Cakile maritima
Sea rocket
Brassicaceae

Cakile maritima is a prostrate or mound-forming to erect fleshy annual with obovate to spoon-shaped, petioled leaves. Fruits are 1.5 - 3 cm, the upper segments conic to cylindrical, with acute to blunt tips. Flowers are lavender or white. This species is found in beach dunes below 50m and is native to Europe. It is gradually replacing *C. edentula*, which is native to eastern North America (Rollins 1996).

Much of the ecological information available for *Cakile* in north America has resulted from interest in the observed ecological replacement of *Cakile edentula* with *Cakile maritima* on the western coasts of North America and Australia. In both cases *C. edentula* var. *edentula* was naturalized first, followed by *C. maritima* from Europe. Currently *C. maritima* is found within large areas of habitat formerly supporting both species (Boyd and Barbour 1993). Replacement of *Cakile edentula* with *Cakile maritima* has attracted attention for a number of reasons. First, it has been extremely well-documented (Barbour and Rodman 1970, Rodman 1974, Heyligers 1985), and there is no evidence that hybridization has occurred that might mask a true replacement event (Rodman 1974, 1986). Secondly, the fact that replacement occurs simultaneously on both continents argues against coincidence in favor of some underlying ecological mechanism (Rodman 1986). Finally, beach communities appear to be relatively open to invasion due to low plant density and high levels of disturbance (Breckon and Barbour 1974).

Several explanations for the observed replacement have been offered. Interference for pollinators (Barbour and Rodman 1970) is a possible mechanism - *Cakile maritima* has larger flowers - but *Cakile edentula* is capable of extensive self-fertilization. Direct interference is unlikely due to low plant densities but was investigated by Barbour (1970) and Barbour and Rodman (1970). A limited growth chamber study by Barbour (1970) showed that *Cakile edentula* outperformed *Cakile maritima* in mixture, so competition or allelopathy seem unlikely explanations. Rodman (1986) suggested that *Cakile edentula* is more r-selected and reproduces more rapidly than *Cakile maritima*, but that the latter outcompetes *Cakile edentula* by preempting limiting safe sites.

Indirect effects have also been considered. Baker (1986) suggested that a virus might be acting differentially on the two species, but little supporting data is available (Rodman 1986). Differential herbivory was considered by Barbour and Rodman (1970), and Boyd (1988) examined the preferences of three *Cakile* herbivores at Point Reyes, using growth chambers or artificial field tests. One herbivore, larvae of the moth *Platyprepia guttata*, preferred *Cakile maritima* but another, the deer mouse, *Peromyscus maniculatus* preferred *Cakile edentula* Boyd concluded that *P. maniculatus* might have accelerated the replacement but was not a major factor because *P. maniculatus* is found both within and outside the extinction zone of *Cakile edentula.*

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Boyd and Barbour (1993) conducted a field experiment to determine why *Cakile maritima* has replaced *Cakile edentula* in most of coastal California but not Oregon or Washington. They found that both species have seed banks persisting for at least 2 years in foredune sandune. No significant interference between the two species was detected in either the foredune or open beach habitat. In the foredune, it was experimentally determined that insect herbivory had no influence on survivorship, though rodent herbivory had a significant and similar effect on both species. Both *Cakile* species grew best in open beach habitat, where reproductive output per plant was similar for the two. *Cakile maritima* was found to have higher survivorship than *Cakile edentula* in the foredune, with enough more individuals surviving into a second reproductive year to produce an 18-fold difference in seed output into the surrounding habitat. The authors conclude that replacement of *Cakile edentula* by *Cakile maritima* is due to the latter's ability to better tolerate foredune conditions and survive into 2nd or 3d reproductive seasons. At more northerly latitudes (e.g. Oregon and Washington) plants may be forced into strictly annual habits by environmental conditions, facilitating coexistence (Boyd and Barbour 1993).

The effects of habitat and predation on the population biology of *Cakile maritima* on the west coast of North America have been investigated by Boyd (1991). Survival patterns of seedlings in adjacent open-beach and foredune habitats differed; open-beach plants were usually killed by winter storms. Approximately 5% of foredune plants survived into a second reproductive season, however, and these plants produced 85% of the seed in the foredune. *Peromyscus maniculatus* removed 95% of the seeds produced by foredune plants.San burial, which is much higher for open-beach plants tht foredune plants, enhanced the probability of escaping predation. Seeds cached by *P. maniculatus* had low survival rates relative to those not cached, so seed dispersal by *P. maniculatus* is not beneficial. While foredune plants produce sufficient seeds for replacement, predation by *P. maniculatus* reduced seed survival to less than 20% of the replacement rate (Boyd 1991).

Maun and Payne (1989) investigated the adaptive significance of fruit and seed dimorphism in *Cakile maritima* and two subspecies of *Cakile edentula*, *Cakile edentula* var. *edentula* and *Cakile edentula* var. *lacustris*. Dimorphic fruit segments were tested for differences in sizes of propagules, dispersal ability, germination behavior, and growth rate. Fruit dimorphism in *Cakile* consists of two morphologically distinct types of fruit segments, upper and lower. The upper fruit segments are deciduous, an adaptation for dispersal, while the lower segments remain attached to the parent plant. The presence of two morphs may contribute differentially to plant fitness because of differences in fruit and seed size, dispersability, germination, growth, and reproduction (Maun and Payne 1989). The mean mass per seed, fruit, and shell to seed mass ration of upper fruit segments of all three taxa were found to be significantly higher than the lower segments. The upper seeds of the two maritime species, *Cakile edentula* var. *edentula* and *Cakile maritima* were similar in mass, but the lower seeds of *Cakile edentula* var. *edentula* were significantly lighter than those of *Cakile maritima* The fruit mass was significantly higher in upper and lower segments of *Cakile maritima*than in either group of *Cakile edentula*

With respect to dispersal, the upper fruit segments of all three taxa did not differ significanly in floating ability from lower fruit segments. Compared with the two groups of *Cakile edentula*, fruits of *Cakile maritima* remained afloat for a long time; 50% of the fruit segments of *Cakile maritima* remained floating after 100 days, compared with 21 days for *Cakile edentula* var. *lacustris* and 15 days for *Cakile edentula* var. *edentula*. Larger upper seeds of *Cakile edentula* var. lacustris emerged from significantly deeper depths than smaller lower seeds; the authors suggest that sand accretion may be a strong selective force in the evolution of *Cakile* seeds. Morphological dimorphism in the fruits of *Cakile edentula* var. *lacustris* is linked with physiological dimorphism in that lower fruit segments germinate better over a wider range of temperatures than do upper segments. Light did not alter the final germinateion percentage of upper or lower fruit segments, but inhibited the rate of germination. The relative growth rate decreased in all three taxa with an increase in the age of a seedling, regardless of it's seed weight (Maun and Payne 1989).

Pakeman and Lee (1991a and b) evaluated environmental factors contributing to differences in the performance of *Cakile maritima* in strandline and foredune habitats. These authors found a marked difference in growth dependent upon their position of establishment. Large, rapidly growing plants are associated with sand containing macroalgal litter, whereas small stunted plants are found on foredunes above the limit of tidal innundation. Edaphic factors and plant nutrient concentrations were measured throughout the 1988 growing season at a site in Wales to determine possible causes for these differences. Pakeman and Lee found that the observed differences in performance were not associated with water or potassium availability, but that nitrogen availability was much higher in the strand habitat as compared with the foredunes, and the concentration of N in the leaves of plants growing in the strand environment was higher than that measured for foredune plants. The authors conclude that nitrogen differences account for the observed growth differences, probably by controlling photosynthetic rates. Phosphorus may also be important (Pakeman and Lee 1991 a and b).

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