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The Biological Flora of Coastal Dunes and Wetlands. 1. *Cakile edentula* (Bigel.) Hook.

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ABSTRACT

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Cakile edentula (Bigel.) Hook. (sea rocket) is an annual or facultative perennial (Brassicaceae) that grows as a pioneer along the shorelines of the Great Lakes, the Atlantic and the Pacific coasts of North America, and the coasts of Japan, the Azores, New Zealand, and Australia. Here we present a summary of ecological, physiological and geomorphological aspects of the biology of *Cakile edentula*. Its success along shorelines may be attributed to the production of large numbers of fruits, short life cycle, high potential for water dispersal, resistance to salt spray, possession of seed dormancy, high level of seedling establishment, rapid growth, and ability to flower under a range of photoperiods. *Cakile edentula* produces dimorphic fruits; distal and proximal. Distal fruits break off from the parent and disperse to new locations while the proximal ones stay with the parent. The species plays a significant role in geomorphology. Single or clumped plants accumulate sand and add organic matter to the soil, thus providing more amenable habitats for the establishment of secondary colonizers. *Cakile edentula* exhibits highest germination at alternating temperatures of 20°C (14.5 hr) and 10°C (9.5 hr) under dark conditions. Light inhibits germination rates but not total germination and fruits require stratification to overcome dormancy. The plants are infested by fungi and are consumed by a variety of phytophagous insects and vertebrates. The species manufactures glucosinolates that protect it from some insects, fungi, bacteria and vertebrates.

ADDITIONAL INDEX WORDS: *Cakile edentula, sea rocket, variation, ecology, population biology, physiology, geomorphological interactions, economic importance.*

I. INTRODUCTION

Habitats along the shorelines of lakes and oceans are subject to major substrate rearrangements in space and time by dynamic forces of wind and wave action. In North America, most erosion occurs in late fall and very early spring; however, throughout the year the coastal beach habitat is highly unpredictable, unstable and temporary. The lower part of the beach is usually the most disturbed because it is under the constant action of waves and hence is not available for colonization by plants. However, the areas above the low beach (*e.g.*, the mid-beach, driftline, and high beach) are free from disturbance for short periods of time and some specialized plant species establish and complete their life cycles there. One of the most characteristic genera of this habitat is *Cakile*. Although the populations suffer high rates of mortality during storms, the outstanding features of the species are resistance to salt spray, rapid growth, and abundant seed production during the short intervals between storms. An elegant review of the systematics and evolution of the genus *Cakile* was presented by RODMAN (1974). In this review, we present information about the ecological, physiological, and geomorphological aspects of the biology of *Cakile edentula* (Bigel.) Hook.

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II. TAXONOMY AND VARIATION

(a) Name

Cakile edentula (Bigelow) Hooker ssp. *edentula* (RODMAN, 1974), Tribe Brassiceae; Family Brassicaceae (Cruciferae), *Cakile edentula* (Bigel.) Hook ssp. *edentula* var. *edentula*, also referred to on the Pacific coast as *C. californica* (FERNALD, 1922) or *C. californica* ssp. *califor-*

nica, Cakile edentula (Bigel.) Hook. ssp. *edentula* var. *lacustris* Fernald, also referred to as *C. americana* Nutt. (MILLSPAUGH, 1900 in FERNALD, 1922); sea rocket.

(b) Taxonomic Description

The following account has been assembled from FERNALD (1922), RODMAN (1974) and ZOHARY (1948).

(i) Seedling Morphology Germination is epigeal (Figure 1) and sometimes the fruit coat appears above the sand surface (PAYNE, 1980). Cotyledons are accumbent to occasionally incumbent.

(ii) Shoot Morphology Stems are initially succulent but developing a woody caudex, smooth or weakly striate, terete in cross-section and up to 8 cm in height. Branches growing outwards and upwards, and the lowermost are often decumbent. Mature leaves are thick, fleshy and entire, broadly ovate and petiolate to obovate or spatulate and attenuate at the base, crenately, sinuately, or dentately lobed but never pinnatifid or pubescent. Younger leaves are smaller, ± oblanceolate and less lobed. Lobing is most obvious in the mature leaf at the basal petiolar end. Leaf tissue of *C. edentula* var. *edentula* is thinly cutinized with heterogeneously sized cells. Stomata are more numerous abaxially and are even with the surface. Parenchyma tissue is not clearly differentiated into palisade and spongy mesophyll and contains cells (irregular in shape and scattered throughout the leaf) thought to be myrosin cells or idioblasts. Hydathodes are usually present at the end of the leaf and the terminals of the three major vascular strands.

(iii) Root Morphology Stout tap root rarely exceeds 40 cm in length and 3 cm in diameter. Several long, fine horizontal roots may extend over 15 cm just a few centimeters below the soil surface (RODMAN, 1974).

(iv) Inflorescence. Flowers are regular, actinomorphic and tetradynamous, and are borne on elongating, terminal ebracteate racemes 1-2 dm long. Sepals are borne in two indistinct series with the outer, lateral pair usually slightly gibbous at the base; erect at anthesis and soon deciduous. Sparse, simple trichomes are observed occasionally at the apex of the sepals. Sepal margins are consistently hyaline and commonly dimorphic at the apex.

Petals are ± obovate, 4.6-9.7 mm long, 1.4-3.3 mm wide and white to pale lavender in color. Elongated, translucent, tubular idioblasts, thought to be myrosin cells, are observed in most petals. Pedicels vary from 1-10 mm long and 0.5-2.5 mm wide. Flowers have four small green nectaries, the two lateral glands, compressed horizontally and usually bilobed, are subtended by the unpaired stamens; the two median glands 0.2-0.4 mm high, conical or pyramidal, subtend the paired stamens. Stamens at first are tetradynamous, but become nearly equal as the flower ages because the unpaired stamens elongate proportionally more than the paired stamens. Filaments are stout and taper abruptly at the point of attachment to the anthers. Anthers of the unpaired lateral stamens are slightly larger than those of the paired median stamens but are in general 0.4-1.4 mm long. At anthesis, the paired anthers are exserted over the stigma, whereas the unpaired lower anthers are level with or below the stigma. Pistil is lanceolate to ± turbinate, ensiform and indistinctly articulated transversely. Short-papillose stigma is capitate and hemispherical to slightly bi-lobed. The articulation of the stigmatic lobes is perpendicular to the plane of the septum.

Ovary is initially unilocular, with the linear placenta disposed vertically in the elongated chamber. The ovules, usually two, are attached at the point of future articulation between the two fruit segments. After fertilization, a thin elongated septum forms with the ovules on one side. Then the ovary wall grows between the two ovules, resulting in a distal segment with an erect ovule, and a proximal segment with a pendulous ovule (BOCQUET, 1959). Fruit, an indehiscent, hard-corky or nucamentaceous two-segmented silique 12-29 mm long, is a special case of the "valvo-nucamentoid" type. Distal and proximal segments are considered to be homologous to the stylar and valvar portions of fruits typical of the tribe Brassiceae (ZOHARY, 1948). Distal segment is beaked and deciduous while the proximal segment remains attached to the raceme. Both segments are falsely one-loculed and usually one-seeded but the proxi-

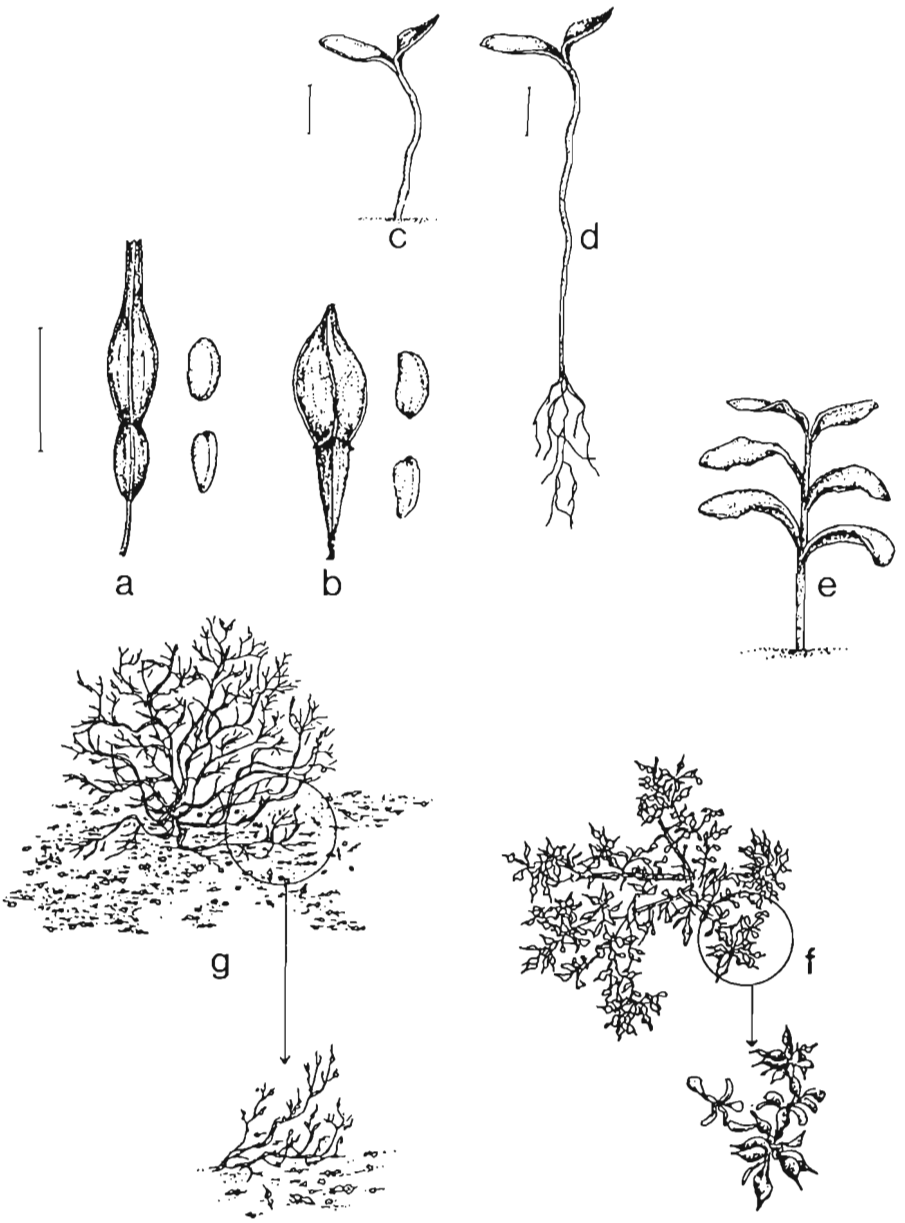

Figure 1. Distal and proximal fruit segments of *Cakile edentula* var. *lacustris* (a), var. *edentula* (b), seedlings (c,d), 28 day old plant (e), mature plant with fruits (f), and a mature plant with dispersed distal fruits (g). Bars equal 1 cm.

mal fruit may be multispermous or abortive. Point of articulation of the two segments is usually ± constricted. Proximal fruit segment is terete, ± cylindric to expanded slightly at the apex; while the distal fruit segment is truncate-fusiform to turbinate. Seeds are smooth, bronze or brown in color and oval or ellipsoid to slenderly oblong and compressed longitudinally.

(c) Variability

(i) Subspecies According to RODMAN (1974), *C. edentula* comprises two subspecies, *harperi* and *edentula*. *Cakile edentula* ssp. *edentula* has four-angled distal and proximal fruit segments, with a ± flat to concave articulating surface and 2(6) small teeth projecting upward. *Cakile edentula* ssp. *harperi* has eight-ribbed distal and proximal fruit segments, with a flat articulating surface and no teeth. The difference in fruit length between *C. edentula* ssp. *edentula* (17.9 mm) and *C. edentula* ssp. *harperi* (23.8 mm) is highly significant ($P < 0.001$) (RODMAN, 1974). Glucosinolate analysis of seeds (Table 1) also supports splitting these taxa into varieties (RODMAN, 1974). In the zone of sympatry between the two subspecies (the Outer Banks of North Carolina) hybridization occurs (RODMAN, 1980).

(ii) Varieties. RODMAN (1974) and FERNALD (1922) described two varieties of *C. edentula* ssp. *edentula:* var. *lacustris* and var. *edentula*. Var. *lacustris* is generally less robust and fleshy than var. *edentula* and has a slender distal fruit segment, 3-5 mm wide, with a long beak equalling or exceeding the length of the seminiferous part and a base with a slight scarious border. Var. *edentula* has a plump distal fruit segment, 5-9 mm wide, with a short beak and a base without a scarious margin (Figure1). In addition, fruits of *C. edentula* var. *lacustris* from the Great Lakes are significantly longer ($P < 0.001$) than those of *C. edentula* var. *edentula* from either the Atlantic coast or the Great Lakes.

(iii) Ecotypes. Differences in fruit length, maturation time and petal length between Atlantic and Pacific coast populations of *C. edentula* var. *edentula* have been attributed to founders effects rather than ecotypic variation (RODMAN, 1976). However, ecotypic variation may explain the incidence of purple coloration on stems, young fruits and flowers in *C. edentula* var. *edentula* populations on both the Atlantic and Pacific coasts. The proportion of purplish forms increases northward on both coasts (RODMAN, 1976).

To test for ecotypic differences between landward and seaward portions of a population of *C. edentula*, KEDDY (1982) grew individuals from both locations under uniform greenhouse conditions. He found no difference in fruit production between plants from these two areas. BARBOUR (1970b) grew individuals of *C. maritima* from 6 populations, separated by up to 1050 km of California coastline, under uniform growth chamber conditions. Temperature effects on germination showed no variation between populations, yet temperature effects on root growth did vary. Variation in root growth did not correlate with water or sand temperature at his sites and was not considered to represent adaptations to these factors.

Table 1. *Glucosinolate composition of the seeds of* Cakile *taxa from different locations. The values are average peak percentages by gas chromatography* (after RODMAN 1974, 1980).

		Composition (%)								
Taxa	Coastal Location	Unknown 1	iso-propyl	allyl	sec-butyl	3-butenyl	unknown 2	4-pentenyl	3-methyl-thio-prophyl	4-methyl-thio-butyl
C. maritima ssp. *maritima*	Pacific	0	18.5	T[a]	50.4	T	0	0	15.8	9.3
C. maritima ssp. *baltica*	Europe	0	T	85.7	12.5	T	T	0	T	0
C. edentula var. *edentula*	Pacific	0	T	70.9	26.5	1.0	T	0	1.6	0
	Atlantic	0	1.9	80.2	16.7	1.1	1.2	0	1.6	0
C. edentula var. *lacustris*	Great Lakes	0	T	93.9	4.4	1.0	T	0	T	0
C. edentula ssp. *harperi*	Atlantic	7.9	0	3.2	T	84.7	0	1.6	T	1.5

[a]T = trace amounts

(iv) Chromosome numbers. 2n = 18 has been reported by KRUCKEBERG (1948), MULLIGAN (1964) and TAYLOR and MULLIGAN (1968).

III. GEOGRAPHICAL DISTRIBUTION

In eastern North America, *C. edentula* ssp. *edentula* var. *edentula* ranges from the Outer Banks of North Carolina to Labrador (Figure 2). *Cakile edentula* ssp. *harperi* occurs from the Outer Banks of North Carolina to southern Florida (AL-SHEHBAZ, 1985). Rare occurrences of *Cakile* in an inland habitat have been documented by GUIRE and VOSS (1963). GEHU and GRANDTNER (1982) defined a subassociation of *Cakiletosum edentulae* along the shoreline of Magdalen Island, Quebec. The variety is also found along the Pacific coast and less frequently on the shores of Lakes Michigan, Huron, Erie, and Ontario, but is not present along Lake Superior. Of 394 herbarium collections studied from the Great Lakes, only 7.6% were clearly *C. edentula* var. *edentula* (RODMAN, 1974). Its sporadic occurrence suggests it is a recent introduction, perhaps as a ballast plant after completion of the Erie Canal in 1825 (RODMAN, 1974). *Cakile edentula* var. *lacustris* is very abundant on the sandy beaches of all the Great Lakes of North America, except Lake Superior, where populations are rare (Figure 2). Occurrence is very sporadic on the St. Lawrence River east of Quebec. This variety does not occur along Atlantic or Pacific coasts.

Cakile edentula var. *edentula* was naturalized around 1880 on the Pacific coast of North Amer-

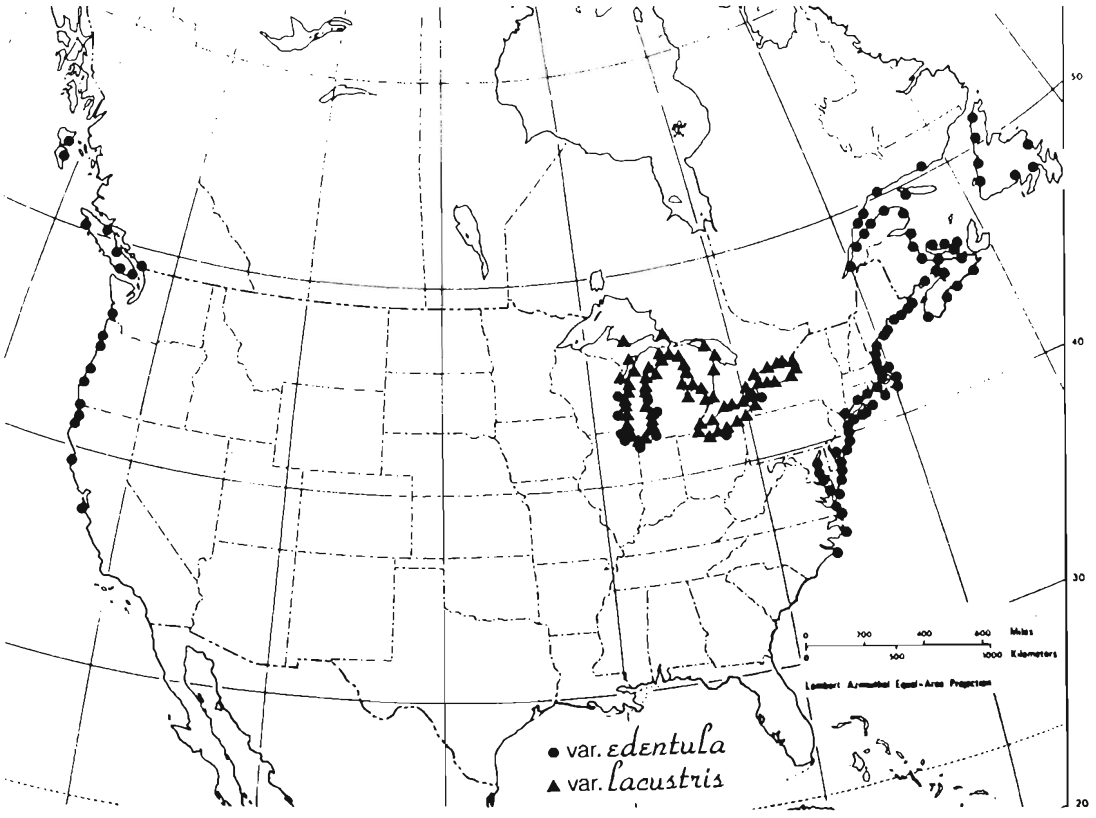

Figure 2. Distribution of *Cakile edentula* varieties *edentula* and *lacustris* in North America. From specimens in the herbaria of Biosystematic Research Institute, Ottawa; National Museum of Canada; University of Western Ontario, London; University of California, Davis; personal observations and from Rodman (1974) and Morton and Venn (1984).

ica near San Francisco, California (BARBOUR and RODMAN, 1970). It spread rapidly north and south, and was reported on Vancouver Island in 1921 and Kodiak Island in 1931. Following the introduction of European *C. maritima* to California in the 1930's and its spread throughout the range of *C. edentula, C. edentula* has disappeared from the southernmost 1,000 km of its range (BARBOUR and RODMAN, 1970). It continues to grow sympatrically with *C. maritima* north of Eureka, California, although it becomes abundant only in central Oregon and beyond (BARBOUR and RODMAN, 1970; BOYD, 1986).

A similar case of early invasion by *C. edentula*, followed by invasion by *C. maritima* and disappearance of *C. edentula* in part of their previous joint range, has occurred in Australia (RODMAN, 1974, 1986). *Cakile edentula* was first introduced near Melbourne in the 1860's, and by the 1970's had spread into Queensland in eastern Australia and into Western Australia. A later introduction of *Cakile maritima* has replaced *C. edentula* in South Australia and Victoria. It currently extends from Perth, West Australia to Sydney in New South Wales (RODMAN, 1986).

Cakile edentula has also been reported from Japan (ASAI, 1982), New Zealand (AL-SHEHBAZ, 1985), and the Azores (AL-SHEHBAZ, 1985).

IV. RANGE OF HABITATS

(a) Zone of Occurrence

Cakile edentula ssp. *edentula* occurs as a pioneer strand species on both marine and freshwater (Great Lakes) shorelines. As such its position is analogous to that of *C. maritima*, which is an integral member of the strand line community in northwest Europe (IGNACIUK and LEE, 1980). In a synecological study of beach vegetation on 34 Pacific beach sites (47-33°N), BARBOUR *et al.* (1976) discovered *C. edentula* on 27% of their sites and considered it a significant component of the seaward edge of vegetation (Table 2). They showed that its cover usually peaked in the middle third of the beach.

The landward extent of *Cakile edentula* is regulated by dispersal (KEDDY, 1982), predation (BARBOUR, 1970b; BOYD, 1988b) and competition (BARBOUR, 1970b; KEDDY, 1982). The seaward (or lakeward) extent of *C. edentula* is regulated by the physical environment through movement of fruits away from the water and high seedling mortality at the water's edge. KEDDY (1982) and JOHNSON (1963) documented the destruction of seedlings growing too close to the water.

(b) Substrate Characteristics

The parent material of the shoreline substrate where *Cakile* grows consists of sand, gravel, and shingle (BALDWIN and MAUN, 1983; KEDDY, 1981). Soil pH generally ranges from about 6.5 to 8.0. Substrate disturbance by both high waves and winds causes continual shifting of the sand, thus creating a rather unstable environment. *Cakile edentula* requires a well drained soil and poor growth of *C. maritima* was obtained in clay soils (SALISBURY, 1952). Along the Lake Huron shoreline, BALDWIN and MAUN (1983) found high levels of calcium carbonate due to fragments of limestone and fresh water invertebrate shells. Substrate organic matter was generally betwen 0.04 and 0.20% by weight, resulting in poor moisture retention as well as poor cation exchange capacity. Four macronutrients (Mg^{++}, K^{+}, N, P) were in short supply. Deposition of detritus by waves may be an important source of nitrogen (HOLTON, 1980) and thus may influence *Cakile* microdistribution.

(c) Climatic Requirements

The major part of *C. edentula*'s distribution lies within KOPPEN's (1931) Dfb climatic region, characterized as humid continental with cool summers and humid winters, no dry season and a snow cover of several months duration. *Cakile edentula* extends to about 53°N latitude along the Pacific coast and 50°N along the Atlantic (Figure 2) in habitats that may be classified as azonal rather than latitudinal in influence (BARBOUR *et al.*, 1976). The moderating influence of water along shorelines may extend its range. Several studies (BARBOUR and ROBICHAUX, 1976; BARBOUR *et al.*, 1976) concluded that microenvironmental factors were more meaningful to *Cakile* abundance

Table 2. *Distribution pattern of plant species on 34 beaches along the Pacific coast (47°-33°N) showing the percentage of beaches on which the species was present in the leading edge and percent cover of the species on the seaward, middle and landward end of the beach. After BARBOUR, DE JONG and JOHNSON* (1976).

Name of Species	Percent of beaches on which the species was represented	Percentage of beaches showing maximum cover on		
		Seaward 1/3	Mid 1/3	Landward 1/3
Abronia latifolia	14	24	24	38
Abronia maritima	40	0	50	50
Ammophila arenaria	31	0	16	72
A. breviligulata	40	0	100	0
Ambrosia chamissonis	21	6	53	35
Atriplex leucophylla	33	50	33	17
Camissonia cheiranthifolia	0	0	33	67
Cakile edentula	27	9	55	0
C. maritima	43	9	26	22
Calystegia soldanella	0	11	11	67
Carex macrocephala	0	0	100	0
Distichlis spicata	0	0	0	100
Elymus mollis	20	8	24	32
Fragaria chiloensis	0	0	0	100
Honckenya peploides	20	40	20	20
Lathyrus japonicus	0	0	0	75
L. littoralis	0	0	0	100
Mesembryanthemum chilense	8	0	20	70
Poa douglasii	0	0	0	100
P. douglasii ssp. macrantha	0	0	50	50

and distribution than latitudinal macroclimatic gradients. The current southern limit of *C. edentula* var. *edentula* on the Pacific coast appears to be indirectly determined by climate (BOYD, 1986). In California, where winters are relatively mild, both *C. edentula* and *C. maritima* can live into a second reproductive season. The proportion of plants surviving into a second season in the open beach microhabitat is similar for both species, but many more *C. maritima* plants flower and fruit during the second year of life in the foredune. As a result, reproductive output of *C. maritima* in the foredune is greater than *C. edentula* by approximately two orders of magnitude. Farther north, where neither species can overwinter, this advantage of *C. maritima* does not occur and the two species coexist.

Cakile edentula is not threatened with extinction on either coast of North America. *Cakile edentula* and *C. maritima* have been sympatric for some time in the northwest (the earliest record of *C. maritima* in British Columbia is 1951), but *C. edentula* is still dominant there (BARBOUR and RODMAN, 1970). On the east coast, *C. maritima* has been introduced in a number of localities (AHLES, 1951; RIEFNER, 1982) but appears to be non-aggressive.

V. PLANT COMMUNITIES

Along the Pacific coast, *C. edentula* was found growing with 19 other typical beach species (Table 2), although at any one beach generally five species comprised the vegetation. Only one or two dominant species had any significant amount of cover, *e.g.*, *Ammophila arenaria* north of 38° latitude and *Mesembryanthemum chilense, Cakile maritima, Ambrosia chamissonis* or *Abronia maritima* south of that latitude (BARBOUR *et al.*, 1976).

RODMAN (1974) stated that *Ammophila breviligulata* and *Hudsonia tomentosa* were two common species associated with *C. edentula* on the Atlantic. VAN ASDALL and OLMSTEAD (1963) found that three species of summer annual dicots: *Euphorbia polygonifolia* L., *Cycloloma atriplicifolium* (Spreng.) Coult., and *Corispermum hyssopifolium* L. were associated with *C. edentula* on open dune sites along Lake Michigan. PAYNE (1980) reported *Corispermum hyssopifolium, Ammophila breviligulata* Fern., *Calamovilfa longifolia* (Hook.) Scribn., *Oenothera biennis* L., *Salsola kali* L., *Xanthium strumarium* L., *Euphorbia polygonifolia* L., and *Artemisia campestris* Michx. as major species occurring with *C. edentula* var. *lacustris* on the

southeastern shoreline of Lake Huron. MORTON and VENN (1984) reported *C. edentula* from the exposed shoreline of Manitoulin Island (northern Lake Huron), occurring in unstable sand on the storm beach. Occasional plants were also found on the strand in association with *Agropyron psammophilum* (Gillett & Senn) Voss, *Juncus balticus* Willd., *Prunus pumila* L., *Artemisia campestris* L., *Potentilla fruiticosa* L., *Equisetum variegatum* Schleich., *E. laevigatum* A. Br., and *E. hyemale* L. At some locations along Lake Erie, *Strophostyles helvola* (L.) Ell. and *Tussilago farfara* L. are the two most abundant co-occurring species. North American strandlines are rarely colonized by more than eight plant species owing to variable salinity levels (along sea coasts), instability of habitat, destructive wave action, drought conditions and low nutrient supply.

VI. PHYSIOLOGICAL ECOLOGY

(a) Physiology

Beach substrates contain relatively low levels of nutrients and available water due to their coarse texture and low organic matter content. As a result, nutrient (KACHI and HIROSE, 1983) and watering experiments (WELLER, 1985) show increased growth in field-grown plants. Addition of ammonium nitrate to field-grown plots of *C. edentula* yielded large plants with higher reproductive outputs than the control (KEDDY, 1981). KEDDY (1980, 1982) also found a positive association between detritus left by wave action and high reproductive output of *C. edentula* in Atlantic coast shingle bar and sand dune habitats. However, the interplay between detritus and fungal/animal "predators" on the shingle bar was complex. Plants growing in the detritus had lower survival and reproductive output, in part due to the greater frequency of damping-off disease early in the season (KEDDY, 1982). However, a heavy infestation of caterpillars on plants growing away from detritus later in the season resulted in higher final fruit production of plants growing in detritus.

Studies of *C. maritima* in Europe (LEE *et al.*, 1983) and California (HOLTON, 1980) concluded that nutrients limited plant growth and that detritus could be an important source of nutrient additions. However, BARBOUR (1972) found no correlation between soil nitrogen and the microdistribution of *C. maritima* on the open beach. The nature of the nutrient limitation in dune or beach soils appears to be variable. Nitrogen, along with phosphorus and/or potassium, seems most commonly limiting (RANWELL, 1972). Seawater contains all essential plant nutrients (EPSTEIN, 1972) although N, P, K are in relatively low concentrations while Na, Cl, Ca and Mg may be present in harmfully large amounts. These salts are supplied to marine beach sand or plant leaves via salt spray. Uptake may be either from the substrate or by the leaves (ROZEMA *et al.*, 1982). One difference in nutrient status between the freshwater habitat of *C. edentula* var. *lacustris* and the marine beach habitat of *C. edentula* var. *edentula* may be a deficiency of Mg or other nutrients in the freshwater environment. Although we know of no attempts to directly test this idea, the ability of var. *edentula* to grow in the freshwater environment of var. *lacustris* indicates that it can tolerate these possible differences.

Salt spray is an important environmental factor in beach habitats, and *Cakile* is relatively tolerant of high salt spray levels. MARTIN (1959) observed that Atlantic coast *C. edentula* was very tolerant of salt spray. BARBOUR and DE JONG (1977) tested the response of west coast *C. edentula* to realistic levels of salt spray and seawater inundation, and combined mortality, morphology and biomass estimates into a tolerance index. Relative to other beach taxa, *C. edentula* was found to have a fairly high tolerance level, which corresponded well with its zonation rank (BARBOUR, 1970b, 1978). RODMAN (1974) estimated that *C. edentula* var. *edentula* and *C. edentula* var. *lacustris* have become morphologically different following reproductive isolation within the last 10,000 years. Besides morphological divergence, BOYD and BARBOUR (1986) have shown that they have diverged in their ability to tolerate salt spray. Artificially applied salt spray decreased reproductive output of var. *lacustris* but not var. *edentula*. However, both varieties tolerated soil salinity and salt spray better than a typical glycophyte and were able to undergo similar degrees of hypertrophy (the thickening of leaves typical of salt spray-tolerant plants) in response to salt spray. At least part of the difference in fleshiness between

field-collected var. *edentula* and var. *lacustris* plants is due to hypertrophy of var. *edentula* induced by exposure to salt spray. Leaves of var. *edentula* exposed to levels of salt spray similar to those found at the leading edge of beach vegetation were 2.3-fold as thick as water-sprayed leaves of var. *lacustris* (BOYD and BARBOUR, 1986). This difference decreased to 1.3-fold when both varieties were sprayed with water.

No water relations studies have been performed on *C. edentula*, but DE JONG's (1979) study of California *C. maritima* revealed that plants survived rainless summers by tolerating higher xylem sap tensions than *Ambrosia chamissonis* or *Abronia maritima* seedlings. Drought, however, has been considered to be an important factor in *C. maritima* seedling mortality (BARBOUR, 1970a). DE JONG (1979) also reported lower xylem tensions in southern California *C. maritima* relative to northern California populations, which he attributed in part to the greater amount and seasonal evenness of precipitation to the north. BALDWIN and MAUN (1983) remarked that soil moisture content, especially at shallow depths (1-10 cm), was the most important discriminating factor in the Great Lakes sand dune environment. Moisture was lowest in June and July, at which time a drastic reduction in the seedling populations of *C. edentula* var. *lacustris* occurred. PAYNE and MAUN (1984) estimated that 32% of the plants in their population died from drought stress.

BARBOUR *et al.* (1985) compared photosynthetic rates and leaf water loss of *C. maritima* under high and low soil nitrogen regimes, finding that plants maintained the same rate of net photosynthesis under both nutrient regimes. However, under low nitrogen conditions there was an increase in leaf conductance and therefore transpiration, resulting in a decline in an already low value for water use efficiency.

All four *Cakile* species investigated to date possess the C_3 photosynthetic pathway (DE JONG, 1978; BARBOUR *et al.*, 1987), and therefore it seems likely that *C. edentula* does as well. DE JONG (1978) compared *C. maritima* and two other C_3 plants to a C_4 *Atriplex* species, finding that the C_4 species reached maximum rates of photosynthesis at higher temperatures and light intensities, but the C_3 species had higher photosynthetic rates at temperatures approximating normal field conditions. Water use efficiency of all the C_3 species was less than *Atriplex*.

(b) Phenology

In far northern latitudes *C. edentula* germinates soon after the ground is fully thawed, and occurs during a relatively short time. Both Great Lakes and Atlantic populations germinate over a period of 4-6 weeks (PAYNE and MAUN, 1984; KEDDY, 1982). Observations at Pinery Provincial Park, Canada over a period of several years showed that the first emergence of *C. edentula* var. *lacustris* occurred in late April on the upper undisturbed beach areas, whereas lakeward seedlings emerged a few days later. Observations by KEDDY (1982) on the Atlantic coast also showed earlier germination of landward seeds, which may have resulted from warmer sand temperatures. Flowering begins in the end of July or beginning of August in the Grand Bend region in southwestern Ontario, Canada. Most plants continue to flower and fruit throughout August and September, but occasional flowering plants may be found in October or November. Fruits mature within about three weeks.

In the mediterranean-climate region of California, flowers and fruits of *C. edentula* may be found almost any time of year. For example, at Eureka in northern California, *C. edentula* flowered from June to January (JOHNSON, 1963). Near San Francisco, some members of an artificially-established population in foredune and open beach habitats survived into a second reproductive season and flowered in late winter and spring (BOYD, 1986). However, the peak of flower and fruit production of both *C. edentula* and *C. maritima* was in the summer and fall.

Germination timing is also less well-defined in California. JOHNSON (1963) observed seedlings from planted seeds in November, March and April and from naturally-dispersed seeds in December. In an artificially-established open beach colony of *C. edentula*, BOYD (1986) recorded seedling emergence from January to May, with a large peak in April. This germination pattern differed from that of *C. maritima* at the same site, which peaked in January and April with no May germination.

RODMAN (1974) found that greenhouse or growth chamber-grown plants of all species he

investigated flowered and fruited within two months of germination, but some populations or species had noticeably faster maturation rates than others. For *C. edentula*, Atlantic coast populations matured in an average of 44 days, in contrast to 33 days for Pacific coast populations. He was unable to determine if this difference had adaptive significance or was due to a founder's effect for Pacific coast *C. edentula*. RODMAN (1986) suggested that historical replacement of *C. edentula* by *C. maritima* in California and Australia may have been due to the faster maturation time of *C. maritima* observed under growth chamber conditions. BOYD (1986) found that *C. maritima* flowered earlier than *C. edentula* in field-grown populations at Point Reyes, California, but that total reproductive output was affected by many other factors that, in some cases, outweighed the reproductive speed of *C. maritima*.

VII. POPULATION BIOLOGY

(a) Perennation

Cakile edentula is a succulent annual (therophyte) that completes its life cycle within one growing season in northern latitudes and survives unfavorable conditions as seeds. In milder climates it acts as a facultative perennial, with a few individuals surviving into a second reproductive season in the foredune habitat (BOYD, 1986).

(b) Population Dynamics

Habitat unpredictability, population size and other biotic and abiotic factors may cause mortality to vary widely from year to year (PAYNE and MAUN, 1984; KEDDY, 1982). For example, PAYNE and MAUN (1984) reported high mortality rates for *C. edentula* var. *lacustris* during 1978 because of extremely low rainfall. Mortality rates were lower the following year but a spring storm that resulted in deep burial of seedlings caused considerable mortality. Differences in microhabitat also caused differences in mortality rates. Driftline and high beach plants suffered about 75% mortality as compared to less than 50% for midbeach plants. Mortality on the high beach may be caused by higher drought stress (PAYNE and MAUN, 1984) and/or macronutrient deficiency (LEE and IGNACIUK, 1985). TYNDALL *et al.* (1986a) showed that on the foredune low soil water potential contributes heavily to seedling mortality and decreased growth rates of *C. edentula*. During summer along Lake Huron (fresh water), low beach plants occasionally may be inundated by high waves and consequently survive and grow better during drought. Similar inundation on marine beaches may be lethal (KEDDY, 1982).

KEDDY (1981) studied the demography of *C. edentula* var. *edentula* on the environmental gradient stretching from seaward to landward ends of a sandy beach. He found that: (1) density-dependence of survivorship changed significantly along the gradient whereas density-independent mortality stayed constant; (2) both density-independent and density-dependent effects significantly influenced reproductive output, and (3) effects of density on survivorship were greatest at the landward end of the gradient, while the effect of density on reproductive output were greatest at the seaward end. Modelling done by WATKINSON (1985) showed that *Cakile* abundance on Martinique beach (data from KEDDY, 1981) was regulated by density-dependent control of fruit production at the seaward end.

Survivorship curves for clumps of *C. edentula* (PAYNE, 1980) showed an increase in mortality rate with increasing initial clump size; however, the rates were not statistically different. Moreover, only large clumps had a significantly higher mean mortality rate than adjacent controls consisting of scattered plants, a result probably due to greater density stress as a function of drought in larger clumps.

Populations of *C. edentula* can be highly ephemeral. BARBOUR (1970b) reported fluctuating appearance and disappearance of sea rockets locally along the California coast. PAYNE (1980) noted that the distribution of *C. edentula* varies from year to year, and even from spring to summer. Spatial patterning of *C. edentula* var. *lacustris* (PAYNE, 1980) on Lake Huron and var. *edentula* (KEDDY, 1981) along the Atlantic coast consisted of three types of groupings: (1) densely clustered plants in clumps 8 to 60 cm diameter occurring at sites occupied by large plants of the previous year. In such clusters density declined rapidly with increasing distance from the center; (2) many plants in a zone along the driftline or high

water mark; and (3) single plants 'scattered' along the beach both above and below the drift-line, resulting from water dispersal of fruits. In addition, a few plants may establish on dune ridges or in blowouts. Small populations in blowouts inland from the shoreline may maintain themselves over many generations as long as the habitat remains open and unoccupied by perennials.

Cakile edentula is a summer annual along the Great Lakes and northern Atlantic and Pacific coasts, although to the south along both coasts it may survive into a second reproductive season (RADFORD *et al.*, 1968; BOYD, 1986; PITTS, 1976). ALong Lake Huron and Martinique Beach, Nova Scotia, germination and seedling emergence occurs in spring within approximately four weeks (PAYNE and MAUN, 1984; KEDDY, 1978), so that the difference in age of plants within a population is relatively small. However, the difference in demography and population dynamics of cohorts (a group of individuals born during the same time interval) of seedlings emerging during these four weeks may be significant. PAYNE and MAUN (1984) found that cohorts differed in fruit production per plant. Mean fruit production per plant was significantly higher ($P < 0.05$) in the second cohort (emergence between May 3-14) than the first and third. Cohorts 1 (April 15-May 2) and 3 (May 15-30) did not show any significant differences.

VIII. REPRODUCTION

(a) Sexual Reproduction

(i) Pollination and Fertilization *Cakile edentula* is principally an inbreeding species; however, cross pollination by wind or insects can occur. For example, BOYD (unpublished data) found a few apparent hybrids among the progeny of an artificially established stand of both *C. edentula* and *C. maritima* in California. The ability of *C. edentula* to self-pollinate is reflected in reduced petal and nectary size. Anthers often dehisce in the bud just prior to anthesis, thus ensuring autogamy (RODMAN, 1974). Flowers usually open in the morning and close at least for the first night. No information on floral visitors is available, but high fruit set of growth chamber-grown plants (RODMAN, 1974, reported 82% for var. *lacustris* and 89% for var. *edentula*) indicated that they are not necessary for fruit production. *Cakile maritima* flowers have patterning visible only in ultraviolent light, which presumably enhances floral attractiveness (HOROVITZ and COHEN, 1972), but *C. edentula* flowers have not been examined for this trait.

(ii) Seed Production Fruit output varies from year to year depending on factors such as violent storms, sand deposition or erosion, biotic factors, and plant density (PAYNE and MAUN, 1984; KEDDY, 1982). For example, in populations of *C. edentula* var. *lacustris* along Lake Huron, high waves eroded part of the beach in April 1979 and caused an 80% reduction in the number of seedlings as compared to 1978 (PAYNE and MAUN, 1984). Estimates showed that in a 5 m wide and 16 m long strip of beach from the lake to the first dune ridge, the total number of fruits produced was 3411 in 1978 and 486 in 1979. The mean number of fruits produced per plant was 35.2 ± 6.2 S.D. and 16.6 ± 3.2 S.D. in 1978 and 1979, respectively. PAYNE (1980) determined fruit production of potted plants from proximal and distal fruit segments in a greenhouse. Fruit output per plant ranged from 25 to 215, but plants originating from distal and proximal fruit segments did not differ in total fruit production. PAYNE and MAUN (1984) found that reproductive output m^{-2} was highest for plants closest to the lake and in general, declined with distance to the first dune ridge. Similarly, after one growing season on the Pacific coast of California, reproductive output per plant of both *C. edentula* and *C. maritima* was 3.4 and 2.1 times higher (respectively) for plants growing in front of the foredune than for foredune plants (BOYD, 1986). KEDDY (1981) suggested that nitrogen shortage and increased competition from *Ammophila breviligulata* could explain the observed landward decrease in reproductive output of *C. edentula*. He showed that increased density resulted in decreased reproductive output at the seaward end of the gradient, whereas at the landward end increased density had little effect on reproductive output.

KEDDY (1980) also observed a negative impact of seedling clumping on reproduction. Reproductive output per plant of *C. edentula* var. *edentula* in both shingle and wrack habitats declined with distance from the cluster cen-

ter. Moreover, comparisons of reproductive output in the two habitats revealed that for scattered plants, reproductive output was equivalent for both shingle and wrack habitats, but for clustered plants, shingle reproductive output was generally greater (15.6 distal fruits per plant) than that of wrack plants (6.0 distal fruits per plant). Fruit production was positively related to the amount of drifted wrack (*Zostera*) along Nova Scotia shoreline (KEDDY, 1978).

(iii) Dispersal Fruits of *Cakile edentula* are well-suited for water dispersal. The corky outer coat of the fruits makes them buoyant in water for long periods of time. PAYNE and MAUN (1981) reported that 38% of fresh distal fruits (agitated to simulate wave action) were still afloat after 52.5 hours. After 20 days of agitation, 22% of distal fruits were floating, whereas only 0.75% of proximal fruits continued to do so. Fruits overwintering in sand also exhibited exceptional floating ability: on day 20, 65.3% of the distal and 87.5% of the proximal segments remained afloat. GUPPY (1917) estimated that distal fruits of *C. edentula* have the potential to travel 208-272 km in seawater. BARBOUR and RODMAN (1970) showed that, once established, *C. edentula* var. *edentula* migrated along the west coast of North America at an average rate of 64 km per year. *Cakile* was the first documented vascular plant to establish on Surtsey Island, probably dispersing by water 32 km from Iceland (RODMAN, 1974).

Fruit dimorphism of *Cakile edentula* reflects two modes of dispersal. The deciduous distal fruit segment falls off the plant and may be dispersed by wind or water (PAYNE and MAUN, 1981). Proximal fruits remain attached to the parent plant and are consequently buried by wind-blown sand, thereby forming clumps of seedlings in a "tried and true" habitat in the next growing season (BARBOUR, 1972). In addition, dead and dried parent plants may become uprooted and be blown like tumbleweeds on the beach, thus dispersing the attached proximal fruits (COWLES, 1899; PAYNE and MAUN, 1981).

Several field studies show surprisingly low dispersal distances for *Cakile* fruits, given its reputation as a highly-dispersible plant. KEDDY (1980), studying *C. edentula* on a shingle bar, and BARBOUR (1970b), studying Pacific coast *C. maritima*, found dispersal over small distances (< 2m). In another study of *C. edentula* on a sand dune, KEDDY (1982) documented landward fruit dispersal on the order of 10 m. The apparent contradiction between these studies and the rapid colonizing ability (and hence dispersal) of *Cakile* introduced to new areas (BARBOUR and RODMAN, 1970; RODMAN, 1986) may be due to a bimodal dispersal pattern for these plants. PAYNE and MAUN (1981), working on the shore of the Great Lakes, showed that painted fruits on plants destroyed by waves or blown about by wind moved great distances. An intact plant sprayed with paint and followed for 6 wk had most of the proximal fruits remaining on its branches or within 2 m of the parent. However, most (87%) of the dispersed fruits were not found. They were either buried by sand or had dispersed beyond the 7 m diameter study area, suggesting that fruits which move a small distance from the parent continue to move, resulting in either long-distance dispersal or practically none at all.

BOYD (unpublished data) found that the seed predator *Peromyscus maniculatus* (deer mouse) dispersed seeds of *C. maritima* on the California coast, caching them in the sand and failing to recover some caches before germination. Abandoned caches contained many (9-44) seeds, shelled from the fruits and buried 2-6 cm deep in the sand on the foredune. Mouse dispersal was not thought to be ecologically important for two reasons: first, cache seedlings had lower survival rates than seedlings not arising from caches and, second, unrecovered caches represented less than 0.2% of all seeds produced on the study area (over 90% of all seeds produced by the population were destroyed by rodent activity).

In some areas of the world birds eat and may disperse *Cakile* seeds. HEYLIGERS (1984) observed seedlings of *C. maritima* emerging from emu scats in Australia. Other birds (rosellas and parrots) were also reported as seed predators and may play a dispersal role as well.

(iv) Seed Bank and Seed Size PAYNE (1980) recovered fruits that had failed to germinate after burial in 20 cm of sand and found that 51 ± 6% had remained viable but dormant, suggesting that a seed bank may occur under natural conditions. This was supported by her

observation that, following a severe winter storm at the Pinery, many seedlings emerged from deeply buried seeds in a wave-cut bank. She estimated seed bank size in the top 15 cm of sand to be about 15 seeds m^{-2}.

BOYD (1986) stapled shelled and unshelled seeds of Pacific coast *C. edentula* into fiberglass sleeves and buried them 10 cm deep on the foredune. After 26 months, 90% of the seeds left in their fruits were still viable, whereas only approximately 15% of the shelled seeds were alive. Seeds from proximal fruit segments, especially when shelled, survived longer than distal seeds under the same treatment.

Seed size in *C. edentula* varies with position within the fruit. Seeds in distal fruit segments are slightly larger and heavier than proximal seeds in all *Cakile* taxa (RODMAN, 1974). RODMAN (1974) recorded mean seed weights (in mg) of 12.3 and 10.7 for distal and proximal *C. edentula* ssp. *harperi* (respectively), and 9.5 and 9.2 for Atlantic coast *C. edentula* var. *edentula*.

(v) Germination Ecology and Establishment of Seedlings Germination requirements differ for distal and proximal segment seeds. PAYNE (1980) conducted seed and fruit germination experiments on *C. edentula* var. *lacustris* under varying temperature and light regimes in a growth chamber. The results showed that: (a) greatest percent germination was obtained at alternating temperatures of 20°C (14.5 hr) and 10°C (9.5 hr) under dark conditions, (b) light inhibited germination rates but not total germination, (c) proximal fruits germinated over a wider range of temperatures than distal fruits, (d) distal fruits had greater percent germination than proximal ones at constant temperature (20°C), (e) most fruits required stratification to overcome dormancy and (f) presence of fruit coats decreased both the percentage and rate of germination. In these experiments, distal fruits had a higher incidence of fungal infection than proximal fruits and more rotted.

In growth chamber experiments some fruits failed to germinate under optimal (20°C (14.5 hr), 10°C (9.5 hr) in dark) germination conditions (PAYNE, 1980). Since these fruits were viable (tetrazolium test), they were probably in a state of induced dormancy. It was calculated that the mean percentage of dormant seeds was 37.0 ± 6.8% (S.E.).

Germination speed and germination percentage usually decrease with increasing salinity in halophytes (LESKO and WALKER, 1969). In a comparison of the effects of salinity on the two varieties of *C. edentula*, BOYD and BARBOUR (1986) exposed seeds (which had been previously stimulated to germinate) to salinities of up to 10,000 ppm. They found no inhibition of germination in seeds from either distal or proximal segments, and concluded that germination in both varieties was relatively tolerant of salinity.

Seedling establishment is affected by the same factors which influence survival of established plants, but their effect is relatively greater due to the heightened vulnerability of seedlings. Seeds germinating too close to the ocean may be destroyed by wave action (KEDDY, 1982). Similar wave inundation on lakes may be either beneficial by supplying water during drought or detrimental by burying seedlings with sand (PAYNE and MAUN, 1984). Seedling establishment can be prevented by erosion of sand (PAYNE and MAUN, 1984) and damping-off disease (KEDDY, 1978; PAYNE and MAUN, 1984). BOYD (1986) noted that recently-germinated seedlings were especially vulnerable to predation by rodents, and removal of both cotyledons of a seedling often killed the plant even though the growing tip was left intact.

(b) Vegetative Reproduction

No natural vegetative reproduction is known in this genus (RODMAN, 1974).

IX. GEOMORPHOLOGICAL INTERACTIONS

(a) Response to Burial

Substrate mobility and prevailing weather conditions may result in burial of fruits. TYNDALL *et al.* (1986b) suggested that *C. edentula* survives on heavily accreting beaches because the buoyancy of its fruits protects them from deep burial. Effects of burial on germination and emergence of seedlings from 0, 2, 4, 6, 8, 10, and 12 cm burial depths were studied in a greenhouse by MAUN and LAPIERRE (1986).

Seed germination was not influenced by burial depth, but seedling emergence was significantly reduced. Seedlings from distal fruits showed greater capability for emerging from greater depths than proximal fruits, owing to their larger size. Fruits required at least some degree of burial since germination was very poor at 0 cm. PAYNE (1980) showed that maximum depth for seedling emergence was about 10 cm. Mean emergence depth under field conditions was 3.8 ± 1.4 (S.D.) cm (range 0.5-9.5 cm). Field studies by PAYNE (1980) showed that seedlings in a clump emerged from significantly greater depths (2.8-9.7 cm), than those of scattered seedlings ($P<0.001$) probably owing to greater collective force of emergence. Seedlings emerging from greater depths require more resources and more time in hypocotyl elongation, and thus tended to have smaller cotyledons.

Burial of plants by sand may be stimulatory, neutral, or fatal, depending upon depth of burial. PAYNE and MAUN (1984) concluded that plants buried early in the season to one half of their height survived and showed greater growth and fruit production than unburied plants. Complete burial reduced survival and no plants survived being buried 1.5 times their maximum height. Conversely, seedlings with sand eroded from their bases became desiccated and died. PAYNE (1980) attributed about 5% of mortality in her study plants to either sand erosion or burial.

(b) Role in Geomorphology

Cakile edentula is one of the first true pioneers of sandy beaches along shorelines of lakes and oceans. It acts to stabilize sand, thereby providing further niche differentiation and more amenable micro-environmental sites for secondary colonizers. However, because of erratic but predictable wave action (PAYNE, 1980) the mid-beach remains in a constant state of primary succession with *C. edentula* as the dominant species. Single and clumps of individuals accumulate sand and form sand mounds. At the end of the season the plants die and add humus to the soil, thereby increasing sand nutrient levels (COWLES, 1899). *Cakile edentula* is also among the first colonizers of dune blowouts (ERSKINE, 1960).

X. INTERACTIONS WITH OTHER SPECIES

(a) Competition

PAYNE (1980) reported the following major species as actual or potential competitors of *C. edentula* var. *lacustris* on Lake Huron beaches: *Corispermum hyssopifolium* L., *Ammophila breviligulata* Fern. and *Artemisia campestris* Michx. *Corispermum hyssopifolium* occurred with clumps of *C. edentula* more frequently than the other two species. Because of shading from the sun, *Cakile* seedlings growing under *A. breviligulata* plants were often both taller and larger than unshaded seedlings (PAYNE, 1980); however, if water became limiting, these larger seedlings usually died. Finally, since *A. campestris* was scattered in distribution and consequently not generally associated with *Cakile*, the possibility for competition was slight.

The decreased size and vigor of *Cakile* individuals growing away from the shoreline is generally believed to be at least partially a result of competition from other plants. KEDDY (1981, 1982) suggested that shortages of nitrogen and competition from *Ammophila breviligulata* were responsible for the poor reproductive output of foredune *C. edentula*. BARBOUR (1970a) found that competition for light kept *C. maritima* from colonizing inland grassy areas.

Competition has been suggested in attempts to explain the displacement of *C. edentula* by *C. maritima* along the Pacific coast of California (BOYD, 1986). BARBOUR and RODMAN (1970) suspected that direct competition was unlikely to play a role, given the low densities often found in Pacific coast populations. Using pure and mixed cultures of the two species in a growth chamber, BARBOUR (1970b) showed that *C. edentula* had an advantage over *C. maritima*. BOYD (1986) grew pure and mixed plots of *C. edentula* and *C. maritima* in foredune and open beach habitats to see if interference (competition or allelopathy) between the two species might explain the displacement of *C. edentula* by *C. maritima* in California. He found that neither species significantly interfered with the other and concluded that direct competition was not involved, although the exact mechanism remained unclear. He also concluded that an important difference between the two spe-

cies was the ability of *C. maritima* to better-tolerate foredune habitat conditions, live into a second reproductive season there, and thereby produce more fruits than *C. edentula*.

(b) Predation and Parasitism

Biotic agents affecting survival of Great Lakes *C. edentula* were white rust (*Albugo candida* (Lev.) Kunze), damping-off fungi (*Pythium* spp.), human disturbance, white tailed deer and a variety of both specialized and generalized insects. PAYNE and MAUN (1984) first observed white rust (*Albugo candida*) on *C. edentula* plants on June 1. Ninety-one percent of the plants in quadrats were infected by July 5 whereas by July 13, 78% of the clump plants and 81% of the scattered control plants were infected. PAYNE (1980) and KEDDY (1978) observed many seedlings infected by damping-off fungi. White-tailed deer grazed the larger lakeward plants, which may resprout and produce seeds late in the season (PAYNE, 1980).

Phytophagous insects included *Euxea* (cutworm), *Pieris rapae* L. (cabbageworm), *Acrolepia xylostella* L. (diamond-back moth), *Hyadaphis erysimis* (aphids), and *Trimerotropis verraculatus* (banded-wing grasshopper). PAYNE and MAUN (1984) noted that at least 9% of young plants were killed by the cutworm, *Euxea* (Notridae) which chewed through the stems of seedlings below the sand surface. *Pieris rapae* L. (Pieridae), were found on 2% of clumped plants and 4.6% of scattered control plants, and caused considerable damage to leaves, flowers, fruits and stems. Larvae of *A. xylostella* L., (Plutellidae) rasped small holes in leaves, flowers, and pods of *C. edentula*; however, this damage was slight. Aphids (Aphididae) were first observed at the end of June, and by mid-July inhabited almost all plants, causing leaf curling and stunting of stems. Severely affected plants often died before fruiting. Although predators of aphids, such as lady-bird beetles, lacewings, and the larvae of certain syrphid flies as well as Hymenopterous parasites such as *Diaertiella* spp. were abundant at the Pinery, aphid populations showed a tremendous increase during periods of no rainfall. The combination of aphid infestation and water stress resulted in high mortality of *Cakile* plants. Banded-wing grasshoppers were very abundant and fed by taking large parts out of *C. edentula* leaves. Twenty-two per cent of clumped plants showed grasshopper damage, as opposed to 44.2% of scattered single plants.

Cakile edentula plants are also infested by crucifer and striped flea beetles (*Phylotretta cruciferae* and *P. striolata*). These introduced species are attracted to cruciferous hosts by allyl isothiocyanate and consequently are serious pests (TAHVANAINEN and ROOT, 1972). Adults rasp small holes in leaf and pod epidermis imparting a typical "shot-holed" appearance; flower buds are also damaged. Under field conditions, many plants at the Pinery showed flea beetle damage. Flea beetle distribution was patchy in both time and space and consequently plant damage was patchy also. Observations by the authors on flea beetle/sea rocket interactions at the Pinery supported the conclusion by FEENY (1977) that the primary defense of crucifer species against insect specialists is one of escape. Further evidence is provided by the fact that when plants of *C. edentula* were placed in an area of "no escape" (cabbage crop) with high flea beetle density and low plant species diversity, 100% damage occurred (OLSON and MAUN, unpublished data).

Cakile edentula is characterized by secondary compounds called glucosinolates (mustard oils), which have taxonomic value for the genus (RODMAN, 1972). Glucosinolates themselves are non-toxic, but upon tissue damage are hydrolysed to reproduce a variety of physiologically active products that are highly toxic to insects, bacteria, and fungi. Glucosinolates occur in roots, stems, and leaves of plants, with the highest concentrations usually found in seeds (TOOKEY *et al.*, 1980). Of 65 species of Cruciferae tested for total isothiocyanate per gram of seed meal, *Cakile edentula* ranked highest, along with *Brassica nigra* (DOXENBICHLER *et al.*, 1964). During the co-evolutionary "war" of plant defense and insect counterdefense, certain insect species have come to utilize glucosinolates as gustatory and egg-laying stimulants and the fission products as attractants (RODMAN and CHEW, 1980). Some species may even sequester these chemicals for their own defense (APLIN *et al.*, 1975).

BOYD (1988a) hypothesized that qualitative and quantitative differences in glucosinolate composition between *C. edentula* and *C. maritima* (Table 1) may affect herbivore preference and hence may have contributed to the replace-

ment of *C. edentula* by *C. maritima* in California through differential herbivory. Tests of this hypothesis were conducted using two insects, the moth *Platyprepia virginalis* (Arctiidae) and the grasshopper *Microtes occidentalis* (Acrididae), and the rodent *Peromyscus maniculatus*. These herbivores were chosen due to their relatively important impact on *C. maritima* in the field. *Microtes* showed no preference and *Platyprepia* preferred *C. maritima*. *Peromyscus* preferred fruits of the larger-seeded *C. edentula*, but this preference was viewed only as a contributing factor in this case of species replacement because *Peromyscus* is found throughout the Pacific coast range of both *Cakile* species.

(c) Symbiosis

As indicated by prolific fruit set under greenhouse conditions, insect pollinators are not required for pollination of *C. edentula*. Mycorrhizae, which are found in most species of higher plants, probably are not formed by *C. edentula* since none have been found in other Brassicaceae.

(d) Grazing and Harvesting

In addition to insect herbivory, some vertebrates eat *C. edentula*. *Peromyscus maniculatus* (deer mouse) eats the herbage of *C. maritima*, but prefers its seeds (PITTS and BARBOUR, 1979). BOYD (1986) found that most of the annual seed production of a foredune population of *C. maritima* was destroyed by mice prior to dispersal. Predation pressure on fruits (and, to some extent, seedlings) resulted in a 3-4 m wide zone of decreased *Cakile* abundance bordering dense stands of *Ammophila*, where the rodents preferred to nest (BOYD, 1988b). PAYNE (1980) observed browsing of *C. edentula* var. *lacustris* by white-tailed deer. Damage occurred mostly to large *C. edentula* plants on the mid-beach during late summer and early fall. However, if enough of the growing season remained, removal of apical shoots stimulated axillary growth and further reproduction. Man has occasionally harvested *Cakile* for livestock forage.

In comparing the morphology of *C. edentula* and *C. maritima* in California, BOYD (1986) found differences in ecological importance. Plants of *C. maritima* had racemes with greater distances between fruits, so that inflorescences tended to sprawl over the sand, whereas *C. edentula* influorescences were held more upright. On the open beach in the fall, storm-generated winds deposited sand over the plants with the result that 83% of *C. maritima* fruits were buried as compared to only 7% for *C. edentula*. Because the fruits were eaten by rodents and the rodents preferred to harvest exposed fruits, *C. edentula* suffered a greater loss of fruits. This difference was thought to be a minor contributor to the decline of *C. edentula* and its replacement by *C. maritima* on this site.

(e) Toxicity and Allelopathy

Since glucosinolate fission products are highly toxic to vertebrates, the ingestion of large amounts of plant material may cause (1) human goiter, (2) mammalian and avian growth depression, (3) thyroid hyperplasia, (4) enlargement of and damage to kidneys and livers, (5) reduced conception, litter size, and weight, and (6) irritation of both skin and mucous membranes (TOOKEY *et al.*, 1980). In general ruminants are less susceptible to these effects than monogastric mammals. White-tailed deer, birds, and small rodents do not seem to be harmed by ingestion of *Cakile edentula*.

It has been suggested that glucosinolates may have an allelopathic effect. ELLIOT and STOWE (1971) showed that significant quantities of indole glucosinolates were excreted by the roots of seedlings of *Isatis tinctoria* L. in culture. They hypothesized that the long known deleterious effect of cruciferous crops on subsequent plantings may be explained by allelopathy. No evidence to indicate allelopathic effects of *Cakile* has yet been found. BARBOUR (1972) examined the effect of leachate from plants of *C. maritima* on the germination of *C. maritima* seeds in a laboratory test. He found no differences in germination of control and treated seeds. In a field test, BOYD (1986) found no evidence of amensalism (competition or allelopathy) between plants of *C. edentula* and *C. maritima* planted in foredune and open beach habitats at Point Reyes, California.

XI. RESPONSE TO WATER LEVELS

Cakile edentula is a terrestrial species and cannot withstand wet soil conditions for long

periods. Plants growing close to the shoreline are subject to occasional flooding by waves. Effects of flooding are variable depending on length of submergence, salinity of the water and the extent of burial or erosion. Sand erosion from the base of plants during flooding causes root exposure and usually leads to death by desiccation. Effects of sand accretion during flooding depend on extent of burial. Burial in moderate amounts of sand may enhance plant survival, growth and reproduction by improving water retention around the root system (PAYNE and MAUN, 1984). Inundation by salt water may be fatal. BARBOUR and DE JONG (1977) subjected *C. edentula* to seawater inundation in a growth chamber experiment. They found it to be relatively tolerant of saline conditions, which combined seawater inundation with high levels of residual soil salinity. Salinity tolerance of *C. edentula* corresponded well to its zonation rank relative to other Pacific beach taxa.

XII. ECONOMIC IMPORTANCE

In modern times, the main benefit of *Cakile* to mankind is its ecological role as a pioneer in beach and dune succession. By stabilizing sand it provides a foothold for the establishment of more permanent perennial species. However, in the past a variety of other uses have been documented.

In North America, Indians of the St. Lawrence River used the powdered roots in a mixture of other flours to make bread during famine (BENSON, 1966). Settlers utilized sea rockets for antiscorbutic purposes as well as a scurvy remedy (SMALL, 1900 in RODMAN, 1974). Leaves of plants have been used for salads (QUESTEL, 1951) and young *Cakile* plants for potherbs by fishermen (FERNALD *et al.*, 1958). Sea rockets have also served as livestock forage. In the Bahamas they served as forage for burros, hogs and goats (HOWARD, 1950). RODMAN (1972) noted that a specimen from Washington was labelled with the comment "cattle are very fond of it."

In Europe, *Cakile* also served a variety of purposes. They were preserved in botanic gardens for variety "if not for beauty" (RODMAN, 1974). As in the New World, they were also used as antiscorbutic, diuretic, and purgative agents. *Cakile* was even cultivated on a small scale in France for salad greens (POBEDIMOVA, 1963).

While *C. edentula* may not be of any significant importance to modern man, this influence is not mutual since man has an important influence (both positive and negative) on *Cakile*. *Cakile edentula* var. *edentula* ssp. *edentula* has been spread to Australia (RODMAN, 1986) and Japan (ASAI, 1982), as well as the west coast of North America and the Great Lakes, apparently through accidental dispersal via ship's ballast. Man has had a negative effect on the plant via habitat destruction. Thus on heavily used beaches, *Cakile* is rare to absent because of trampling and erosion (PAYNE, 1980).

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☐ ZUSAMMENFASSUNG ☐

Cakile edentula (Bigel., Hook.) ist eine annuelle oder fakultativ perennierende Pflanze, die als Pionier im Spülsaum der großen Seen, der atlantischen und pazifischen Küste Nordamerikas sowie an der Küste von Japan, der Azoren, Neuseeland und Australien wächst. In diesem Artikel wird eine Zusammenfassung der ökologischen, physiologischen und geomorphologischen Aspekte in der Biologie von *Cakile edentula* gegeben. Ihre erfolgreiche und weite Verbreitung entlang der Küstenlinien mag auf die Fruchtproduktionsrate, den kurzen Lebenszyklus, das Potential für Wasserabgabe, die Resistenz gegenüber Salzgischt bzw. -nebel, der

Besitz einer Samenruhe, eine hoher Prozentsatz von sich entwickelnden Sämlingen, schnelles Wachstum und die Fähigkeit bei verschiedenen Tageslänge (Photoperioden) zu blühen zurückzuführen sein. *Cakile edentula* produziert dimorphe Früchte: distal und proximal. Die vom Fruchtknoten weiter entfernten Früchte brechen von der Pflanze ab und gelangen zu neuen Standorten während die näher am Fruchtknoten sitzenden Früchte an der Pflanze verbleiben. Für die Geomorphologie des Spülsaumes spielt diese Spezies eine bedeutende Rolle. Einzelne oder verklumpte Pflanzen akkumulieren Sand und organisches Material, welches als Bodensubstrat in der Lage ist für Sekundärkolonisten als neuer Standort zu dienen. *Cakile edentula* zeigt die höchste Keimungsrate bei zwischen 20°C (14,5 Std.) und 10°C (9,5 Std.) schwankenden Temperaturen und Dunkelheit. Licht vermindert die Keimungsrate, verhindert sie aber nicht vollständig; Keimung und Fruchtbildung benötigen eine Termperturgradienten um die Ruhe zu überwinden. Die Pflanzen werden von Pilzen heimgesucht und von einer Vielzahl von pflanzenfressenden Insekten und Vertebraten verzehrt. Die untersuchte Spezies produziert als Schutzschicht gegen verschiedene Insekten, Pilze, Bakterien und Vertebraten Glucosinolate.—*Ulrich Radtke, Geographisches Institut, Universität Düsseldorf, F.R.G.*

☐ RÉSUMÉ ☐

Cakile edentula (Bigel) Hook est une plante pionnière littorale annuelle ou parfois perenne (Brassicacae). Son aire de répartition couvre: les Grands lacs, les côtes Atlantique et Pacifique d'Amérique du Nord, Japon, Açores, Nouvelle Zélande et Australie. Un résumé de l'écologie, de la physiologie et des conditions géomorphologiques propres à la biologie de Cakile edentula est présenté ici. Le succès de cette plante sur les littoraux est dû aux facteurs suivants: production d'un grand nombre de fruits, cycle de vie court, potentiel élévé à la dispersion de l'eau, résistance aux embruns, dormance des graines, bonne tenue des jeunes pousses, croissance rapide et possibilité de floraison dans des photopériodes données. Cakile edentula produit des fruits dimorphiques distaux et proximaux. Les fruits distaux se détachent de la plante mère et se dispersent en de nouveaux sites, alors que les fruits proximaux demeurent avec la plante mère. L'espèce a un impact significatif sur la géomorphologie. Les plantes isolées ou en groupes accumulent le sable et apportent des matières organiques au sol, ce qui fournit un habitat plus amène à l'établissement de colonisateurs secondaires. Cakile edentula détient le plus haut pouvoir de germination à températures alternées (14,5 h à 20°C, 9,5 h à 10°C) dans la pénombre. La lumière altère le taux de germination, mais pas la germination totale, et une stratification est nécessaire aux fruits pour venir à bout de la dormance. Les plantes sont infectées de champignons et attaquées par des insectes phytophages et des vertébrés. L'espèce produit des glucosinoles qui la protègent de quelques parasites (insectes, champignons, vertébrés).—*Catherine Bressolier, Labo. Géomorphologie E.P.H.E., Montrouge, France.*

☐ RESUMEN ☐

Cakile edentula (Bigel.) Hook es una planta vivaz anual o facultativa (Brassicaceae) que crece como una pionera a lo largo de las orillas de los Grandes Lagos, las costas del Atlántico y Pacifico de América del Norte y las costas de Japón, las Azores, Nueva Zelanda y Australia. Presentamos un sumario de aspectos ecológicos, fisiológicos y geomorfológicos de la biologia de la Cakile edentula. Su éxito de implantación en las orillas puede atribuirse a la producción de un gran número de frutos, un corto ciclo de vida, alto potencial de dispersión de agua, resistencia a las salpicaduras salinas, alto nivel de enraizamiento de las semillas, rápido crecimiento y habilidad para florecer en un rango de fotoperiodos. La Cakile edentula produce frutos dimórficos; distantes y próximos del centro. Los frutos distantes del centro se separan del padre y se dispersan a nuevas localizaciones mientras que los próximos permanecen junto al padre. La especie juega un papel importante en la geomorfologia. Las plantas individuales o agrupadas acumulan arena y añaden materia orgánica a suelo, de tal forma que proporcionan habitats más adecuados para el establecimiento de colonizadores secundarios. La Cakile edentula muestra la más alta germinación para temperaturas alternantes entre 20° (14,5 hr) y 10°C (9,5 hr) en condiciones de oscuridad. La luz inhibe los niveles de germinación pero no la total germinación y los frutos requieren una estratificación para superar el letargo. Las plantas están plagadas de fungi y son consumidas por una gran variedad de insectos fitofangos y vertebrados. Las especies producen glucosinolatos que la protegen de algunos insectos, fungi, bacterias y vertebrados.—*Department of Water Sciences, University of Cantabria, Santander, Spain.*