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MATERNAL DETERMINANTS OF SEED DISPERSAL IN *CAKILE EDENTULA*: FRUIT, PLANT, AND SITE TRAITS

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Abstract. Seed dispersion patterns are largely determined by the maternal plant. Characters of the progeny, such as dispersal, that are determined by the maternal parent and that vary with the maternal environment are said to exhibit maternal environmental effects. Because dispersal is maternally determined, the response to selection on dispersal depends on the correlations between generations for maternal traits that influence dispersal. These correlations depend on the direction and degree to which the maternal plant responds to its environment. Although it is widely appreciated that seed dispersal is maternally determined, the evolution of dispersal has not yet been addressed within the context of maternal character evolution. In this study, I identify maternal traits that influence seed dispersion patterns and characterize their variation as a function of maternal environmental conditions in order to determine whether maternal environmental effects on dispersal are possible and to predict the direction of correlations between generations for these traits. The traits included morphological traits of the fruits and architectural traits of the maternal plant. Laboratory and field studies were combined to investigate dispersal of *Cakile edentula* var. *lacustris*, an annual beach plant with heteromorphic fruit segments. Fruit traits influenced dispersal under laboratory conditions and in the field. Taller, more sparsely branched plants with a greater percentage of fruits on their primary stem had impeded dispersal, and plants with more fruit segments had denser seed shadows. Path analysis revealed that the total effect of a trait on dispersal often differed from its direct effect because of intercorrelations among variables. Environmental factors influenced dispersal directly, but they also strongly influenced the expression of plant traits. By considering both the effects of plant traits on dispersal and the influence of environmental variables, such as density, on the expression of these plant traits, this study predicts positive phenotypic correlations between maternal and progeny generations for some traits and negative correlations for others. The extent to which each maternal trait influences dispersal, the extent to which it varies with the environment, and the extent to which the environment varies as a function of dispersal will all influence phenotypic correlations between maternal parent and offspring. Consequently, these factors are expected to influence the response of dispersal to selection.

Key words: *Cakile edentula*; density; dispersal; evolution of dispersal; maternal characters; plasticity; seed dispersal.

Dispersal, or migration as it is often referred to in the population genetics literature, is one of the primary factors that influence the rate and outcome of evolution, and it was recognized as such even in the earliest years of theoretical population genetics (Fisher 1930, Wright 1931). Since those early years, the possibility has emerged that dispersal itself is an evolving character rather than a constant rate of genetic exchange among populations. But how should we approach the evolution of dispersal?

Theoretical and empirical studies of seed dispersal have gone far in predicting or documenting how natural selection operates on dispersal. Nearly every published

study of selection on seed dispersion patterns has found that dispersal is not a selectively neutral character. That is, whether a seed remains near the maternal plant or is dispersed from it influences the fitness of the seed (for example, Kozłowski 1949, Smythe 1970, Gibson 1971, Janzen 1971, 1972, Liew and Wong 1973, Burdon and Chilvers 1975, Platt 1976, Vandermeer 1977, Augspurger 1983a, b, Horvitz and Schemske 1986, 1994; reviewed in Howe and Smallwood 1982). Theoretical studies of the evolution of dispersal have modeled how different selective agents, such as sibling competition (Hamilton and May 1977, Comins et al. 1980, Asmussen 1983) and environmental variability (Balkau and Feldman 1973, Roff 1975, Hastings 1983, Levin et al. 1984, Holt 1985, Venable 1985), influence the evolution of dispersal. Much empirical and theoretical evidence exists, therefore, that dispersal is under selection.

Despite the abundant evidence for selection on dis-

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persal, ecological selection models of seed dispersal and genetic models in which dispersal is determined by the dispersing organism itself (e.g., many animals) are limited in their ability to predict the response to selection on seed dispersion patterns. This is because seed dispersal is maternally determined (Theide and Augspurger 1996). Traits that influence seed dispersion patterns could be traits of the seeds and fruits or architectural traits of the maternal plant. Seed and fruit size and shape influence dispersal in many species (Small 1918, Zohary 1950, Burrows 1975, Casper 1992, Venable and Levin 1985, Augspurger 1986, Augspurger and Franson 1987, McEvoy and Cox 1988, Andersen 1992, 1993, Emig and Leins 1994). Plant morphological traits, such as height, branch orientation, spatial distribution of fruits on the plant, plant size, and fruit production also influence seed dispersal (Swaine and Beer 1977, Rabinowitz and Rapp 1981, Waller 1988, McCanny and Cavers 1989, Sinha and Davidar 1992). All of these traits are maternal traits (Westoby and Rice 1982, Roach and Wulff 1987).

The reason ecological selection models cannot accurately predict responses to selection is that they necessarily postulate that correlations between parent and offspring dispersal traits are positive. In maternally determined characters, however, phenotypic correlations between the maternal parent and offspring can be either positive or negative, and the magnitude and direction of these correlations determine in part the magnitude and direction of responses to selection (Kirkpatrick and Lande 1989, 1992). Negative correlations between maternal and offspring phenotypes can arise through variation in the expression of maternal or progeny characters in response to maternal environmental conditions (Schmitt 1995). That is, they can arise through maternal environmental effects.

The first step towards applying models of maternal character evolution to the evolution of dispersal is to identify maternal traits that influence seed dispersion patterns and to characterize their variation as a function of maternal environmental conditions. The interaction of maternal traits with the environment is important because this interaction determines, in part, whether the correlations between parental and offspring dispersal traits are positive or negative. This study attempts this first step by identifying fruit traits, maternal plant traits, and environmental variables that influence dispersal of *Cakile edentula* var. *lacustris* fruits under controlled conditions and in the field. It also investigates the possibility of maternal environmental effects on dispersal by characterizing how these traits interact with each other and with environmental variables to influence seed dispersal. Although it is widely appreciated that maternal characters influence seed dispersal, the evolution of dispersal has not yet been addressed within the context of maternal character evolution. Moreover, although many maternal traits that potentially influence seed dispersal are known to be highly

plastic (Donohue and Schmitt 1997), the possibility of maternal environmental effects on dispersal has rarely been investigated and has not yet been interpreted within an evolutionary context.

In addressing the evolution of dispersal within the context of maternal character evolution, this study has the following specific aims: (1) to identify fruit traits that influence dispersal under controlled conditions, (2) to identify maternal plant morphological traits that influence seed dispersion patterns in the field, (3) to characterize how fruit traits and plant morphological traits interact to influence seed dispersion patterns in the field, (4) to identify other ecological variables within the maternal environment that influence dispersal in the field, and (5) to characterize how plant traits interact with maternal environmental variables to influence seed dispersion patterns in the field. Path analysis was employed to investigate the relationship between maternal traits and maternal environment and how their interactions influence progeny dispersion patterns.

MATERIALS AND METHODS

The study species

Cakile edentula var. *lacustris* (Brassicaceae), or the Great Lakes sea rocket, is an annual, primarily selfing (Rodman 1974, Donohue 1998) lakeshore plant with heteromorphic, (proximal and distal) fruit segments. Each fruit segment typically has only one seed (Rodman 1974). The distal fruit segments usually detach from the proximal fruit segments through an abscission layer and can be dispersed independently from them. The proximal fruit segments often remain attached to the dead and often buried maternal plant through germination. Both types of fruit segments float and can be dispersed by wind and water, and the buoyant pericarp usually remains intact until germination. Both segment types can exhibit between-year dormancy, and distal segments have a slightly higher germination fraction within a given year (K. Donohue, *unpublished data*) and germinate over a wider range of experimental conditions (Maun and Payne 1989). The difference in germination behavior between the two segment types suggests that dispersal and germination could be interacting in this system (Venable and Brown 1988). *Cakile edentula* grows on the beach along the shores of the Great Lakes and rarely encounters other plant species in this habitat. It occurs in a wide range of densities, ranging from hundreds of seedlings within a square meter area, usually associated with the dead maternal plant, to widely scattered individuals elsewhere on the beach, whose nearest neighbors are often tens of meters away. Increased dispersal leads to higher progeny fitness, and selection on seed dispersion patterns is through the effects of sibling density rather than of dispersal distance per se (Donohue 1997).

Detachment under controlled conditions

One-hundred seeds were collected from 30 plants growing at Mount Baldy at the Indiana Dunes National

Lakeshore. The seeds were forced to germinate by soaking and removing the seed coat, and plants were grown to maturity in a greenhouse in 10-cm (four-inch) clay pots filled with Terragreen (a clay-based growing medium, Oil-dry, Inc., Chicago, Illinois USA). Segments of branches that contained mature fruits were clipped and stored in uncovered paper bowls inside a box for 12 mo. The plants were allowed to dry thoroughly. Twenty-five proximal and 25 distal fruit segments were arbitrarily selected from 25 plants. The following traits were recorded: length of the segment, diameter of the abscission layer on distal segments, and length of the pedicel on proximal fruit segments.

The force required for detachment of these segments was measured using a tensiometer (assembled by M. LaBarbera at the Department of Anatomy of the University of Chicago). To measure the force required to detach distal fruit segments, proximal fruit segments with attached distal fruit segments were clamped into a stationary, upright position, and a small metal rod contacted the distal fruit segment at 0.5 cm above the abscission layer, pushing the distal segment off. To measure the force required to detach a proximal fruit segment from the branch, a small portion of a branch having a single proximal fruit segment was glued to a bent bobby pin, which was then clamped into a fixed position. The rod contacted the proximal fruit segment at 0.5 cm from the bottom of the fruit segment, detaching the proximal segment from its pedicel usually by breaking the pedicel. The rod was connected to a 0.1 Newton transducer (Schaevitz brand), which recorded the force with which the rod pushed against the fruit segment at the time of detachment. The distance (in centimeters) the rod moved from initial contact with the fruit until the fruit was detached, multiplied by force, gives a measurement of the work required for detachment. Force and work required for detachment were compared between the two fruit segment types using independent *t* tests on normalized (natural-log transformed) data. The extent to which seed traits influenced detachment was investigated using regression analysis.

Dispersal after detachment under controlled conditions

One-hundred distal, 100 proximal fruit segments, and 100 fruits with both proximal and distal segments still joined were randomly selected from the sample of 30 families grown in the greenhouse. The following traits were measured on each fruit segment: length, length of the pedicel on proximal and joined fruits, maximum diameter, and mass. A composite trait, "wing loading," was calculated as mass divided by the area of the fruit. The area of each fruit segment was estimated as the total length (including the pedicel, if present) multiplied by the average diameter (both dimensions measured in millimeters), where the average diameter was estimated as one-half the maximum di-

ameter, since both fruit segment types taper on one end to a diameter close to zero (the proximal fruit segments tapering through the pedicel). Wing loading has been used extensively in previous studies of seed dispersal and has been shown to influence dispersal distance and rate of descent (e.g., Green 1980, Augspurger 1986, Augspurger and Franson 1987, Green and Johnson 1989).

Wind speeds of 8.1 km per hour and 16.1 km per hour were used in the wind tunnel, and fruit segments were released at heights of 33 cm and 16 cm. The wind speeds were chosen to represent typical speeds during the summer and autumn months when fruits are dispersing in the field. Although wind speeds are sometimes much higher, a lower speed was chosen to accommodate the limited length of the wind tunnel. The two heights were also constrained by the design of the wind tunnel, but they represent a typical plant of 10–20 cm and a plant twice as tall. Twenty-five fruit segments of each type were individually released at a vertical orientation into the wind tunnel for each of the four treatments. The distance traveled by each fruit segment was recorded. Analysis of covariance (SYSTAT, Multivariate General Linear Hypothesis) was performed on normalized (natural-log transformed distance or square-root transformed wing loading) variables to determine the effect of wing loading (continuous covariate), segment type, wind speed, height of release, and interactions on the distance traveled in the wind tunnel.

Dispersal in the field

Six populations of *C. edentula* along the south and the east shore of Lake Michigan were sampled in late September when most fruits had ripened. The sites were Mt. Baldy (East and West) of the Indiana Dunes National Lakeshore, and the following state parks in Michigan: Saugatuck, Hoffmaster, Silver Lake, and Ludington. I chose plants that had mature, ripe fruits but had not yet dispersed many of their fruits. Some fruits had already dispersed on the selected plants, however. When possible, a wide range of plant phenotypes was sampled to establish a stronger regression relationship between plant traits and seed dispersion patterns. In each population, the exact location of 15 plants was marked with a wooden stake. All fruits present on each plant were colored with various colors of durable ink (Script's brand permanent artists' ink), which was absorbed into the corky pericarp without altering the fruit surface and consequently did not alter fruit detachment or dispersal. Plants were revisited twice within the following month to color any fruits that had ripened within that time. They were visited again in late December to record percentage of fruit detachment. A total of 7707 fruit segments were colored.

Plant morphological or seed traits that are known to influence seed dispersion patterns in other species were measured for this study. "Height" the distance, in cen-

timeters, from the base of the stem, is defined as the point from which the stem emerges from the sand, to the top of the primary, or central, stem. Occasionally, a plant lay prostrate, so its height can more accurately be interpreted as length. "Branches / cm" is the number of secondary branches per centimeter of primary stem. This is a measure of compactness of branch placement. Its inverse is the length between branches. "Total segments" is the total number of fruit segments produced within the lifetime of the plant. "Percentage primary fruits" is the percentage of the total number of fruits that were located on the primary stem. Primary fruits are located higher on the plant than fruits on secondary or tertiary stems, and they are placed closer to the center of the plant. Therefore, if fruit location is important, its effect is most likely to be evident in primary fruits. This is used as a measure of the spatial distribution of fruits on the plant. "Percentage detachment" is the percentage of fruit segments that detached from the maternal plant early in the dispersal season. This was recorded three months after all fruits had been colored, well after fruit maturation and the death of the plant and after many, but not all, fruits had detached. This measure estimated the facility with which fruits detach from the maternal plant. Plants vary greatly for this trait, with some plants releasing newly matured, green fruits and some plants retaining dry, corky fruits throughout the winter (*personal observation*).

The following site traits were also recorded. "Beach width" is the distance between the base of the dune and the water level, classified on a scale from zero to four, recorded at the location of the focal plant. This is related to the probability that a dispersing *C. edentula* fruit segment will reach the water. "Slope" is the degree of incline on which the focal plant was growing, classified on a scale from zero to five. "Number of plants in clump" is the number of plants within a 25-cm radius of the focal plant. Plants occurring singly had a value of one.

The following spring, before seed germination but after seed dispersal, the sites were revisited to recover the colored fruit segments. Fifty of the 92 original plant locations were found. Perhaps the largest discrepancy between dispersal in this sample of plants and dispersal by the population is due to the sample of plants that were not found after dispersal. Plants were not found for several reasons. One probable reason is that the stakes marking their location were missing, whereas the plant could have remained in place. Another possibility is that both the stake and the plant were washed away or buried. The fact that so many plants were not found suggests that entire plants can be washed or blown away, so that segments of plants with attached fruits may be dispersed far away as a unit. The extent to which this dispersal mode occurs, however, cannot be estimated from this study. Although general patterns of dispersal by the populations can be seen from this study, such generalizations should be made with cau-

tion since the sample of plants used for this field study was not a random sample. The sampling used in this study was chosen because the primary purpose of the study was to identify maternal traits that influence dispersal rather than to characterize dispersal of the population.

Burial of some plants occurred over the winter. Recovery of seeds entailed digging until the dead maternal plant was recovered, recording the depth at which it was recovered, and sifting the sand to the same depth in continuous transects in three equiangular directions. A 25 cm by 50 cm sampling area was used for each sample, approximating the area occupied by a dead maternal plant. In each 1250-cm² sample, the number of colored and uncolored proximal and distal fruit segments was recorded, as was the distance and direction of the sample. Sampling was discontinued in a given direction if no colored fruit segments were recovered during two consecutive samples. A criterion of constant, low density of recovered colored fruits was used for discontinuing sampling rather than a criterion of constant distance for the following reasons. Asymmetry of dispersal direction due to wind or slope would result in some directions being sampled beyond their dispersal limit while other directions being sampled less than their dispersal limit. Continued sampling as long as fruits were still being recovered allowed the recovery of a greater proportion of the fruit segments. This recovery method is limited by the necessary assumption that no recovery of fruits in one sample predicts a low probability of recovery in the following sample. That is, it decreases the probability of recovering segments that may occur in high abundance but that were dispersed farther than fruits that occur in low abundance. However, 12 preliminary transects that sampled up to 2.5 m in each direction (between 1 and 2 m beyond the extent to which segments were recovered) showed no evidence of this. This preliminary sampling also indicated that all fruits that were recovered were within one sample of previously recovered fruits. Moreover, in the entire sample of segments recovered for this study, only 2% of all recovered fruits were recovered following a sample that had no fruits. Therefore, the criterion of two consecutive samples with no fruit recovery was used to discontinue sampling, and the assumption was made that no additional fruits would be recovered in that direction (although they may have been dispersed beyond recovery in that direction). Dispersal measures derived using a truncation distance (the greatest distance at which all plants were sampled symmetrically in all directions) were highly correlated with dispersal measures derived using the entire sample of recovered fruits as described above, and results did not differ appreciably when these dispersal measures were used instead. The results presented, therefore, are based on dispersal measures derived from the entire sample of recovered fruits.

Analysis employed measures of local dispersal and

measures of wide-scale dispersal. Local dispersal measures were derived only from those fruits that were recovered within the area of census, whereas wide-scale dispersal measures were derived from all marked fruits, whether they were recovered or not. The wide-scale measures of dispersal have a larger sample size than do local dispersal measures since plants for which no fruits were recovered (although the maternal plant site was found) had no measures of local dispersal. Local dispersal measures are of interest because they give detail on local seed dispersion patterns. From 3% (Silver Lake) to 79% (Mount Baldy West) (62.2% averaged over all populations) of the standing population of seedlings in different populations were located in high density clumps associated with dead maternal plants or within 50 cm of them (K. Donohue, *unpublished data* based on seedling censuses of 10 504 seedlings in a total area of 144.5 m² distributed equally among the six populations used for this study). Therefore, a significant proportion of the standing population could be influenced by local dispersal patterns. The measures of local dispersal, based only on recovered fruit segments, are as follows. "Distance" refers to the average distance from the home site (site of the maternal plant) at which the colored fruit segments were recovered, corrected for sampling. This measure includes fruit segments that were not dispersed from the home site as well as those that were dispersed and recovered. "Local mean crowding index" is the number of neighbors an average recovered fruit segment had within a sampling area (1250 cm²) plus one (itself), corrected for sampling (Lloyd 1967). It is calculated as:

$$\frac{1}{N} \sum_{i=1}^s n_i^2$$

where N = total number of recovered colored segments, n = number of colored segments per sample, and s = number of samples. This measure also includes fruit segments that were not dispersed from the home site as well as those that were dispersed and recovered.

Wide-scale measures of dispersal describe dispersal of both recovered and unrecovered fruit segments. Because a large proportion of fruit segments can be dispersed beyond recovery, incorporating this proportion into additional dispersal measures allows comparison with local dispersal measures to determine whether any patterns observed locally still apply when the potentially large proportion of unrecovered segments is considered. The wide-scale measures of dispersal are as follows. "Wide-scale mean crowding index" is the number of neighbors an average fruit segment has within a sampling area (1250 cm²) plus one (itself), corrected for sampling, and assuming that the fruit segments that were dispersed beyond the census area occur singly, or at a density of one per sampling area. "Percentage segments far dispersed" is the estimated per-

centage of colored fruit segments that were dispersed beyond the census area, after correcting for sampling.

The wide-scale mean crowding index is based on the approximation that the fruit segments that were dispersed out of the census area occur at low densities. This is likely to be the case in most of the populations studied, although in one population very high densities of water-dispersed fruits were washed up onto the beach. However, because the water-dispersed fruits did occur in low densities in most of the sites, and because the percentage of fruits that were water dispersed (as opposed to wind dispersed along the beach) was unknown, the estimate of one fruit per sampling area is the most reasonable approximation of the density of far-dispersed fruits, with these caveats included. Even if this assumption is not accurate, the wide-scale measure of crowding can be considered a method to weight the local estimate of crowding by the percentage of fruits that could not be accounted for.

Correction for sampling consisted of determining the percentage of the total area around the plant that was actually sampled at each distance (100% of the area was sampled at the home site, and the percentage decreased with increasing distance) and weighting the number of fruits recovered at each distance by that factor. The correction for the mean crowding index involved calculating the average mean crowding index at each distance for each plant and attributing this value to the estimated number of fruits that were present at that distance but not recovered. All measures of dispersal were corrected for sampling.

Plant traits and dispersal measures were transformed to normality using natural-log transformation or arcsine-square root transformation of proportions. Analysis included a separate multivariate analysis of variance of local and wide-scale measures of dispersal, with plant traits as the independent variables and dispersal measures as the dependent variables.

Path analysis (Wright 1925) was employed to characterize how plant and site traits interacted to influence fruit dispersion patterns. Path analysis is a multiple regression analysis that is based on a priori causal and correlational hypotheses. Direct effects reflect causal pathways from the dependent to independent variables, independent of all other traits included in the analysis. Indirect effects are mediated by correlations and direct effects among measured variables. The magnitudes of indirect effects are obtained from the sum total of all paths of influence, where the magnitude of the influence of a single path is the product of the path coefficients in that path. Total effects are the sum of direct and indirect effects. Results from path analysis are presented in terms of standardized regression or correlation coefficients, which show the influence of variables in standard deviation units. Significance of direct effects are based on t tests in a multiple regression analysis. Significance of total effects were based on t tests in a simple regression model. Indirect effects were not

TABLE 1. Means \pm 1 SE of traits of fruit segments used in the wind tunnel. $N = 100$ for each type.

Trait	Distal segment	Proximal segment	Joined segments
Mass (mg)	0.020 \pm 0.001	0.018 \pm 0.002	0.027 \pm 0.003
Length (mm)	14.36 \pm 0.19	7.47 \pm 0.10***	Distal: 13.53 \pm 0.20 Proximal: 6.93 \pm 0.11
Length of pedicel (mm)	...	4.08 \pm 0.12	3.33 \pm 0.12
Total length (mm)	14.36 \pm 0.19	11.59 \pm 0.17***	23.80 \pm 0.35
Diameter (mm)	4.23 \pm 0.06	2.89 \pm 0.05***	Distal: 3.91 \pm 0.07 Proximal: 1.80 \pm 0.04
Wing loading (mg/mm ²)	0.04 \pm 0.001	0.10 \pm 0.01***	0.07 \pm 0.01

Note: Asterisks indicate significant differences ($P < 0.001$) between the values for proximal and distal fruit segment based on independent t tests.

tested for significance since they were summed over multiple causal pathways. This path analysis was based on four hierarchical causal hypotheses. (1) *Site traits influence the number of plants in a clump, plant morphological traits, depth of burial, and dispersal.* Slope or distance from the water could influence water availability and thereby plant traits, and slope and exposure to water could influence the probability of burial. Moreover, slope and distance from the water could influence dispersal and likewise the number of plants in the maternal plant clump because both gravity (slope) and access to water (beach width) could influence dispersal distance. (2) *The number of plants in a clump influences plant traits, depth of burial, and dispersal.* Competitive interactions often influence plant morphology, and a group of plants may be more effective at trapping sand or dispersing seeds than single plants. (3) *Intercorrelated plant morphological traits influence depth of burial and dispersal.* For example, larger plants with more branches may entrap more sand or seeds than smaller plants. (4) *Depth of burial influences dispersal.*

Buried plants probably cannot disperse their seeds effectively. Some reciprocal interactions were not considered; for example, burial cannot influence plant traits or number of plants in the maternal clump, since plant traits are expressed before burial in the winter. Likewise, plant traits cannot influence number of plants in the maternal clump since the clump was established before the plants' traits were expressed. Moreover, no measured variable can influence slope or beach width.

Dispersal by proximal and distal fruit segments was compared using paired t tests. The influence of plant traits on differences in dispersal by proximal and distal segments was investigated using regression analysis.

RESULTS

Dispersal under controlled conditions

Distal fruit segments were significantly longer and wider than proximal segments and had significantly lower wing loading ratios, although mass did not differ between the two segment types (Table 1). The difference in wing loading between the segment types, therefore, is due more to differences in shape than in mass. A significantly greater force was required to detach proximal fruit segments than distal segments (Fig. 1), and work showed a very similar pattern. Upon detachment of proximal segments, pedicels broke midway, allowing some of the pedicel (mean \pm 1 SD = 3.94 \pm 0.12 cm) to be dispersed with the fruit segment. Fruit traits explained a significant amount of variation in force required for detachment of distal fruit segments ($R^2 = 0.26$, model significance = 0.034, $N = 25$) with the diameter of the abscission layer (1.72 \pm 0.05 cm, coefficient = 12.32, $t = 1.91$) having the stronger effect (segment length coefficient = 1.33, $t = 1.06$). No traits significantly explained variation in force required for detachment of proximal segments ($R^2 = 0.03$, model significance = 0.73, $N = 25$), indicating that the measured fruit traits are unlikely to influence detachment of proximal segments (segment length coefficient = 1.30, $t = 0.67$; pedicel length coefficient = -0.55, $t = -0.40$). Regressions of fruit traits on work required for detachment showed a very similar pattern as regressions on force (not shown). Field observations verified the result that distal fruit segments detach more

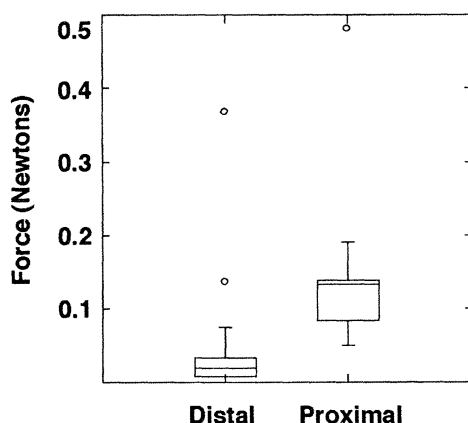


FIG. 1. Force required to detach proximal and distal segments during tensiometer trials. Box plots show median, quartiles, range, and outlying points of untransformed data. Independent t tests of normalized (natural-log transformed) data show highly significant differences between proximal and distal fruit segments for force ($t = 4.632$, $P < 0.001$, $N = 25$ for each fruit segment type) and work ($t = 9.002$, $P < 0.001$, $N = 25$).

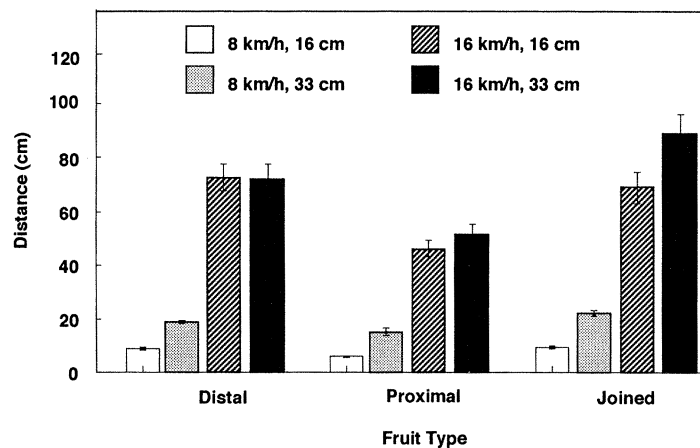


FIG. 2. Distance traveled by fruit segments in a wind tunnel (± 1 SE) at two wind speeds and at two heights of release. $N = 25$ for each bar.

easily than proximal segments, since a significantly greater proportion of distal segments detached from the sample of field plants than did proximal segments ([mean ± 1 SD] distal = $38 \pm 3.5\%$; proximal = $8 \pm 4.0\%$; $t = 12.72$, $P < 0.001$, $N = 50$).

Dispersal after detachment also differed among fruit segment types under experimental conditions. In general, distal segments traveled farther than proximal segments in the wind tunnel, and joined segments traveled the farthest (Fig. 2, Table 2). Higher wind speed and higher height of release caused all segment types to travel farther in the wind tunnel, and wind speed had a greater influence on distance traveled than did height of release. Joined segments showed the greatest increase in distance traveled as the height of release increased. Height of release had a stronger influence on dispersal differences between proximal and distal segments at the lower wind speed. Differences in dispersal by proximal and distal segment types were greatest under the high wind speed but at the lower height of release. Segments with lower wing loading ratios traveled farther, but wing loading explained less of the

variation in distance traveled at the lower height of release at high wind speed (Table 2, Fig. 3). Because both segment type and wing loading were included in the ANCOVA, the significant effect of wing loading indicates that variation in wing loading within segment types affected travel distance. The analysis also suggests that proximal and distal segments differ in traits other than wing loading, and that these traits have aerodynamic consequences. Significant interactions indicate that, although fruit traits influence travel distance, the strength of effect of these traits depends on wind speed and height of release; they are weakest at the shorter height and higher wind speed (Fig. 3). Wind speed could vary according to microenvironment or geographic location, while height of release could depend on location or on plant morphological traits, such as height or percentage of fruits located on the primary stem. Therefore, the extent to which seed traits influence dispersal could depend on these environmental and biotic factors.

Force required for detachment and dispersal after detachment could interact to influence dispersal of the

TABLE 2. Analysis of covariance of distance traveled in a wind tunnel.

Source	df	MS	F	P
Wing loading	1	3.885	45.252	<0.001
Segment type	2	2.783	32.415	<0.001
Wind speed	1	17.687	206.025	<0.001
Height of release	1	4.918	57.284	<0.001
Segment type \times height of release	2	0.567	6.603	0.002
Segment type \times wind speed	2	0.017	0.200	0.819
Segment type \times wind speed \times height of release	2	0.092	1.070	0.344
Wing loading \times height of release	1	2.677	31.186	<0.001
Wing loading \times wind speed	1	0.925	10.769	0.001
Wing loading \times wind speed \times height of release	1	10.362	120.695	<0.001
Residual	285	0.086		

Notes: Wing loading was square-root transformed to normality, and distance was natural-log transformed to normality. Results are based on Type III sums of squares. $N = 300$, $R^2 = 0.910$.

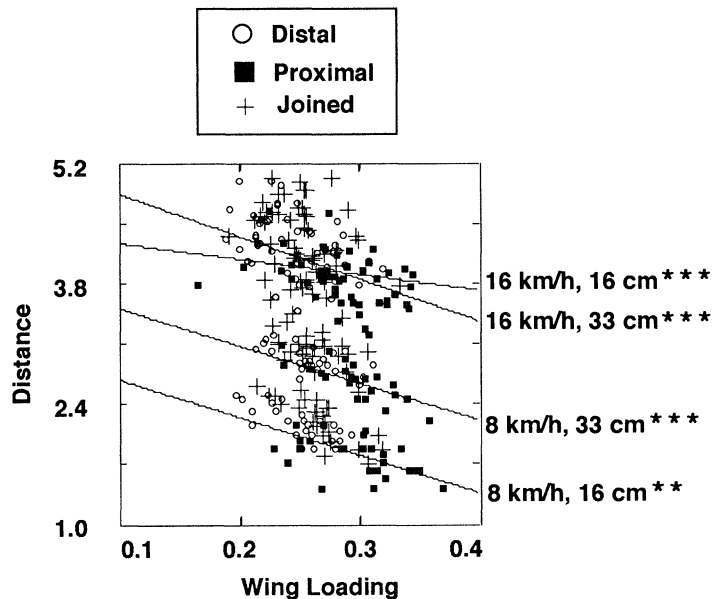


FIG. 3. Relationship between wing loading and distance traveled in a wind tunnel for four treatments. Wing loading was square-root transformed to normality, and distance was natural-log transformed to normality. All regressions were significant. ** $P < 0.01$; *** $P < 0.001$.

two fruit segments in the field. A greater force required for detachment of proximal fruit segments could result in those segments being dispersed only at higher wind speeds. Because wind speed had such a strong effect on dispersal distance, even stronger than that of height of release, dispersal at higher wind speed could mitigate other differences between the two segment types and result in more similar dispersal of the two segment types, provided they detach at all. In addition, variation in the diameter of the abscission layer could influence the wind speed at which distal segments are released, because abscission-layer diameter influenced the force required for detachment.

Dispersal in the field

Before discussing how maternal plant and site traits influenced dispersal in the field, we need to know how well the recovered fruit segments reflect the actual frequency distribution of fruits around the maternal plant. A total of 3352 colored fruit segments was recovered. All recovered segments were within 2 m of the home site, and most segments were recovered within 1 m of the home site. Thirty-seven percent of all marked segments were recovered immediately beneath their maternal plant site, and 48% of all colored segments were estimated to be within the census area after correcting for sampling, with the remaining 52% having been dispersed beyond recovery. Forty-three percent of those segments that were recovered exactly at the maternal home site were still attached to the dead maternal plant, while only 2% of the segments recovered beyond the maternal plant site were attached to plant fragments, indicating that detachment from the maternal plant,

rather than shoot fragmentation, is the typical mode of local dispersal in this system. The average local mean crowding index was 33.5 segments per 1250 cm² sample ($SD = 52.4$) and the average wide scale mean crowding index was 13.2 segments per sample ($SD = 28.6$).

Colored fruit segment recovery generally decreased monotonically with distance from the home site, with the highest number of segments being recovered directly beneath the dead maternal plant (Fig. 4). In addition to colored fruit segments, uncolored fruit segments were also recovered. The uncolored fruit segments could be from four different sources. They could be segments that (1) had detached before any segments were colored, (2) had been colored but that did not look colored because of degradation of the pericarp, (3) had dispersed into the census area from other plants, or (4) were present before the colored plant grew and produced fruits. Two very large dead uncolored maternal plants with attached fruit segments were found buried directly beneath colored maternal plants and contributed >1000 uncolored segments to the sample of recovered segments (in Mount Baldy East and Mount Baldy West, Fig. 4). These dead plants could have been captured by the colored plant as they were blown across the beach, they could have been the parents of the colored plants from the previous year, or they could have captured the seed from which the colored plants grew.

In most sites, the number of colored segments in a sample reflected the total number of segments in a sample, as shown by highly significant Spearman rank correlations (Fig. 4). If background dispersal from other

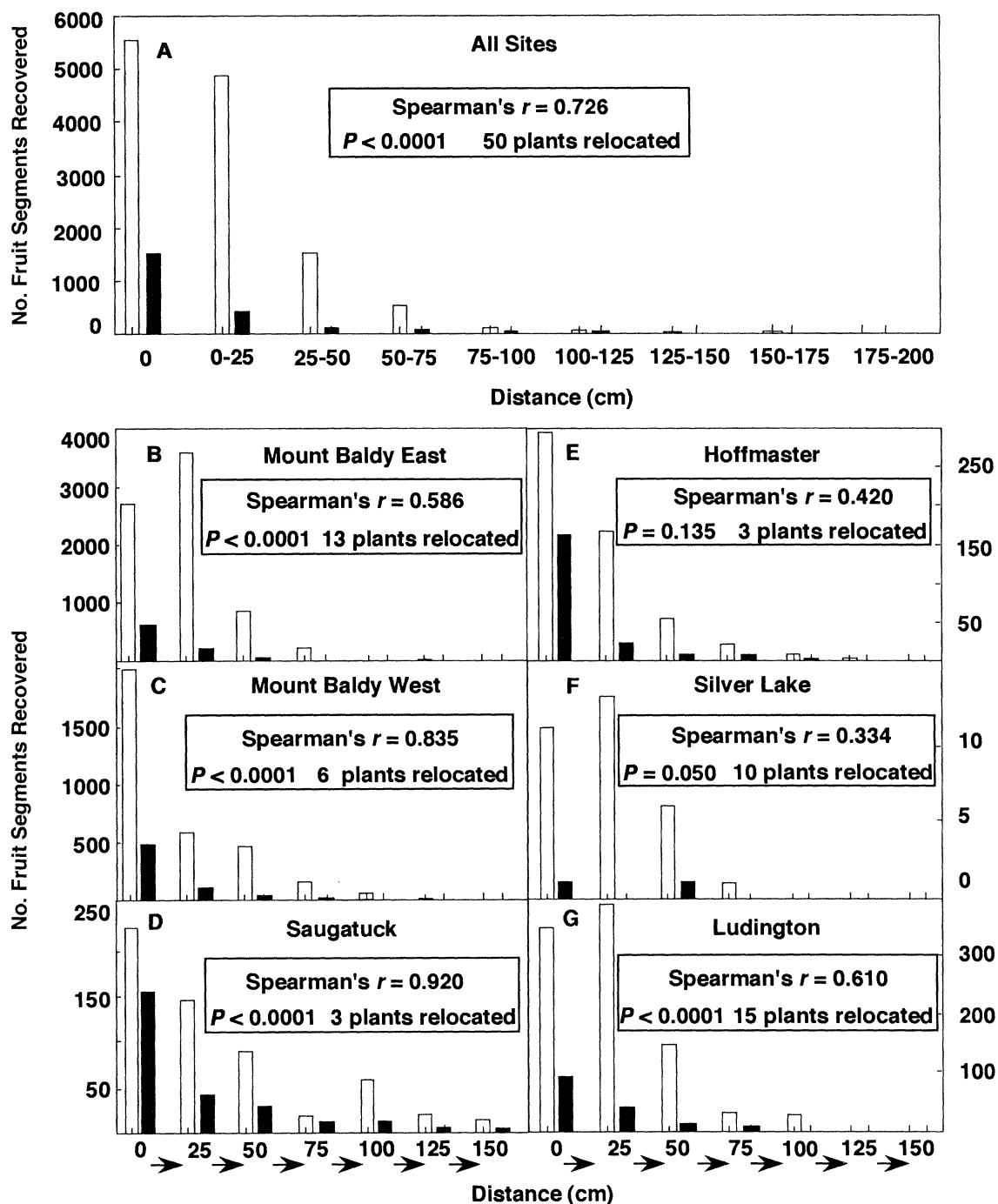


FIG. 4. Seed recovery as a function of distance. Values are not corrected for sampling. Number of colored fruit segments (black bars) and the total number of recovered fruit segments, including colored and uncolored fruit segments (white bars), are shown as a function of distance from the maternal home site. First graph (A) shows the values pooled over all sites. Following graphs (B–G) show values separately for each site. Spearman rank correlations measure the correlation between the number of colored segments recovered in a sample and the total number of segments recovered in a sample, pooled over all plants within a site. The Spearman rank correlation for “All Sites” uses samples pooled over all plants and all sites.

TABLE 3. Descriptive statistics of frequency distributions of colored fruit segments and all fruit segments as a function of distance from the maternal plant site. The last column shows maximum difference in frequencies between the two distributions.

Site	Colored fruit segments					All fruit segments					
	Mean distance (cm)	SD	CV	Skew	Kurtosis	Mean distance (cm)	SD	CV	Skew	Kurtosis	K-S
Pooled	7.1	18.7	2.6	4.5	25.6	13.0	20.0	1.5	2.8	11.9	0.624***
Mount Baldy East	3.9	9.0	2.3	4.2	31.2	12.0	14.2	1.2	1.8	3.2	0.684***
Mount Baldy West	5.6	13.3	2.3	3.5	15.2	12.3	20.9	1.7	2.1	5.3	0.618***
Saugatuck	21.2	39.2	1.8	2.0	3.8	35.4	47.7	1.3	1.3	0.8	0.347***
Silver Lake	18.5	26.2	1.4	0.0	-2.0	14.2	16.0	1.1	1.2	0.8	NA
Hoffmaster	5.4	15.5	2.9	3.5	12.6	11.9	19.8	1.7	2.4	6.5	0.523***
Ludington	7.8	13.8	1.8	2.3	5.3	15.6	20.1	1.3	1.9	3.4	0.526***

Notes: Asterisks indicate significant differences between the frequency distribution of colored fruit segments and that of all recovered fruit segments using Kolmogorov-Smirnov (K-S) tests: ** $P < 0.01$, *** $P < 0.001$. Silver Lake could not be analyzed due to low recovery of colored segments.

plants significantly overlapped with the local dispersal area of the focal plant, as would be the case in a more continuous stand, then one would expect low correlations. These high correlations therefore suggest that the number of seeds that a seed interacts with at a local scale is determined primarily by the maternal plant rather than by random background dispersal and that neighboring seeds are likely to be siblings from the same maternal plant. This is not unexpected for a plant such as *C. edentula* that has such a scattered distribution. In sites such as Hoffmaster or Silver Lake that have nonsignificant correlations on the other hand, background dispersal may contribute more strongly to a seed's biotic interactions. Despite the high Spearman's correlations, Kolmogorov-Smirnov tests that compared frequency distributions of colored fruit segments to that of all recovered fruit segments indicated that the distributions differed significantly in all sites and in the sample of all fruit segments pooled over all sites (Table 3). The frequency distribution of noncolored segments had less skewness and kurtosis, lower coefficients of variation, and a higher average distance of recovery. That is, they were more evenly distributed

than were the colored fruit segments, as would be expected if background dispersal contributes more to the distribution at greater distances from the home site.

Plant morphological traits significantly influenced local dispersal in the field (Table 4). Increased height, increased branching (or decreased spacing of branches), increased fruit segment production, and increased fruit detachment were associated with increased crowding locally. A smaller percentage of primary fruits was associated with increased dispersal distance within the census area. Overall, height, number of branches per centimeter, and detachment influenced local dispersal most strongly. Plant morphological traits did not influence wide scale measures of dispersal as strongly, although a trend for increased height to increase crowding was apparent, as was a trend for increased fruit production, decreased height, decreased branching, and decreased percentage of primary fruits to enhance long distance dispersal (Table 5). Even without considering the maternal plants' site characters, plant characters alone accounted for a substantial amount of variation in dispersal, particularly at the local scale.

Further resolution of the effects of these traits and

TABLE 4. Multivariate analysis of variance of local dispersal measures as a function of plant traits. The analysis was performed on transformed data.

Trait	Regression coefficients		MANOVA results		
	Distance	Local MCI	Wilks' λ	F	P
Constant	3.875	-7.703**	0.687	5.694	0.009
Total segments	-0.224	0.531*	0.803	3.076	0.064
Height	0.175	1.213**	0.677	5.956	0.008
Branches/cm	1.852	2.788*	0.759	3.974	0.032
Percentage primary fruits	-2.859*	1.366	0.835	2.474	0.105
Percentage detachment	-1.657†	2.145*	0.751	4.153	0.028
R ²	0.381	0.470			

Notes: Results of the analyses of variance for the univariate test for each of the dispersal measures are shown separately in the first two columns. Regression coefficients are given with the significance level indicated by asterisks († $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). For the multivariate analysis of variance, the F statistic is based on Wilks' λ , the likelihood ratio criterion for the multivariate test. The P value for the multivariate hypothesis is shown in the next column. "MCI" represents mean crowding index. $N = 32$.

TABLE 5. Multivariate analysis of variance of wide-scale dispersal measures as a function of plant traits. The analysis was performed on transformed data.

Trait	Regression coefficients		MANOVA results		
	Wide MCI	% far	Wilks' λ	F	P
Constant	-1.347***	2.303†	0.646	11.768	<0.001
Total segments	-0.010	0.111	0.844	3.965	0.026
Height	0.295*	-0.251*	0.893	2.583	0.087
Branches/cm	0.863†	-0.863*	0.906	2.325	0.119
Percentage primary fruits	0.920†	-0.811*	0.915	2.001	0.148
Percentage detachment	0.493	-0.446†	0.936	1.478	0.240
R ²	0.243	0.284			

Notes: See Table 4 for explanation of column headings. † $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. "% far" = percentage segments far dispersed. $N = 50$.

their interaction with each other and with maternal site variables can be acquired through path analysis. The relationships among the variables are presented first since they define the indirect effects on dispersal. Following, the effects of the plant and maternal site characters on dispersal are presented.

Plant and site traits interacted in complex ways (Fig. 5). The site traits beach width and slope were intercorrelated, and slope strongly influenced many plant traits. Plants growing on steep slopes were shorter, had more branches per centimeter, had a smaller percentage of primary fruits, and had fewer fruit segments. Plants growing on wide beaches had fewer branches per centimeter. Slope and beach width could influence plant growth by influencing exposure to wind and sun, water

availability, and nutrient availability, since the bases of dunes tend to accumulate organic debris. Surprisingly, site and plant traits did not significantly influence depth of burial.

The number of plants in a clump significantly influenced plant traits (Fig. 5). Plants in large clumps were taller, had fewer branches per centimeter (showed greater spacing of branches), had more primary fruits, produced fewer fruit segments, and had less detachment. Plants in large clumps were also buried to significantly greater depths, suggesting that clumps of plants may accumulate sand.

Some plant traits were significantly intercorrelated (Fig. 5). Taller plants had fewer branches per centimeter and a greater percentage of primary fruits. Plants

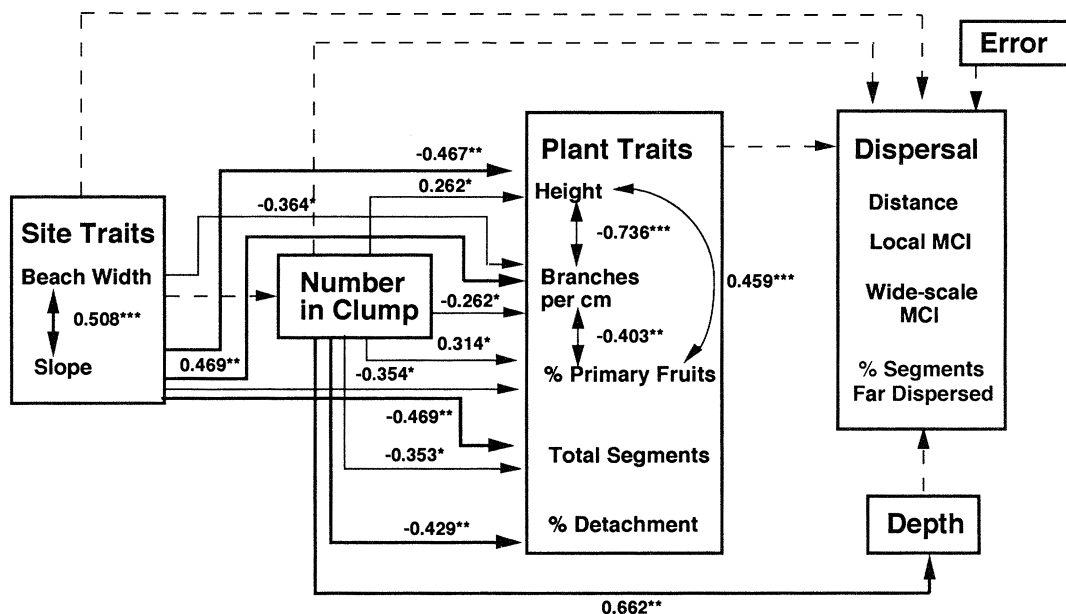


FIG. 5. General path diagram with path coefficients indicating the relationships among variables. Only statistically significant relationships are shown. Width of lines increases as level of significance increases. * $P < 0.01$; ** $P < 0.001$; *** $P < 0.0001$. Results are based only on plants that were found again after dispersal. Single-headed arrows represent partial regression coefficients, and double-headed arrows represent correlations (relationships that have no direction of causality). Dashed lines represent potential causal relationships between variables and dispersal. Actual relationships with dispersal measures are presented in Tables 6 and 7. (See *Materials and methods: Dispersal in the field* for explanation of plant and site traits and dispersal measures.)

TABLE 6. Path analysis of local dispersal measures. (A) Path analysis of average distance dispersed by recovered fruit segments. (B) Path analysis of local mean crowding index.

Variable	Direct effect	Indirect effect	Total effect
A) Average distance dispersed by recovered fruits ($R^2 = 0.488$, $N = 32$)			
Maternal plant traits			
Total segments	-0.470†	0.462	-0.008
Height	0.094	-0.366	-0.272
Branches/cm	0.355	0.053	0.408*
Percentage primary fruits	-0.448*	0.056	-0.392*
Percentage detachment	-0.296†	0.056	-0.240
Maternal site traits			
Beach width	-0.149	-0.031	-0.108
Slope	-0.311	0.377	0.066
No. plants in clump	0.175	-0.168	0.007
Depth	-0.364	0.106	-0.258
B) Local mean crowding index ($R^2 = 0.695$, $N = 32$)			
Maternal plant traits			
Total segments	0.821***	-0.465	0.356*
Height	0.663**	-0.290	0.373*
Branches/cm	0.486*	-0.630	-0.144
Percentage primary fruits	0.087	-0.011	0.076
Percentage detachment	0.369**	-0.309	0.060
Maternal site traits			
Beach width	0.261	-0.267	-0.006
Slope	0.227	-0.493	-0.266
No. plants in clump	-0.040	0.026	-0.014
Depth	0.691**	-0.405	0.286

Notes: † $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Indirect effects were not tested for significance. All coefficients are in standard deviation units. See Fig. 5 for paths of indirect influence.

with more branches per centimeter had a smaller percentage of primary fruits. Plant traits showed great plasticity as a function of site traits and crowding, yet they did not influence burial. Therefore, their effects on dispersal are primarily direct effects, or indirect effects through their correlations with other plant traits but not with other measured environmental variables.

Now consider the effects of maternal plant and site traits on dispersal. Each plant trait measured had a significant direct or total effect on at least one measure of dispersal (Tables 6 and 7). The direct effects of the plant characters on dispersal did not differ appreciably from those shown in the univariate tests of the MAN-OVA's for any of the measures of dispersal (Tables 6 and 7). This is to be expected since the plant traits did not have paths of indirect influence through other measured environmental variables. However, direct effects can differ from total effects due to correlations among the plant traits themselves.

Considering the total effects of plant traits on dispersal, a consistent trend was apparent for taller, more sparsely branched plants with a greater proportion of primary fruits to have impeded dispersal (Tables 6 and 7). Height may be an indicator of plant size, such that larger plants have impeded dispersal, as indicated by increased crowding (Tables 6B and 7A) and decreased dispersal beyond recovery (Table 7B). This interpretation is consistent with the observation that large plants with more total segments also have more crowd-

ed segments after dispersal (Table 6B). Primary fruits may be less likely to escape branches and be dispersed, which may explain the direction of the relationship between percentage of primary fruits and dispersal distance (Table 6A), crowding (Table 7A), and dispersal beyond recovery (Table 7B).

Path analysis also revealed that correlations among plant traits may have enhanced or diminished the effect of a trait on dispersion patterns. The total effect of a trait on dispersal often differed from its direct effect because of intercorrelations among traits. This was particularly pronounced in the effect of number of branches per centimeter on dispersal. This trait was negatively correlated with height and percentage of primary fruits (Fig. 5). Although its total effect on mean crowding was negative (Table 6B and 7A), when the other traits were held constant it was shown that more densely placed branches actually impeded dispersal and resulted in more dense seed distributions. This result may be due to branches inhibiting the movement of segments away from the plant by trapping them beneath the maternal plant.

Maternal site variables also influenced dispersal. Direct effects of increased beach width, slope, and depth of burial were associated with shorter local dispersal distance (Table 6A) and increased crowding (Table 6B), although only the effect of depth of burial was significant at the local scale. Plants on narrow beaches and on steep slopes also tended to have a greater percentage

TABLE 7. Path analysis of wide-scale dispersal measures. (A) Path analysis of wide-scale mean crowding index. (B) Path analysis of percentage of fruits dispersed beyond recovery.

Variable	Direct effect	Indirect effect	Total effect
A) Wide-scale mean crowding index ($R^2 = 0.498$, $N = 50$)			
Maternal plant traits			
Total segments	0.262	-0.174	0.088
Height	0.204	0.136	0.340*
Branches/cm	0.386*	-0.534	-0.148
Percentage primary fruits	0.156	0.149	0.305*
Percentage detachment	0.205	-0.152	0.053
Maternal site traits			
Beach width	0.312*	-0.225	0.087
Slope	-0.087	-0.073	-0.160
No. plants in clump	-0.008	0.311	0.121
Depth	0.627***	-0.112	0.515***
B) Percentage segments far dispersed ($R^2 = 0.482$, $N = 50$)			
Maternal plant traits			
Total segments	0.015	0.123	0.138
Height	-0.217	-0.056	-0.273*
Branches/cm	-0.423*	0.506	0.083
Percentage primary fruits	-0.145	-0.222	-0.367**
Percentage detachment	-0.234†	0.156	-0.078
Maternal site traits			
Beach width	-0.158	0.160	0.002
Slope	0.137	-0.007	0.130
No. plants in clump	-0.061	-0.164	-0.225
Depth	-0.538**	-0.045	-0.583***

Notes: † $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. See Table 6 for explanation of path coefficients.

of segments dispersed beyond recovery (Table 7B), as would be expected if erosion of dunes and exposure to winter storm waves contributed to long distance dispersal. Surprisingly, however, these effects were not significant in this sample. The variable that had the strongest effect on both wide scale measures of dispersal was depth of burial (Table 7). Burial could easily prevent detachment of segments that had not yet detached, and prevent secondary dispersal of segments that had detached and fallen beneath the maternal plant. Indirect effects diminished the effects of environmental variables on local measures of dispersal, and even changed the direction of the effect of beach width and slope on local mean crowding (Table 6B). Environmental variables strongly influenced burial and the expression of plant traits (Fig. 5). Because plant traits and burial, in turn, influenced dispersal, the mag-

nitude of indirect effects of environmental variables on dispersal was large.

A particularly interesting relationship revealed by path analysis is the reciprocal interaction between plant traits and density (Table 8). Both the number of plants in the maternal clump and mean crowding are measures of density. In this study, density influenced the phenotypic expression of plant traits, and plant traits, in turn, influenced density in the following generation. Plants with more fruits and more detachment had more crowded progeny (Tables 6B and 7A), and these progeny would grow into plants with fewer fruits and less detachment (Fig. 5). Taller plants with fewer branches per centimeter and more primary fruits had more crowded progeny (Tables 6B and 7A), and these progeny would grow into tall plants with fewer branches

TABLE 8. Reciprocal relationship between phenotype and density.

Trait	Density → Phenotype	Phenotype → Density	Between-generation phenotypic correlation
Total segments	negative	positive	negative
Height	positive	positive	positive
Branches/cm	negative	negative	positive
Percentage primary fruits	positive	positive	positive
Percentage detachment	negative	positive	negative

Notes: Between-generation phenotypic correlations are the products of the two paths of influence (columns 1 and 2). Column 1 entries are based on Fig. 5. Column 2 entries are based on total effects in Tables 6 and 7. The correlation between generations for crowding is the sum of phenotypic correlations, which is equivalent to the sum over all paths of influence.

per centimeter and more primary fruits (Fig. 5). This leads to a positive correlation between the maternal and progeny generations for height, branches, and primary fruit production but a negative correlation between generations for fruit production and detachment (Table 8). The correlation between generations for density itself would depend on the magnitudes of phenotypic correlations for the plant traits, since it is the combined effect of all the plant traits that determines density in the next generation. This study alone, however, cannot predict these phenotypic correlations very well because only a narrow range of densities was sampled; establishing a strong regression relationship between plant phenotype and dispersal restricted the densities sampled because greater phenotypic variation was expressed only at the lower densities. However, another experiment explicitly addressed the influence of density on phenotypic expression of these traits and allowed estimates of these correlations between generations (Donohue 1993).

All measured variables accounted for 49.8% of the variation in wide-scale mean crowding index and 48.2% of the variation in percentage of segments dispersed beyond recovery, whereas plant traits alone accounted for only 24.3 and 28.4% of the variation in these dispersal measures, respectively (Tables 5 and 7). Environmental variables explained somewhat less of the variation in local dispersal measures; the variance explained increased from 38.1 to 48.8% for local distance and from 47.0 to 69.5% for local mean crowding when environmental variables were included. The significant improvement in explaining variation in both measures of wide-scale dispersal when traits other than plant traits are included suggests that the environmental traits influence wide-scale dispersal more strongly than do the plant traits. In general, however, the direction of the effects of all variables were quite similar for local and wide-scale mean crowding, suggesting that the measured variables influence both of these measures in the same way, but that they influence local dispersal more strongly.

Interaction between fruit traits and plant traits in the field

A nonintuitive result from the path analysis is that a greater percentage of fruit detachment was associated with increased crowding (Table 6B). This result could have two causes. First, a trait not included in the path analysis could simultaneously cause increased detachment but impeded dispersal. Regression of the number of higher level branches (tertiary, quaternary, and quintary branches) against the percentage of detachment showed that a significant association existed between a high percentage of detachment and a large number of branches (coefficient = 0.210, $P = 0.021$, $N = 50$). This result is consistent with the hypothesis that plants with many branches have a large percentage of segments knocked from the branches, but that these seg-

ments are impeded by the branches from secondary dispersal from the maternal site. Another possibility is that this result could be because segments that were less likely to be detached from the maternal plant were those that were colored. This could account for the unexpected result that a greater percentage of fruit detachment results in the recovery of more crowded colored fruits. However, analysis of covariance showed no significant effect on mean crowding of the interaction between percentage detachment and proportion of all fruit segments on a plant that were colored ($N = 30$, $MS = 1.016$, $F = 0.860$, $df = 1$, $P = 0.364$). Moreover, when the percentage of fruits that had already detached and consequently were not colored during the first visit was included in all analyses, the direction and magnitude of the effect of detachment on dispersal did not change, suggesting that detachment before coloring did not appreciably influence the effect of detachment after coloring. The effect of censusing after some fruit detachment may have had some effect on the magnitude of influence of detachment on dispersal, but other factors, such as correlation with traits not included in the analysis, seem to have operated more strongly.

As expected from the results of the dispersal of proximal and distal segments under controlled conditions, the field study showed that recovered colored distal segments were dispersed to significantly greater distances within the census area and were significantly less crowded at both the local and the wide scale (Fig. 6). A marginally significant trend existed for a greater percentage of distal segments to be dispersed beyond recovery. Differences in morphology and detachment of proximal and distal fruit segments, therefore, effected differences in dispersal even under natural field conditions.

To examine the effect of plant traits on the difference in dispersal by proximal and distal segments, dispersal measures were calculated separately for proximal and distal segments on each plant. The difference between these dispersal measures was then regressed against the plant traits (Table 9). Plants with fewer segments had greater differences in mean crowding (both local and wide scale) between segment types, and a weak trend existed for plants with fewer primary fruits to have greater differences in mean crowding. The influence of fruit traits on crowding, therefore, is expected to be strongest on plants with few segments and perhaps those with a smaller percentage of primary fruits. This suggests that even if a fruit character does not, itself, vary substantially with the environment, its influence on dispersal may. This is because it interacts with other plant traits that do vary with the environment. Plant traits, however, explained very little of difference in dispersal by proximal and distal segments as measured by distance dispersed by recovered segments and by percentage of segments dispersed beyond recovery. This result indicates that the fruit traits do not interact

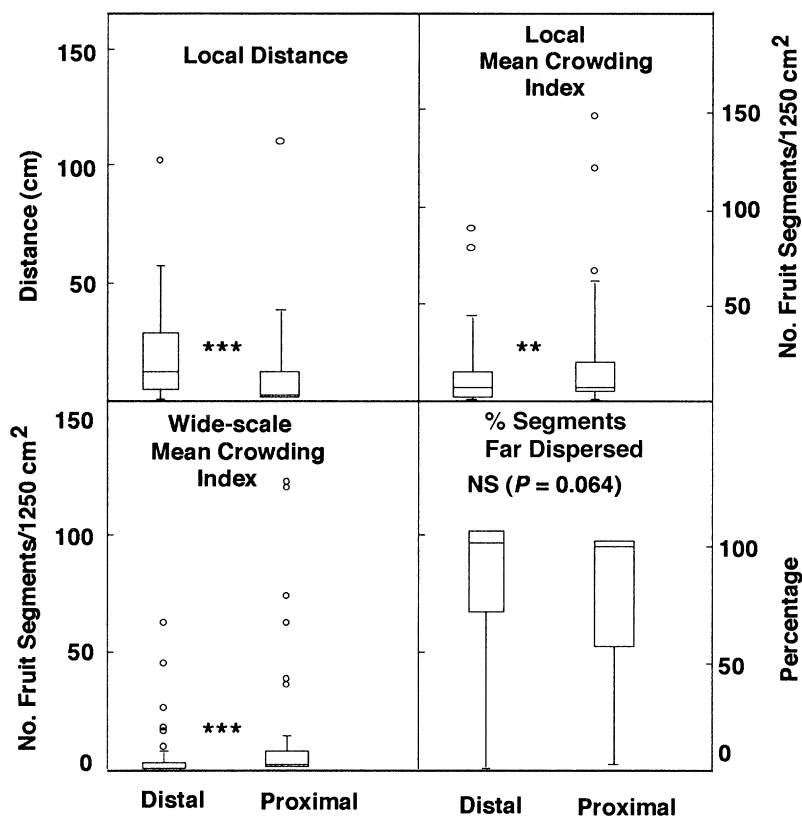


FIG. 6. Dispersal by distal and proximal fruit segments in the field. Box plots show median, quartiles, range, and outlying points of four untransformed dispersal measures of distal and proximal fruit segments. Asterisks indicate significance level of the difference in dispersal measures of distal and proximal fruit segments based on paired t tests of normalized data (natural-log transformed for local distance, local mean crowding index, and wide-scale mean crowding index; arcsine square-root transformed for “% segments: far dispersed”). ** $P < 0.01$, *** $P < 0.001$. $N = 28$ for local dispersal measures, and $N = 50$ for wide-scale measures. See Table 9 for explanation of sample sizes.

significantly with plant traits to influence these measures of dispersal.

DISCUSSION

Fruit traits, plant traits, and maternal site environmental traits all influenced dispersal in *C. edentula*. Very ordinary plant architectural traits, such as height and branching patterns, influenced dispersal in conjunction with highly specialized fruit characters hypothesized to be adaptations for dispersal, such as seed heteromorphism. This result emphasizes the need to view seed dispersal as a character of the maternal plant; all plants have dimensions of height and branching, whereas not all of them have highly developed “dispersal adaptations.” Moreover, these maternal plant traits deserve special attention simply because they are ordinary; the architectural characters shown to influence seed dispersal in this study are likely to influence dispersal in many other systems as well (see Sheldon and Burrows 1973, Harper 1977, Rabinowitz and Rapp 1981, McCanny and Cavers 1989 for other examples).

These same traits exhibit significant variation as a function of the maternal environment. Similar traits

often show great variation in response to environmental conditions in many other systems (e.g., Turner and Rabinowitz 1983, Weiner 1985, Schmitt et al. 1986, 1987, Aarssen and Burton 1990, Sultan and Bazzaz 1993a,b), although in these systems the relationship of these traits to dispersal was not investigated (Donohue and Schmitt 1998). This study, therefore, provides unusual evidence that seed dispersal can exhibit maternal environmental effects (see also Baker and O’Dowd 1982, Peroni 1994).

Previous studies have demonstrated that plant architectural characters influence seed dispersal, and numerous other studies have shown that plant architecture varies with the environment. Fewer studies have shown that the maternal environment can influence dispersal directly (e.g., Theide and Augspurger 1996). However, this study demonstrates that all of these separate factors influence dispersal in conjunction, through their combined influences on each other.

The interaction between dispersal and conspecific density, or crowding, is of particular interest. Conspecific density varies enormously in this system. A high degree of colored segment recovery immediately be-

TABLE 9. Regression of difference in dispersal measures of distal and proximal fruit segments as a function of plant architectural traits.

Trait	Coef- ficient	<i>t</i>	<i>P</i>
Average distance of recovered fruit segments ($N = 28$, $R^2 = 0.034$)			
ln height (cm)	-1.826	-0.621	0.540
ln branches/cm	-9.317	-0.877	0.390
Percentage primary fruits	0.767	0.081	0.936
ln total segments	0.378	0.214	0.832
Local mean crowding index ($N = 28$, $R^2 = 0.253$)			
ln height (cm)	10.788	1.212	0.238
ln branches/cm	5.787	0.180	0.859
Percentage primary fruits	-50.131	-1.759	0.092
ln total segments	-13.337	-2.495	0.020
Wide-scale mean crowding index ($N = 50$, $R^2 = 0.133$)			
ln height (cm)	4.229	1.010	0.318
ln branches/cm	-6.062	-0.400	0.691
Percentage primary fruits	-23.807	-1.539	0.131
ln total segments	-6.320	-2.363	0.022
Percentage segments far dispersed ($N = 50$, $R^2 = 0.092$)			
ln height (cm)	-0.127	-1.345	0.185
ln branches/cm	-0.375	-1.097	0.278
Percentage primary fruits	0.515	1.476	0.147
ln total segments	0.090	1.487	0.144

Notes: "Percentage primary fruits" was arcsine square-root transformed to normality. Sample size for local dispersal measures is lower than that used in the MANOVA and path analysis because a substantial number of segments from four plants could not be identified as distal or proximal.

neath dead maternal plants corresponds to seedling censuses (K. Donohue, *unpublished data*) that indicate a high proportion of seedlings in discrete high density clumps with isolated individuals elsewhere on the beach. Although dense seed deposition beneath maternal plants is not uncommon in other species (for example, Eriksson 1994, Scherff et al. 1994, Lott et al. 1995) *C. edentula* seems somewhat unusual in the extremes of its dispersal potential; it ranges from no dispersal, in the form of retention of segments on the dead maternal plant, to potentially very long distance dispersal by water. This variation in density is predicted to cause variation in plant phenotypes, which in turn could cause variation in dispersal itself.

Plant responses to conspecific density could influence phenotypic correlations between parents and offspring for dispersal traits, depending on how density varies with dispersal. Because of its sparse distribution, crowding of *C. edentula* decreases with increasing distance, whereas abiotic factors do not seem to vary systematically with dispersal (Donohue 1997). Interactions of plant phenotype with crowding in this system result in positive correlations between the maternal and progeny generations for some traits but negative correlations between generations for others. Positive or negative phenotypic correlations between generations could have significant effects on the rate and direction of the response to selection (Kirkpatrick and Lande

1989, 1992), with positive correlations leading to an accelerated response to selection and negative correlations leading to a retarded or even negative response to selection.

The maternal traits that influence dispersal in this study are known to be correlated with maternal fitness in this and many other systems (Weiner 1985, Menges 1987, Berntson and Weiner 1990, Weiner and Thomas 1992, Sultan and Bazzaz 1993b, Dudley and Schmitt 1996; K. Donohue, *unpublished data*). In *C. edentula*, these maternal traits that influence dispersal are strongly associated with maternal plant fitness, sometimes allometrically and sometimes through directional or stabilizing selection (K. Donohue, *unpublished data*). Not only the traits themselves, but the responses of traits to environmental conditions may have selective consequences of their own. Phenotypic plasticity in response to competitive, light, or resource environment has been hypothesized to be adaptive (Via and Lande 1985, Weis and Gorman 1990, Van Tienderen 1991, Gomulkeiwicz and Kirkpatrick 1992, Schmitt and Wulff 1993). The observed response of *C. edentula* to clump size in the form of increased distance between branches and increased height is a common response to density in many plants, and one which has been shown to be adaptive in *Impatiens capensis* (Dudley and Schmitt 1996). Common plant traits influence dispersal, and these traits vary substantially with the environment in this and other systems. Such traits, moreover, are likely to have fitness consequences to the maternal plant.

The ordinariness of the maternal traits that influence dispersal in this system and the ubiquity of their variation in response to environmental conditions in other systems offer a very general starting point for the investigation of selection on and response to selection by seed dispersal. The observation that these architectural traits are known to be so variable in so many systems creates the unavoidable conclusion that seed dispersal is very likely to be highly plastic, that it shows maternal environmental effects, and that these traits and their plasticity are likely to be correlated with maternal plant fitness. Selection on progeny after dispersal, therefore, is likely to be only the second episode of selection that occurs on seed dispersal—the first being selection on the maternal plant that created the seed dispersion pattern. The likelihood that maternal plant characters have fitness consequences of their own has never been investigated in empirical studies of selection on seed dispersal, but its importance now seems unavoidable, considering what sorts of maternal traits influence progeny dispersal. If the fitness consequences of dispersal traits to the maternal plant are considered, we may eventually be able to explain such ubiquitous observations as inefficient dispersal, even when dispersal increases progeny fitness. Moreover, if phenotypic correlations between generations for maternal traits and dispersal are not assumed to be strongly positive, as they have been in the past, then we may also

be able to investigate responses to selection on dispersal.

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