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Seed dispersal in *Cakile edentula* var. *lacustris*: decoupling the fitness effects of density and distance from the home site

Abstract A factorial design of three densities of siblings at three local distances from seed parents was employed to distinguish effects of density from effects of dispersal distance on lifespan and fruit production of *Cakile edentula* var. *lacustris*, a plant with heteromorphic seeds. The segmented fruits produce two seed types: proximal and distal, with distal seeds having greater mass and greater dispersibility. Effects of longer distances (0.5 km and 30 km) on lifespan and fruit production were investigated using plants at low density. The prediction was tested that the greater seed mass of distal seeds increases fitness when seeds are dispersed into sites of unknown quality away from the home site or when seeds are dispersed to low density. High density caused earlier mortality and lower probability of reproduction. Distance from the maternal plant did not influence lifespan or reproduction at distances of 15 m or less, but lifespan was longer 0.5 km from the home site. No interaction was detected between the effects of density and distance on either lifespan or total fitness. Environmental conditions that influence fitness did not vary as a function of dispersal distance in this system, and favorable conditions at the home site did not persist between generations. Therefore, selection on dispersion patterns in natural conditions is likely to be through effects of density rather than dispersal distance. Proximal seeds had greater reproduction than distal seeds at the home site, and distal seeds had greater reproduction at the more distant sites (but not the most distant site), as expected, but these performance differences could not be attributed to differences in mass between the two seed types. Reduced seed mass was favored at the most distant site, but larger seed mass was favored most strongly at low density. Seeds that are dispersed to low density are larger, suggesting that although kin selection may limit the effectiveness of individual selection to increase seed mass under conditions of sibling competition, density-dependent individual selection on seed mass, rather than distant-dependent selection, also contributes to the observed associations among seed type, seed mass and dispersal ability.

Key words Density · Dispersal · Dispersion patterns · Seed heteromorphism · Seed size

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Introduction

Seed dispersal from the maternal parent often has fitness consequences for progeny. Nearly every published study of dispersal concludes that dispersal is not a selectively neutral character. The agent of selection could be either distance from the home site or high sibling density. Distance and seed density often covary in natural dispersion patterns, such that sibling density decreases with increasing distance from the seed parent (e.g., Janzen 1978; Augspurger 1983a, b). To isolate the selective effect of these factors on dispersal and to determine how these factors interact, experimental manipulations are necessary. Previous studies investigating selection on dispersal have measured progeny fitness (reviewed in Howe and Smallwood 1982) in naturally occurring distribution patterns around the seed parent or "home site" (Janzen 1978; Augspurger 1983a), in experimental patterns approximating natural dispersion patterns (Kelley et al. 1988), or in a fixed density at different distances from the home site (Schmitt and Gamble 1990). In this study, I experimentally decouple density and distance from the home site in order to investigate how two possible selective agents on dispersal interact.

Increased distance from the seed parent can reduce progeny fitness if the home site in which the parent grew is intrinsically superior or if the maternal plant, and thereby the progeny, are adapted to the microenviron-

ment of that site (Balkau and Feldman 1973). High sibling density, on the other hand, can reduce progeny fitness at the home site (Liew and Wong 1973; Hamilton and May 1977). If both favorable microenvironment and unfavorable density co-occur, then investigating the fitness effects of only one of these factors may greatly bias estimates of fitness effects of dispersal. Distinguishing between the fitness effects of distance and density and acquiring information on how these factors vary in natural environments are necessary steps towards predicting how dispersal might evolve.

Many models of the evolution of dispersal investigate the effects either of local adaptation or of density. Models that include local adaptation in a heterogeneous environment predict that selection on dispersal will favor decreased dispersal and will cause the maternal home site to be superior to a random site in the environment (e.g., Balkau and Feldman 1973; Hastings 1983; Levin et al. 1984). Models that investigate the effects of density on the evolution of dispersal, on the other hand, predict that increased dispersal will evolve to decrease competitive interactions among relatives (Hamilton and May 1977; Comins et al. 1980). The primary difference between these two classes of models is that the former (models of local adaptation) include environmental heterogeneity, whereas the latter (models of density effects) usually assume a constant physical environment, but postulate variation in the spatial structure of genetic relatedness among individuals. Therefore, distinguishing between fitness effects of dispersal distance versus sibling density is relevant in the context of distinguishing effects of local adaptation in a heterogeneous environment from those of density and local genetic structure in a constant environment.

A second motivation for this study was to investigate factors hypothesized to influence the evolution of seed heteromorphism. Plants with heteromorphic seeds often have one seed type that is smaller, has limited dispersal ability and greater dormancy. The other seed type usually is larger, has greater dispersal ability, and has little dormancy (Venable and Brown 1988). Increased seed size increases seedling survival in certain environments but not others (Baker 1972; Gross 1984; Winn 1988). In particular, seeds that are dispersed away from the home site may experience unpredictable stress in a spatially heterogeneous environment. Increased seed size may be a risk-reducing strategy that improves establishment by providing the embryo with more reserves (Venable and Brown 1988). Thus, increased seed size may be selected to be correlated with increased probability of dispersal, leading to the evolution of heteromorphism with respect to both dispersal ability and size. However, other studies have shown that increased seed mass is selected more strongly under competitive conditions (Stanton 1984; Waller 1984; Wulff 1986). Since high density is associated with non-dispersal, individual selection to increase seed mass at high densities could act in conjunction with individual selection to increase seed mass at greater dispersal distances, leading to no observable association

between seed mass and dispersal if both selective agents are of equivalent magnitude. If so, the observed association could be the result of the limited effectiveness of individual selection on seed mass under conditions of sibling competition. That is, maternal allocation to increase the initial size of all competing offspring may do very little to increase the fitness of any one of them, since relative size rather than absolute size is likely to be important in competitive situations (Stanton 1984). Furthermore, production of different sized offspring may not result in higher family fitness if selective allocation to superior offspring were not possible because all progeny were genetically very similar, as would be the case in highly selfing species such as, *Cakile edentula*. Production of larger offspring may only be favored, therefore, if they are not in competition with siblings – that is, if they are dispersed from the site of intense sibling competition. This mechanism of kin selection could lead to an association between seed mass and dispersal ability even if selection to increase seed mass did not interact with dispersal distance, as previously hypothesized, provided increased seed mass is favored under any conditions. By measuring the magnitude of the interactions between seed mass, distance, and density and their influence on fitness components, one can acquire some information on the relative importance of kin selection and individual selection on seed mass to the evolution of associations between seed mass and dispersal ability.

This study distinguished between the importance of environmental heterogeneity and sibling competition for selection on seed dispersion patterns and measured the magnitude of their interaction. Using a factorial design of three sibling densities at three distances from the seed parent, I distinguished the fitness effects of sibling density from those of distance from the site of the seed parent in the annual beach plant, *Cakile edentula* (Bigel.) Hook.var. *lacustris* (Brassicaceae; *C. edentula* hereafter). I also investigated how seed type and seed size influenced progeny fitness at different distances and densities and thereby tested hypotheses concerning the evolution of seed heteromorphism in *C. edentula*. Specifically, I asked:

1. Does sibling density influence progeny fitness?
2. Does distance from the site of the seed parent influence fitness, such that progeny have greatest fitness at the home site, as predicted by several models of dispersal in heterogeneous environments?
3. Do density and distance from the seed parent interact to influence fitness?
4. Do seed size and distance interact to influence fitness, such that the larger seed size of distal seeds increases fitness at greater distances from the home site?
5. Do seed size and density interact to influence fitness?

Answering these questions can help determine whether selection on dispersal promotes local adaptation, or alternatively, whether dispersal is selected through its

effects on the intensity of sibling competition, independent of the underlying spatial heterogeneity of the environment.

Materials and methods

C. edentula is an annual lakeshore plant with heteromorphic fruit segments. *C. edentula* occurs in a wide range of densities, ranging from hundreds of seedlings within a square meter area to widely scattered individuals elsewhere on the beach. *C. edentula* has segmented fruits with a deciduous distal segment which often detaches from the proximal segment and can be dispersed independently from it. The proximal segment often remains attached to the dead maternal plant, and thereby often remains at the maternal home site. Each segment usually has a single seed, and distal seeds are larger on average than proximal seeds (proximal seeds = 0.007g, SE = 0.001; distal seeds = 0.009g, SE = 0.002). Distal segments are dispersed to lower densities and longer distances at the local scale (within 3 m) (Donohue 1993).

Twenty-nine plants of *C. edentula* were identified at the end of the 1991 growing season at Mount Baldy in the Indiana Dunes National Lakeshore on the southern shore of Lake Michigan. Large plants were chosen to ensure that they had enough seeds to complete the experimental design, and approximately equal numbers of plants were chosen from three different habitats in the dunes: the open beach, the base of the dune, and the dune slope. The exact location of each plant was marked with stakes and compass readings. Seeds from each plant were randomly selected for each treatment, but with equal numbers of proximal and distal seeds from each plant for each treatment. For each seed, mass and seed type – proximal or distal – were recorded. During spring 1992, each seed was planted in Pro-Mix (Premier Brands, an artificial soil) in a plug tray in the greenhouse, and then transplanted into the field immediately after the first true leaves appeared. Plants that died within 2 days from transplant shock were replaced. Seedlings were used instead of seeds because the unstable substrate of the beach would have buried or blown away seeds or newly emergent seedlings.

Each home site was designated as a plot of 75 cm by 50 cm, with the maternal plant located at its center. This plot was divided into six 25 cm by 25 cm subplots. Each subplot was assigned one of three possible density treatments. Four of the subplots received 1 seedling each, as the low-density treatment. One subplot received 8 seedlings, and the remaining subplot received 20 seedlings. In each of the four low-density subplots, the single seedling was the focal plant. In the medium- and the high-density subplots, four centrally positioned seedlings were designated focal plants. For the distance treatments, similar 75 cm by 50 cm plots were established at 3 m and 15 m from each home site. These plots were necessarily located in the same type of dune habitat (open beach, base of dune, dune slope) as the respective home site, and their direction was randomly chosen to be east or west of the home site, the lake being to the north. Both replicates were planted in the same direction. The planting pattern of plots was identical within a family at the three distances, but spatial arrangement of the subplots differed randomly among families. All plants used in the three plots were siblings, including the non-focal plants. All plots were within locations in which *C. edentula* was growing, although no plot occurred on the exact site on which a plant or clump of plants was growing.

The three densities were chosen to span the range of densities in which *C. edentula* naturally occurs. The low density represents plants growing singly on the beach. Plants at the intermediate density were arranged in two rows. The linear arrangement of the intermediate density treatment represents the spatial arrangement of seedlings that grow from fruits that were washed on shore and grow at the storm line. The high-density treatment represents the high-density clumps that grow from fruits that were not dispersed from the maternal plant site or that did not detach from the dead

maternal plant. This treatment was not able to replicate the extremely high density of the natural situation, so it under-represents the density effects expected under natural situations.

In addition to the plots mentioned above, four seedlings from each family were planted singly at distances of 0.5 km and 30 km (at West Beach of the Indiana dunes National Lakeshore) from the maternal plant site. They were planted in a random order 50 cm from each other, as single plants were in the other three distance treatments. All five experimental distances are likely to be within the dispersal range of water-dispersed fruits, since *C. edentula* fruit segments can remain viable after being afloat for over a month (Payne and Maun 1981). The habitat of planting sites was the same for all distance treatments within a family, and equal numbers of families were planted in each of the three habitats. Because of the impracticality of replicating long-distance sites independently for each of the 29 sibships along a two-dimensional lakeshore, this experiment estimated only the fitness consequences of long-distance dispersal in a single direction. That is, because only one long-distance site was used for each distance, site and distance effects are confounded. However, natural long-distance dispersal along the lakeshore is also directional. Although replicating long-distance sites would have allowed estimation of effects of long-distance dispersal independently of those of specific site conditions, replication within a single site allows one to determine if differences among sites exist and how such differences could influence selection on dispersal.

Seedlings were censused weekly, and their survival and fruit production were monitored throughout the growing season until the first snow. Lifespan and total number of fruit segments produced were recorded. Since plants tend to self (Donohue 1993) and because fruit segments are single-seeded, the number of fruit segments produced closely approximates total lifetime fitness. Cause of mortality was also recorded.

Mixed model analysis of covariance was used, with "maternal sibship" as the random variable, nested within habitat (fixed), to test for the effects of habitat, density (fixed), distance (fixed), and seed mass (continuous covariate) or seed type (proximal or distal, fixed) on lifespan. Lifespan was natural log transformed to normality. Proc Mixed of the SAS statistical package, which employs restricted maximum likelihood, was used for all mixed-model analyses of variance. Proc Lifetest (SAS) tested for significant differences in mortality curves among density treatments pooled over distance classes and among distance treatments pooled over density classes.

Plants were classified as reproductive or non-reproductive, and logistic regression, using an iteratively reweighted likelihood approach based on a mixed model, was performed using the macro Glimmix available from the SAS Web site. Probability of reproduction was the dependent variable, density, distance and seed type were fixed effects, seed mass was a continuous covariate, and maternal sibship was a random effect. Significant interactions with seed mass or seed type that were detected in the maximum likelihood analysis were characterized by comparing seed mass of reproductive and non-reproductive plants in each class and by comparing percent reproduction by proximal and distal seed types in each class respectively.

Analysis of covariance (Proc GLM of SAS) was performed on a subset of natural log-transformed data on seed production which included only reproductive plants. "Maternal sibship" could not be used as a random variable since only two families had representatives in all of the nine density and distance treatments due to high mortality and lack of reproduction. However, mean values within a family for each density and distance were used to prevent pseudoreplication within families.

The effect of longer dispersal distance on fitness traits of plants grown singly at all five distances was examined with the same methods as above.

All analysis of variance models were constructed a priori to test hypotheses concerning the influence of the fixed effects, covariates, and their interactions on different components of fitness. "Habitat" was included as a main effect in all models since position on the dune was hypothesized to influence fitness, and the equal sampling

across habitats was designed to control for the influence of habitat. Interactions with habitat were not included because the goal of the experiment was to determine how the other factors influenced fitness components throughout the range of habitats experienced by *C. edentula* rather than how these factors might interact with unspecified environmental variables that vary across habitats. The model presented includes both seed mass and seed type, and in a sub-model, seed mass and its interactions were excluded. These two models together test (1) whether the seed type that is typically dispersed (the distal type) performs better at either greater distances or at lower densities than the typically non-dispersing (proximal) type, and if so (2) whether performance differences between the two seed types are due to differences in their seed mass or due to other unmeasured differences between the two seed types.

Results

Plants at intermediate densities had longer lifespans (Fig. 1A), but distance did not influence lifespan at the three local distance classes (Table 1). The rate of mortality over the season was highest for high-density plants
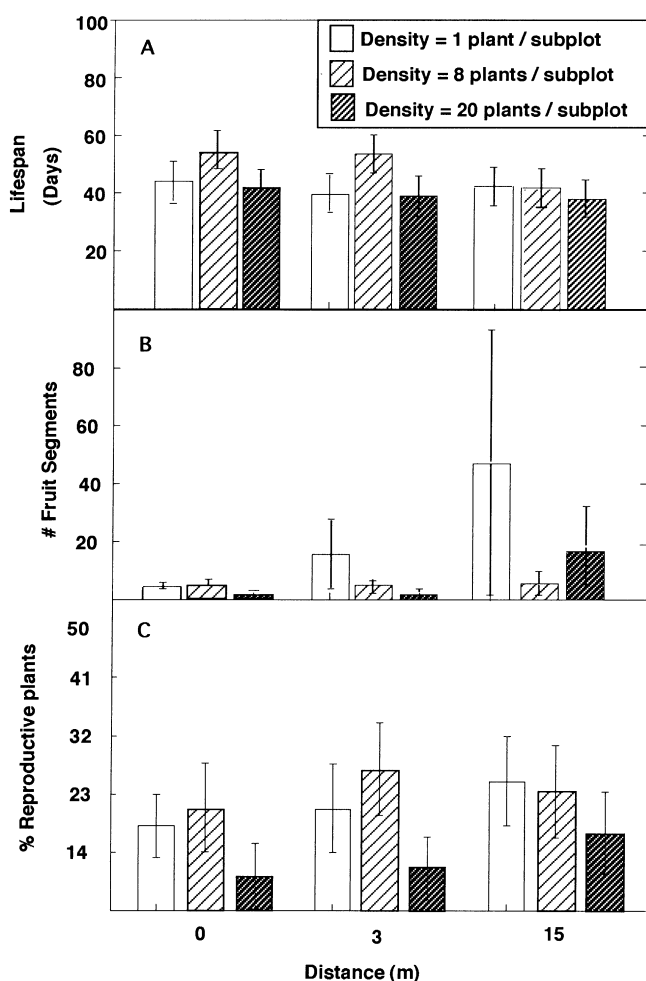

Fig. 1 A Lifespan, **B** fruit segment production, and **C** percent reproduction as a function of distance and density. Mean values of maternal sibships within each treatment class were used to calculate sample means and standard errors. Reproductive and non-reproductive plants were used ($n = 29$ sibships for each sample)

and lowest for plants at intermediate densities (based on the Wilcoxon χ^2 test using individual values: $\chi^2 = 12.81$, $P = 0.002$; using mean values of maternal sibships: $\chi^2 = 5.01$, $P = 0.082$), but it did not differ among local distance classes (using individual values: $\chi^2 = 4.21$, $P = 0.122$; using mean values of maternal sibships: $\chi^2 = 1.82$, $P = 0.403$). The difference in mortality curves among the density classes was constant over time, as opposed to large differences occurring at specific times in the life cycle. A slower death rate of plants at intermediate densities could be the result of facilitation processes that decrease the probability of dessication and early mortality (Bertness and Yeh 1994). Alternatively, a slower death rate could be due to a slower growth rate. Plants from larger seeds had longer lifespans, but no interactions with density or distance were detected. A regression of lifespan against seed mass and its quadratic term revealed highly significant stabilizing selection on seed mass, as estimated with this fitness component [relative lifespan = 0.57(seed mass)*** − 0.55(seed mass2^x)***, using standardized regression coefficients; ***$P < 0.001$]. Seed type and its interactions remained non-significant even when seed mass and its interactions were dropped from the model, suggesting that although proximal and distal seeds differ in seed mass, this difference is not great enough to account for differences in longevity between the two seed types (seed type $F = 1.69$, $P = 0.194$; seed type × density $F = 2.40$, $P = 0.091$; seed type × distance $F = 2.42$, $P = 0.89$).

Lifespan was positively associated with total number of fruit segments produced, although it explained a small proportion of the variance in fruit segment production (regression line: ln (total seeds) = −0.337 + 0.017 (lifespan); $t = 27.00$, $P << 0.0001$, $r^2 = 0.408$). Plants at lower densities produced more fruit segments, on average (Fig. 1B). This is because a greater proportion of plants reproduced at low densities (Table 1, Fig. 1C), not because high density limited fruit production of reproductive plants (ANCOVA of fruit production by reproductive plants showed that all fixed effects, covariates, and interactions were non-significant). Plants from larger seeds had a greater probability of reproduction at the lowest density but not at the other densities, which explains the significant interaction between density and seed mass on probability of reproduction (Table 1, Fig. 2A). Proximal seeds had a greater probability of reproduction than distal seeds at the home site, while distal seeds had a greater probability of reproduction at 15 m (Fig. 2B). Although the difference in reproduction by the two seed types was not statistically significant at any distance class, the direction of the effect of seed type on reproduction changed over distance, leading to a significant interaction between seed type and distance at the local distance classes (Table 1). The reproductive performance differences between the seed types are due to factors other than seed mass differences, since seed mass was controlled for in this analysis. This pattern of proximal seeds performing better at the home site while distal seeds perform better away from the home site, and

Table 1 Analysis of lifespan and reproduction probability as a function of density and distance ($n = 1044$). Only distances of 0, 3, and 15 m were used ($r^2 = 0.811$ for lifespan, and $r^2 = 0.731$ for reproduction probability, based on least squares). The maternal sibship component for lifespan was significant (mean square = 12.19, $F = 2.11$, $P = 0.008$). The maternal sibship component for reproduction probability was significant in logistic regression ($\chi^2 = 132.54$, $P < 0.001$). Distance had no significant effect even when seed mass, seed type, and their interaction terms were dropped

Source	df	Lifespan		Probability of reproduction	
		F-ratio	P	F-ratio	P
Habitat	2	94.29	< 0.001	6.82	0.001
Density	2	3.38	0.035	8.37	<0.001
Distance	2	0.11	0.892	1.58	0.207
Density × distance	4	1.28	0.277	0.47	0.760
Seed mass	1	4.41	0.036	1.21	0.273
Seed mass × density	2	1.87	0.154	15.58	<0.001
Seed mass × distance	2	0.31	0.733	2.02	0.133
Seed type	1	0.02	0.897	0.00	0.966
Seed type × density	2	1.03	0.356	1.29	0.277
Seed type × distance	2	0.90	0.405	13.89	<0.001
Seed type × seed mass	1	0.29	0.592	0.06	0.809

the pattern of larger seeds performing better at low density both support the adaptive hypothesis for the evolution of seed heteromorphism.

Plants growing on the dune slope had the shortest lifespan [mean(95% CI): slope = 16.4 (143.2–20.5); base of dune = 43.4 (36.2–51.9); beach = 35.5 (26.8–47.0); $F_{(habitat)} = 94.29$, $P < 0.001$] and lowest total number of fruit segments [slope = 1.6 (1.1–2.3); base of dune = 11.7 (5.4–25.7); beach = 4.7 (2.8–7.8); see Table 1 for *F*-values], and plants growing on the base of the dune had the longest lifespan and produced the most fruit segments. Nearly half the plants died through senescence, less than 10% died from herbivory, and 12% died from dessication. Approximately one-third of the plants died due to disturbance events such as erosion, trampling, or water disturbance. Disturbance events occurred more frequently at 15 m than expected, assuming random distribution of cause-specific mortality over all treatments ($\chi^2 = 7.887$, $P < 0.05$), a result that suggests that disturbance events are not randomly distributed throughout the landscape, but occur less frequently near large, successful maternal plants. In other words, disturbance may tend to recur year after year in specific sites on the beach, such that a safe maternal site in one year may be more likely than random to be a safe site the next year.

Plants growing at low density at a distance of 0.5 km had less than expected mortality due to disturbance ($\chi^2 = 14.986$, $P < 0.01$) and more due to senescence ($\chi^2 = 12.24$, $P < 0.05$), than plants at the other distance classes. This is apparent as a significant effect of distance

Fig. 2 A Seed mass of reproductive and non-reproductive plants as a function of density. **B** Probability of reproduction by seeds from proximal and distal fruit segments as a function of local distance. Mean values and standard error bars are shown for each density class separately. Reproductive plants grew from larger seeds in the lowest density class ($t = 2.801$, $P = 0.014$), but no difference in seed mass was detectable between reproductive and non-reproductive plants in the other two density classes (8 plants/subplot: $t = -0.108$, $P = 0.914$; 20 plants/subplot: $t = -0.584$, $P = 0.560$) n ranges from 164 to 183
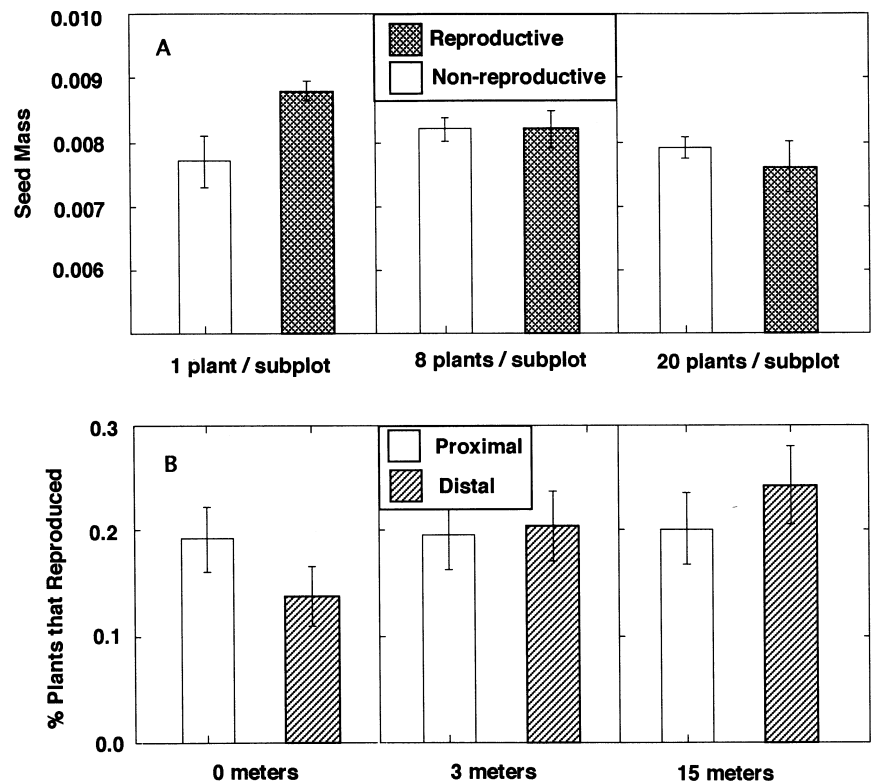
Table 2 Analysis to test for effects of distance seed mass, and seed type on lifespan and reproduction probability. Only plants grown at a density of one plant per 25 cm by 25 cm subplot were used for this analysis ($n = 574$, $r^2 = 0.985$ for lifespan, and $r^2 = 0.737$ for reproduction probability, based on least squares). Maternal sibship had no significant effect on lifespan (mean square = 0.80, $F = 0.85$, $P = 0.655$). The maternal sibship component significantly influenced reproduction probability based on logistic regression ($\chi^2 = 54.74$, $P = 0.002$). The significant seed mass × distance interaction in the full model with lifespan is due to a significant positive effect of seed mass on lifespan at a distance of 0 m and a nearly significant negative effect of seed mass at a distance of 30 km (based on an ANCOVA with habitat and seed type as fixed effects and seed mass as the covariate (0 m: coefficient = 32.51, $F = 4.24$, $P = 0.042$; 30 km: coefficient = -157.14, $F = 3.59$, $P = 0.060$)

Source	df	Lifespan		Probability of reproduction	
		F-ratio	P	F-ratio	P
Habitat	2	0.63	0.563	10.73	<0.001
Distance	4	4.84	0.043	4.12	0.004
Seed type	1	0.32	0.590	0.90	0.352
Seed type × distance	4	1.70	0.267	2.58	0.041
Seed mass	1	4.60	0.041	33.94	<0.001
Seed mass × distance	4	2.76	0.048	3.71	0.006
Seed mass × seed type	1	0.01	0.987	0.11	0.744

on lifespan (Table 2), since plants that senesced tended to live longer. Plants lived longest 0.5 km from the home site (Table 3). Less mortality occurred at the beginning of the season in the distant sites than in the local sites (comparison of mortality curves based on the Wilcoxon χ^2 test using individual values: $\chi^2 = 20.95$, $P < 0.001$; using mean values of maternal sibships: $\chi^2 = 8.14$, $P = 0.087$).

Plants grown from smaller seeds had a longer lifespan at 30 km from the home site [lifespan = -0.13 (seed

mass)**; using standardized regression coefficients; **$P < 0.01$ based on regression of transformed (normal) data]. However, seed mass had no significant effect on lifespan at the local distance classes, which explains the significant interaction between distance and seed mass (Table 2). Recall that larger seeds had significantly longer lifespans at the home site when pooled over all density classes, and that larger seeds in general had significantly longer lifespans when pooled over the local distance classes. These trends would contribute to the significant interaction between seed mass and distance. Seed type did not significantly influence lifespan even when seed mass was dropped from the model (seed type $F = 1.32$, $P = 0.254$; seed type × distance $F = 1.65$, $P = 0.165$), again suggesting that the difference in seed mass between the two seed types is not large enough to effect performance differences.

Plants at intermediate distances had a greater probability of reproduction than plants at the maternal home site or plants at the most distant site (Tables 2, 3). Distance did not influence seed production of plants that did reproduce, however ($F_{(distance)} = 0.36$, $P = 0.836$, $df = 4$). Plants from larger seeds had a greater probability of reproduction when pooled over all distance classes [mean seed mass of reproductive plants (SD) = 0.0084 g (0.0024); mean seed mass of non-reproductive plants (SD) = 0.0078 g (0.0033); $t = 2.29$, $P = 0.023$). Larger seed mass significantly increased reproduction only at the home site (Table 3), which explains the significant interaction between seed mass and distance. Seed type also interacted significantly with distance to influence reproduction, suggesting that differences between the two seed types other than seed mass caused performance differences. Proximal seeds had a higher probability of reproduction at the home site, while distal seeds had a higher probability of reproduction at distances up to 0.5 km, leading to a significant interaction between seed type and distance (Tables 2 and 3).

Table 3 Lifespan, reproduction probability, seed mass of reproductive and non-reproductive plants, and percent reproduction of proximal and distal segments at five distances. Mean values and standard error (in parentheses) are shown for each distance class separately for plants grown at low density. **Reproductive plants

grew from larger seeds at the home site ($t = 2.89$, $P = 0.006$), but no difference in seed mass was detectable between reproductive and non-reproductive plants in the other distance classes (3 m: $t = 0.65$, $P = 0.520$; 15 m: $t = 1.56$, $P = 0.124$, 0.5 kilometer: $t = 0.70$, $P = 0.48$, 30 km: $t = -0.32$, $P = 0.715$)

Distance	Lifespan (days)	% Reproductive plants	Seed mass (g)		% Reproductive plants	
			Non-reproductive	Reproductive	Proximal	Distal
0 m	44.0	18.1	0.00771	0.00947**	23.730	12.280
	(6.3)	(4.9)	(0.00033)	(0.00051)	(5.590)	(4.390)
3 m	39.5	17.2	0.00785	0.00834	14.040	20.339
	(6.3)	(4.8)	(0.00035)	(0.00065)	(4.642)	(5.285)
15 m	43.2	22.4	0.00758	0.00856	20.000	24.590
	(6.3)	(6.7)	(0.00035)	(0.00052)	(5.443)	(5.559)
0.5 km	60.5	29.0	0.00770	0.00803	26.786	31.034
	(5.2)	(6.5)	(0.00037)	(0.00030)	(5.971)	(6.128)
30 km	49.6	21.3	0.00795	0.00773	26.786	17.857
	(5.4)	(4.8)	(0.00034)	(0.00050)	(5.971)	(5.164)

Discussion

At the local scale, density strongly influenced lifespan and probability of reproduction, whereas distance did not. High levels of sibling competition had adverse fitness consequences, so selection on dispersal to decrease sibling competition would favor increased dispersal distances. There was no evidence for an interaction between density and distance in their effects on either lifespan or reproduction, so density should be able to act as a selective agent on dispersal regardless of the underlying spatial heterogeneity of the environment. This is not to say that environmental factors, such as water or nutrient availability that may vary throughout the environment, are unimportant influences on the intensity of density effects on fitness (Keddy 1981). It does indicate, however, that these environmental factors do not vary systematically as a function of local dispersal distance in this system.

Spatial heterogeneity does not seem to favor decreased dispersal in this system in the way formulated by the theoretical models mentioned above, and consequently it will not promote adaptation to local environmental conditions. For spatial heterogeneity to favor decreased dispersal, environmental conditions must be temporally invariant, or the local habitat must improve over time. Despite the fact that all the maternal sites used in the study supported maternal plants that produced much more than the average number of seeds, any favorable conditions at these sites apparently did not persist through the progeny generation. In fact, the pattern was that these sites became more unfavorable for progeny survival and reproduction rather than remaining favorable. Selection on dispersal at a local scale due to environmental heterogeneity does not seem to favor decreased dispersal, but rather favors increased dispersal from the home site. Temporal heterogeneity in environmental conditions itself is hypothesized to favor increased dispersal as a "risk-reducing strategy" (Venable and Lawlor 1980).

Local spatial and temporal heterogeneity allow little opportunity for adaptation to very localized environmental conditions, but more persistent differences between distant sites could allow adaptation at a larger spatial scale. In this study, lifespan and reproduction tended to increase with distances up to 0.5 km, but then decreased again at 30 km. Significant effects of distance at the longer distance classes but not the local distance classes was very likely to be because only one site was used for the farther distance classes, whereas effects of local distance were averaged over several microsites. The specific trends observed at the farthest distance class could therefore be due either to poorer conditions in the distant site used for the study or to local adaptation to the native site. Since large plants were used for this study, plants that were particularly well adapted to the native site could have been sampled preferentially, although this possibility seems unlikely, since Dudley

(1996a) found that *C. edentula* from a different population performed as well at this study site as did plants native to this site. However Dudley (1996a, b) did detect local adaptation in physiological characters of this same population of *C. edentula* when transplanted into the more xeric site used for the long distance site in this study. It is possible, therefore, that the decrease in reproduction at the distant site observed in this study is due to the same site-specific local adaptation observed by Dudley. Despite evidence for local adaptation at a large spatial scale (Dudley 1996a, b; possibly observed again in this study) selection on dispersal at this spatial scale would act only on those rare individuals that are dispersed such long distances.

Density, however, varies greatly in natural situations at a local scale – even more than in this experiment – and density strongly influenced important fitness components. Moreover, since environmental conditions seem to vary randomly at a local scale, but density systematically decreases with distance, dispersal is more likely to determine the density of progeny than it is to determine the abiotic environment of progeny. Therefore, selection on dispersion patterns in natural conditions is likely to be through effects of density rather than distance. This study suggests that temporal variation in environmental conditions, coupled with density effects on fitness, could both be selecting for increased dispersal in *C. edentula*.

Seed mass differences between the two seed types did not lead to performance differences, so qualities other than seed mass would account for performance differences between the two seed types. It is possible that proximal and distal seeds differ in their genetic composition due to differences in the probability of inbreeding or quality of the pollen donor due to pollen competition. They could also differ in the content of specific nutrients.

Seed mass influenced both lifespan and reproduction and interacted with both density and distance. Because seedlings, rather than seeds, were necessarily used for this study, the effects of seed mass observed in this study are likely to be underestimated. The use of seedlings may have prevented very early selection on seedlings when they are most dependent on reserves in the seed. At the home site (in plants grown at low density) larger seed mass was favored, whereas at the most distant site smaller seed mass resulted in longer lifespan. These results do not support the prediction that increased seed size should necessarily increase the fitness of seeds dispersed to unpredictable conditions away from the home site. Rather, it supports other studies that document that seed size has variable influence on fitness, depending on particular environmental conditions (Gross 1984; Winn 1988).

The observation that proximal seeds had greater reproduction at the home site and distal seeds had greater reproduction at farther distances is in accordance with predictions concerning the adaptive evolution of seed heteromorphism, since proximal seeds remain at the home site more frequently than do distal seeds. More-

over, larger seeds were favored at low density. Because low density occurs away from the home site, the seeds that are dispersed are likely to be under selection to increase in size, which again is in accordance with the observed association between seed mass and dispersal propensity. Although the direction of selection on seed mass is in the same direction as that hypothesized, the mechanism of selection is different. Specifically, it has been proposed that dispersing seeds would be selected to be larger to cope with unpredictable post-dispersal environments due to spatial variation in environmental conditions. Results from this study, however, suggest that density-dependent selection could account for the evolved association between dispersal and seed mass, whereas environmental unpredictability, apparent as distance effects, may have lead to the evolution of other qualitative differences between the two seed types. In fact, in this study, the pattern of selection on seed mass as a function of distance is the opposite of that predicted. It would be worth investigating the possibility of density-dependent selection on seed mass, as opposed to distance-dependent selection, in other systems with heteromorphic seeds to determine if the patterns of selection observed in this study are more widespread.

In conclusion, selection is likely to favor increased dispersal in this system to reduce sibling competition and possibly to reduce risk in a temporally variable environment. Moreover, the typically dispersing seed type performs better at greater distances while the non-dispersing seed type performs better at the home site. Although increased seed mass is favored most strongly at low density, the performance differences between the two seed types cannot be attributed to differences in seed mass alone. It appears that, although kin selection may limit the effectiveness of individual selection to increase seed mass under conditions of sibling competition, individual selection to increase seed mass at low density and individual selection for as yet unidentified traits that improve performance of the dispersed seed type at longer distances could have promoted the observed associations among seed mass, seed type and dispersal ability.

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