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## RELATIVE SALT TOLERANCE OF *CAKILE EDENTULA* (BRASSICACEAE) FROM LACUSTRINE AND MARINE BEACHES<sup>1</sup>

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### ABSTRACT

Seeds of *Cakile edentula* ssp. *edentula* var. *edentula* (hereafter *edentula*) were collected from the Pacific Ocean shore of Washington, and *Cakile edentula* ssp. *edentula* var. *lacustris* (hereafter *lacustris*) seeds were collected from the Lake Huron shore of Ontario. Germination rates of the two varieties showed equal tolerance of substrate salinities ranging from 0-10,000 ppm. Early root growth of *edentula* seedlings was significantly stimulated by 1,000 ppm salts, but otherwise both varieties showed equal tolerance to 10,000 ppm. *Edentula* plants exposed for 4 wk to salt spray intensities of 0, 20, and 90 mg dm<sup>-2</sup> d<sup>-1</sup>, applied in a growth chamber environment, showed no significant changes in shoot or root biomass, plant morphology, or reproductive effort. *Lacustris* plants exhibited significant declines in stem length and reproductive effort with increasing levels of salt spray. Our results suggest that *lacustris* and *edentula* have diverged physiologically over the past 9,000 years, and field observations from the literature corroborate our conclusion that this divergence in salt tolerance has ecological significance.

THE GENUS *Cakile* (Cruciferae) is comprised of (mainly) annual herbaceous species which inhabit marine beaches in diverse parts of the world. In his monograph of the genus, Rodman (1974) concluded that the only taxon in the genus to be found on freshwater beaches was *Cakile edentula* (Bigel.) Hook. ssp. *edentula* var. *lacustris* Fernald, which is confined to parts of North America's Great Lakes. Following the last glacial retreat, the Saint Lawrence Seaway was flooded by the ocean, forming a dispersal route by which marine species colonized the newly-formed inland beaches. Uplift of the Saint Lawrence area forced the sea to retreat ca. 9,000 years ago, isolating lacustrine from marine populations. Rodman has speculated that the closely-related *Cakile edentula* (Bigel.) Hook. ssp. *edentula* var. *edentula*, now present along the Atlantic Coast of North America, was ancestral to the modern lacustrine variety. They are vegetatively indistinguishable, but differ in petal size and fruit beak length. The marine variety was introduced to the Pacific Coast strand of central California in the 1880's and has since spread north to British Columbia and south to Baja California (Barbour and Rodman, 1970).

*Cakile* species are among the most salt-tolerant of Pacific Coast strand taxa, often occurring at the leading edge of vegetation and exhibiting considerable resistance to artificially-applied salt spray (Barbour and DeJong, 1977; Barbour, DeJong and Johnson, 1976; Boyd, 1986). Studies of *Cakile maritima* have demonstrated physiological adaptations to salinity in the marine beach environment (Rozema et al., 1982; Beer, Shomer-Ilan and Waisel, 1975). Our objective was to determine whether the lacustrine and marine varieties of *C. edentula* have diverged in their physiological tolerances, in addition to their existing morphological differences. Important environmental differences between marine and freshwater beaches are substrate salinity and salt spray intensity. In a recent review, Barbour, DeJong and Pavlik (1985) concluded that temperate zone beach sand may exhibit root zone salinities as high as 10,000 ppm for brief periods following wave inundation, although 1,000 ppm is more typical during the growing season. In contrast, lacustrine beach sand reflects the low salinity of the offshore water, which in the case of the Great Lakes is <100 ppm (Reid and Wood, 1976). Marine salt spray loads at the height of herbaceous plant canopies range between 1-200 mg dm<sup>-2</sup> of vertical intercepting surface d<sup>-1</sup>, with typical values falling between 10-50 mg dm<sup>-2</sup> d<sup>-1</sup> (Barbour, 1978). Salt spray quantity declines steeply with distance from shore. Marine coastal dunes only 600 m inland receive two orders of magnitude less salts than the seaward edge of vegetation

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(Barbour et al., 1973; Clayton, 1972; Martin, 1959).

The specific questions addressed in this paper are: do the two varieties differ in their tolerance of substrate salinity and salt spray and, if so, are the differences ecologically significant?

**MATERIALS AND METHODS—Collection of fruits**—Mature distal fruit segments of *Cakile edentula* (Bigel.) Hook. ssp. *edentula* var. *lacustris* Fernald (hereafter *lacustris*) were collected from a population of plants growing on the shore of Lake Huron, Ontario, in September 1981. Mature fruits (both distal and proximal segments) of *Cakile edentula* (Bigel.) Hook. ssp. *edentula* var. *edentula* (hereafter *edentula*) were collected from a population of plants at Copalis Beach, Washington, in October 1982. Both collections were stored in paper sacks at room temperature until used in mid-1983.

**Germination and early root growth**—Seeds were removed from the fruits and stratified at 4 C for 2 wk. The seed coats were then removed, and the embryos were placed in petri dishes containing solutions of different salinities. Salt solutions were prepared with artificial seawater (Rila Marine-Mix®) to concentrations of 10,000, 1,000, 100, and 0 ppm salt. The 10,000 ppm level was chosen as representative of extreme marine beach sand salinity (as might be expected following storm wave surges); 1,000 ppm was representative of more typical marine beach sand salinity during the growing season; 100 ppm represented lacustrine sand salinity; and 0 ppm was a control. Four ml of these solutions were used to saturate two layers of filter paper lining each 5 cm petri dish. Five embryos were placed in each dish, and eight replicates were used for each variety, seed position (distal or proximal segment), and salinity level. The embryos were then incubated in the dark at a 17 C-16 hr/11 C-8 hr temperature regime in a growth chamber for 10 d. This temperature regime was a compromise between measured temperatures in the field at the time of germination and optimum germination temperatures determined for West Coast *Cakile maritima* (Barbour, 1970a, b, 1972). At the end of 10 d, root lengths were measured. An embryo was considered germinated if measurable root growth had occurred.

**Salt spray trials**—Seedlings germinated from distal *edentula* and *lacustris* fruits, by the procedure described above, were planted in 4,000 cm<sup>3</sup> pots filled with sterilized sand. The pots were placed in a Percival Model PGW 108

growth chamber under a 17 C day/11 C night temperature regime and a 16/8 hr thermo- and photoperiod (300  $\mu\text{E m}^{-2} \text{sec}^{-1}$  irradiance, combination of fluorescent and incandescent bulbs). Plants were sub-irrigated with half-strength Hoaglands solution, the formula of which corresponded to Solution 1 of Hoagland and Arnon (1950). Within the first week of planting, each pot was thinned to five equally vigorous seedlings. Spray treatments began 2 wk later and continued for 4 wk.

Three salt spray levels were used: 0, 20, and 90 mg dm<sup>-2</sup> d<sup>-1</sup>. Preliminary work showed that hand-held mist bottles, containing either full-strength natural seawater, a 1:4 dilution of seawater, or only deionized water, delivered the desired salt loads with approximately equivalent amounts of spray. Plants were sprayed twice daily in such a manner that all parts of all plants were equally exposed to the spray. Salt loads applied were checked by spraying test patches of filter paper (as imitation plants), eluting the paper, and measuring the fluid's conductivity (see Barbour, 1978). Four replicate pots were used for each variety and spray level. Natural seawater for this experiment was obtained from the University's Bodega Marine Laboratory and was stored in sealed containers at 4 C until used.

At the end of the 4 wk treatment period, plant morphology (general condition, leaf senescence and succulence, total stem length), above- and below-ground biomass, and reproductive effort (total number of flowers and fruits) were recorded. Leaf succulence was quantified by removing the sixth leaf from the plant apex and placing it in FAA fixative. Serial sections were made from a block of tissue removed from each leaf and examined under the microscope. The tissue block was removed from the area half-way between the leaf tip and the petiole, and extended from the leaf margin to the midrib. Four leaves were selected for each variety and salt spray level, and five random sections of each leaf were measured for leaf thickness with an ocular micrometer. Above- and below-ground plant material was harvested, dried to constant weight at 100 C, and weighed on a per-pot basis.

As an indirect check of the salt load deposited by the end of the treatment period, the fifth leaf from the plant apex was cut off the stem, its surface area was measured, and the surface was washed with deionized water (taking care to keep the cut end of the petiole out of the water). The conductivity of the wash-water was then measured, and salt load calculated as mg mm<sup>-2</sup> leaf surface.

We designed this experiment to separate the

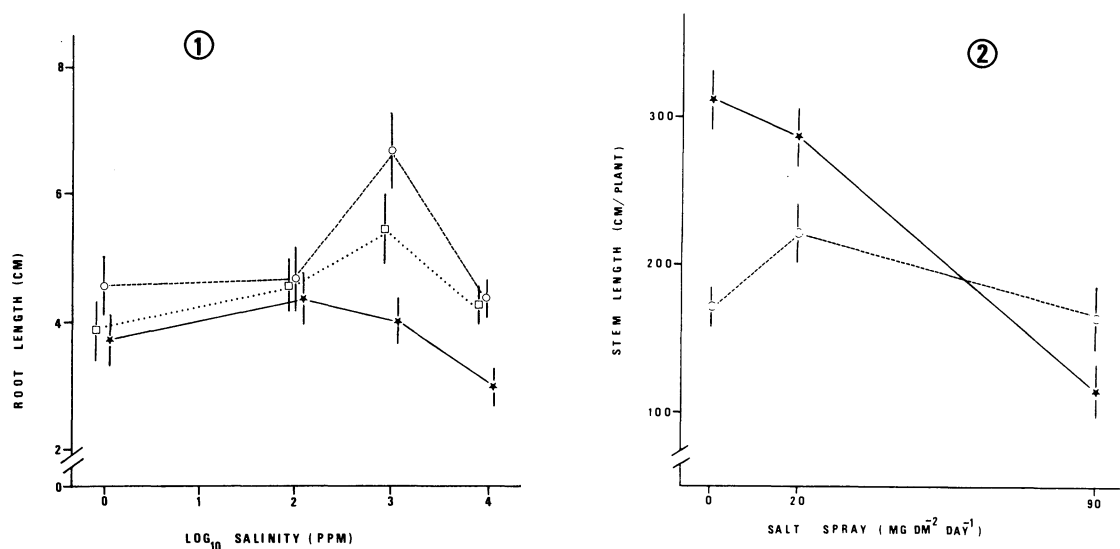


Fig. 1, 2. 1. Root lengths of 10 d old seedlings grown in substrate salinities ranging from 0 to 10,000 ppm artificial sea salt. ★ *lacustris* seedlings from distal fruit segments, □ *edentula* seedlings from proximal segments, ○ *edentula* seedlings from distal segments. Vertical lines are  $\pm 1$  S.D. 2. Stem length (total length of main and lateral axes) of plants following 4 wk exposure to different salt spray intensities. ★ *lacustris* and ○ *edentula* plants grown from distal segment seeds. Vertical lines are  $\pm 1$  S.D.

effect of salt spray from that of substrate salinity. As a check on sand salinity at the end of the treatment period, a  $2.5 \times 3.0$  cm core of sand was removed from each pot, beginning at a depth of 1 cm below the sand surface. Each core was dried to constant weight at 100 C and weighed, eluted with deionized water, and the conductivity of the fluid was determined.

Statistical analyses of the data were performed by analysis of variance, with multiple comparisons of means by the Newman-Keuls multiple range test (Zar, 1974). Significance was at  $P < 0.05$  unless otherwise stated.

**RESULTS AND DISCUSSION—Germination and early root growth**—Germination rates were high for all treatments, regardless of variety, seed position, or substrate salinity. Germination ranged from 83 to 100%. No differences were statistically significant.

Root length, however, showed more variation between varieties (Fig. 1). Root growth was statistically similar at 0, 100, and 10,000 ppm, but separation of the means was significant at 1,000 ppm. Both distal and proximal *edentula* seedlings reached maximum root lengths at 1,000 ppm, the level chosen as representative of marine beach sand salinity during the growing season, although only the distal seedling peak was statistically different from the other means. *Lacustris*, in contrast, showed little fluctuation in root growth with salinity. For both varieties, root growth at the highest

salinity was not significantly different from growth at 0 ppm salt.

Seneca and Cooper (1971) performed similar experiments on the substrate salinity tolerance of another beach plant which has a similar history of invasion and isolation in the Great Lakes—*Ammophila breviligulata* Fernald. They reported that germination of seeds from a Great Lakes population was more sensitive to salinity levels when compared to a marine beach population, but seedling growth showed an equal lack of tolerance to high levels of salinity. Our results for *Cakile* are the opposite: no difference in germination response, but a significant difference in seedling growth response.

**Salt spray trials**—The effect of salt spray on plant morphology was marked only in terms of total stem length (the sum of the main axis length and the lengths of all laterals). *Lacustris* stem growth showed a significant decline at the highest level of salt spray, whereas *edentula* was relatively indifferent to salt spray, with no significant differences between any spray levels (Fig. 2). At the 0 and 20 mg spray levels, *lacustris* plants were significantly larger than *edentula* plants, but stunting of *lacustris* at the 90 mg spray level caused plant size for both varieties to be statistically equal for that treatment.

Salt spray did not significantly affect root or shoot biomass of either variety, although some trends are apparent. Total biomass (root +

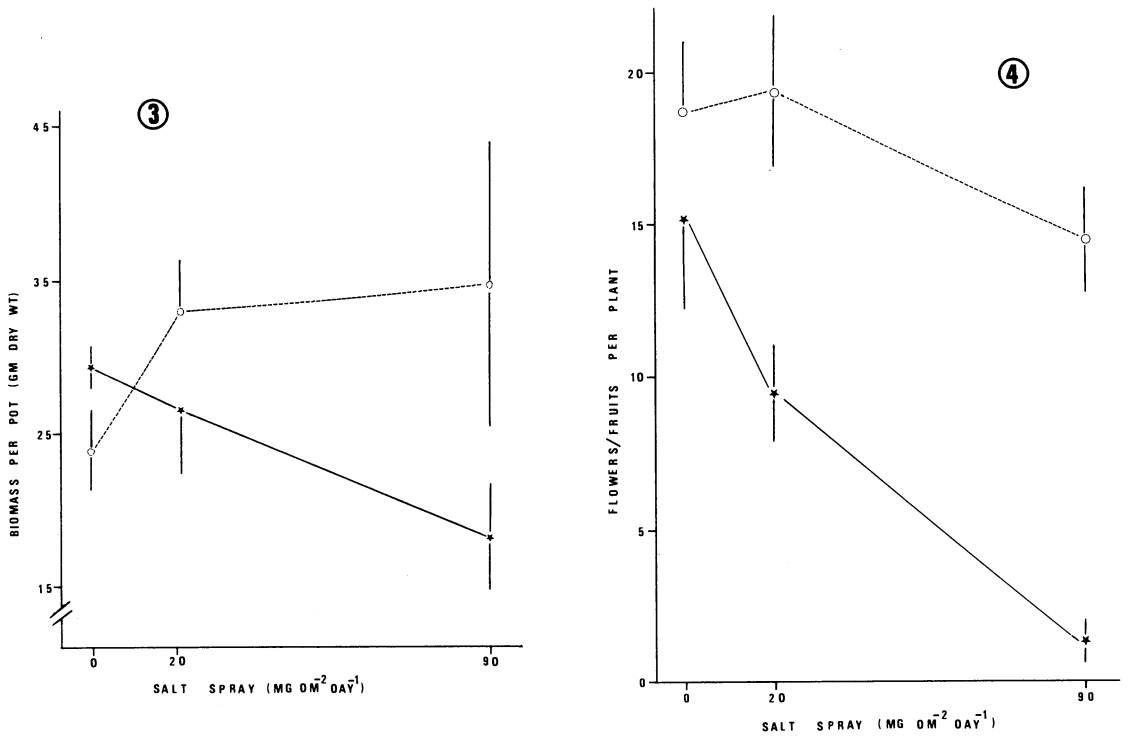


Fig. 3, 4. Results of salt spray trials following 4 wk exposure to different salt spray intensities. ★ *lacustris* and ○ *edentula* plants grown from distal segment seeds. Vertical lines are  $\pm 1$  S.D. 3. Total plant biomass (dry wt., root + shoot on per-pot basis). 4. Reproductive effort (number of flowers and fruits) per plant.

shoot, per pot basis) values for *edentula* were lowest at the 0 mg spray level and increased with increasing salt spray, whereas the opposite was true with *lacustris* (Fig. 3). However, the amount of variation was so high that none of the trends was statistically significant.

Salt spray had a marked differential effect on the reproductive output of the two varieties (Fig. 4). The number of flowers and fruits produced by *edentula* plants was not significantly affected by salt spray load, but that of *lacustris* declined dramatically by about 85% at the highest level of salt spray (reproductive output at 90 mg is statistically different from that at 0 and 20 mg). *Edentula's* reproductive output was statistically greater than that of *lacustris* at both the 20 and 90 mg treatment levels.

Leaf salt loads measured at the end of the experiment are summarized in Table 1. For each variety, residual loads increased significantly with increasing spray intensity. At a given spray intensity, residual loads are not statistically different for the two varieties, except for the 90 mg level, where *lacustris* leaves retained significantly more salts. Increasing salt spray from 20 to 90 mg dm<sup>-2</sup> d<sup>-1</sup> (a 4.5-fold increase) resulted in a 4.3-fold increase in the residual leaf salt load of *edentula*, but a 7.5-

fold increase for *lacustris*. It is not clear why more salts were retained on *lacustris* leaves, as leaf morphology and plant size seemed to be similar between the two taxa.

Analyses of pot sand at the end of the experiment showed modest increases in salinity with increasing salt spray. Pots with plants sprayed at the 0 mg level exhibited < 100 ppm salts, while pots with plants sprayed at the 90 mg level exhibited about 300 ppm salts. Although the increased salt level was statistically significant at the 90 mg level, it is doubtful that it was physiologically or ecologically important. According to Richards (1954), all soil salinities below 500 ppm are classified as non-saline, and are capable of supporting the most sensitive glycophytes.

In summary, the major ecologically significant difference between lacustrine and marine varieties of *Cakile edentula* was the effect of salt spray on reproductive output, i.e., the output of the marine variety was unaffected by salt spray, while that of the lacustrine variety was markedly depressed by increasing salt spray concentrations. Because both taxa are annuals, survival from year to year is heavily dependent on the number of seeds produced. A comparison of the reproductive outputs of both va-

TABLE 1. Leaf thickness and residual salt loads (all  $\pm 1$  S.D.) following 4 wk exposure to several salt spray intensities. All plants were grown from seeds from distal fruit segments

Salt spray (mg dm <sup>-2</sup> d <sup>-1</sup> )	Variety	Leaf thickness ( $\mu$ m)	Residual salt (mg mm <sup>-2</sup> )
0	<i>edentula</i>	462 $\pm$ 10	0
	<i>lacustris</i>	357 $\pm$ 20	0
20	<i>edentula</i>	558 $\pm$ 19	1.97 $\pm$ 0.085
	<i>lacustris</i>	473 $\pm$ 11	1.77 $\pm$ 0.12
90	<i>edentula</i>	820 $\pm$ 39	8.47 $\pm$ 0.88
	<i>lacustris</i>	757 $\pm$ 33	13.3 $\pm$ 1.81

rieties under freshwater spray conditions showed no difference, leading us to conclude that the two varieties could coexist under natural lacustrine conditions. Under the salt spray treatment similar to that commonly measured for marine beaches (20 mg dm<sup>-2</sup> d<sup>-1</sup>), *edentula* was able to produce twice as many flowers and fruits as *lacustris* and its growth was as vigorous as under 0 mg salt spray. This difference could drive *lacustris* to extinction on marine beaches.

A typical response of spray-tolerant plants to salt spray is leaf hypertrophy (enlargement of cells), resulting in a doubling or tripling of leaf thickness (Boyce, 1951, 1954; Martin and Clements, 1939). Generally, in dicots, the degree of salt tolerance seems positively correlated with the ability to undergo hypertrophy and to become succulent (Barbour et al., 1985). Table 1 shows that leaves of both taxa increased equally in leaf thickness with increased levels of salt spray. Leaf thickness at the highest spray level was 80–90% greater than that at the 0 mg spray level. The two varieties, therefore, have equivalent abilities to undergo hypertrophy, but the correlation between degree of salt tolerance and hypertrophy does not seem to hold in our study of these two closely-related taxa. Both varieties have similar abilities to undergo hypertrophy, but *lacustris* is less salt-tolerant than *edentula*.

Chrysler (1904) measured leaf thicknesses for a number of coastal taxa from the vicinity of Woods Hole, Massachusetts and inland taxa from the vicinity of Chicago, Illinois, including *Cakile*. He found that coastal *Cakile* had leaves 1.5 times as thick as leaves from inland plants. This difference in his field measurements is similar to a comparison of our *lacustris* under Great Lakes conditions and *edentula* at the 20 mg spray level.

In conclusion, *lacustris* and *edentula* have diverged in their ability to tolerate environmental salinity during the 9,000 yr they have been separated. *Lacustris*, in the absence of salinity as a selective force, has declined in its

ability to tolerate salts. This does not mean that it is now a glycophyte. Comparison of its responses with other beach taxa (Barbour and DeJong, 1977) shows that it is still quite salt-tolerant. In a marine beach environment, it may even be able to reproduce sufficiently to maintain a viable population in pure stands. In a mixed marine beach population of *lacustris* and *edentula*, the ability of *edentula* to produce more fruits than *lacustris* would result in a successively greater proportion of *edentula* individuals in future generations. After a number of years, this process would result in the eventual disappearance of *lacustris* from the population.

Without actually performing a reciprocal transplant experiment, extrapolation of our experimental results and conclusions to the field must be done with caution. However, Rodman (1974) reported that at least part of such a transplant experiment has been performed, albeit in an uncontrolled manner. *Edentula* was accidentally transported into the Great Lakes as early as the 1880's as a result of shipping traffic between the Atlantic Coast and major cities along the shores of the lakes. Intermixed populations of the two varieties can be found at a number of locations, most of which are in the vicinity of Chicago. Although *edentula* has invaded the Great Lakes, Rodman was not able to find any evidence that *lacustris* has invaded the marine coast. Thus, the present-day distributions of *lacustris* and *edentula* are consistent with our experimentally-derived conclusions: *lacustris* and *edentula* are equally fit under freshwater beach conditions, but *edentula* is better-adapted to the marine beach environment.

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