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Intrapopulation Variation in Reproduction and Seed Mass of a Beach Annual; *Cakile edentula* var. *lacustris*

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ABSTRACT

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A field study was conducted to examine phenotypic plasticity in reproduction and seed mass (weight per seed) variability of *Cakile edentula* var. *lacustris* (Brassicaceae). This beach annual exhibited large intrapopulation variation in plant size, seed production, and seed mass. The plants grew large in favourable microenvironments on the beach. For example, close to the lake the plants had significantly greater crown area and number of seeds per plant than those farther inland primarily due to higher soil moisture and nutrient content of occupied microsites. A large number of seeds within fruits were aborted but abortion was significantly higher (74%) in lower than upper fruits (14%). The coefficient of variation for mass per seed was 53% for upper seeds and 48.5% for lower seeds. Mean seed mass per plant decreased as the season progressed from July to September. The data suggest that *C. edentula* responds to unstable shoreline habitat by phenotypic plasticity in plant size, reproduction, and fruit abortion.

ADDITIONAL INDEX WORDS: *Seed production, fruit abortion, plant size, phenotypic plasticity, shoreline, beach, dunes, Cakile.*

INTRODUCTION

On the shores of Lake Michigan (OLSON, 1958) and Lake Huron (MAUN, 1985) significant changes in beach profile occur in the fall and early spring of each year by wind and wave action. Annual plant species adapted to unstable habitats show large intrapopulation variation in plant size and reproductive output (VAN ASDALL and OLMSTED, 1963; PAYNE and MAUN, 1984; KEDDY, 1982). This size hierarchy is also found in some other plant populations and may be established early in the life cycle through rapid relative growth rate (RABINOWITZ, 1979), greater seed weight (STANTON, 1984a), presence of cohorts of different ages (PAYNE and MAUN, 1984), and microenvironmental variation (LEE and IGNACIUK, 1985). Phenotypic plasticity is exhibited only by certain individual characters in response to certain specific environmental variables (BRADSHAW, 1965). For example, large variation in plant size, biomass and reproductive output per plant, has been recorded under conditions of high or low density (BRADSHAW, 1965; KEDDY, 1981), microhabitat variability (PAYNE, 1980), variable nutrient conditions (LEE and IGNACIUK, 1985) and date of maturity (CAVERS and STEELE, 1984).

BRADSHAW (1965), HARPER *et al.* (1970) and SOLBRIG (1981) suggested that seed mass (weight per seed) may remain remarkably constant or vary within very narrow limits under conditions that impose phenotypic plasticity for plant size and reproduction. However, recent studies (STANTON, 1984a,b; THOMPSON, 1984; CAVERS and STEELE, 1984) have shown that seed mass within a population may be more variable than had been expected previously. STANTON (1984b) suggested that differences in seed mass may contribute to the creation of early size hierarchy in a seedling population and affect dispersal, germination, seedling emergence and establishment. In the unstable conditions of the shoreline, seeds of greater mass would be of adaptive significance, since seedlings from larger seeds would emerge from greater depths of burial in sand (MAUN and LAPIERRE, 1986) and would probably have a better chance of establishment and sur-

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vival to maturity (WEIS, 1982; MOORE and CAVERS, 1985).

In this paper we address how *Cakile edentula* (Bigel.) Hook. var. *lacustris* responds to the fluctuating conditions of the shoreline. We present some aspects of phenotypic plasticity and seed size variability of this beach annual, which grows in abundance on the micro-gradient along Lake Huron shoreline at Pinery Provincial Park. The objectives of this study were to determine the variation in crown area, reproductive output per plant, the extent of seed mass variation, the effect of position of seed within fruit on seed mass, the effect of percent abortion on seed mass, and relationship between seed mass and number of seeds per plant. The data should provide useful information on the adaptive response of the species to changing beach morphology.

MATERIALS AND METHODS

The Species

Cakile edentula var. *lacustris* (Brassicaceae) is a fast-growing annual, endemic to the shorelines of the Great Lakes. The species is self-compatible in that the anthers often dehisce in bud just prior to flowering (RODMAN, 1974) and it reproduces only by seed. The immature ovary is initially unilocular and consists of two ovules. Following fertilization, the ovary wall between the two ovules grows inward thus separating it into an upper and a lower fruit segment each homologous to, respectively, the "stylar" and "valvar" portion of the fruit typical of the tribe Brassiceae (RODMAN, 1974). The fruits of *Cakile* are therefore dimorphic, and both upper and lower fruit segments are typically one-seeded. A certain proportion of fruits may, however, be multispermous (> 1 seed) or abortive (fruits are either empty or contain shrivelled remains of ovules). Along the shoreline, the plants follow a ruderal opportunistic strategy (GRIME, 1979) and respond to moisture stress by curtailment of vegetative growth and diversion of photosynthates into sexual reproduction (PAYNE, 1980). Following disturbance by wind and wave action, fruit dispersal, seed dormancy, germination and establishment of seedlings ensure rehabilitation.

Study Site

Intrapopulation variation of *Cakile edentula* was studied along the shoreline at the Pinery Provincial Park, Ontario, Canada (43° 15′ N 81° 50′ W). The study site, located on the beach in the northeast corner of the Park, is accessible only by foot and is not heavily used for recreation. Storm waves in spring 1985 eroded the mid-beach and created a scarp at the point of farthest inland reach of waves.

Plant Distribution

At this site a rectangular study plot (55 x 6 m) was laid out with the long axis parallel and short axis perpendicular to the shoreline. The location of the wave-cut scarp was marked with permanent stakes in order to separate the upper and high beach (the area above the scarp which is beyond the highest inland reach of waves) from the mid-beach (the area below the scarp). Line transects were drawn at 1 m intervals along the entire length of the study plot (Figure 1). The study plot was then divided along its width into six, one meter wide zones; upper beach (2 m) and high beach (2 m) were above the beach scarp while mid-beach (2 m) was below the scarp closer to the water (Figure 1). Thus in all, there were 330 one m^2 quadrats in the study plot. A portion of the study plot (16 x 6 m) is shown in Figure 1.

Date of Maturity, Plant Size and Seed Production

On July 9, 1985, all *Cakile edentula* var. *lacustris* plants within the study plot were mapped and tagged with an aluminum tape bearing an identification number. Since germination begins in the end of April and ends by the first week of June (PAYNE, 1980), the tagged plants presumably comprised a mixture of cohorts. In all, 500 plants were tagged; however, only 169 of these survived and reproduced by September 21. The plants were monitored on weekly intervals from July 25 until September 21. As soon as a plant reached maturity (the fruits started to turn yellow), the date of maturity was recorded. Size of each plant was then determined by measuring its crown diameter and then calculating its crown area using the equation πr^2. Each plant was then harvested

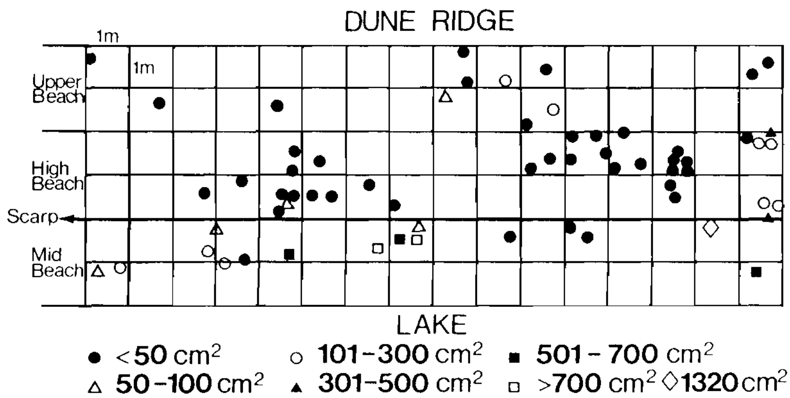

Figure 1. Map of part of the study plot (55 x 6 m) showing 18 transect lines (1 m wide and 6 m long). Each square is 1 m x 1 m. Each symbol indicates the location of the individual plants of *Cakile edentula* var. *lacustris* within the plot. The double line indicates the location of scarp. Upper beach is farthest from the lake shore, high beach is in the center and mid-beach is the closest to the lake shore.

and all the fruits (upper and lower) were collected in a paper bag and brought to the lab. Here, seed production per plant in each microhabitat was determined for each date of collection, by counting the number of upper and lower fruits from each plant.

Seed Mass

The upper and lower fruits per plant were air dried at room temperature in a lab for about 2 months and then shelled individually by removing their fruit coats. Seeds from each fruit were examined carefully and a fruit was considered aborted if it was empty or seed was shrivelled or very small in size (< 0.5 mg). Each sound unshrivelled seed from each plant was placed in a coin envelope and then dried at 70°C for 24 hours. The weight per seed (seed mass) was then recorded in mg on a digital balance to two decimal places. To determine the departure of observed frequency distribution from normal, skewness (g_1) and kurtosis (g_2) were calculated and their significance was tested using a "t" test (SOKAL AND ROHLF, 1981).

Statistical Analysis

For statistical analysis a log transformation of data for crown area and seed number was undertaken to normalize it due to the dependence of the variance on the mean. Analysis of variance was then performed on the log transformed data using the GLM procedure in the Statistical Analysis System (SAS) package (1985). Seed mass data required no transformation.

RESULTS

Plant Size and Distribution

The population of *Cakile edentula* var. *lacustris* consisted mostly of small plants (85% of the plants had a crown area of < 100 cm^2) and a few large plants (Figure 1). A two-way analysis of variance on the log transformed data indicated that both date of collection ($F = 14.7$, $p < 0.0001$) and zone of occurrence ($F = 9.9$, $p < 0.0001$) had a significant effect on crown area but there was no significant interaction between zone and date ($F = 1.27$, $p > 0.26$). Plants on the mid-beach had a significantly ($P < 0.05$) larger mean crown area per plant (246.1 ± 58.5 cm^2) than those on the upper (19.1 ± 5.7 cm^2) and high beach (35.3 ± 7.5 cm^2) zones (Figure 2). The few particularly large individuals were usually located on the mid-beach. The largest of these had a crown area of 1320 cm^2 (Figure 1). The upper and high beach plants did not differ significantly in crown area. All plants of the upper beach remained small and bore mature fruits on or before August 15, whereas plants of the high beach continued to reach

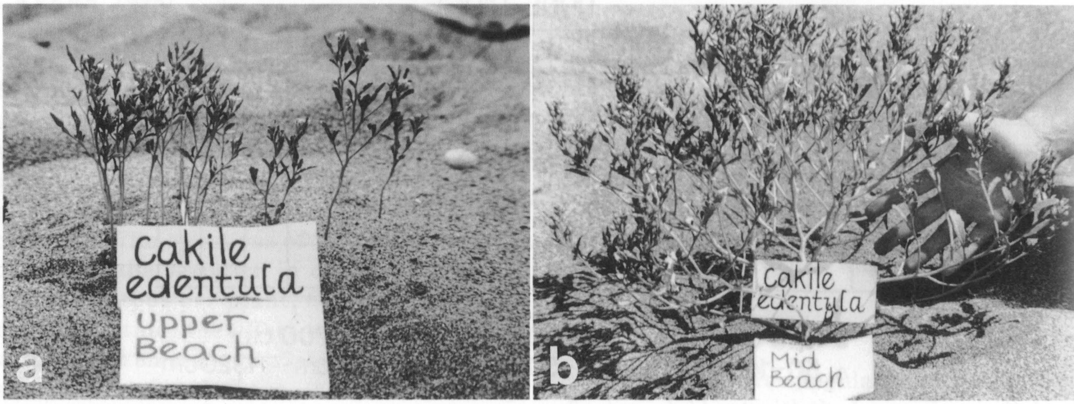

Figure 2. A comparison of 17 individual plants (1) of *Cakile edentula* typical of small plants on the upper beach compared with a single plant (b) on the mid-beach.

maturity throughout the summer (Table 1). On the mid-beach, the plants started to mature on August 8 and continued to do so for the rest of the season. The time of maturity affected plant size because plants maturing early in the season (July 25 to August 15) were significantly smaller in size (Table 1) than those maturing later (with the exception of 9 plants collected on August 29). Plants collected on September 21 had the largest crown area of all the plants collected during the summer (mean = 500.4 cm^2).

Date of Maturity and Seed Production

The mean total number of seeds per plant was usually under 10 (Table 2) early in the season (July 25 and August 1) but as the season progressed, each plant produced more seeds (up to 100). For example, plants maturing on September 21 produced significantly greater number of seeds per plant than those maturing on July 25 and August 1 (Table 2). A two way analysis of variance on log transformed data indicated that both date of collection ($F = 8.2$, $p < 0.001$) and zone of occurrence ($F = 14.5$, $p < 0.0001$) had a significant effect on the mean number of upper seeds per plant but there was no significant interaction ($F = 0.94$, $p < 0.49$). The result was similar for lower seeds, with date of collection ($F = 9.4$, $p < 0.0001$) and zone ($F = 4.1$, $p < 0.01$) having a significant effect while the interaction was non-significant.

Plants produced significantly ($P < 0.05$) greater number of upper and lower seeds per

Table 1. *The crown area per plant (cm^2) of* Cakile edentula *var.* lacustris *plants collected on different dates from the upper, high and mid-beach zones at the Pinery Provincial Park during summer 1985*.*

Date	Upper beach	High beach	Mid-beach	Overall Mean**	n
July 25	19.4 ± 12.4	12.0 ± 4.2		16.0 ± 6.7 c	15
Aug. 1	13.1 ± 2.2	14.5 ± 2.4		13.8 ± 1.6 c	60
Aug. 8	29.9 ± 16.8	45.1 ± 17.4	232.3 ± 0.0	43.4 ± 12.8 c	44
Aug. 15	0.2 ± 0.0	14.2 ± 5.9	75.3 ± 36.0	33.6 ± 14.1 c	15
Aug. 22		44.5 ± 34.7	189.1 ± 52.4	155.8 ± 44.0 ab	13
Aug. 29		64.6 ± 26.8	324.6 ± 313.3	122.4 ± 67.9 bc	9
Sept. 13		124.1 ± 45.6	319.9 ± 190.6	276.4 ± 146.6 ab	9
Sept. 21		394.1 ± 0.0	500.4 ± 167.0	473.8 ± 121.1 a	4

*Statistical analysis was performed on $\log_{10}$ transformed data. The overall means followed by the same letter are not significantly different at $P < 0.05$ according to Tukey's test.
**Overall mean equals sum of all plants maturing on the beach on a particular date divided by n.

Table 2. *Mean number (actual values) of upper and lower seeds per plant of* Cakile edentula *maturing on different dates at Pinery Provincial Park during summer 1985. n is the number of plants in the sample.*

Data	n	Mean number of seeds +2 S.E.* Upper	Lower
July 25	14	5.9 ± 1.3 a	1.9 ± 0.6 a
August 1	60	6.7 ± 0.8 b	1.4 ± 0.2 a
8	44	12.5 ± 2.6 bc	2.5 ± 0.2 bc
15	15	16.7 ± 5.5 b	3.8 ± 1.2 ab
22	13	27.8 ± 7.4 bc	8.9 ± 3.2 bc
29	9	13.9 ± 8.5 bc	2.2 ± 0.9 bc
September 13	9	33.9 ± 16.0 c	17.2 ± 9.3 c
21	4	80.5 ± 13.2 c	16.7 ± 3.1 bc

*Statistical analysis was performed on $\log_{10}$ transformed data. Means in each column followed by the same letter are not significantly different at $P < 0.05$ according to Tukey's test.

Table 3. *Mean number (actual values) of upper and lower seeds per plant of* Cakile edentula *growing on the upper, high and mid-beach zones at the Pinery Provincial Park during summer 1985. n is the number of plants in the sample.*

Zone	n	Mean number of seeds +2 S.E.* Upper	Lower
Upper beach	54	6.5 ± 1.2 b	1.8 ± 0.5 b
High beach	87	10.4 ± 1.7 b	2.1 ± 0.3 b
Mid-beach	28	41.2 ± 6.8 a	12.7 ± 3.4 a

*Statistical analysis was performed on $\log_{10}$ transformed data. Means in each column followed by the same letter are not significantly different at $P < 0.05$ according to Tukey's Test.

plant on the mid-beach than on the upper and high beach zones which were not significantly different from each other (Table 3). A large proportion of plants produced few seeds per plant while a small proportion produced a large number of seeds.

Seed Mass Variation

The effects of fruit abortion, time of maturity, microhabitat conditions, seed position within fruits and number of seeds per plant on seed mass variation were examined. We consider each aspect separately.

Fruit Abortion. The proportion of aborted lower fruits ± 2 S.E. per plant (n = 169 plants) was significantly higher (73.5 ± 4.4%) than that of aborted upper fruits (14.1 ± 2.8%)

Table 4. *Mean mass per upper and lower seed of* Cakile edentula *from plants growing in the upper, high and mid-beach zones of the study area at the Pinery Provincial Park during summer 1985. n is the number of plants in the sample.*

Zone	Mean number of seeds +2 S.E.* Upper	n	Lower	n
Upper beach	4.17 ± 0.21 a	363	3.07 ± 0.26 a	87
High beach	4.21 ± 0.15 a	905	3.03 ± 0.20 a	192
Mid-beach	3.58 ± 0.12 b	1148	2.88 ± 0.16 a	368

*Means in each column followed by the same letter are not significantly different at $P < 0.05$ according to Tukey's Test.

according to the t test ($t = 20.3$, d.f. $= 336$, $p < 0.0001$). The percent abortion of seeds in upper fruits was not significantly different between plants on the upper (11.9 ± 4.6), high (15.5 ± 4.2) or mid-beach (13.8 ± 5.4) zones. Similarly, there were no significant differences between percent abortion of seeds in lower fruits growing on plants on the upper (71.6 ± 8.6), high (75.9 ± 5.8) and mid-beach (69.6 ± 10.0) zones.

Date of Maturity and Microhabitat. A two way ANOVA revealed that date of collection ($F = 5.7$, $p < 0.0001$) and zone (microhabitat) of occurrence ($F = 20.3$, $p < 0.0001$) had a significant effect on mean upper seed mass. There was also a significant interaction between date and zone ($F = 8.71$, $p < 0.0001$). Mean mass per upper seed was significantly ($P < 0.05$) lower in the mid-beach plants than those on the upper and high beach zones (Table 4). Seeds collected on August 1 had a significantly greater seed mass than those collected on any other date except July 25 (Table 5). The results of the two way ANOVA for lower seed mass were somewhat different than for upper seed mass (Table 4, 5). Date of maturity was still highly significant ($F = 5.8$, $p < 0.0001$) and there was a significant interaction ($F = 2.3$, $p < 0.02$) but zones were non-significant (Table 4) ($F = 2.5$, $p < 0.08$). Similarly, seed mass per lower seed over different dates did not show any detectable pattern (Table 5) although significantly ($P < 0.05$) smaller seed mass for lower seeds was found on September 21. The mean mass per upper seed was significantly higher than that of lower seeds in all three zones (Table 4).

Fruit Position. The frequency distribution of

Table 5. *Mean mass per upper and lower seed of* Cakile edentula *from plants maturing on different dates at the Pinery Provincial Park during summer 1985. n is the number of seeds in the sample.*

	Upper seeds		Lower seeds	
Date	n	Mean mass* ±2 S.E. (mg)	n	Mean mass* ±2 S.E. (mg)
July 25	112	3.87 ± 0.31 ab	40	2.51 ± 0.34 ab
Aug. 1	394	4.40 ± 0.22 a	75	3.21 ± 0.32 a
Aug. 8	562	3.93 ± 0.18 b	105	3.09 ± 0.28 a
Aug. 15	289	3.88 ± 0.27 b	52	2.38 ± 0.33 bc
Aug. 22	373	3.75 ± 0.19 b	149	3.07 ± 0.24 a
Aug. 29	114	3.31 ± 0.42 b	28	2.57 ± 0.59 abc
Sept. 13	495	3.84 ± 0.19 b	181	3.12 ± 0.22 a
Sept. 21	77	3.38 ± 0.49 b	17	1.47 ± 0.43 c

*Means in each column followed by the same letter are not significantly different at $P < 0.05$ according to Tukey's Test.

upper seeds (Figure 2) was significantly skewed to the right ($g_1 = 0.71$, $p < 0.0001$) and platykurtic ($g_2 = -0.19$, $p < 0.01$). A platykurtic distribution has fewer values at the mean and in the tails than would be expected for a normal distribution. Similarly the distribution of lower seeds (Figure 3) was also significantly skewed to the right ($g_1 = 0.74$, $p < 0.001$); however, it was leptokurtic ($g_2 = 0.43$, $p < 0.01$) indicating that both large and small seeds were less frequent than expected for a normal distribution. The frequency distribution of seed mass also changed at different times during the summer for upper and lower seeds (for details see Hawke 1987). The smaller seeds became more frequent as the season progressed in both upper and lower seeds of *C. edentula*.

Number of Seeds per Plant. A linear regression of mean seed mass per plant vs total number of seeds per plant (Figure 4) did not show a significant relationship ($F = 2.9$, $p < 0.1$). Thus, a plant of *C. edentula* producing a small number of seeds did not necessarily have greater mass per seed.

DISCUSSION

The plants of *Cakile edentula* var. *lacustris* exhibited clear differences in plant size (Figures 1,2). Generally the mid-beach plants were larger in crown area (Table 1) and produced significantly greater number of upper and lower seeds per plant (Table 3) than those on the upper and high beach. These results agree with

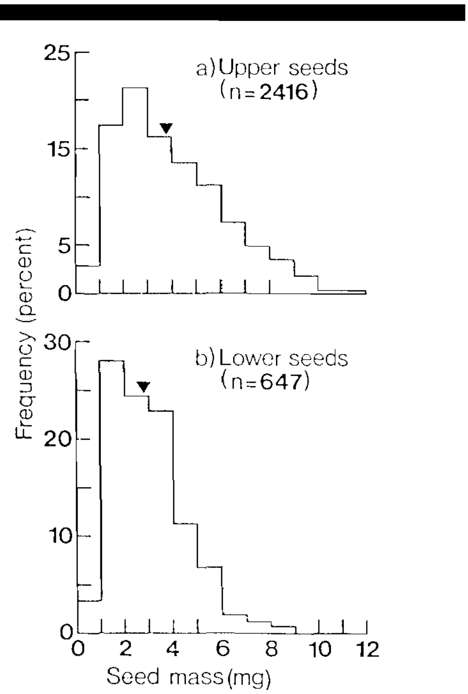

Figure 3. Frequency distributions (percent) of seed mass of upper and lower seeds of *Cakile edentula* from 169 plants growing at different locations on Lake Huron beach at Pinery Provincial Park.

those of other studies on *Cakile* (PAYNE, 1980; KEDDY, 1982; BOYD, 1986). Usually, plants maturing earlier in the season were smaller in size and produced fewer seeds per plant than those maturing later in the season (Table 2). The observed hierarchy in plant size at different locations and at different dates of maturity may be due to a number of reasons. For example, closer to the lakeshore the availability of moisture is higher than inland (TYNDALL *et al*, 1986) and the mid-beach plants are inundated by freshwater from the lake one or twice each summer (PAYNE, 1980). Also, the plants growing on the mid-beach had virtually no competition for light or resources from other species, while those on the upper and high beach not only had to contend with intraspecific competition (PAYNE, 1980) but were growing among the vigorous shoots of the perennial dune grasses, *Ammophila breviligulata* and *Calamovilfa longifolia*. The simplest explanation, however, is the differential availability of macronutrients in the vicinity of individual plants. By using hydroponics, HAWKE and

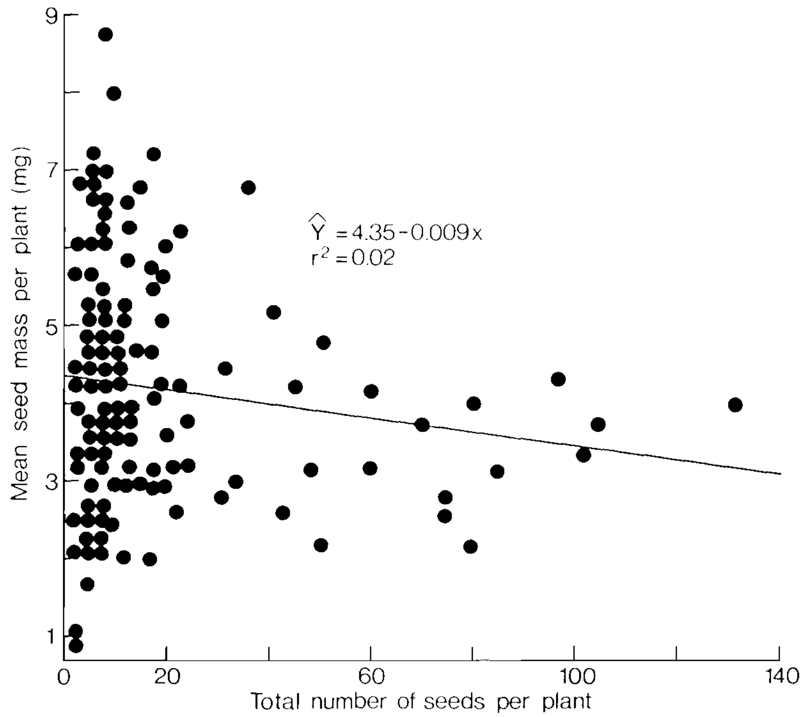

Figure 4. Scatterplot of mean seed mass per plant vs total number of seeds per plant for 169 *Cakile edentula* plants collected from Pinery Provincial park during 1985.

MAUN (1988) showed that high or low concentrations of macronutrients (N, P, K) may create differences of several orders of magnitude in the biomass of individual plants. Similar results were also reported in *Salsola kali* populations by LEE and IGNACIUK (1985).

The frequency distribution of seed mass showed a strong positive skewness to the right for both upper and lower seeds, thus rejecting the null hypothesis of normality. ERNST (1983) suggested that a skewed distribution indicates stress which may result from a shortage or excess of moisture, nutrients, salt content, and other environmental factors. A large proportion of upper seeds was heavier than lower seeds (Figure 3); however, there was a large overlap of area beneath histograms. There was a 21.5-fold difference in the mass of largest and smallest upper seed and a 16.4-fold difference in the mass of the largest and smallest lower seed. These values are high compared to 15.8-fold differences for *Lomatium grayi* (THOMPSON, 1984), 12-fold for *Raphanus raphanistrum* (STANTON, 1984a), 3.5-fold for *Cassia grandis* (JANZEN, 1977), 5.6 fold for *Lupinus texensis* (SCHAAL, 1980) and 2.3-fold for *Aster acuminatus* (PITELKA *et al.*, 1983).

Seed mass of an individual may be influenced by a number of plant characters. The effects of five of these, namely (a) abortion of ovules, (b) date of maturity, (c) microhabitat variation, (d) fruit position, and (e) number of seeds per plant were studied.

The abortion of lower seeds (74%) of *Cakile edentula* was significantly higher than upper seeds (14%). Similar results were reported by KEDDY (1982), PAYNE (1980) and RODMAN (1974) thus indicating that lower seeds are being selectively aborted. Levels of fruit abortion in other species may also be high. For example, 28% abortion was reported in *Lupinus texensis* (SCHAAL, 1980), 35 to 43% in *Lithospermum caroliniense* (WESTELAKEN and MAUN, 1985), 20 to 48% in *Ammophila breviligulata* (KRAJNYK and MAUN, 1982), and 51% in *Yucca whipplei* (UDOVIC and AKER, 1981). The abortion of seeds in *Cakile edentula* may be of adaptive significance because larger quantity of assimilates would be available for fewer ovules thus increasing or maintaining their size above a certain minimum probably at the expense of the number of seeds. MAUN and CAVERS (1971) where they showed an increase in seed size of *Rumex crispus* when a certain proportion of fruits was manually removed.

Plants maturing earlier in the season produced larger seeds than those maturing later. This was particularly true for upper seeds. Few studies have examined differences in seed weight of early and late maturing plants, however, in a recent study, CAVERS and STEELE (1984) showed that on several indeterminate plants seeds produced first were larger in size than those produced later. In *C. edentula*, the early and late maturing plants probably belong to different cohorts (PAYNE and MAUN, 1984), and thus experience different environmental conditions. Generally there is a moderation of temperature, decrease in photoperiod, increase in the number of cloudy days, and increase in rainfall during August and September that may reduce the grain filling efficiency of plants maturing later in the season.

Plants of *C. edentula* nearest the lake (mid-beach) produced seeds with a significantly lower mean seed mass than those on the upper and high beach (Table 4). In a similar study KEDDY (1982) reported that upper fruits (shell plus seed) produced seaward were significantly heavier than those produced landward. The reasons for lower seed mass of plants near the lake are obscure, especially because moisture (TYNDALL *et al.*, 1986) and nutrient status (HAWKE and MAUN, 1988) are more favorable for the production of large plants and many seeds.

The position of dimorphic fruits of *C. edentula* influenced their seed mass. The seeds from lower fruits (near the pedicel) were significantly lighter in mass than upper seeds. The position effects have been documented for *Lupinus texensis* (SCHAAL, 1980), *Raphanus raphanistrum* (STANTON, 1984a) and a number of other species and may result from competition between ovules for limited resources (UDOVIC and AKER, 1981), earlier of later fertilization of ovules (KRAJNYK and MAUN, 1982) and possibly hormonal control of fruit development.

In contrast to *Solidago* species in which seed size and numbers are negatively correlated (WERNER and PLATT, 1976), there was no correlation between mean seed mass per plant and number of seeds per plant of *C. edentula* (Figure 4). WULFF (1986) found no relationship between seed size and number of seeds per plant in *Desmodium paniculatum* suggesting that perhaps seed sizes and numbers in indeterminate plants are regulated independently.

Earlier studies (PAYNE AND MAUN, 1984) suggested that *Cakile edentula* var. *lacustris* is very well adapted to the unstable habitat conditions of the shoreline owing to its superior dispersal ability, fruit dimorphism, and seed dormancy. The storm waves that cause drastic changes in beach geomorphology also disperse fruits of *Cakile* within and between habitats. Thus, by early spring the fruits are deposited at different microsites on the beach, which may differ in moisture content, nutrient status, and organic detritis (HAWKE AND MAUN, 1988). This microsite variability is probably the major cause of high phenotypic plasticity in biomass and seed production per plant shown in this study. Phenotypic plasticity would be of adaptive significance because, inspite of the harsh environments, the population as a whole is able to produce rather large quantities of fruits of different seed sizes. Moreover, since sand accretion is a major hazard along shorelines, fruits of *Cakile* are buried in sand to various depths. Large seeds would be favored in accreting sites because their seedlings would emerge from greater depths of burial in sand (MAUN AND LAPIERRE, 1986) than those from small seeds.

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□ ZUSAMMENFASSUNG □

In einer Feldstudie wurde die phänothypische Veränderung in der Reproduktions- und Samenmassenvariabilität von *Cakile endentual* var. *lacustris* untersucht. Diese annuelle Strandpflanze zeigt innerhalb der Population eine große Spannbreite von Pflanzengröße, Samenproduktion und Samenmasse. Die größten Formen treten an den ökologisch bevorzugten Standorten des

Strandes auf, insbesondere in Seenähe aufgrund der im Gegensatz zum binnenwärtigen Bereich höheren Bodenfeuchtigkeit und des höheren Nährstoffgehaltes. - Eine große Anzahl der Samen in den Früchten verkümmerte, aber diese Erscheinung war in den unteren Früchten signifikant höher (74%) als in den oberen Früchten (14%). Der Schwankungskoeffizient für die Samenmasse lag bei 53% für die oberen Samen und 48,5% für die unteren Samen. Die durchschnittliche Samenproduktion je Pflanze nimmt im Zeitverlauf von Juli bis September ab. - Die Untersuchungsergebnisse legen den Schluß nahe, daß *C.edentula* auf Lageveränderungen der Küstenlinie mit einer phänotypischen "Plastizität" hinsichtlich Pflanzengröße, Reproduktion und Samenabsterben antwortet.—*Ulrich Radtke, Geographisches Institut, Universität Düsseldorf, F.R.G. (West Germany).*

□ RESUMEN □

Se realizó un estudio de campo para examinar la plasticidad fenotipica de la reproducción y la veriabilidad del peso de las semillas de *Cakile edentula* var. *lacustris* (Brassicaceae). Esta planta maritima anual exhibió gran variación intrapoblacional en el tamaña de las plantas, producción de semillas y peso de las mismas. Las plantas crecieron bien en macorambientes favorables de play. Por ejemplo, cerca del lago las plantas tenian significantivamente mayor desarrollo y mayor número de semillas por planta que las que crecieron en zonas más interiores primeramente debido a la mayor humedad del suelo y contenido de nutrientes, de los microespacios ocupados. Un gran número de semillas dentro de los frutos degeneraron pero este hecho fue significativamente más frecuente (64%) en los frutos más bajos que en los más altos (17%). El coeficiente de variación del peso por semilla fue el 53% para las semillas altas y el 48.5% para las bajas. La media del peso por semilla por planta disminuyó de Julio a Septiembre. Los datos sugieren que *C. edentula* responde al habitat inestable de la costa variando fenotipicamente en el tamaño de la planta, en la reproducción y en la degeneración de frutos.—*Department of Water Sciences, University of Cantabria, Santander, Spain.*

□ RÉSUMÉ □

Une étude de terrain a permis d'examiner la plasticité phénotypique dans la reproduction et la masse (poids par graine) des graines de *Cakile edentula* var. *lacustris* (Brassicaceae). Annuellement, la plage montre une large variation intrapopulation dans la taille, la production de graines et leur masse. Par exemple prés du lac, les plantes ont des couronnes significativement plus grandes, et plus de graines par plante que celles du continent, ce qui est originairement dû à une humidité du sol plus forte et à la teneur en éléments nutritifs des microsites occupés. Un grand nombre de graines dans les fruits ont avorté mais l'avortement était significativement plus élevé dans les fruits situés plus bas (74%) que dans ceux situés plus haut (14%). Le coefficient de variation de la masse des graines est de 53% pour les graines situées plus en hauteur, et de 48,5% pour les plus basses. La masse moyenne des graines par plante décroît avec la progression de la saison de juillet à septembre. Les donées suggèrent que *C. edentula* répond à un habitat littoral instable par une plasticité phénotypique de la taille, la reproduction et l'avortement du fruit.—*Catherine Bressolier, UA 910 CNRS, EPHE, Montrouge, France.*