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Biological flora of the British Isles: *Cakile maritima* Scop.

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Summary

1 This account reviews information on all aspects of the biology of *Cakile maritima* that are relevant to understanding its ecological characteristics and behaviour. The main topics are presented within the standard framework of the *Biological Flora of the British Isles*: distribution, habitat, communities, responses to biotic factors, responses to environment, structure and physiology, phenology, floral and seed characters, herbivores and disease, history and conservation.

2 *Cakile maritima* (sea rocket) is a succulent, annual species that is confined to maritime strandlines on sand or shingle, and associated foredunes. British material is ssp. *integrifolia* (= ssp. *maritima*), found around the Atlantic and Mediterranean coasts of Europe. *Cakile maritima* shows considerable variation, within and between subspecies, especially in fruit morphology and leaf shape. A very closely related species, *Cakile edentula*, is native to the east coast of North America. Both species have been introduced to Pacific North America and Australia.

3 Populations of *C. maritima* tend be ephemeral and shifting, depending on dispersal by tides and wind. The fruits are 2-segmented: the distal segments are readily detached and can float considerable distances in seawater; the proximal segments tend to shed their seed while attached to the maternal plant. Seeds require cold stratification and do not germinate at high salinity, or usually while retained in intact fruit segments. There is often a flush of germination in strandlines left by early season, equinoctial spring tides. *Cakile maritima* shows great phenotypic plasticity of form and reproductive output. Work on *C. edentula* suggests that abundance is regulated by a combination of density-dependent and density-independent processes. Landward dispersal of seeds from strandline populations may subsidise foredune populations, which themselves experience severe mortality from predators.

4 *Cakile maritima* is tolerant of salt spray and transient seawater inundation. Although beach and dune sand is a meagre source of macronutrients, *C. maritima* shows large growth responses to nitrogen addition and can exploit local nitrogen enrichment associated with mineralisation of organic detritus washed up on the strandline. Growth is stimulated by burial with blown sand and plants sometimes form the nuclei of early successional foredunes. The tissues are rich in glucosinolates; these may be responsible for the limited ranges of herbivores and fungal pathogens, and the absence of mycorrhiza.

Key-words: coastal distribution, communities, conservation, ecophysiology, genetic variation, germination, herbivory, parasites and diseases, phenotypic plasticity, reproductive biology, soils

Cakile maritima Scop. (Brassicaceae), the sea rocket. A glabrous, succulent annual herb. Tap-root to 40 cm, slender to stout, with extensive laterals. Stem prostrate or ascending, branched, 15–45 cm, succulent at first but becoming corky with age. Highly branched, decumbent stems in larger plants produce a bush-like form up to 1 m in diameter. Leaves alternate and fleshy; lower leaves 3–6 cm, narrowed into a stalk-like base, entire obovate or oblanceolate to deeply pinnately lobed. Leaf lobes oblong, distant, entire or distantly toothed. Upper leaves less lobed, or entire and sessile. Inflorescences are dense, many-flowered racemes, terminating the main stem and branches. Flowers up to 25 mm in diameter with 4 petals, strongly scented; petals clawed, white, lilac-coloured or purple, 6–10 mm, bearing long basal hairs, and twice as long as the sepals (3–7 mm). Sepals, petals and stamens are shed after pollination, leaving maturing fruits attached to the stem by alternate, thick pedicels (2–4 mm long). Distinctive fruits 20–25 mm, consisting of 2-jointed siliquas, green and fleshy when unripe, maturing to become brown, tough and corky. Upper (terminal) segment mitre-shaped, up to 15 mm, twice as long as lower (proximal) segment and terminating in a laterally compressed beak; it has two broadly triangular basal teeth that fit over the convex top of the lower segment. Lower segment to 11 mm long, tub-shaped, usually bearing two lateral projections just below the joint; sometimes infertile, then becoming small and stalk-like. One seed (occasionally 2, rarely 3) is produced by each segment. Early, independent dispersal of the upper fruit segment occurs when the transverse joint splits, the lower fruit segment remaining attached to the parent plant. Seeds yellow, brown, smooth. Seed mass *c.* 9 mg.

Cakile maritima is essentially a European species. British material is all referable to ssp. *integrifolia* (Hornem.) Hyl. ex Greuter & Burdet [= ssp. *maritima*] (Stace 1997). At least three other subspecies have been recognised, differing mainly in fruit and leaf shape: ssp. *baltica* (Jordan ex Rouy & Fouc.) Hylander ex P.W Ball, of the Baltic and south-east Norway; ssp. *aegyptiaca* (Willd.) Nyman, of the Mediterranean; and ssp. *euxina* (Pobed.) E.I. Nyárády, of the Black Sea (Fl. Eur. 1, edn 2). The ssp. *aegyptiaca* is extremely variable and doubtfully distinct from ssp. *integrifolia* (Ball 1964; Rodman 1974; Atl. Fl. Eur.). A very closely related species, *Cakile edentula* (Bigelow) Hooker, is native to the east coast of North America and the shores of the Great Lakes, in similar habitats (Maun *et al.* 1990). It differs mainly in not having projections on the lower fruit segment, its 4-angled upper fruit segments, shorter pedicels and smaller petals (Fl. Eur. 1, edn 2). Reports of *C. edentula* from the Hebrides (Allen 1952; Heslop Harrison 1952) are in error, although not known to be among Heslop Harrison's misrepresentations of the Hebridean flora (Pearman & Walker 2004). They may have led to misrecording of it from Britain. Plants from Iceland and arctic Europe have traditionally been referred to *C. edentula* ssp. *islandica* (Gand.)

A. & D. Löve, because they lack projections on the lower fruit segments. However, the frequent occurrence of intermediates between them and *C. maritima* ssp. *integrifolia* has led to them being treated as *C. maritima* ssp. *islandica* (Gand.) Hyl. ex Elven (see Atl. Fl. Eur.; Fl. Eur. 1, edn 2). This undermines the argument for retaining *C. edentula* as a distinct species. Furthermore, the two species are sympatric as introductions in parts of their ranges and, on beaches in southern Australia, they are no longer separable into morphologically distinct entities, apparently because of introgression (Cody & Cody 2004). Consequently, comparative information for *C. edentula* is provided in this account.

There is considerable variation, even within *C. maritima* ssp. *integrifolia*, which forms a virtual continuum with the other subspecies (Ball 1964). Much of this is likely to be due to phenotypic plasticity in growth form. Leaf shape frequently shows marked plasticity within individual plants and phenotypic variation between populations. Differences of leaf shape and petal colour observed within field populations suggest that some intrapopulation genetic heterogeneity exists. Evidence from plants grown in a common environment from seed collected at different locations has confirmed a morphological cline from types with entire leaves and unadorned fruit in the north, to types with pinnatifid leaves and more ornate fruits in south-east England (R. Scott, unpublished). This pattern parallels the trend on a larger scale across the subspecies around the coast of mainland Europe (see VI A; Ball 1964). Herbarium sheets indicate that single-seeded fruits are more frequent in ssp. *integrifolia* than in the other subspecies. Hebridean plants, although distinct in the field, became less so when raised collaterally from seed.

Native. A variable, annual species confined to maritime strandlines on sand or shingle and associated foredunes.

I. Geographical and altitudinal distribution

Cakile maritima occurs in suitable habitats all around the coast of the British Isles (Fig. 1). Local populations may be ephemeral and annually shifting but numbers are more consistent on foreshores fronting, or in the vicinity of, large dune systems. Similarly, *C. maritima* ssp. *integrifolia* is found from arctic Norway (69° N), all the way around the Atlantic, North Sea and Mediterranean coasts of Europe (Fig. 2). It is largely replaced by ssp. *baltica* in much of the Baltic area and entirely replaced by ssp. *euxina* on shores of the Black Sea. It shares part of its distribution in arctic Europe with ssp. *islandica* (Atl. Fl. Eur.), and in the Mediterranean region and south Portugal with the doubtfully distinct ssp. *aegyptiaca* (Fl. Eur.). *Cakile maritima* has been introduced to the coasts of Pacific North America (Barbour & Rodman 1970), Atlantic South America (Cordazzo 1994) and southern Australia (Rodman 1986), where it has formed extensive populations.

Cakile edentula ranges from North Carolina to Labrador on the Atlantic coast of North America and is
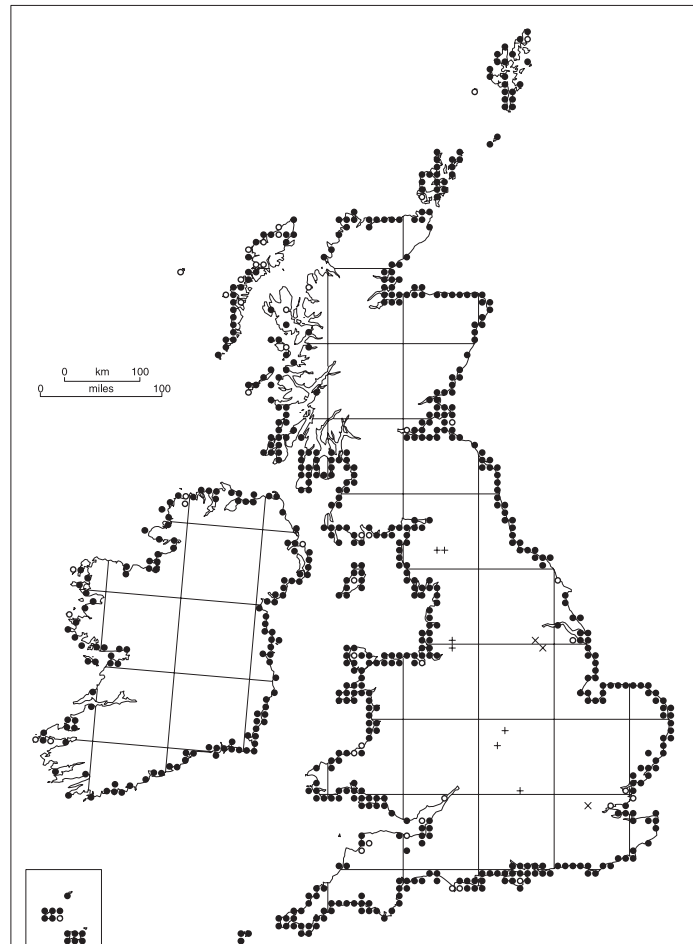
Fig. 1 The distribution of *Cakile maritima* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. Native (○) pre 1950, (●) 1950 onwards; introduced (×) pre 1950, (+) 1950 onwards. Mapped by H.R. Arnold, using Dr A. Morton's DMAP software, Biological Records Centre, Centre for Ecology and Hydrology, Monks Wood, mainly from data collected by members of the Botanical Society of the British Isles.

naturalised over a similar latitudinal range on the Pacific coast; its var. *lacustris* is abundant on the shores of the Great Lakes (except Lake Superior) and parts of the St. Lawrence River (Maun *et al.* 1990). *Cakile edentula* has also been introduced to south and east Australia (Rodman 1986).

Cakile maritima is always found close to sea level, at or above the level of the highest equinoctial spring tides. It has been recorded at up to *c.* 40 m above normal tide levels on very exposed sites (e.g. at Perranporth, Cornwall), where seeds have been carried to higher levels by wind.

II. Habitat

### (A) CLIMATIC AND TOPOGRAPHICAL LIMITATIONS

Cakile maritima shows no obvious climatic limitation in the British Isles, although there is a morphological cline with latitude (see above). On a larger scale, it tolerates climates ranging from arctic to Mediterranean, reflecting its latitudinal distribution. The buffering effect of the sea from extremes of temperature may allow some extension of its distribution. The effective length of the growing season is determined by different constraints in different parts of its range. On the meso- and macro-tidal British strandlines, the 6-month window in summer between equinoctial spring tides is important (Ignaciuk & Lee 1980); further north summer temperature is limiting, whereas in the microtidal Mediterranean summer drought tends to terminate a mild, winter growing season (Watkinson & Davy 1985).

Annual colonisation, through dispersal by tides and wind, is determined in part by local beach and dune topography. Once established, *C. maritima* may play a role in trapping blown sand, thus initiating foredune formation and dune succession, especially on prograding coasts.

(B) SUBSTRATUM

The sands and gravels inhabited by *Cakile maritima* represent a range of particle sizes but none tends to retain much water. Typically, foredune sands usually
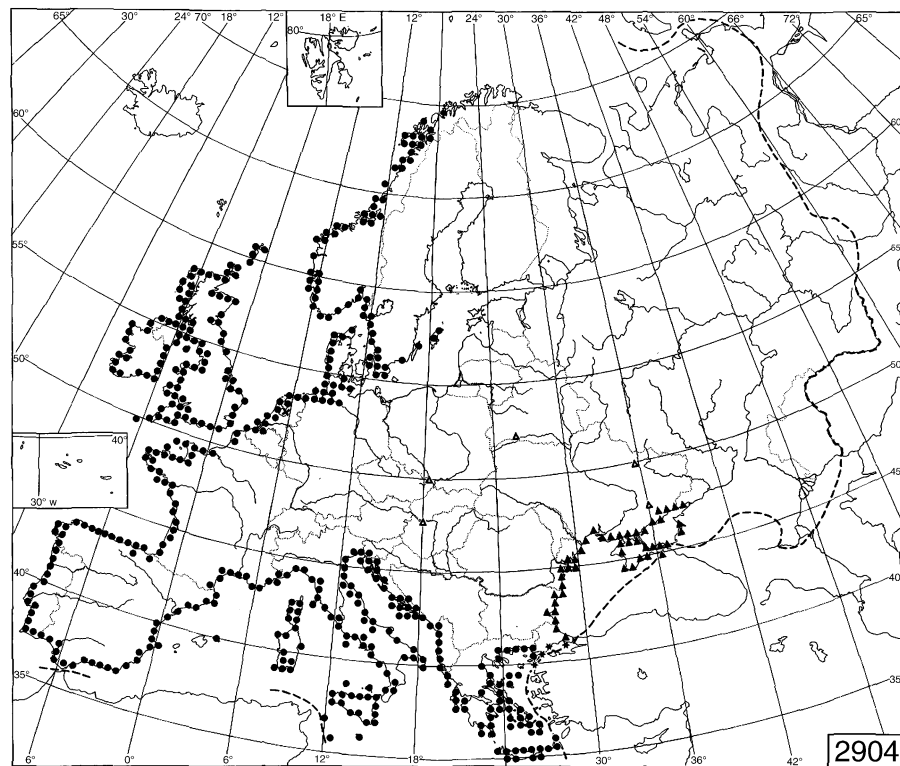
Fig. 2 The European distribution of *Cakile maritima* ssp. *integrifolia*, including ssp. *aegyptiaca* (●) and ssp. *euxina* (▲) on a 50-km square basis; subspecies unknown (★). The range of the *C. maritima* is extended in the Baltic by ssp. *baltica* and around the coasts of Iceland, Faeroe and the Arctic mainland by ssp. *islandica*. Reproduced from Atl. Fl. Eur. vol. 11, by permission of the Committee for the mapping of the Flora of Europe and Societas Biologica Fennica Vanamo.

have little organic matter content and generally very low macro-nutrient availability. Strandline sands may receive periodic inputs of organic matter, which usually decompose rapidly. Both substrates can be subject to varying amounts of seawater spray, which represents both a source of salinity and inorganic nutrients (van der Valk 1974; Rozema *et al*. 1982), and to occasional inundation with seawater. Leaching also tends to be rapid, because of the high porosity and good drainage, and the concentrations of many ions represent the balance between input from the sea and losses from leaching. Coastal sands are physically unstable, as they are continually disturbed and reworked by tides and the wind. Both loss of substrate by erosion and burial by sand accretion are frequent events. Permanently damp sand is seldom more than 10 cm below the surface (Salisbury 1952). Observations made over a whole growing season on dunes at Morfa Harlech, Wales, showed that the water content of the upper 30 cm of sand remained remarkably constant, mostly in the range 4–5% (Pakeman & Lee 1991a). Conditions experienced by *C. maritima* on the strandline and foredunes were rather different: the Na^+ concentration of the interstitial water was between 23 and 90 mM on the foredunes, whereas it exceeded 150 mM early and late in the growing season on the strandline; total nitrogen concentrations in the sand at 30 cm were significantly higher on the strandline (peaking at 150 µg g^{-1}), which reflects the higher organic matter content, but

total nitrogen declined during the growing season in both habitats (Pakeman & Lee 1991a). Local deposition of organic detritus, particularly seaweeds, along the strandline by equinoctial spring tides provides a pulse of mineral nitrogen as organic matter is decomposed, and this corresponds with a period of fastest growth in *Cakile* (Lee & Ignaciuk 1985). Roots of *C. maritima* often follow horizons of buried organic litter.

Beach and foredune sands are typically rich in calcium carbonate from shelly debris brought ashore by waves and onshore winds. Most contain at least 1% $CaCO_3$ and machair sands in Scotland can contain 70% or more (Gimingham *et al*. 1948; May 2003). However, 0.3% $CaCO_3$ represents sufficient buffering capacity to produce a calcareous system. *Cakile* also grows on more acidic sands.

III. Communities

Cakile maritima is characteristic of ephemeral strandline communities on sandy shores in many parts of the world (Doing 1985). These communities may represent the earliest stages of dune succession (Davy & Figueroa 1993) or, more commonly, they may be destroyed annually by equinoctial tides and winter storms. Strandline plant species tend to be sparsely distributed; they appear to be independent of each other and capable of growing alone or in association with any of the others. In Britain *Salsola kali* is the most frequently associated

species on strands fronting extensive mobile dunes, an important habitat for *C. maritima*. On stabilised foredunes, *C. maritima* occurs typically with *Honkenya peploides*, *Elytrigia juncea* and *Leymus arenarius* and, at higher elevations, *Eryngium maritimum* and *Ammophila arenaria*. *Cakile maritima* can also grow with *Suaeda vera*, *Elytrigia atherica*, *Atriplex portulacoides*, *Festuca rubra* and *Puccinellia maritima* on sandy soil at the upper tidal limit of saltmarsh. There it occurs above an abrupt vegetation boundary at the highest High Water Spring Tide (HWS) level, where the gradients can be steeper and the frequency of tidal inundation is much less than at lower levels.

Cakile maritima is often a component of a relatively species-diverse community found on strandlines composed of organic litter that has accumulated at the base of seawalls or against rocky outcrops. In this situation it often occurs with *Atriplex* spp., *Beta maritima* and *Rumex crispus*, and shingle species such as *Silene uniflora*, but its growth is usually poor compared with that on sandy strandlines.

Treatment of *C. maritima* in the National Vegetation Classification is limited to its occurrence in five strandline and sand-dune communities (Rodwell 2000). Its main representation is as a constant in the patchy strips of strandline vegetation classified as the *Honkenya peploides–Cakile maritima* strandline community (SD2). Apart from the constant, *H. peploides*, it is frequently accompanied by other strandline plants, especially *Atriplex prostrata* and *Elymus farctus* ssp. *borealiatlanticus* [*Elytrigia juncea* ssp. *boreoatlantica*]. In addition, *Ammophila arenaria*, *Atriplex glabriuscula*, *A. laciniata*, *Leymus arenarius*, *Matricaria maritima* and *Salsola kali* are represented at frequencies up to 40% (Rodwell 2000). Another 21 species are also recorded at low frequency. This community is considered to be the characteristic pioneer vegetation of sand and fine shingle on flat and gently sloping beach tops. Rarely (in north Norfolk), it may itself be a successional development of the *Rumex crispus–Glaucium flavum* shingle community (SD1).

Cakile maritima is found as a minority component of several other strandline and sand-dune communities. It achieves 21–40% frequency in the *Matricaria–Galium aparine* strandline community (SD3) and the *Elymus farctus* ssp. *Boreali–atlanticus* [*Elytrigia juncea* ssp. *boreoatlantica*] foredune community (SD4). *Cakile maritima* has a frequency of up to 20% in several further subcommunities: the *Leymus arenarius* mobile dune community (SD5) *Festuca rubra* subcommunity, and the *Ammophila arenaria* mobile dune community (SD6) *Elymus farctus* [*Elytrigia juncea*], Typical, *Festuca rubra* and *Poa pratensis* subcommunities (Rodwell 2000).

Continental European phytosociological classifications refer strandline communities to the class Cakiletea maritimae Tx. et Preising 1950, including halo-nitrophilous communities that are represented on all European coasts from the subarctic to Mediterranean regions (Westhoff & Schouten 1979). The more important taxa are listed as *Salsola kali*, *Cakile maritima*, *Suaeda maritima*, *Bassia hirsuta*, *Atriplex littoralis*, *A. prostrata*, *Matricaria maritima* ssp. *inodora*, *Suaeda vera* and *Lepidium latifolium*.

IV. Response to biotic factors

Cakile maritima exploits ephemeral sandy habitats and gaps in dune vegetation. It competes poorly with perennial dune grasses, particularly *Ammophila arenaria*, *Elytrigia juncea* and *Leymus arenarius*. Disturbances such as fire, trampling, excavation or wind erosion, which remove existing vegetation cover, provide opportunities for colonisation by *C. maritima*. It cannot survive heavy human trampling, such as on tourist beaches.

The local distribution of *C. maritima* on a Californian beach, specifically its absence from the vicinity of patches of *Ammophila arenaria*, was explained as predation of its fruits by the deer mouse (*Peromyscus maniculatus* (Wagner)), which nests in the *Ammophila* clumps and forages from them (Boyd 1988). This mouse removed 95% of fruits in the foredunes and, although some plants germinated from its buried caches, they represented only 0.002% of all seeds removed; hence there was no seed dispersal benefit to *C. maritima* (Boyd 1991). *Cakile edentula* showed compensatory growth responses to low or moderate intensities of defoliation in experiments designed to simulate herbivory (Gedge & Maun 1992). Plants placed in an unsprayed cabbage field were defoliated by insects within 11 days, confirming that they are potentially vulnerable in the field. Clipping and fruit removal to simulate deer browsing (Gedge & Maun 1994) resulted in delayed maturity and the diversion of resources to the production of new flowers and fruits. The production of glucosinolates (Section VI F) is likely to be a chemical defence against pathogens and predators.

On the Pacific coast of the USA, both *Cakile edentula* and *C. maritima* have become naturalised, in turn (Barbour & Rodman 1970). On the Californian coast, the latter has largely replaced the former but the two species coexist further north in Oregon and Washington. The replacement appears to be due to the superior reproductive output of *C. maritima* on the foredunes, where its appears to be better adapted and can survive into a second reproductive season; further north, a strictly annual life-cycle is enforced by the climate (Boyd & Barbour 1993). A similar sequence of colonisation and replacement has occurred in Australia (Rodman 1986).

V. Responses to the environment

(A) GREGARIOUSNESS

Localised sand and litter deposition combine with erratic dispersal to ensure that *Cakile maritima* has an aggregated and often ephemeral distribution. Locally, aggregations can occur around previous year's plants,

Table 1 The total population of *Cakile maritima* on the north Norfolk coast, UK, in September 1975

	Number of individuals	Fraction of population (%)	Habitat type
Holme	19	1.8	Stable foredune
Brancaster	32	3.0	Mobile foredune
Scolt Head	28	2.7	Stable foredune
Holkham West	747	71.0	Unstable sandy backshore
East Hills	86	8.2	Sand/shingle and stable foredune
Blakeney Point	140	13.3	Sand/shingle spits and embryo dune
Total	1052	100.0	

probably as a result of their longer retention of the lower fruit segments (see VIII C), until they are covered with sand. Barbour (1970b) recorded 90% of all seedlings arising within 1-m radius of parent clumps on Californian beaches. Even in the densest stands there is rarely 100% vegetation cover. The largest numbers occur in the dense stands on sites of recent strandline litter but the same location may not contain a similar number of plants in the following growth season. On the Norfolk, UK, coast (Table 1) there are relatively low numbers at stable sites and fluctuating high numbers in the intermittently stable dune strands. For example, the Holkham west population varied between 0 and 3000 individuals over a 5-year period, dependent on whether there had been accretion or loss of strandline during the winter months.

Periodic appearance and loss of large stands suggest that tidal transport is the major factor in population mobility. Dune succession and predation by animals may also restrict the ability of *C. maritima* to persist on the same site in successive years. However, on high energy shorelines, it is possible that the strandlines eroded in equinoctial tides during the winter will be replaced by spring deposition and that predation and competition from rooted perennials will be reduced. On sites of dune deposition, the progradation of the shoreline will continually renew the strandline in the direction of build up of the dune system.

(B) PERFORMANCE IN VARIOUS HABITATS

Individual plant size is highly variable, depending on conditions of growth. There is also great plasticity in form of leaves and fruits. An individual about 50-cm tall × 70-cm diameter was taken from a patch of vigorous, well-spaced plants at Holkham, Norfolk. It had 1447 upper fruits (less than the total number produced, as some had already fallen), 313 lower fruits, and a total dry weight for the above-ground portions of 100 g, of which the fruits accounted for 41%. Flowering also occurs in very small plants, but seed set rate and seed size are reduced, and in extreme cases no seed is produced. Growth is much reduced under conditions of extreme nutrient paucity, excess soil water, or lack of space.

The population dynamics of *C. edentula* have been examined in some detail. In Nova Scotia, Candada, its abundance varied along an environmental gradient from the sea across a dune system, rising to a maximum near the centre of its distribution, although survivorship and reproductive output declined to landward (Keddy 1981) as a result of both density-dependent and density-independent processes. Large fecund plants at the seaward edge showed density-dependent reproductive output and plants at the landward end showed density-dependent survivorship. At the landward end, mortality was balanced by an influx of seeds carried by onshore winds from the seaward end, and the species' landward limit was determined by this dispersal (Keddy 1982). Population modelling can explain the pattern of distribution and shows that without this migration populations would not persist in those areas where the species is actually most abundant (Watkinson 1985). A similar pattern of distribution and population dynamics has been reported for *C. edentula* var. *lacustris* on the shore and dunes of Lake Huron (Payne & Maun 1984).

A population study of *C. edentula* in an environmental mosaic on a shingle bar in Nova Scotia, Canada, showed marked differences in performance between populations growing on open shingle and mats of dead *Zostera* wrack; survivorship and reproductive output were greater on the shingle but caterpillar grazing in late summer resulted in net reproductive output being greater on the wrack (Keddy 1980).

(C) EFFECT OF FROST, DROUGHT, ETC.

In outdoor cultivation at Norwich, pregerminated plants of *Cakile maritima* grew slowly but showed no direct visible damage under normal winter conditions. Germination in the field occurs as early as March when frost is still frequent, and seedlings appear to be unaffected. Drought by itself apparently is not harmful to the species in the British Isles.

VI. Structure and physiology

(A) MORPHOLOGY

Small plants are upright in habit but lengthening of stems eventually leads to sprawling; side branches ascend vertically to 50 cm from the axils of the alternately borne leaves. The horizontal stems spread to
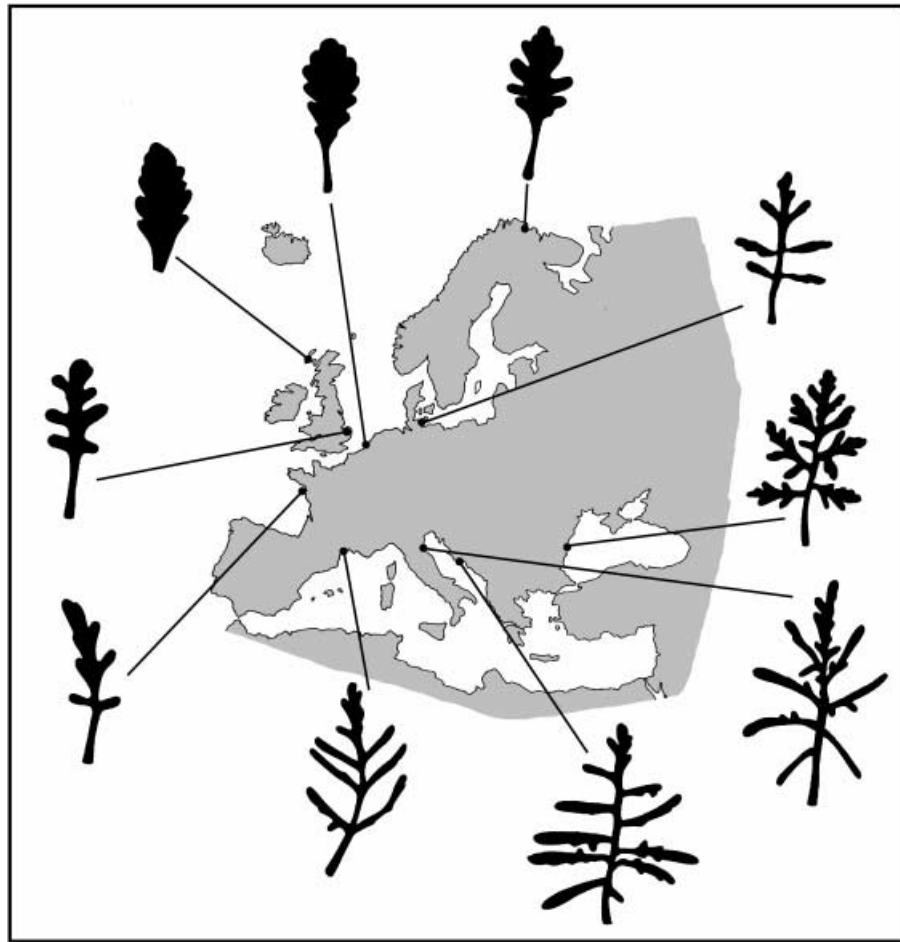
Fig. 3 Variation in the leaf shape of *Cakile maritima* originating from around the coasts of Europe. Outlines are characteristic leaves from plants under collateral cultivation in a glasshouse at Colney, Norwich, Norfolk, UK (data of R. Scott). This range includes plants referable to several subspecies: Britain, the Netherlands and France, ssp. *integrifolia*; Mediterannean, ssp. *aegyptiaca*; Black Sea, ssp. *euxina*; Baltic, uncertain but possibly ssp. *baltica*; arctic Norway, ssp. *islandica*.

give a symmetrical clump with radiating branches. A detailed description and interpretation of the morphology of *C. maritima* are given by Wright (1927). The more or less glaucous leaves tend to be oblong with a deeply serrated outline and tapering towards the base. When they are young the margin is entire except for notches flanking the apex. However, leaf shape is variable, becoming more pinnatifid towards the south and east of Europe (Fig. 3; Ball 1964); this parallels a cline of increasing leaf dissection seen in *Geranium sanguineum* (Lewis 1969) and may reflect selection for favourable thermal balance, with less transpiration, under higher irradiance during hotter, drier summers. Leaves produced early, or under adverse environmental conditions, tend to remain less pinnatifid. Although the leaves are succulent, they have thin cuticles and their epidermal cells are not regular in size, with a small fraction of slightly projecting cells 4–5 times the size of the others (Wright 1927). There are more stomata on the abaxial (96 mm^{-2}) than on the adaxial (64 mm^{-2}) surface. They are typically Cruciferous, with three subsidiary cells of which one is smaller than the other two. The mesophyll is all chlorophyllous and undifferentiated

but becomes more spongiose towards the periphery. North American *C. maritima* has been depicted with palisade layers two deep below both surfaces (Harshberger 1908). The leaf trace consists of three meristeles which leave the stem stele at a distance of two bundles apart (Wright 1927). They each pass along the leaf and end in a hydathode. There is thus one hydathode at the leaf apex and one at each of the two flanking teeth. The meristeles produce branches singly, on alternate sides, forming a reticulum.

Leaf protoplasts (20–50 m diameter) showing large vacuoles with peripheral cytoplasm and chloroplasts have been isolated successfully (2.31 × 10^6 g^{-1} fresh material) from field-grown material (Balestri *et al*. 2001).

The stems are green and succulent, with a low density of stomata (36 mm^{-2}). The epidermal cells are strongly thickened and include giant cells, as in the leaf. The chlorophyllous tissue consists of isodiametric cells, three cells deep, with large intercellular spaces. There is an inner cortex of thin-walled parenchyma and a vascular cylinder of open collateral bundles, enclosing a large, parenchymatous pith. Secondary thickening of the lower stems gives rise to a corky appearance.

The branching roots have a diarch central stele and a pericycle of thin-walled cells two cells deep. Secondary thickening is initiated very early in the roots, the stelar cambium becoming active only slightly ahead of the cork cambium, which is derived from the pericycle. Even after secondary growth has been established, the roots may remain narrow (180–200 μm) as a result of early decortification (Wright 1927). All parts of the plant contain special secretory cells containing myrosinase (see Section VI F).

Developing seeds have a pale green hyaline testa which suberizes on ripening and becomes orange to brown in colour. The apparent genetic variation which exists in fruit shape may be related to different dispersal mechanisms, as plants from the north and west part of the range have barrel-shaped fruits virtually lacking the distinct lateral appendages seen in the southern populations.

(B) MYCORRHIZA

Cakile maritima has no definitely known mycorrhizal associations, although Harley & Harley (1987) record one doubtful report of an arbuscular mycorrhiza, along with multiple reports of its absence. The lack of mycorrhiza may be related to the presence of glucosinolates within the tissues (see VI F).

(C) PERENNATION: REPRODUCTION

Cakile maritima is strictly annual in the British Isles and is wholly dependent on seed for survival. The usual life-span of plants in the field is 4–5 months. Perennation is reported from California, USA (Rodman 1974), and glasshouse-grown plants have survived for over 1 year through repeated production of new stems from axillary buds (facultative perennation).

(D) CHROMOSOMES

Cakile maritima appears to be uniformly $2n = 18$ and counts on plants from the Isles of Harris and Lewis have all confirmed that number. However, these neither support nor contradict erroneous reports of Hebridean *C. edentula* plants (Allen 1952; Heslop Harrison 1952), because a report of $2n = 36$ on apparently convincing meiotic cells for *C. edentula* (Löve & Löve 1947) has been discounted by Rodman (1974), who states that the chromosome numbers of *C. edentula* and *C. maritima* are identical.

(E) PHYSIOLOGICAL DATA

Photosynthesis

Assimilation of CO_2 in *Cakile* is normally by the C_3 pathway. Photosynthetic rates in the field (Pakeman & Lee 1991b) generally followed the diurnal pattern of photon flux density (PAR). CO_2-uptake rates in plants on a strandline (peaking at *c.* 28 μmol m^{-2} s^{-1}) were significantly higher than in those on foredunes (peaking at

c. 20 μmol m^{-2} s^{-1}); however, if rates were expressed as photosynthetic nitrogen-use efficiency, there was no difference, reflecting the higher nitrogen concentrations in strandline plants. Plants from California achieved a net CO_2 exchange rate of *c.* 37 μmol m^{-2} s^{-1} at an optimal temperature of 25 °C under growth-cabinet conditions (De Jong 1978). Light saturation was at a PAR of 1000–1200 μmol m^{-2} s^{-1}. However, work in Israel, on material of unspecified origin, showed that phosphoenolpyruvate (PEP) carboxylase activity was increased by 30% after culture under saline conditions (100 mm NaCl), and activity was stimulated by up to 200 mm NaCl in the reaction mixture irrespective of prior salt treatment (Beer *et al.* 1975). Diallo & Queiroz-Claret (1983) subsequently reported increased PEP carboxylase capacity and malate production during the night after 18–21 days' growth on a saline medium (50 mm NaCl), suggesting the induction of CAM by salinity. Absence of net $^{14}CO_2$ incorporation into malate indicated that PEP carboxylase might be fixing mainly endogenous (respiratory) CO_2.

Water relations

At a cool, relatively wet site in northern California, xylem water potentials at dawn (measured with a Scholander pressure bomb) were fairly consistent in *C. maritima* at *c.* −0.5 MPa throughout an annual cycle, although mid-day values in summer dropped to *c.* −1.5 MPa; on a warmer drier, more southerly beach, dawn values ranged from *c.* −0.5 MPa in winter to *c.* −2 MPa in late summer, but reaching mid-day values lower than −2.5 MPa then (De Jong 1979). Neither salinity nor water-table depth in the sand varied greatly during the year and, although the sand dried out superficially in rainless periods, it remained moist at about 1-m depth. Populations of *C. edentula* in North Carolina experienced lower sand water potentials in the foredunes than on the beach and this resulted in correspondingly lower leaf water potentials and stomatal conductances (Tyndall *et al.* 1986). *C. maritima* is not tolerant of waterlogging.

Salt tolerance

Cakile maritima is tolerant of salt spray and transient seawater inundation, slightly more so than *C. edentula* where they grow together in California, and both of these tolerances were correlated with position in the beach zonation of 12 species (Barbour & De Jong 1977). Rozema *et al.* (1982) reported that NaCl (supplied at 150–300 mm) absorbed via the root system reduced growth significantly in *C. maritima* but it was resistant to airborne salinity. There was foliar uptake of Na$^+$, K$^+$, Cl$^-$, Ca^{2+} and Mg^{2+} ions. The Na$^+$ and Cl$^-$ ions absorbed from seawater droplets induced succulence. Shoot tissues contained appreciable concentrations of methylated quaternary ammonium compounds that were not affected by the salt treatments and therefore presumably not contributing to any osmoregulation. A

laboratory experiment with British material showed salt stimulation of growth, with maximal growth (dry mass) at 50 mM NaCl (Lee & Ignaciuk 1985). Vegetative growth of plants from Tunisian populations was stimulated by NaCl concentrations in the range 50–100 mM and plants were able to grow at up to 500 mM; concentrations up to 400 mM increased succulence of the leaves and large amounts of Na^+ were transported to the leaves (Debez *et al*. 2004). In contrast, Rozema *et al*. (1983) found that growth in *C. maritima* was strongly reduced by 60 mM NaCl in the rooting medium. Boyd & Barbour (1986) detected difference in salt tolerance between inland (var. *lacustris*) and coastal forms of *C. edentula*: in particular, the latter showed significant stimulation of seedling root elongation at 0.1% sea salt concentration and the former was progressively stunted by salt-spray treatments of up to 9 g m^2 day^{-1}. Nitrate reductase activities induced in leaves and roots of *C. maritima* by 3 months' cultivation with Hoagland nutrient solution were decreased to only 3–8% of their control values when 16 or 32 g L^{-1} of NaCl (corresponding with approximately half- and full-strength sea water, respectively) were included in the nutrient solution, even though the tissue NO_3^- concentrations were maintained (Garcia Novo 1976).

Inorganic nutrition

Although beach and dune sand is generally a very meagre source of macronutrients, *C. maritima* can be regarded as a nitrophile. In nutrient addition experiments on dune sand, it showed a large growth response that was primarily due to nitrogen (Lee *et al*. 1983) with little additional response to phosphorus or potassium. This agrees with the high nitrate reductase activities that could be induced in its tissues (e.g. 183 and 154 mM NO_2^- h^{-1} g^{-1} dry mass, in shoot and root, respectively); only about 1–2% of these activities were realized in the field on the beach and embryo dunes at Tentsmuir Point, Scotland (Garcia Novo 1976). *Cakile maritima* is a potentially fast growing plant that can exploit local nitrogen enrichment associated with mineralisation of organic detritus washed up on the strandline (Lee & Ignaciuk 1985). The greater nitrogen supply in the strandline is reflected in the fact that plants there maintained a total leaf nitrogen concentration at *c.* 4% for most of the growing season, whereas it dropped progressively from that initially high value (associated with seed reserves) to *c.* 1.3% on the foredunes (Pakeman & Lee 1991a). Furthermore the foredune plants allocated a higher fraction of their nitrogen to stress metabolites. An experimental investigation of the complex interactions between soil nutrients, water stress and sand burial on various aspects of performance of *C. edentula* indicated that nutrient supply was the most important factor influencing plant traits (Zhang 1996). High nutrient availability enhanced the photosynthetic capacity of water-stressed plants and increased the biomass allocation to their root systems.

Response to burial with sand

Partial burial by blown sand is usually beneficial to *C. maritima* plants, which sometimes form the nuclei of mini-dunes. Adventitious rooting does not occur, but burial acts as a stimulus to the production of new vertical branches from the axils of prostrate stems, thereby increasing the number of flowering shoots. *Cakile maritima* responds to sand accretion with increased stem elongation and can withstand accretion rates of 5 cm $week^{-1}$ (Rozema *et al*. 1985). (Lee & Ignaciuk 1985) reported growth stimulation in a sand accretion experiment, with maximal dry mass attained under 4 mm $week^{-1}$ accretion. Partial burial with sand promoted biomass allocation to the root systems of water-stressed plants of *C. edentula* (Zhang 1996).

(F) BIOCHEMICAL DATA

Wright (1927) first noted the presence of myrosinase (in specialised 'myrosin' cells) and its substrate sinigrin, mustard oil (in ordinary parenchyma cells) in *C. maritima*. Subsequently, 16 different glucosinolates (mustard oil glucosides) deriving from three major biosynthetic pathways have been identified in *Cakile* species (Rodman 1976). The predominant forms in collections from northern and Atlantic Europe are isopropylglucosinolate, allylglucosinolate and *s*-butylglucosinolate. Hydrolysis of these glucosinolates by myrosinase, as a result of tissue damage, releases corresponding strongly smelling, volatile isothiocyanates. The distribution of glucosinolates in populations has provided valuable evidence for taxonomic (Rodman 1972, 1974, 1976) and phylogeographical (Rodman 1976, 1980, 1986) studies in *Cakile*.

In common with other crucifers, *C. maritima* contains appreciable quantities of phenolic choline esters (Bouchereau *et al*. 1991). Nine compounds were differentiated but 45% of the total of 20.6 μmol g^{-1} dry mass in seeds was in the form of sinapine (3,5-dimethoxy-4-hydroxycinnamoylcholine). Two unidentified compounds were distinctive to *C. maritima* in a comparison of 28 cruciferous taxa. In addition, four flavonol glycosides have been identified in the flowering shoots of *C. maritima* (kaempferol 7-*O*-rhamnoside, kaempferol 4′-*O*-glucoside, kaempferol 3 -*O*-glucoside 7-*O*-rhamnoside and quercetol 7-*O*-rhamnoside) and phenolic acids belonging to the benzoic and cinnamic series (*p*-hydroxybenzoic, vanillic, protocatechic, syringic, ferulic, isoferulic, *p*-coumaric, caffeic and sinapic acids) have been found in the shoots (Dauguet *et al*. 1985).

The elemental composition of leaves, fruits and seeds of *C. maritima* is given by Hocking (1982).

VII. Phenology

Sporadic germination in Britain begins before March but the main flush of germination and seedling emergence usually starts in April. Seedlings can be found well into the summer. On strandlines in North Wales,

Table 2 Insects recorded as visiting flowers of *Cakile maritima* in north-west Europe (from Knuth, Poll. 2)

Coleoptera	**Hymenoptera**
Anoncodes melanura L.	*Apis mellifera* L.
Coccinella septempunctata L.	*Bombus lapidarius* (L.)
Meligethes aeneus F.	*Bombus lucorum* (L.)
Phyllopertha horticola L.	*Bombus ruderatus* (F.)
Psilothrix cyaneus Ol.	*Bombus terrestris* (L.)
	Chrysis ignita (L.)
	Halictus calceatum Scop.
Diptera	*Pompilus chalybeatus* Schjödte
Aricia albolineata Fall.	*Pompilus cinereus* (F.)
Bombylius canescens Löw.	*Psithyrus rupestris* (F.)
Calliphora vomitoria (L.)	*Psithyrus vestalis* (Fourcr.)
Dasysyrphus venustus (Mg.)	*Tiphia femorata* F.
Eristalis arbustorum (L.)	
Eristalis intricarius (L.)	
Eristalis pertinax (Scop.)	**Lepidoptera**
Eristalis tenax (L.)	*Aglais urticae* (L.)
Melangyna umbellatarum F.	*Aphantopus hyperantus* (L.)
Melinda sepulcralis (Mg.)	*Autographa gamma* (L.)
Musca domestica L.	*Maniola janira* (L.)
Platycheirus podagratus (Zett.)	*Pieris brassicae* (L.)
Rhingia campestris Mg.	*Pieris napi* (L.)
Scaeva pyrastri (L.)	*Pieris rapae* (L.)
Scathophaga stercoraria (L.)	*Zygaena filipendulae* (L.)
Syritta pipiens (L.)	
Tropidia milesiformis (Fall.)	

germination was first observed in the last week of April, some 4 weeks after the equinoctial spring tides, with the main germination period extending into May (Ignaciuk & Lee 1980). Plants usually begin to flower about a month after emergence, but this can be delayed by cold, wet weather. There is no specific stimulus for floral initiation, but warm weather speeds development of heads. The progressive maturation of seed heads ensures that some fruits are ripe if the plant is disturbed before becoming fully mature. On strandlines, the growing season tends to be truncated by equinoctial spring tides or storms in late September. At protected sites, plants may grow and set seed into early winter.

In Mediterranean climates, germination is mainly in autumn, after the dry season. In California, most growth was in winter and spring at a southern site, whereas most growth was in spring and summer at a more northerly location (De Jong 1979). On the coast of southern Brazil, it is possible to find new seedlings throughout the year after episodes of rainfall; flowers and fruits may also be found at almost any time of the year but the peak of their production is in late summer and autumn (Cordazzo 1994).

VIII. Floral and seed characters

(A) FLORAL BIOLOGY

Cakile maritima is mainly outbreeding and insect-pollinated but low rates of selfing have been recorded (Rodman 1974) from North America. In contrast, *C. edentula* is principally inbreeding, with a low incidence

of cross pollination, and has smaller petals and nectaries (Rodman 1974; Maun *et al.* 1990). Nevertheless, substantial inbreeding depression has been measured in *C. edentula* var. *lacustris* (Donohue 1998a). *Cakile maritima* exhibits S-locus gametophytic self-incompatibility and the same mechanism has been implicated in interspecific, unilateral incompatibility with other members of the Brassicaceae (Hiscock & Dickinson 1993). Hence, bagged heads of British *C. maritima* remain sterile. When four plants were grown in isolated inland localities, an individual at Colney, Norfolk, *c.* 1 km from its nearest pollen source produced some seed. In the highly linear field habitat such a distance would not provide an effective barrier to pollen flow. *Cakile maritima* is visited by a variety of bees, hover-flies, butterflies and beetles that are attracted by its scented flowers and copious nectar production (Table 2; Knuth, Poll. 2). As in the Brassicaceae generally, there are six stamens, two outer transverse ones with short filaments and two inner pairs with long filaments. Two lateral, horizontally compressed nectaries are subtended by the outer unpaired stamens, and a median conical or pyramidal nectary subtends each of the pairs of stamens (Hildebrand 1879; Rodman 1974). The flowers can be half full of nectar, in a cup comprising the erect sepals and petal claws (Knuth, Poll. 2). The petals have a low ultra-violet reflectance (i.e. appear dark in the near-UV part of the spectrum perceived by insects) and this reflectance is lower in white-flowered forms than in violet-flowered ones (Horowitz & Cohen 1972). Pollen grains are spheroidal (*c.* $35 \times 32\ \mu m$), tricolpate and have a reticulate surface, with an oily coating (Rodman 1974).

Flowering can be protracted, as a result of continued raceme elongation and the production of new inflorescence shoots from axils. Maturation is from the base upwards, with proximal fruits ripening first.

(B) HYBRIDS

Rodman (1974) succeeded in crossing *C. maritima* with *C. edentula*, and apparent hybrids have been found among the progeny in an artificially established mixed stand of the species in California (Maun *et al.* 1990). A few putative hybrids have also been found in British Columbia, Canada, but extensive introgression between the two species has apparently occurred in southern Australia (Cody & Cody 2004).

(C) SEED PRODUCTION AND DISPERSAL

The bicarpellary ovary is initially unilocular and composed of two elongated lateral carpels separated by anterior and posterior linear placentas. These placental zones have been interpreted as highly reduced median carpels (Wright 1927) each bearing two ovules. After fertilization a thin, elongated, membranous septum forms in the posterior–anterior plane with all four ovules on one side of it. Whilst each median placenta

initiates two ovule primordia, the left posterior one aborts at an early stage, leaving three to develop into campylotropous ovules. The right posterior and the left anterior turn upwards, whereas the right anterior turns downwards. Subsequently, the left anterior is crushed and destroyed by mechanical pressure during development. In about 5% of cases the right anterior ovule does not develop, probably because of lack of fertilisation as its micropyle is furthest from the stigma; in this case the left anterior ovule is allowed space to develop and, either way, the number of seeds produced per fruit is typically two (Wright 1927). Less commonly, all three seeds may survive or abortion may reduce their number to one. Meristem growth in the two sterile (lateral) carpels leads to the separation of the fruit into basal and terminal segments by a corky layer. At maturity the fruit fragments, allowing the terminal segment to be dispersed before dehiscence, whereas the basal segment remains attached to the senescing parent until dehiscence.

A plant of above average size has been recorded as having 5628 fruits (Rep. Capac.) with potentially *c.* 10 000 seeds. On southern Brazilian coastal dunes (Cordazzo 1994) the average fruit production was 1056 235 SE (range 15–3561, *n* = 25). Reproductive output depends on both density-dependent and density-independent factors (see IV A). Although fruit segments are typically one-seeded, Cordazzo (1994) recorded 8% of upper (distal) segments and 20% of lower (proximal) segments with two seeds; 11.4% of lower and 9.3% of upper segments were abortive, and 0.8% of lower segments had more than two seeds. Hawke & Maun (1989) suggested that the abortion of seeds in *Cakile edentula* may be of adaptive significance in maintaining seed mass, in a trade-off between seed mass and number, when resources are limiting. Cold, wet weather can result in the production of abortive fruits, presumably because of a reduction in insect pollinator activity. Seed mass varies considerably between populations in different parts of the world (Table 3); upper seeds are heavier on average than lower ones, although their ranges usually overlap. The relatively large seed size is probably a selective response to burial with coastal sand or shingle (Salisbury 1974; Davy *et al.* 2001).

Dispersal can be by water (tides and sea currents) or more locally by wind. The easily detached upper fruit segments are more suited to dispersal over long distances and thus the exploitation of new habitats, perhaps escaping from the density-dependent effects of predators and local resource limitation; the lower-fruit segments that are retained by the maternal plants are more likely to disperse their seeds locally and exploit a proven habitat. However, remains of whole plants with only lower fruit segments left can be deposited at new sites by the autumn equinoctial tides. *Cakile edentula* var. *lacustris* has been used in a series of detailed evolutionary studies of dispersal. An experiment to distinguish between the effects of density and dispersal distance on fitness showed that high density caused earlier mortality and lower probability of reproduction at the local scale but dispersal distance did not have any influence on them. Lifespan was longer at 0.5 km from the home site (Donohue 1997). Dispersal of progeny is strongly determined by maternal traits and varies with the maternal environment (Donohue 1998b) such that there were positive phenotypic correlations between maternal and progeny generations for some traits and negative ones for others. Consequently, a response that increased progeny fitness by increasing dispersal was often associated with reduced maternal fitness, an association that would greatly reduce the overall selective advantage of dispersal (Donohue 1999).

Fruit segments can remain buoyant in seawater for long periods because of spongy tissues in their corky pericarps (Guppy 1917; Disp. Pl.). Agitation of the water prolonged flotation in buoyancy experiments with *C. edentula* var. *lacustris* (Payne & Maun 1981). The buoyancy of upper and lower fruit segments of Brazilian *C. maritima* after 70 days in agitated seawater was 60% and 58%, respectively (Cordazzo 1994). In contrast, only 4% of upper fruits of British material remained buoyant after 30 days' immersion in an agitated 600 mm NaCl solution (Ignaciuk & Lee 1980).

Table 3 Mean individual mass (mg) of seeds in upper and lower fruit segments of *Cakile maritima* reported from populations in different parts of the world

Upper fruit segment	Lower fruit segment	Location	Reference
7.4	7.2	Norfolk, UK, 1970	Unpublished data, R. Scott
10.3	9.0	Norfolk, UK, 1972	Unpublished data, R. Scott
13.0	4.5	England	Guppy (1917)
9.3	8.5	Baltic coast	Becker (1912)
9.7	8.5	Central Europe	Repr. Cap.
4.3	2.4	Atlantic France	Binet (1961)
8.3	6.6	S.W. Spain	Cordazzo (1994)
8.2	6.0	California, USA	Barbour (1970a)
8.0	6.2	California, USA	Maun & Payne (1989)
8.4	6.5	Pacific coast USA	Rodman (1974)
4.3	3.9	Southern Brazil	Cordazzo (1994)
11.9	11.0	Australia	Hocking (1982)

Germination is inhibited by salinity but a fraction of seeds remain viable after long exposure to seawater. The efficiency of dispersal was illustrated on Surtsey, a new island that arose south-east of Iceland from a volcanic eruption that started in November 1963. *Cakile maritima* ssp. *arctica* (= *C. edentula* ssp. *arctica*) was the first vascular plant colonist on its sandy shores, seen growing as early as 1965, even though the nearest sources of fruits were 20–40 km away across the sea (Fridriksson 1987).

At sites not subject to disturbance by tides, most seeds initially fall close to the parent plant and as the upper fruit portions are deciduous the majority of later-falling seed is derived from lower segments. On Brazilian foredunes seedlings appeared within 3 m of mother plants, dispersed mainly in the direction of the dominant wind (Cordazzo 1994). Seedlings of *C. maritima* were found emerging from emu droppings in Australia and so dispersal by birds may occur exceptionally (Heyligers 1984).

(D) VIABILITY OF SEEDS: GERMINATION

Seeds of *Cakile maritima* from upper (terminal) fruit segments exhibit dormancy that can be relieved by prolonged cold stratification (Binet 1961) or treatment with 3 mM gibberellic acid (Ignaciuk & Lee 1980). Dormancy can be partially removed by treatment at high constant temperature (30 °C) or diurnally alternating temperatures (Ignaciuk & Lee 1980). There is evidence that the mechanical properties of pericarp and testa are involved in dormancy, as removal of the embyro from mature or unripe seeds results in growth and no evidence of inhibitory substances has been found (Binet 1961). In the field, upper fruits do not germinate while retained within intact fruit segments, whereas 15–19% lower fruits germinated from sown fruit segments (Barbour 1970b). Studies with *C. edentula* suggest that apparent faster germination of lower seeds is an effect of mass rather than fruit position, as smaller seeds germinate faster and the lower ones tend to be smaller (Zhang 1993).

There was virtually complete germination of GA$_3$-treated seed of British *C. maritima* populations in the temperature range 10–30 °C, but germination was significantly reduced at 5 °C (Ignaciuk & Lee 1980). Barbour (1970a) reported a temperature optimum of *c*. 26 °C for seeds from upper and lower fruit segments of a Californian population. In comparison, a Brazilian population showed a sharp germination peak, which was almost identical in upper and lower seeds, at 20 °C on a gradient of constant temperature (Cordazzo 1994); however, alternating temperatures of 15/20 and 20/30 also yielded very high germination rates. Diurnal alternation of temperature is attenuated rapidly with depth in sand and may therefore provide a signal that seeds are not buried beyond their capacity to emerge.

Overall germination and velocity of germination are progressively inhibited by salinity. At the optimum temperature of 20 °C (in British material), 60 mM NaCl had little effect on GA$_3$-treated seed but the temperature range for germination was substantially narrowed by salinity; there was almost no germination at 600 mM NaCl (Ignaciuk & Lee 1980). Seeds returned to optimal germination conditions after immersion for up to 30 days in 600 mM NaCl showed significant reductions in germinability, suggesting that irreversible salt toxicity was involved rather than just osmotic inhibition. However, immersion of the upper fruits in seawater may weaken them and actually promote subsequent germination (Barbour 1972). There was no inhibition of germination in seeds from upper and lower fruit segments of a Californian population up to 17 mM (0.1%) but substantial effects at 171 mM (1.0%) NaCl and higher concentrations (Barbour 1970a). A concentration as low as 45 mM NaCl reduced the germination of upper seeds of a Brazilian population (Cordazzo 1994) and they showed very poor germination at 215 mM. It has been suggested that the concentrations of salts that can be accumulated in the pericarps would be sufficient to enforce dormancy of both upper and lower fruit-segment seeds (Hocking 1982). The inability to germinate in seawater is likely to be important for long-distance dispersal (Rodman 1974) and the leaching of salt from the fruits may be important in determining the timing of germination (Hocking 1982). There is evidence of light inhibition of germination in Californian (Barbour 1970a) and Mediterranean populations (Thanos *et al*. 1991), at least. Exposure to light also delays the germination of upper and lower seeds of *C. edentula* var. *lacustris* (Maun & Payne 1989).

Most seeds that are successful in contributing to the next generation will have become buried in sand, which in Britain remains sufficiently damp in winter for seeds to be in a fully imbibed state. Rising temperatures and leaching of salts by rainfall after the equinoctial spring tides are probably the stimulus to germination in the field. Spring rainfall (at least 2 weeks averaging 15–25 mm day^{-1}) has been identified as important in California (Barbour 1970b, 1972).

Seeds can remain viable for many years whether deeply buried in the sand, or in dry storage at room temperatures. Seeds stored dry for up to 6 years showed up to 48% germination and there may be loss of dormancy in dry storage. Seed from 10-year-old herbarium sheets germinated very readily but 50- and 80-year-old seed was inviable.

Buried seed of *C. maritima* can germinate from a depth of 10 cm in sand-filled pots and in the field it is common to find hypocotyls of at least this length, with their cotyledons just above the surface. Burial to a depth of 2 cm or more in sand enhanced germination of *C. edentula*, compared with seeds at the surface, although subsequent emergence of the seedlings was severely reduced from the greater depths (Maun & Lapierre 1986; Adair *et al*. 1990). The mean depth of emergence of seedlings in the field was 3.4 cm (Maun & Lapierre 1986).

Table 4 A summary of reports of insect feeders on *Cakile maritima*

	Species	Mode of feeding and its effects	Reference
Hemiptera			
Aphididae	*Brevicoryne brassicae* (L.)	Larvae and adults feed on Brassicaceae	1
	Myzus persicae (Sulzer)	Non-specific aphid	1
	Lipaphis erysimi (Kaltenbach)		1
Miridae	*Lygus maritimus* Wagner	Polyphagous bug	2
Lepidoptera			
Incurvariidae	*Adela rufimitrella* (Scopoli)	Caterpillars phytophagous, non-specific	3
Noctuidae	*Agrotis ripae* (Hübner)	Caterpillars	4, 5, 6
	Sideridis albicolon (Hübner)	Caterpillars, adult feeding excluded	5
	Trichoplusia ni (Hübner)	Caterpillars, adult feeding excluded	7
Tortricidae	*Cnephasiella incertana* Treitschke		8
Plutellidae	*Plutella xylostella* (L.)	Diamond back or Cabbage moth, caterpillars	8
Arctiidae	*Estigmene acrea* (Drury)	Salt Marsh Moth caterpillar strips and kills plants of *C. edentula* in Canada	9
Pieridae	*Pieris brassicae* (L.)	Large White caterpillars	10
	Pieris napi (L.)	Green-veined White caterpillars	4, 8
Diptera			
Cecidomyiidae	*Contarinia nasturtii* (Kieffer)	Larvae cause galls	11
Agromyzidae	*Scaptomyza flava* (Fallén)	Larvae mine leaves and eat through veins	8
	Phytomyza horticola Goureau		8
	Liriomyza brassicae (Riley)		8
Coleoptera			
Curculionidae	*Baris laticollis* (Marsham)	Weevil larvae	12
	Ceutorhynchus quadridens (Panzer)	Weevil larvae and adults form galls and mines	13
	Ceutorhynchus contractus (Marsham)	Weevil larvae and adults form galls and mines	14
	Ceutorhynchus floralis (Paykull)	Weevil larvae and adults	12, 14
	Ceutorhynchus pleurostigma (Marsham)	Weevil larvae form galls	12
Chrysomelidae	*Psylliodes marcida* (Illiger)	Host-specific flea beetle. Larvae mine leaves, stems and fruits.	
		Adults feed on green parts of the plant	15, 16
	Meligethes ?*aeneus* Fab.	Blossom beetles; larvae and adults feed on pollen and damage flower buds of Brassicaceae. Seen in Norfolk, UK	17
	Lixus albomarginatus Boh.	Adults of feed on *C. maritima* ssp. *euxina* in coastal regions of the southern Ukraine. Larval development occurs on the same plant	18

1, Börner, Aphides; 2, Woodroffe (1966); 3, Emmet (1979); 4, Noble (1975); 5, Heath & Emmet (1979); 6, Allan (1949); 7, Heath & Emmet (1983); 8, M.G. Morris (pers. com.); 9, Keddy (1980); 10, Feltwell (1982); 11, Buhr, Gallen; 12, Hoffmann (1954); 13, Read (1987); 14, Scherf (1964); 15, Read (1980); 16, Volovnik (1996); 17, R. Scott (pers. observ.); 18, Mohr (1966).

(E) SEEDLING MORPHOLOGY

The embryo, which completely fills the interior of the seed, is pleurorhizal with an accumbent radicle. Reserves of proteins and oil are generally distributed in the axis and the cotyledons (Wright 1927). Emergence is either from the protection of the corky fruit segment, which splits (see Fig. 4), or sometimes from the bare seed after release from the pericarp. Germination is epigeal, with the fruit case sometimes being carried above ground along with the testa (Fig. 4). Seedlings developing from seeds that have germinated near to the surface of the sand secure stability by producing abundant adventitious roots from the base of the hypocotyl, whereas seedlings from more deeply buried seeds are stabilised by the elongation of their hypocotyls and taproots within the sand (Wright 1927). The cotyledons are horizontally orientated, and lanceolate with a moderately acute to obtuse apex; in large plants they may grow to over 5 cm in length and be persistent. Seedlings with three cotyledons have been seen, the resulting plants showing trimeric leaf orientation, but they flowered normally and gave rise to seeds with only two cotyledons.

IX. Herbivory and disease

(A) ANIMAL FEEDERS OR PARASITES

Insects

A limited range of insect feeders has been recorded on *Cakile maritima* (Table 4) and this may be related to the presence of glucosinolates in its tissues (see VI F). The host-specific flea beetle *Psylliodes marcida* (Illiger) can have a large impact on individuals, especially in high density populations of *C. maritima*. Its mining larvae damage leaves, stems and fruits, and often allow
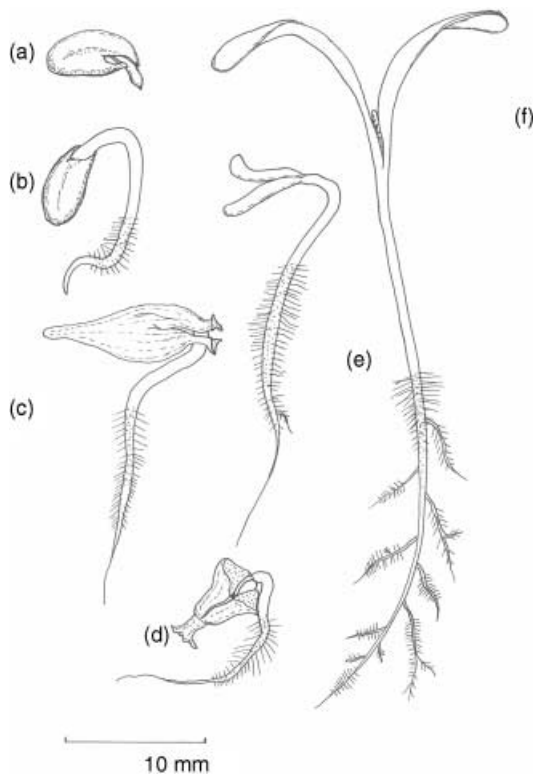
Fig. 4 Stages in the germination of seeds of *Cakile maritima*.
(a) germinating bare seed; (b) radicle emergence from bare
seed at 7 days; (c) radicle emergence from upper fruit at
7 days; (d) radicle emergence from lower fruit at 7 days; (e)
seedling at 14 days; and (f) seedling at 28 days.

secondary infections or make the plants susceptible to
fracture by wind. The adults also feed on *C. maritima*,
nibbling and scarring all green parts of the plant. These
beetles are long-lived and highly mobile, isolated plants
frequently being found with several resident beetles.
Caterpillars of cabbage white butterflies (*Pieris* spp.)
can also cause serious damage in Norfolk.

Birds

Emu (*Dromaius novaehollandiae* Latham), rosellas and
other parrots have been reported to eat the fruits in
Australia (Heyligers 1984).

Mammals

Rabbits (Rowan 1913) and domestic ungulates eat the
plants, and are capable of eradicating whole populations;
indeed grazing may be one of the mortality factors
excluding *C. maritima* from dune vegetation where con-
ditions for germination are in fact very good. The fruits
are heavily predated by the deer mouse (*Peromyscus
maniculatus* (Wagner)) in California (see IV). *Cakeli eden-
tula* is damaged by deer browsing in Canada (see IV).

Cakile maritima and its relatives have been eaten tra-
ditionally as an antiscorbutic, diuretic and purgative in
folk remedies; it has been cultivated on a small scale
and its leaves used for salads, amongst other culinary
uses (Rodman 1974).

(B) PLANT PARASITES

See (C).

(C) PLANT DISEASES

The metapopulation dynamics of the *Cakile maritima–
Alternaria brassicicola* host–pathogen association have
been studied extensively on naturalised populations of
C. maritima along the south-east coast of Australia
(Thrall *et al*. 2001). *Alternaria brassicicola* is a necro-
troph that causes black lesions on leaves, stems and
developing fruit; most of the individuals in a popu-
lation can become infected towards the end of the
growing season. *Alternaria brassicicola* has no known
sexual cycle but nevertheless maintains moderate levels
of genetic variability (Bock *et al*. 2002) and the genetic
structure of its populations suggests genetic recom-
bination in an unidentified sexual stage (Bock *et al*.
2005). Although it produces no overwintering spores,
infection of seeds and fruits in diseased populations of
C. maritima is likely, and vertical transmission can lead
to infection of up to 60% of seedlings germinating from
diseased fruits (Oliver *et al*. 2001). Local *Cakile*,
populations experience epidemics that depend on time,
age-class, density and distance from the sea. Both host
and pathogen populations were highly dynamic, with
frequent extinction and colonisation events, and seed
dispersal appears to be a very effective method of infect-
ing populations (Thrall *et al*. 2001). Local *Alternaria*
populations also vary in their aggressiveness (Thrall
et al. 2005).

Infection with the biotroph *Albugo candida* (Pers.)
Kuntz (Oomyces) caused a wide range of physiological
and biochemical disturbances in Egyptian *C. maritima*
(Aldesuquy & Baka 1992).

A black mould frequently occurs during ripening
and on mature fruits, leading to high seed mortality. A
fungus isolated by the Commonweath Mycological
Institute at Kew from a batch of affected fruits
proved to be *Cladosporium cladosporoides* (Fres.) de
Vries (M.B. Ellis, pers. com.). Other microorganisms
have adverse effects on the species, especially after
drought, disturbance or predation but the organisms
responsible have not been identified. There are non-
British records of species of *Ascochyta, Macrophoma,
Rhabdospora* and *Peronospora* mainly found on mori-
bund or dead plants and all have been listed with forms
specific to *Cakile* (M.B. Ellis, pers. comm. to R. Scott).

X. History

The genus *Cakile* comprises a small number of species
from strandline and desert habitats probably derived
from the genus *Erucaria* (Pobedimova 1963; Rodman
1974). The two-segmented fruit represents a trend to
simplification of the characteristic beaked, many seeded
siliqua of the Brassicaceae. The natural distribution of
strandline species of the genus *Cakile* implies that they

evolved after the closing of the Tethys Sea (Scandone 1975) in Pliocene times but there is no palynological record. *Cakile* was probably one of the first members of re-invasion floras after successive glaciations, and the specialisation of northern forms could be a result of rapid radiation into previously uninhabitable areas. Analysis of genetic variation, uncovered by examination of random amplified polymorphic DNAs (RAPDs) and intersimple sequence repeats (ISSRs), has suggested a reconstruction of the glacial and postglacial phylogeography of *Cakile maritima* (Clausing *et al.* 2000). Comparison of material from 21 locations around the coast of Europe revealed two clusters, from the Atlantic and Mediterranean, separated by a genetic distance of 0.037. This pattern may represent recolonisation from distributions separated during the Würm glacial.

The first British record of *C. maritima*, as 'Cakile Serapionis vulgo Eruca marina' was from the Isle of Wight ('Angliæ insulam meridionalem Vectem') in 1570 (First Rec.).

XI. Conservation

Cakile maritima exists as often ephemeral populations that occupy sensitive or fragile habitats in dunes and beaches. It is extirpated by heavy human trampling. An extreme adverse effect of human activity is the building of seawalls along the HWS level, precluding *C. maritima* from many stretches of shoreline which would otherwise have provided suitable habitats. In these areas there may be suboptimal habitats in foredunes or on the beach below the seawall. Its habitats are likely to be affected by increasing storminess and sea-level rise (Łabuz 2004).

Acknowledgements

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