

Biological Flora of the British Isles: *Crambe maritima*

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Summary

1. This account presents information on all aspects of the biology of *Crambe maritima* L. (Sea-kale; *Crambe pontica* Stev. ex Rupr) that are relevant to understand 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. *Crambe maritima* is found predominantly on southern and western coasts of Britain but also in Scotland, Ireland and elsewhere. It occurs primarily on neutral or slightly alkaline soils on shingle and sand beaches above the drift line, out of reach of average high tides. Equinoctial tides or storms can increase soil salinity, requiring it to be salt tolerant.

3. *Crambe maritima* is a rosette plant with a fleshy taproot, which is the main perennating organ with a capacity for vegetative propagation. Flowering can take 5–8 years when grown from seeds. Reproduction is predominantly by seeds. Root and stem cuttings can be used for vegetative propagation. In winter, each branch ends at ground level in a leafless crimson bud, and in spring, it produces a succession of cabbage-like leaves just above ground level, the first being purple and successive leaves becoming greener.

4. *Crambe maritima* produces weakly protogynous hermaphrodite flowers. Self- and cross-pollination occurs. Pollination is by insects, flies and bees. The plants usually produce 1000–10 000 seeds per year.

5. In Britain, *Crambe maritima* has been reported to have declined in certain areas but increased in other areas and currently does not have rare or scarce status. There has been an expansion in range in Ireland since the 1960s as it has been recorded at new sites, and while the species has disappeared from some sites in France, it has also been identified in several new sites.

Key-words: climatic limitation, communities, conservation, ecophysiology, geographical and altitudinal distribution, germination, herbivory, mycorrhiza, parasites and diseases

Sea-kale. Brassicaceae. *Crambe maritima* L. is a long-lived, deciduous, glabrous, perennial herb, rarely sub-shrub, which grows to a height and diameter of 0.6 m. Taproot thick, cylindrical, brittle, branched, fleshy (Scott & Randall 1976), gemmiferous; frequently surmounted by a massive, much branched, vertical underground stem 3–6 cm in diameter, resembling a taproot. Lateral roots extend horizontally to

200 cm in sand. In winter, each branch ends at ground level in a leafless crimson bud after the abscission of leaves and inflorescences. During the growing season, a mass of glaucous leaves and flower branches form a large, almost hemispherical thicket resting on the ground. In spring, each branch produces a succession of cabbage-like leaves at its apex just above the ground; first leaves deep crimson-purple, successive leaves becoming greener (Scott & Randall 1976). Basal and lower stem leaves with glaucous petioles, 2–3 cm. Mature basal leaf laminae 14–40 × 7–30 (50) cm, ovate, thick, fleshy, bluish green with an intense waxy bloom; margins, wavy and crisped, irregularly and variably toothed

*Nomenclature of vascular plants follows Stace (2010) and, for non-British species, *Flora Europaea*. This account supersedes that of *Crambe maritima* by Scott & Randall (1976).

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(Scott & Randall 1976) with pinnatifid to pinnatisect lobes. Upper leaves smaller, transitional in size and shape when compared to the lowermost bracts of the inflorescence. Inflorescence developing from near the apex of each branch, an erect, bushy, bracteate, corymbose panicle; stalk 40–60 × 2–3 cm; bracts in a series, decreasing in size up the inflorescence, uppermost ± rhomboidal, sometimes as small as 2 × 1 cm (Scott & Randall 1976). Flowers 0.8–1.5 cm. Sepals subequal, glabrous, ovate or oblong. Petals white, flushed with pink, 6–9 mm with green claws, blade widely oblong, sometimes slightly cleft at apex. Stamens 6, tetradynamous, filaments of the four longer stamens forked (Scott & Randall 1976). Concave sides of filaments form an apparent staminoid tube around the ovary (Prina 2009). Fruit 12–14 × 6–10 mm, on a 20–25 mm stalk, indehiscent, globose, single-seeded (rarely two-seeded), with a thick corky pericarp (Scott & Randall 1976). Seeds *c.* 20 mg, 2 × 5 mm in diameter, wingless, yellow and oily within; testa leathery, black when ripe.

Details of the taxonomic position, genetic variation and phylogeny of *Crambe maritima* are presented in section X.

Crambe maritima is a native species mainly of sparsely vegetated coastal shingle and sands, but it is occasionally found also on rocks and cliffs.

I. Geographical and altitudinal distribution

In England, *Crambe maritima* occurs mainly on the south-eastern, southern and western coasts (Fig. 1), especially in Sussex and Kent, where suitable habitats are plentiful, but is apparently decreasing (Scott & Randall 1976). In Wales, it is mainly on the north coast, and in Scotland, it extends as far north as the Clyde on the west coast and Fife on the east coast. However, it is declining on the east coast. Populations have shown a decline in abundance during the twentieth century. It is extinct on North Uist on the west coast where it was recorded earlier (Scott & Randall 1976). It is reported to be recovering from a decline in the Republic of Ireland, where there are now many sites. *C. maritima* has declined in parts of its British range in Suffolk (Walmsley & Davy 1997b) and in South Wales. On the other hand, it seems to be increasing in some areas of southern England, such as Chesil Beach.

In continental Europe, *Crambe maritima* occurs in northern France and around the Baltic, with outlying populations in northern Spain, Sweden, Belgium, the Netherlands, Finland and southern Norway (Fig. 2; Scott & Randall 1976; Asen & Andreassen 1976, 1978; Rappe 1984; Glazkova 1998). In France, except for Cayeux and Gatteville, Sea-kale populations have disappeared from most of the sites previously

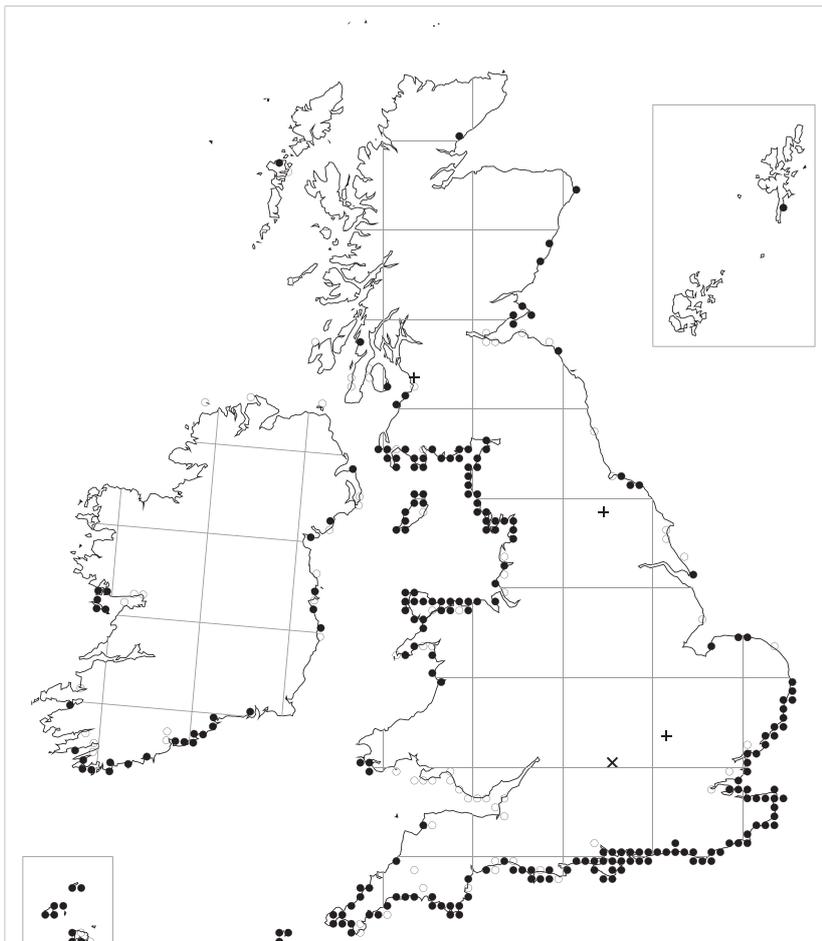


Fig. 1. The distribution of *Crambe maritima* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. (●) native 1970 onwards; (○) native pre-1970; (x) non-native 1970 onwards; and (+) non-native pre-1970. Mapped by Colin Harrower, Biological Records Centre, Centre for Ecology and Hydrology, mainly from records collected by members of the Botanical Society of the British Isles, using Dr A. Morton's DMAP software.



Fig. 2. The European distribution of *Crambe maritima*. Data were obtained from the Global Biodiversity Information Facility.

described, while several large new sites with extensive populations have been found (Briard, Horvais & Péron 2002). Among them, three sites were particularly large: from north to south, they are Locquemeau, Kerlouan and Trévignon (Briard, Horvais & Péron 2002). In Norway, *C. maritima* was first documented in the Oslofjord area in southern Norway, and less than a century ago, it was considered a rarity, occurring in only a few locations (Nordhagen 1940). Today, it is common in Oslofjord and no longer confined to this area (Byre 2001). The northernmost known locality of Sea-kale in the world was reported at Sor-Trondelag County in central Norway at 64°05 'N (Aune & Frisvoll 1984). *C. maritima* was found recently at Borkum on the East Frisian Islands in north-western Germany. This is the only currently known record of the species on the East Frisian Islands (Junghans 2010). There is also a population on the Black Sea coast (Schulz 1919; Fig. 2).

II. Habitat

(A) CLIMATIC AND TOPOGRAPHICAL LIMITATIONS

Crambe maritima is found in cool, temperate oceanic climates and open sunny positions (Chittendon 1956; Halpin 1978; Huxley 1992), often sheltered from strong winds (Huxley 1992). However, as its habitat is on sea shores, it is very tolerant of strong maritime winds, but less so of cold northerlies.

Hill, Preston & Roy (2004) characterized it as a European temperate species. An Ellenberg indicator value of 9 has been ascribed to *C. maritima*, suggesting that it is found mostly in full sun (Ellenberg *et al.* 1991; Hill, Preston & Roy 2004). The mean annual precipitation in the 10-km squares in Britain, Ireland and Channel Islands that it occupies is 938 mm, and the annual mean temperatures in January and July are 4.8 °C and 15.5 °C, respectively (Hill, Preston & Roy 2004). The northern limit of its distribution in the Baltic corresponds closely with the 0.6‰ isohaline of surface sea water (Eklund 1931). *C. maritima* is restricted to coastal habitats (Clapham, Tutin & Warburg 1962; Scott & Randall 1976) that are subjected to sea spray in winter, but are beyond the reach of high spring tides. However, equinoctial tides or storms can inundate the plants (Scott & Randall 1976; de Vos *et al.* 2010).

Sea-kale occurs primarily near sea level, occasionally on cliffs and has been recorded at a maximum altitude of 25 m (Druce 1932; Scott & Randall 1976).

(B) SUBSTRATUM

C. maritima is typically found on coastal shingle and on sand when it is overlying shingle (Preston, Pearman & Dines 2002). It prefers a well-drained soil, and mostly a neutral pH of 7 or slightly alkaline soil at pH 8.9–9.4 (Géhu & Géhu 1959). This is supported by the Ellenberg indicator value for soil acidity (*R*) of 8 indicating a preference for pH between 7

and 9 (Ellenberg *et al.* 1991; Hill, Preston & Roy 2004). A pH of 5.9 has been recorded in Cemlyn Bay in Anglesey (Géhu & Géhu 1959). Sea-kale is a nitro-halophile and grows on substrates more or less rich in organic matter and nitrogen compounds from the decomposition of seaweed at high drift lines. An Ellenberg indicator value of 7 for nitrogen was ascribed to the plant indicating richly fertile conditions (Ellenberg *et al.* 1991; Hill, Preston & Roy 2004). It can, however, grow in nutritionally poor and saline soils. An Ellenberg indicator value of 5 indicates a moist site of average dampness (Ellenberg *et al.* 1991; Hill, Preston & Roy 2004). A luxuriant growth at Cuckmere Haven (Sussex), the embankments of Dungeness Ranges and the Dungeness-Camber road may be accounted for by good drainage, while it is absent or less abundant at the foot of the embankments (Scott & Randall 1976). The mixture of clay and grit at Cemlyn Bay, Anglesey, probably provides the maximum moisture content the plant can tolerate (Scott & Randall 1976). Géhu & Géhu (1959) recorded chemical analyses of soils from three *C. maritima* sites at Burton Bradstock in Devon, the western end of Cemlyn bar in Anglesey and the middle of Cemlyn bar (Table 1).

The coarse substrates supporting Sea-kale usually comprise pebbles and gravel derived from rock fragments, with colloidal elements, and traces of humus derived from the decomposition of algae: shingle beaches or shingle with buried seaweed (Nordhagen 1940; Géhu & Géhu 1969), shingle with clay (e.g. Cemlyn Bay, Anglesey), shingle with sand (Llandulas, Clwyd) or sand (typically coarse) at Formby at Lancashire, the Baltic (Steubing 1949) and in Brittany (Géhu & Géhu 1959). In Brittany, Géhu & Géhu (1959) recorded 75% sand at the surface reducing to 60% at 60 cm depth, representing the sandiest extreme of its ecological range. In the Netherlands, colonization only occurred after the establishment of the basalt-stone sea dikes in the 1950s (Mennema, Quené-Boerenbrood & Plate 1985), which resemble an

artificial pebble beach habitat. Since that time, an explosion of the occurrence of *C. maritima* has been observed with the majority occurring on sea dikes (Mennema, Quené-Boerenbrood & Plate 1985; van der Meijden 2005). The absence of *C. maritima* from parts of the southern coast of the Baltic is due to the presence of fine silt derived from boulder clay, as the plant is confined to areas with alluvial sand mixed with stones (Bauch 1943). Thus, distribution is determined by soil particle size and also by buried algal humus to an extent (Nordhagen 1940; Géhu 1964; Géhu & Géhu 1969; Westhoff & Den Held 1969). The coastal substrates of *C. maritima* are often physically unstable, with movements of shingle or sand and cast-up wrack.

C. maritima can also occasionally grow on rocks and sea cliffs (Druce 1932) in areas subject to sea spray, such as at Sidmouth, Devon, where it grows at 25 m on well-drained, coarse sandstone with *Crithmum maritimum* (Scott & Randall 1976). An Ellenberg indicator value of 3 for salt tolerance supports occurrence on non-saline soils inland, cliff crevices and sand dunes that are not obviously salt-affected (Ellenberg *et al.* 1991; Hill, Preston & Roy 2004). More rarely, it is found on screelike slopes of calcareous sea cliffs in UK only (Bond, Daniels & Bioret 2005). It has also been observed in grasslands near to shingle beaches in Britain and in Scandinavia (Eklund 1931).

III. Communities

In the British Isles, *Crambe maritima* occurs in the communities of coastal shingle (Randall 2004) that are found in two habitat types of Annex I of the Habitats Directive (JNCC 2004), namely H1210 Annual vegetation of drift lines and H1220 Perennial vegetation of stony banks. These correspond with British plant community types SD2 and SD1, respectively (Rodwell 2000).

Although rare, *Crambe maritima* is characteristic of the main British community of coastal shingle, the *Rumex crispus* – *Glaucium flavum* (SD1) community (Rodwell 2000). This occurs from north Norfolk around the coast of south-east England, with a few sites on the west coast as far north as the Firth of Forth. Associated species often include *Silene uniflora*, *Beta maritima* ssp. *maritima* and *Atriplex prostrata*; rather, less frequent are *Senecio jacobaea*, *S. viscosus*, *Cirsium arvense*, *C. vulgare*, *Sonchus arvensis*, *S. asper* and *Lactuca serriola*. With increased amounts of sand mixed into the shingle, *Honkenya peploides* may be found. Other possible associates are *Crithmum maritimum*, *Matricaria maritima*, *Geranium robertianum*, *Euphorbia paralias*, *Sedum acre*, *Cerastium fontanum*, *Potentilla anserina* and the grasses *Festuca rubra*, *Elytrigia atherica*, *E. juncea*, *Ammophila arenaria*, *Arrhenatherum elatius* and *Holcus lanatus*. The less common *Lathyrus japonicus* can occur in more sheltered situations (Rodwell 2000).

In the typical subcommunity, equivalent to the Crithmo-Crambetum maritimae (Géhu 1960a; Géhu & Géhu 1969), *Crambe maritima* is preferentially frequent and occurs in 41–60% of the vegetation samples with Domin values ranging

Table 1. Soil data for *Crambe maritima* habitats from (i) Burton Bradstock, Devon (1959); (ii) W. end of Cemlyn bar, Anglesey (1959); and (iii) Middle of Cemlyn bar, Anglesey (1958) (Géhu & Géhu 1959)

Constituents	Site a	Site b	Site c
Total exchangeable bases (m-equiv. 100 g ⁻¹ air-dry soil)	16	1.2	30
Total exchangeable hydrogen (m-equiv. 100 g ⁻¹ air-dry soil)		4	
Sodium (m-equiv. 100 g ⁻¹ air-dry soil)	0.122	0.135	0.326
Potassium (m-equiv. 100 g ⁻¹ air-dry soil)	0.066	0.113	0.615
Phosphate	0.009	0.008	0.005
pH	7.9	5.9	8.9
Carbonate (% air-dry soil)	1.87	–	1.75
Nitrogen (% air-dry soil)	0.03	0.21	0.06
Humus (% air-dry soil)	9.8	5.17	1

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from 1 to 6. In the *Lathyrus japonicus* subcommunity (the Lathyrus-Crambetum of Géhu & Géhu 1969), *C. maritima* is only occasional and occurs in 21–40% of the vegetation samples with Domin values ranging from 1 to 3 (Rodwell 2000). *Crambe maritima* can also occur in the transition of SD1 to the *Honkenya peploides* – *Cakile maritima* strandline (SD2) community where a sandy beach top runs along the front of the shingle deposits that are beyond the reach of all but very extreme tides (Rodwell 2000). The other British community in which *Crambe maritima* occurs is the *Festuca rubra* – *Daucus carota* ssp. *gummifer* maritime grassland (MC11), where it is occasional in the *Ononis repens* subcommunity (20% of the vegetation samples with Domin values ranging from 1 to 5; Rodwell 2000).

A survey of 12 sites (20–100 quadrats per site) in Britain (Scott & Randall 1976) found 49 species associated with *C. maritima*. *Festuca rubra* and *Rumex crispus* were recorded in 11 and 10 sites, respectively. *Galium aparine*, *Sedum acre* and *Lathyrus japonicus* were observed at 7, 5 and 3 sites, respectively, but all three were found in all 100 quadrats at one of the sites. Other species recorded in five or fewer sites but more than 50 quadrats in one or more sites were as follows: five sites, *Beta maritima* and *Glaucium flavum*; four sites, *Senecio jacobaea*; three sites, *Arenaria serpyllifolia* and *Hypochoeris radicata*; two sites, *Anthriscus caucalis*, *Geranium robertianum*, *Poa pratensis* and *Rumex acetosa*; and one site, *Honkenya peploides*, *Scilla verna* and *Senecio sylvaticus*. At the mid-beach Cemlyn Bay site, six associated species (*Rumex crispus*, *Galium aparine*, *Silene uniflora*, *Tripleurospermum maritimum*, *Sonchus arvensis* and *Atriplex glabriuscula*) grew in humus and sand on the shingle surface. At the Dungeness site, *C. maritima* grew on the shingle embankment carrying a road, in association with 16 other species, some of which are weeds of roadsides and waste places (Scott & Randall 1976). In regions where the interstitial fine material in the shingle is humus rich, 25 associated species included halophytes like *Cochlearia danica* and agricultural weeds like *Sonchus oleraceus* and *S. arvensis* (Scott & Randall 1976).

Twenty-nine species were associated with *C. maritima* in a survey of ten locations from Europe ranging from Holland to the Baltic (Mayer 1936). The predominant species observed were: *Eryngium maritimum* (eight sites); *Elytrigia juncea* and *Elytrigia × littorea* (six sites); *Ammophila arenaria* and *Carex arenaria* (five sites); *Cakile maritima*, *Leymus arenarius*, *Salsola kali* and the natural hybrid × *Calammophila baltica* (four sites); *Honkenya peploides* and *Plantago maritima* (three sites); and 17 other species (two sites) (Scott & Randall 1976). Six species were predominant in Norway (*Beta maritima*, *Glaucium flavum*, *Solanum dulcamara*, *Angelica littoralis*, *Ligusticum scoticum* and *Mertensia maritima*) (Nordhagen 1940). These were typically the shingle beach plants.

The plant communities including *C. maritima* on the French coast were classified into nine vegetational units (I–IX; Géhu & Géhu 1969) within three classes. In class A, in five associations and subassociations (I–V), *Atriplex glabriuscula*, *A. laciniata* and *Euphorbia peplis* were the most

abundant species. In the two associations (VI–VII) in class B, *Euphorbia paralias* and *Honkenya peploides* were the most abundant species in some of the regions. In the two associations (VIII–IX) in class C, *Ammophila arenaria* was the most abundant species in some regions. A total of 50 species present in the nine vegetational units was observed in association with *C. maritima* on the French shore (Scott & Randall 1976).

Several plant communities associated with *C. maritima* on the French shore correspond to the British plant community classification system. The *Lathyrus* subcommunity of SD1 is similar to the Rumici-Lathyretum (Géhu & Géhu 1969; Géhu & Géhu-Franck 1979; Rodwell 2000) community. Furthermore, SD1 is very similar to some forms of the *Crithmo-Crambetum* community described from the British shingle, except for the absence of *Crithmum maritimum* from most of the British stands of this kind of shingle vegetation (Géhu & Géhu 1969; Géhu & Géhu-Franck 1979; Rodwell 2000). The *Bromus* subcommunity of the MC11 community is similar to the typical subassociation Armerieto-Daucetum gummiferi described from the French Channel coast (Géhu 1964). However, this association is much broader than MC11 grassland and includes vegetation that is closer to the *Festuca rubra-Holcus lanatus* (MC9) community of Rodwell (2000).

An extensive survey which compared the floristic composition of plant communities with *Eryngium maritimum* from all over Europe, including 3605 relevés distinguished by TWINSpan classification of species frequency (%), revealed eight biogeographical regions from Europe and adjacent countries. The species frequency of *C. maritima* is highest (41%) in the *E. maritimum* communities around the Black Sea. The species frequency of *C. maritima* in the biogeographical regions of NE Black sea, SW Black Sea and N North Sea and NW Baltic Sea was high at 46%, 32% and 25%, respectively. The species frequency in the biogeographical regions of Black Sea, Mediterranean Sea, SW Atlantic and in the NW Atlantic-S North Sea, SW Baltic were only 4% and at the NW Atlantic, North Sea, Baltic Sea and NW European, Atlantic and North Sea were 3% and only 1% at N North Sea and Baltic Sea (Isermann & Rooney 2014).

IV. Response to biotic factors

Brushwood deployed for beach stabilization on the Belgian coast also slowly decayed to increase the organic content of the sand, facilitating the establishment of nitrophilous species including *Crambe maritima*, *Beta maritima* and *Glaucium* spp. (Rappe 1984). Similarly, it has also been suggested that cast-up algal drift provides a suitable seed bed for germination and establishment, but it is not an obligate requirement, at least in Britain (Scott & Randall 1976). Establishment of *C. maritima* in Britain (south coast beaches including parts of Dungeness and Climping in Sussex) and also the Belgian coast has been affected by heavy trampling by tourists (Scott & Randall 1976; Rappe 1984), by vehicular traffic and, to some degree, by coastal development (Walmsley & Davy 1997b). The Wadden sea dike in the Netherlands is regularly

mowed, precluding *C. maritima* as a perennial plant that does not flower in its first year, even though fruits have drifted on to the shore (Cadée 2005).

V. Response to environment

(A) GREGARIOUSNESS

Crambe maritima grows singly or in small groups, usually occurring at the drift line (de Vos *et al.* 2010) on beaches, which have been stable over 5–20 year periods (Doody & Randall 2003). Individuals are generally well-spaced in the open shingle vegetation and can form large colonies (Scott & Randall 1976). Plants can become large, for example 1.6 m in diameter at Mecklenburg on the Baltic (Bauch 1943) and 2 m in diameter at Dungeness (Scott & Randall 1976). Stands of *C. maritima* tend to be even-aged. Patches of seedlings can be observed near parent plants, sometimes in rings, but they generally do not reach maturity there (Scott & Randall 1976).

(B) PERFORMANCE IN VARIOUS HABITATS

Crambe maritima is found in a limited range of habitats in the British Isles. However, it can show good vegetative and reproductive growth on a range of well-drained soil types (Scott & Randall 1976) (see **II B**) and is tolerant of salt spray (de Vos *et al.* 2010; see **VI E**).

In a transplant study conducted at Sizewell in Suffolk (UK), *C. maritima* produced more leaves per plant growing on shingle (4–9.5 mm and > 9.5-mm-diameter particles) than on sand (< 2-mm-diameter particles). The growth of roots and shoots was also significantly larger at the shingle site (Walmsley & Davy 1997c).

Poor fruiting has been observed in plants from Finland at the Baltic at the northern limits of its range (Eklund 1931).

(C) EFFECTS OF FROST, DROUGHT, ETC

Sea-kale can withstand temperatures as low as $-20\text{ }^{\circ}\text{C}$ (Phillips & Rix 1991). Plants may be partially killed by frost at $-15\text{ }^{\circ}\text{C}$ to $-18\text{ }^{\circ}\text{C}$. The roots are damaged by temperatures below $-15\text{ }^{\circ}\text{C}$ (Péron 1990). Established plants are very drought tolerant (Chatto 1982). Excessive moisture and water logging result in diseases, such as the black rot of stems and black spot diseases of stems, leaves and fruits (see **IX C**).

VI. Structure and physiology

(A) MORPHOLOGY

Crambe maritima is a rosette plant, with a brittle, fleshy root system that is extensive and deep. A deep taproot helps stabilize the plants in the face of disturbance by waves (Doody & Randall 2003). In older plants, the short stems at ground level divide into short stiff branches, which remain above ground level. These side branches may emerge as a complete ring of

shoots around the parent axis when the plants get buried. Stems may be buried from 50 cm to 1 m below the ground (Scott & Randall 1976). The rosette leaves are followed by bractlike cauline leaves on the flowering stems. In some populations, the developing rosette leaves are initially deep crimson in colour, gradually changing to green-blue. The crimson colour may persist at base of the petioles. The early leaves are much crisped, and even in mid-summer, the leaves have undulating margins.

The leaves have a waxy layer that is water-repellent. The relative frequencies of the stomata on the upper and lower surface of the leaves are 12:16 (Darwin 1887). Starch grains are densely packed in the parenchyma cells of the cortex and stele of both the roots and the stems and remain unused even during spring. This possibly enables the plants to send up shoots to the surface even after being buried beneath the shingle (Scott & Randall 1976).

(B) MYCORRHIZA

Members of the Brassicaceae were generally believed to be non-mycorrhizal (Gerdemann 1968). However, reports including those by Medve (1983), Tommerup (1984), Glenn, Chew & Williams (1985) and Harley & Harley (1987) for both field and glasshouse conditions have revealed arbuscular mycorrhiza (AM) in 30 of 80 crucifer taxa examined (DeMars & Boerner 1996). It was observed that AM was absent in *Crambe maritima*, as well as in *C. abyssinica*, *C. hispanica*, *C. kotschyana*, *C. orientalis*, *C. pinnatifida* and *C. tatarica*; it was only observed in *C. filiformis* (DeMars & Boerner 1996).

(C) PERENNATION: REPRODUCTION

Crambe maritima is a chamaephyte or hemicryptophyte (Prina 2009). Only the underground plant parts survive in winter. The taproots have a strong capacity to reproduce and regenerate (Briard, Horvais & Péron 2002). The extensive root and rhizome systems provide the resources necessary for reproduction by subterranean growth and emergence, and also enable renewed growth after erosion, because of their ability to regenerate from plant fragments (Walmsley & Davy 2001). Effective reproduction is predominantly by seeds, which are produced every year. Vegetative propagation has been observed in Cremlyn Bay and Dungeness following eroding seas and winter storms. The cuttings of older plants may flower within a year after establishment. Hence, the age of the plant may determine the onset of flowering, which usually takes at least 5 years (Scott & Randall 1976) in *C. maritima*, and subsequently seed production (see **VII**).

(D) CHROMOSOMES

Crambe maritima is highly polyploid with tetraploid number of $2n = 60$ (Jaretsky 1932; Manton 1932; Litardière & Doulat 1942; Montgomery *et al.* 1997; Lysak *et al.* 2007). Parnell (1986) also recorded $n = 30$ in Irish populations. Haploid chromosome numbers of $n = 15$ and 30 have been reported

(Gómez-Campo 1980). In Bulgaria near Zlatny pjasatzi on the Black Sea coast, *C. maritima* plants with $2n = 30$ have also been reported (Ancev 1981). A comparative chromosome painting (CCP) analysis of block F of the crucifer ancestral karyotype (AK; $n = 8$) revealed six copies of the block F in *C. maritima* ($2n = 60$), indicating that they are neopolyploids similar to the allopolyploid *Brassica* species (Lysak *et al.* 2007). Based on CCP analysis, it has been predicted that *Crambe* ($2n = 30$) are quasi-diploid species which possess three copies of the ancestral blocks as other Brassicaceae species (Lysak *et al.* 2007). The base compositions of 'AT' and 'GC' have been reported to be 65.01% and 34.99%, respectively (Lysak *et al.* 2007).

(E) PHYSIOLOGICAL DATA

C. maritima can be classified as a salt-spray-tolerant plant that is sensitive to root zone salinity (RZS) treatments exceeding 100 mM NaCl. There was a reduction in the relative growth rate (RGR) by 41% and 56% at 200 mM NaCl RZS and 300 mM NaCl RZS largely due to reduced specific leaf area (SLA) caused by increased leaf succulence and leaf dry matter content (LDMC). Salt spray tolerance of *C. maritima* seemed to be based on preventing salt from entering the leaves. Salt spray did not affect the RGR of *C. maritima*, but increased the leaf thickness and succulence (de Vos *et al.* 2010). This increased succulence has been interpreted as a halophytic adaptation, promoting conservation of internal water, water storage and dilution of accumulated salts (Storey & Wyn-Jones 1979; Flowers, Hajibagheri & Clipsom 1986; Breckle 2002; Dimmit, Wiens & Van Devender 2005; Munns 2005; Koyro & Lieth 2008; Munns & Tester 2008). Seawater spray can provide important nutrients, particularly NO_3^- , which may induce positive growth responses in *C. maritima* as has been reported in several strand-line species (Rozema *et al.* 1982; Lee & Ignaciuk 1985).

Salt spray had a negative effect on the K^+ concentration of the new leaves, but only to a minor extent when compared with the RZS treatments. Salt spray significantly increased the proline concentration (*c.* $80 \mu\text{mol g}^{-1}$ dry mass) when compared with the control spray and the 0 mM NaCl RZS ($< 20 \mu\text{mol g}^{-1}$ dry mass) treatment and was not significantly different from the proline concentrations at 50 and 100 mM NaCl treatments (*c.* > 90 to $< 160 \mu\text{mol g}^{-1}$ dry mass). Increased RZS at 300 mM NaCl resulted in increased Na^+ concentration (4.74 mmol g^{-1} dry mass), $\text{Na}^+ : \text{K}^+$ ratio (400% increase when compared with the 100 mM treatment) and proline concentrations (25-fold increase when compared with the 0 mM NaCl treatment) in new leaves. The K^+/Na^+ selectivity in new leaves increased at 50, 100, 200 and 300 mM NaCl RZS treatments when compared with the 0 mM NaCl RZS treatment, but no differences occurred between the 50, 100, 200 and 300 mM NaCl RZS treatments. The difference in K^+/Na^+ selectivity between 50 and 200 mM NaCl RZS treatment was nearly significant ($P = 0.051$). Reduction in K^+ , Ca^{2+} and Mg^{2+} and N concentrations (2.65 mmol g^{-1} dry mass, as opposed to $3.50\text{--}4.00 \text{ mmol N g}^{-1}$ dry mass under other treatments), lower osmotic potential and increased

antioxidant capacity (when compared with the 0 mM NaCl treatment) were observed in the new leaves under RZS treatment. The osmotic potentials recorded for the control spray, salt spray and RZS treatments of 0 and 50 mM NaCl were $> 1 < 2$ MPa and were not significantly different from each other. The osmotic potential of the 100 mM NaCl treatment (< 2 MPa) was significantly different from the osmotic potential of the control spray and the 0 mM NaCl treatment. The osmotic potential of the 300 mM NaCl treatment (< 4 MPa) and the 200 mM NaCl treatment ($> 4 < 5$ MPa) was not significantly different from each other but were significantly different from all the other treatments ($P \leq 0.05$) (de Vos *et al.* 2010). Proline concentrations of the leaves correlated strongly ($r = 0.95$) with RZS concentrations and not with plant growth (de Vos *et al.* 2010).

Furthermore, the soluble sugar concentrations showed a gradual but not significant decrease with increasing salinities, with values ranging from 116 to $175 \mu\text{mol g}^{-1}$ dry mass. These findings suggest that *C. maritima* is not able to adapt to high (*c.* 300 mM NaCl) salinity. However, it can tolerate higher salinity than typical glycophytes like *Arabidopsis thaliana* where concentrations higher than 50 mM NaCl inhibit plant growth (Xiong & Zhu 2002). Furthermore, it appears that the observed growth reduction between the 100 mM and the 200 mM NaCl RZS was caused by the combined reduction in SLA and the unit leaf rate (ULR) (the rate of increase in dry mass per unit leaf area). The SLA and the LDMC are involved in a trade-off between rapid production of dry mass (high SLA, low LDMC species) and an efficient conservation of nutrients (low SLA, high LDMC species) (Garnier *et al.* 2001). Thus, *C. maritima* adapted to increased salinity by changing from fast growth to slow growth with conservation of water and nutrients (de Vos *et al.* 2010).

Physiological studies on seeds showed that salt concentration is kept low during ripening and drying by transporting salt to the ovary wall (Pompe 1941).

A study by Molisch (1912) found that the stomata were partly open at night, contrary to what might be expected, but the conditions are unknown. Previous studies with *C. maritima* have shown that variations in the osmotic value, O_g , (relative concentration of the cell sap at incipient plasmolysis; sucrose is usually employed as a plasmolysing agent) of a given tissue can serve as an indicator of the physiological activities in that tissue (Beck 1931). The guard cells showed the greatest variation between light (0.950 molal) and shade (0.625 molal) under the shade of umbrella and 0.500 molal under the shade of tin foil, indicating that it is most responsive to natural factors that influence the plants during the day. Variations in O_g were observed in all three tissues, but only guard cells responded to light and shade treatments. Variations in O_g were also observed between the lower epidermis (0.375 molal), the guard cells and the spongy parenchyma (0.65 molal for both) when treated with sucrose, indicating the ability of the different cell types in taking up water. Recent studies have used osmotic potential as a direct measure of the physiological activities within a tissue due to salt spray or RZS treatment (de Vos *et al.* 2010).

The maximum potential photosynthetic rate ($17.4 \mu\text{mol m}^{-2} \text{s}^{-1}$), maximum water vapour conductance ($1133 \text{ mmol m}^{-2} \text{s}^{-1}$), transpiration rate ($6.7 \text{ mmol m}^{-2} \text{s}^{-1}$) and photosynthetic water-use efficiency ($2.6 \text{ mmol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$) were predicted by modelling from stomatal measurements of the adaxial [pore length = $32.1 \pm 4.4 \mu\text{m}$ ($\pm\text{SD}$), density = $101.8 \pm 15.9 \text{ mm}^2$] and abaxial (pore length = $33.4 \pm 3.8 \mu\text{m}$, density = $104.2 \pm 20.4 \text{ mm}^2$) leaf surfaces, and assumptions of environmental conditions and biological features (Davy, Willis & Beerling 2001). The environmental conditions set and the biological assumptions made in the model are described by Davy, Willis & Beerling (2001). The coupled energy balance-gas exchange model was derived from Beerling & Woodward (1997). *C. maritima* has been reported to be a higher CO_2 -compensating species ($> 50 \mu\text{L L}^{-1} \text{CO}_2$) in spite of having chlorenchymatous vascular bundle sheaths in the leaves, a feature generally associated with C4 species with low CO_2 compensation points (Crookston & Moss 1970).

Root cuttings of *C. maritima* have been widely used for hormone and polarity investigations (Jones 1925; Priestley & Swingle 1929; Stoughton & Plant 1938; Plant 1940; Camus 1947) and have shown strong stem and root polarity. If 5- to 10-cm-long root cuttings are allowed to regenerate while lying in a horizontal position, the cut surfaces at both ends develop callus which produces buds from the shoot-apex end and roots from the root-apex end in the course of 2 or 3 weeks. This polarity is maintained when the cuttings are placed vertically in the reversed position with the root-apex end upwards (Jones 1925). Expression of this polarity is slightly affected by gravity and to a greater extent by centrifugal force. This is only apparent in the manner of regeneration of the lateral callus developed by longitudinally split pieces of root cuttings in the case of gravity. Since gravity has little effect, when the plant cutting is planted the right way up, the lateral callus from which buds and chlorophyll develop are concentrated towards the shoot apex, and if the cutting is planted upside down, these callus go farther down towards the shoot apex of the cutting as the polarity is maintained. Further, centrifugal force can influence the position of bud and chlorophyll development on the laterally exposed surface of a longitudinally split piece of root, and also induce the growth of bud and chlorophyll at the root-apex end of an unsplit root cutting. The position of the root formation could not be shifted by gravity or centrifugal force. Short lengths of root, 2 mm or less in length, always produce shoot buds from both ends, but roots from one end only. If conditions are otherwise favourable for bud development, it takes place in regions where processes like respiration and metabolic activity are most vigorous (Jones 1925) and the differentiation of meristematic tissue is determined, in part, by specific concentrations of growth substance, a relatively high and low concentration of growth substance influencing root and bud production, respectively (Plant 1940). A local rise of temperature by 2°C is sufficient to make the warmed region of the cutting dominant so far as shoot production is

concerned, even though the region in question occupies the root-apex end of the cutting (Jones 1925).

(F) BIOCHEMICAL DATA

The total content of potentially antimicrobial glucosinolates (GSL) in the wild seeds of *C. maritima* is $153 \mu\text{mol g}^{-1}$ fresh matter (Daxenbichler *et al.* 1991), the same as in the seeds of the reference clone CCo (see X; Quinsac *et al.* 1994). The GSL content of etiolated sprouts was between 5.4 and $7.3 \mu\text{mol g}^{-1}$ of fresh matter, indicating the concentration of GSL in seeds is greater than in the sprouts (Quinsac *et al.* 1994). Epiprogoitrin was the major GSL representing 80–85% of the total in etiolated sprouts and 95% in seeds. An indolylglucosinolate, 4-OH glucobrassicin was present in notable proportions (10% of total GSL content) in the etiolated sprouts. Six other GSLs were identified in the sprouts (progoitrin, gluconapin, glucobrassicinapin, sinalbin, gluconasturtiin and glucobrassicin), whereas only five GSLs were identified in the seeds. Glucoalysyn was present in seeds, but not in the etiolated sprouts, and 4-OH glucobrassicin was nearly absent in seeds (Quinsac *et al.* 1994). Freezing and thawing cause a nearly complete decomposition of GSLs into unidentified compounds which are most probably 5-vinylloxazolidine-2-thione and nitriles. Cooking for 4 min (blanching) reduces the GSL content by 30% due to leaching, and a cooking time of 20 min reduces the GSL content by 76%. The amount of GSLs found in Sea-kale poses no risk when consumed when compared with other commonly eaten cruciferous vegetables. Further, *C. maritima* contains five types of flavonol glycosides, derived from kaempferol (3-glucoside, 3,4'-di-glucoside, 3-(p-coumaryl) glucoside-4'-glucoside), 3-(2-hydroxypropionyl) glucoside-4'-glucoside) and quercetin (3-glucoside, 3,4'-di-glucoside, 3-feruloylglucoside-4'-glucoside, 3-malonylglucoside-4'-glucoside) (Aguinagalde & Gómez-Campo 1984). In addition, phytoalexin secondary metabolites such as camalexin and brassinin are produced and studies have confirmed the *in vitro* antifungal effects of these two phytoalexins on the development of *Alternaria* spp. at different growth stages (Sellam *et al.* 2007).

A study of nutritional composition (expressed as 100 g^{-1}) of fresh, raw etiolated sprouts of Sea-kale (Péron, Gouget & Declercq 1991) revealed a low calorific value at 16.9 kcal, a low nitrate content (17 mg), low carbohydrate (1.6 g), low lipids (0.2 g), low sucrose (0.1 g) and reducing sugars (2.4 g), low calcium (73 mg), low sodium (3.6 mg), low sulphur (28 mg), high protein (2.10 g), fibre (3.1 g) and potassium (430 mg) content. The presence of trace elements, copper (0.5 mg), iron (0.6 mg), manganese (0.2 mg) and zinc (0.3 mg) was recorded. Certain peculiarities in the vitamin content have been observed. The proportions of ascorbic acid (27 mg), pyridoxine (0.21 mg), riboflavin (0.05 mg) and β -carotene (0.01 mg) are average, while the content of thiamine (0.27 mg), which is uncommon in vegetables, is high and total folic acid is 0.10 mg. The contents of phosphates and sulphates were 37 and 45 mg, respectively. The analysis of the amino acid profile indicates that the essential amino

acids represent a little over 50% of the total. The content of amino acids with branched structure is relatively low with the exception of valine, histidine and tryptophan, which are found in a relatively high concentration (0.07, 0.03 and 0.05 mg). When *C. maritima* was cooked for 4 min, the proportions of β -carotene, ascorbic acid, thiamine, pyridoxine and ascorbic acid decreased. Previous studies showed that the proportion of vitamin B1 in leaves and tops was 27 International Units 100 g⁻¹ (Pyke 1940) and vitamin C was 18 mg 100 mg⁻¹ (Harborne & Baxter 2001). An interesting distribution of minerals (high potassium/low sodium; excellent calcium/phosphorus ratio at 0.90) was recorded. The seed oil content was reported to be 41.7% (Dolya *et al.* 1973), and the seed oil composition of *C. maritima* contains eight fatty acids (FAs) whose proportions are $\geq 1\%$. The major FAs are 16:0 (1.8–2%), 18:0 (0.3–0.5%), 18:1 (18.8–25.3%), 18:2 (21.2–24.7%), 18:3 (5.8–8.6%), 20:1 (13.9–18.5%), 22:1 (26.3–32.6%), 24:1 (0.1–0.2%) and other FAs (1.2–1.3%) (Appelqvist 1971). The purple heads yielded a solution of cyanidin 3:5-dimonoside (Robinson & Robinson 1932). The purplish tips contain a diglycoside anthocyanin which can be readily hydrolysed by hydrochloric acid only after boiling with aqueous sodium hydroxide yielding cyanidin (Robinson & Robinson 1934).

VII. Phenology

The growth of roots and leaves of established plants begins in late February or, more commonly, early March. Lateral roots arising 2–3 cm below the hypocotyl proliferate, extend horizontally for up to 2 m and may supplant or supplement the main taproot (Scott & Randall 1976; see VIII E). Most plants are leafy by early April, but buds have been seen as late as 26 April (Scott & Randall 1976).

The flower buds appear around the third week of April and open in early May. Flowering takes place during mid-May to early June and continues till August. Few plants flower after mid-August. Plants usually take at least 5 years to produce flowers and subsequently seeds, and in some cases, flowering can occur even after 8 years (Scott & Randall 1976). The earliest flowering recorded in cultivated plants was 4 years on 27 May at Giessen (Hoffman 1886). The number of years before flowering first occurred was recorded as eight for one specimen on Shingle Street in Suffolk (Scott & Randall 1976). Fruits are ripe by early September approximately 2–3 months after flowering. The entire flowering stalk with its fruits dries as it ripens. Both the leaves and flowering stem wither leaving a short shoot with leaf scars by late November. The withered above-ground vegetation may be blown away or form a dry, protective covering over and around the dormant buds at ground level (Scott & Randall 1976). Only the underground parts survive in winter.

Studies in Angers in France have shown that the total growth of the Sea-kale plants in the field 5 months after transplanting (on 17 May 1994) was 10.47 t ha⁻¹ (dry matter). The amount of growth in these months was as follows: fifth month > the third month > the second month > the

fourth month > the first month. The concentrations of B, S, Ca and P were the highest in the second month and the lowest in the fifth month; the concentrations of Cu, Fe and Mn were the highest in the first month and then declined sharply. Concentrations of Zn and Mg decreased with continued growth, but the concentrations of K and Na were relatively stable. The total uptake of the various nutritional elements during the entire growing season was as follows: K > Ca > S > P > Mg > Na > Fe > Mn > Zn > B > Cu, and (except for Mn) the amounts taken up of followed the same monthly order as dry mass (Fusheng & Peron 1998).

VIII. Floral and seed characters

(A) FLORAL BIOLOGY

The flowers may be self- or cross-pollinated by flies, bees or beetles (Knuth 1908). The nectar-producing flowers aggregated in large inflorescences have a strong honey scent (Scott & Randall 1976). The largest upper median nectaries are found at the base of the long stamens in *C. maritima* (Knuth 1908; Clemente-Munoz & Bermejo 1978). The lower lateral nectaries – that is, those at the bases of the short stamens – are always present, but are almost vestigial in *C. maritima* (Knuth 1908; Clemente-Munoz & Bermejo 1978). There is no evidence of automatic self-pollination, cleistogamy, apomixis or vivipary (Scott & Randall 1976). The habitat being maritime the plant is not open to insect visits in great numbers. Genetic variation studies corroborate this as geographically close populations show genetic separation, a phenomenon that would not be expected if gene flow via pollen dispersal was high (Bond, Daniels & Bioret 2005).

(B) HYBRIDS

Hybrids of *Crambe maritima* are generally not known. There have been suggestions of hybridization between *C. maritima* and *C. tataria* based on their phylogenetic relationships, similar chromosome numbers (*C. maritima* has $n = 15, 30$ and *C. tataria* has $n = 15, 30, 60$) (Francisco-Ortega *et al.* 1999) and geographical distribution. The internal transcribed spacer (ITS) phylogeny of *Crambe* reveals that *C. maritima* and *C. tataria* are sister species (Francisco-Ortega *et al.* 1999), but *C. tataria* is sister to *C. orientalis* in the cpDNA tree. This incongruence may be due to hybridization, a phenomenon that has been implicated in many plant groups (Rieseberg & Soltis 1991; Rieseberg, Whitton & Linder 1996), as the two species are sympatric by the Black Sea.

(C) SEED PRODUCTION AND DISPERSAL

Crambe maritima has heteroarthrocarpic fruits, with disarticulation of the joint (Hall *et al.* 2011). The fruit breaks transversely into two chambers: the proximal one is sterile, slender and stalk-like, whereas the distal one contains a single seed and is practically an indehiscent achene (Ward 1908), which is the unit of dispersal. Rarely fruits can

contain two seeds. Each plant usually produces 5–10 000 seeds. A large plant with eighteen flowering branches was estimated to produce 22 500 seeds, but small plants with only a few smaller inflorescences may produce ≤ 1000 seeds (Scott & Randall 1976).

The branches with fruits may be dispersed by wind and the sea (Eklund 1927; Straka 1959; Cadée 2005). The presumed modes of seed dispersal over short distances are by fruits being blown along the beach, and over longer distances via tidal currents (Scott & Randall 1976). The pericarps of the globose fruits have a spongy structure, and the seed does not completely fill the space within the pericarp (Ridley 1930). *C. maritima* fruit examined under a scanning electron microscope showed large amounts of intracellular cell space aiding in seed buoyancy (S. Devlin, A. Mina-Vargas, K. Dinnan, C. Spillane, unpubl. data). This corky coat allows fruits to remain afloat and viable in seawater for long periods and thus aids dispersal (Hall *et al.* 2006). The floating times recorded in the literature vary: 13 days (Sernander 1901), 1–4 weeks (Guppy 1906), a maximum 4 weeks (Straka 1959), 37 days (Darwin 1857) and > 45 days but not viable (Martins 1857). Scott & Randall (1976) showed that 50% remain afloat after 14 days and some over 26 days. In a recent study by Cadée (2005), 50% of the 60 fruits were floating for at least 6 months. Even after buoyancy has been lost, some seeds remain viable following 4 months of immersion in seawater (J. Bond, pers. com.). Wind dispersal is also seen when dry twigs with fruits attached are blown as tumble weeds along the shore, shedding their fruits as they go (Straka 1959; Cadée 2005). Inflorescences blown along the beach may be caught around the persistent stalks of *Rumex crispus* and *Glaucium flavum*, scattering seeds (Scott & Randall 1976). The dried branches are seen floating loaded with fruits but without leaves and roots (Cadée 2005).

The effects of sea currents on dispersal are reflected in patterns of genetic variation. Gene flow, via seed dispersal, is possible between UK and French populations on either side of the English Channel, which maintains the genetic variation (Bond, Daniels & Bioret 2005). In contrast, French populations on the Bay of Biscay coast are effectively isolated by the direction of currents and consequently show a greater degree of genetic differentiation due to lesser opportunity for exchanging genes (Bond, Daniels & Bioret 2005). Localized currents also play an important role in determining if seeds will land on the beach (and conversely if seeds will be dispersed from the site) as seen in populations in Sillon de Talbert in Brittany in France, where populations separated by only 1 km were genetically different (Bond, Daniels & Bioret 2005). Long-distance dispersal can only occur when seeds escape the localized currents produced by coastal morphology. Thus, populations that are geographically close may be isolated because of currents, while geographically distant populations may be linked by currents (Bond, Daniels & Bioret 2005). Tidal patterns, coupled with small population size, may also explain exceptionally low levels of genetic diversity within the population at Crozon Peninsula, France. Since the currents in this region are relatively slow and eddies are fre-

quent (Koutsikopoulos & Le Cann 1996), the rate of seed exchange will also be slow.

(D) VIABILITY OF SEEDS: GERMINATION

Seed germination takes place freely at 15 °C (Bird 1989). However, optimal germination at 15 °C on moist filter paper in petri dishes in the laboratory was increased by splitting open the seeds (Scott & Randall 1976). Walmsley & Davy (1997a) showed that only 20% of seeds of *C. maritima* germinated from fresh fruits and none of the fruits stored dry for up to 7 years germinated without pre-treatment; in contrast, seeds manually removed from the hard fruits irrespective of storage time had a germination rate of 40–90%. Germination tests on pre-treated (non-dormant) seeds at constant temperature, using a thermogradient bar, showed that *C. maritima* germinated in reasonable numbers only over a relatively narrow temperature range of 23–30 °C (Walmsley 1995), but showed optimal germination under more realistic, diurnally alternating temperature regime of 15/5 °C, which corresponds approximately to soil temperatures in the field in March and April (Walmsley & Davy 1997a). High, alternating temperature treatment (25/15 °C) of pre-treated seeds (pericarp removed) slightly reduced the germination rate of 1-year-old seeds; significant reduction in germination was observed in 7-year-old seeds at 25/15 and 20/10 °C. Seed ageing did not decrease viability, as the germination percentages for both 1- and 7-year-old seeds were similar at 15/5 °C. However, increased seed age led to a general narrowing of the optimum temperature and hence reduced germination at supra-optimal temperatures (Walmsley & Davy 1997a). A cold treatment at 2 °C for 12 days had no significant effect, with 30% seeds germinating compared to 33% in controls (Scott & Randall 1976). Fusheng, Peron & Blanchard (1998) explored the pre-treatments for improving the slow and low germination rate of *C. maritima* seeds due to the influence of seed dormancy and slow water imbibition rate because of a thick and hard seed coat. They recommended the following strategies: (i) decortication of seeds can greatly improve germination; (ii) soaking seeds in a solution of 0.025% gibberellic acid for 18 h had the best effect on germination and seedling growth; and (iii) soaking seeds in a solution of 10% sodium hypochlorite for 5 min can also improve germination and reduce seedling mortality. Other studies also showed that the removal of the hard, corky pericarp and pre-soaking the seeds were effective in releasing dormancy (Walmsley & Davy 1997a), and the removal of testa has also been recommended (Baron & Binet 1964).

Seed germination requires leaching of inhibitory substances present in the fruit. Temperature treatments of 25 °C for 1 month followed by a period of 2 months at 4 °C can remove inhibitory substances from seeds placed 2 cm deep in wet silica sand (Baron & Binet 1964). The leaching associated with sandy soil allowed the elimination of inhibitory substances, and the cold temperature promoted seed germination. On the other hand, if the cold period was preceded by a longer hot and humid period (2 or 4 months at 25 °C),

germination rate decreased, possibly due to an increase in inhibitors (Lacroix & Le Bail 2006). Hard seed or physical dormancy may be regarded as long-term insurance against episodic catastrophe in shingle species like *C. maritima*. Even when innate or induced forms of dormancy have been overcome, the timing of germination can be determined by responses to the environment that can be regarded as enforced dormancy, which may also be important in coastal shingle species to allow fine-tuning germination to a window of opportunity: major disturbances frequently result from equinoctial storms in the spring (Davy & Figueroa 1993), and drought and high surface temperatures are likely to limit the potential.

Seed germination was completely inhibited by 50% and 100% seawater treatment. Less extreme 10% and 25% treatments reduced the germination rate of 1-year-old seeds by 40% and 70%, respectively, and 7-year-old seeds by 66% and 85%, respectively, when compared to the control; thus, ageing reduced their ability to tolerate and regulate osmotic changes, and again led to narrowing of the environmental conditions that allow maximal germination (Walmsley & Davy 1997a). However, studies have shown that seeds pre-treated with sea water germinated rapidly when transferred to fresh water and that the 'salt stimulation' increased with increasing salt concentration in the pre-treatment (Woodell 1985). Darwin (1857) also noted that the seeds germinated well after 37 days of immersion in sea water. This response confers upon *C. maritima* the potential of rapid establishment after dispersal by the sea, followed by rain (Woodell 1985). Soil salinity is generally low in beaches and strandlines (Boyce 1954; Scott 1960; Barbour, De Jong & Pavlik 1985), but winter storms could cause seawater flooding. Dormancy enforced by salinity during winter might prevent premature germination before spring, when salt would be leached easily by rainfall from shingle and sand substrates (Walmsley & Davy 1997a). Seed germination in the field occurs in the spring in mid-April (Scott & Randall 1976).

Cast-up algal drift could be advantageous for germination, especially if it is buried well beforehand to form a suitable seed bed, although this is not an obligate requirement at least in Britain (Géhu 1960b). Growth of roots in the pockets of organic matter within beds of gravel or pebbles has been reported (Géhu & Géhu-Franck 1979). Walmsley & Davy (1997b) showed that seedling emergence was greater in organic-matter-treated plots on shingle, because of improved seed-water relationships and retention of seeds within the surface layers of the substrate. Conversely, the addition of organic matter to sandy substrates caused the surface of the plots to dry out and had adverse effects (Walmsley & Davy 1997b). However, on mixtures of shingle and sand, *C. maritima* showed greater seedling emergence in sandy plots compared to plots which were dominated by coarse shingle, which had lower moisture retention capacity. Thus, substrate physical composition was probably the primary determinant of the differences in performance across the beach profile (Walmsley & Davy 1997c; see **V B**). It is likely that burial of fruits, in relatively moist conditions, degrades the impermeable pericarp. The large seeded *C. maritima* suffered reduced

emergence at higher coarse-shingle contents in its substrate than the small seeded *Glaucium flavum*, reflecting their different probabilities of deep burial (Walmsley & Davy 1997b). Four hundred *C. maritima* seeds sown on the soil surface in pots outdoors at Bangor did not germinate in the course of a year (Scott & Randall 1976).

(E) SEEDLING MORPHOLOGY

In *Crambe maritima*, the seeds generally germinate inside the fruit wall, which ruptures when the radicle emerges if it has not been damaged before. Germination is epigeal (Fig. 3). A robust primary root develops into a taproot, and lateral roots are produced later. The taproot can penetrate at least 15 cm into the soil. Frequently, in the field, the 2-cm section below the cotyledons remains swollen and fleshy, but below that, the root withers to a dry threadlike structure when the seedling is growing in dry sand; it is then very likely to be vulnerable to drought and disturbance. The shoot does not elongate and produces a succession of small petiolate leaves in a spiral above the hypocotyl (see **VII**).

IX. Herbivory and disease

(A) ANIMAL FEEDERS OR PARASITES

The eating of the fruits by *Chloris chloris* (Greenfinches) has been observed in Sussex (Scott & Randall 1976), and a migrant flock of birds (possibly finches) has been observed eating the fruits so intensively in Macklenburg that by late winter and spring, few of the seeds are not split open and their cotyledons eaten (Bauch 1943). There has been evidence of seed excavation and predation in sown experimental plots, probably by small mammals at Sizewell in Suffolk. The large, oil-rich nutritious seeds could be very attractive to granivores (Walmsley & Davy 1997b). Eating by birds and also grazing by sheep and cattle have been recorded in Finland (Eklund 1931). Container-grown plants of *C. maritima* have been shown to be highly palatable and readily destroyed by rabbit grazing (Walmsley & Davy 2001).

Plants in the wild are sometimes infested with the caterpillars of Lepidoptera: *Pieris brassicae* L., Large White Butterfly, and *Pieris rapae* L., Small White Butterfly, (DBIF 2015). These defoliate the plants partially, but are not important ecologically (Scott & Randall 1976). A beetle (Coleoptera), *Psylliodes crambicola* Lohse (family Chrysomelidae), feeds specifically on *C. maritima*. It has been reported from northern Germany, Denmark, Sweden and Finland, lately expanding westwards into southern Norway (Wanntorp & Odegaard 2005). Two other species of Chrysomelidae feed on *C. maritima*: *Psylliodes napi* Fabricius have been observed on leaves and stems and *Phyllotreta nemorum* L. on the leaves (DBIF 2015). Beetles of the weevil family Curculionidae feed on the leaves, fruits and seeds: *Ceutorhynchus cakilis* Hansen, *Ceutorhynchus contractus* Marsham, *Ceutorhynchus timidus* Weise, *Ceutorhynchus syrtes* Germar and *Ceutorhynchus floralis* Paykull (DBIF 2015).

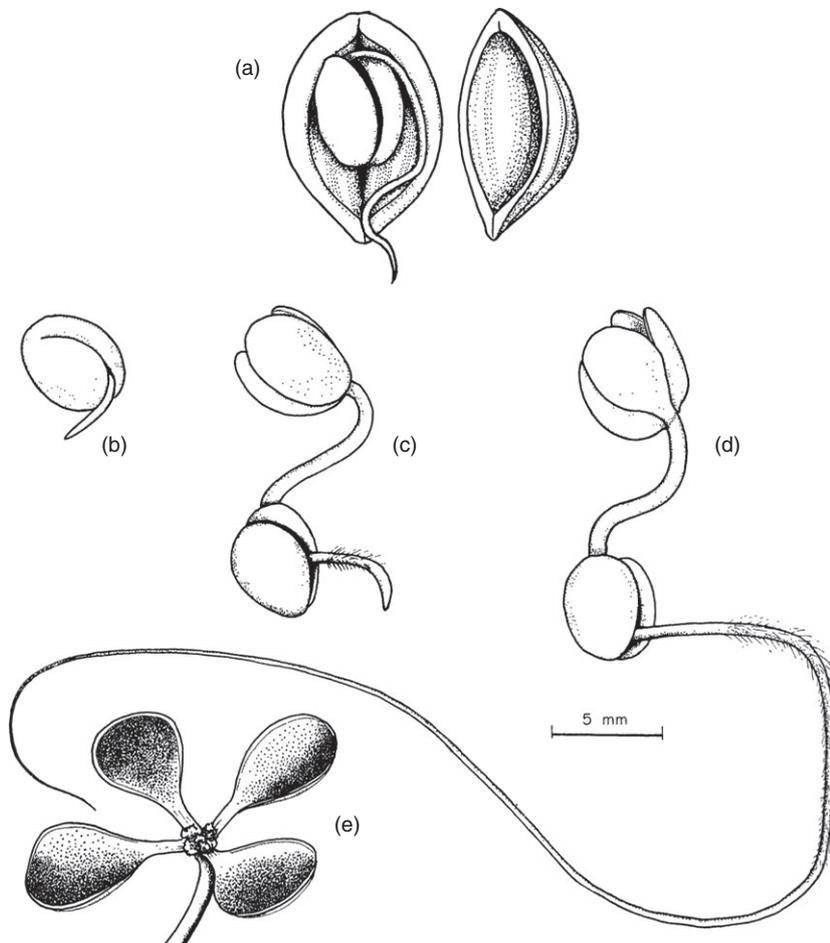


Fig. 3. Stages in the development of seedlings of *Crambe maritima*: (a) germination of seed within the fruit; (b) seedling after 10 days; (c) after 20 days; (d) after 30 days; and (e) after 40 days. Grown in sand culture. Reprinted with permission from Scott & Randall (1976).

(B) PLANT PARASITES

A small number of fungi has been recorded as associated with *Crambe maritima* (Table 2).

(C) PLANT DISEASES

Bacterial black rot of the stems appears to be the most common disease in Britain, and nearly all the older plants in Cemlyn Bay had the centre of their stems decomposed. The primary reason appears to be poorly drained soil (Scott & Randall 1976). As with other brassicas in cultivation, club root disease caused by the phytomyxean protist *Plasmodiophora brassicae* can be troublesome, especially in soils deficient in lime (Taylor 1927; Moore 1959). Several other diseases have been reported by Brown (1937) on cultivated Sea-kale.

X. History

INTRODUCTION AND NATURALIZATION HISTORY

Sea-kale was a traditional crop in Britain and France. It was first cultivated in the large private gardens of castles and manors in Britain and also grown in market gardens (Evans 1982). It became established as a garden vegetable by the

early 18th century, later being introduced and naturalized in parts of Oregon in the USA (Horwood 1919; Halpin 1978), where it became a delicacy. Prior to 1765, the seeds were sold at a high price as a rarity. It is still grown in Britain on a small scale, but the crop has almost disappeared as the cultivation became uneconomic (Fusheng & Peron 1998; Bogemans & Erdet 2012). J. Y. Péron in France has developed new cultivation and propagation systems to increase yield and quality, and decrease seed dormancy in *C. maritima*. Continuing improvement of production techniques and forcing in the glasshouse has been instrumental in reviving the crop. There has been commercial production in northern France since 1988 following the experiments conducted in 1985 in England, then in the Loire Valley in 1987 in France (Péron 1990).

CULTIVATION

C. maritima is of interest not only as a wild relative of other Brassicaceous crops and a crop in its own right, but also because it has potential as a new halotolerant crop. Studies of genetic variability have been conducted with the aim of diversifying vegetable crops and bringing *C. maritima* closer to commercial production, and also for conservation purposes in France, UK and Ireland. A breeding programme initiated in 1992 resulted from a systematic search for wild populations

Table 2. Fungi associated with *Crambe maritima*

Phylum	Order	Species	Host part	
Ascomycota	Pleosporales	<i>Alternaria brassicae</i> (Berk.) Sacc.	Seed pods	
		<i>Pleospora herbarum</i> (Pers.) Rabenh.		
	Helotiales	<i>Botrytis cinerea</i> (De Bary) Whetzel	Twigs	
	Hypocreales	<i>Gibberella intricans</i> Wollenw.		
			<i>Gibberella avenacea</i> R. J. Cook	
		Hypocreales	<i>Nectriella bloxamii</i> (Berk. & Broome) Fuckel	
	Pezizales	<i>Iodophanus carneus</i> (Pers.) Korf		
Oomycota	Peronosporales	<i>Hyaloperonospora parasitica</i> (Pers.) Constant.		
Basidiomycota	Cantharellales	<i>Thanatephorus cucumeris</i> (A. B. Frank) Donk		
		<i>Rhizoctonia solani</i> J. G. Kühn		
		<i>Rhizoctonia crocorum</i> (Pers.) DC.		
		Agaricales	<i>Typhula variabilis</i> Riess	
		Helicobasidiales	<i>Helicobasidium purpureum</i> (Tul.) Pat.	

Data from the Fungal Records Database of Britain and Ireland (FRDBI 2015).

in France, along the Channel and Atlantic coasts, especially from Quiberon (south Brittany) to Dunkerque (north France near Belgium) that aimed to capture its genetic variability. Morphological characters and molecular markers, such as random amplified polymorphic DNA (RAPD) (Briard, Horvais & Péron 2002) and inter simple sequence repeats (ISSR) (Bond, Daniels & Bioret 2005), were used to characterize the phenotypic and genetic variability. Great variability in leaf and leaf-stalk colour, stem, flowers and silique size was observed. A study of 66 wild plants from five sites (Kerlouan, Gatteville, Cayeux, Trévignon and Locquemeau) showed that they nearly all differed from 20 plants of a reference laboratory genotype, CCo. Some of this variation may be phenotypic, particularly as dispersal by sea water allows gene exchange all along the Channel and Atlantic coasts. Within a site, clonal spread may result from extensive underground ramifications, and movements of sand and shingle by tides and storms could be responsible for vegetative propagation (Briard, Horvais & Péron 2002).

Molecular studies have also aimed to determine the genetic variation in *C. maritima* in order to minimize the cost of developing 66 new inbred lines. Twenty polymorphic RAPD

markers were used for the molecular analysis of 12 plants (two plants from each of the five sites and from the CCo clones) (Briard, Horvais & Péron 2002). The molecular similarity between the wild plants was 25–85%, and the mean distance between the wild genotypes and the reference (CCo) was large (50%). The wild genotypes of all the populations were distant from CCo except for the Locquemeau site. The most distant individual was from Gatteville with only 20% similarity to CCo. Molecular analyses of morphologically similar pairs of plants at two sites, to determine whether they were clonal in origin, revealed 80% similarity between plants from the Locquemeau population, but only 45% similarity between those from Trévignon. To decide whether morphologically similar plants from two different sites could be sister lines resulting from seed dispersal, C2 from Cayeux was compared with L2 and L5 and showed only 75% and 65% similarity. Two phenotypically different plants (Kerlouan 3 and C2) from different sites showed 50% similarity, which was greater than between T2 and T10 (45%) from the same site. This suggests that phenetically similar plants were not clonal in origin, and provides no evidence of seed dispersal by seawater. It also means that vegetative multiplication within a site was not as important as assumed, or the sampling method was efficient enough to avoid collecting plants from the same stock.

The other genotypes enabled evaluation of the reliability of the morphological descriptors for genome variability assessment. The molecular similarity (35%) between the two Cayeux plants was consistent with their morphological distinction. Finally, the morphological examination of the 20 CCo plants revealed one quite different violet plant (CCo7), with anthocyanin present in leaves and stalks, which was most similar to a standard type (CCo10) of all the genotypes studied (90%); the 10% difference could be partly explained by a certain degeneration of the cutting due to virus infestation of the stock (Brown (1937), or by somaclonal variation. It could also possibly be compared to the off-types or 'aberrant plants' described as hybrids, inbred lines or population varieties of *Brassica oleracea* (Ruffio-Châble, Chatelet & Thomas 2001). Some off-types whose origins could not be determined were also observed by Briard, Horvais & Péron (2002) while multiplying clones. Studies undertaken to identify the underlying agronomic factors and the genetic mechanisms involved in creating the aberrant plants suggested the involvement of epigenetic phenomena causing modification in gene expression. Changes in chromatin structure and/or DNA methylation may be induced by environmental stresses. Reactivation of mobile elements could also be possible. The aberrant *Crambe* plants could be a complementary model to the *Brassica* study.

From these results, no clear correlation between morphological and molecular data was shown, possibly due to the neutral nature of the RAPD markers. Therefore, it appears that morphological characteristics have to be interpreted with caution, especially colours, because foliage colour and presence of anthocyanin are deeply influenced by environmental conditions as for other Brassicaceae. The only morphological

characters that seem consistent with molecular results were leaf–stalk thickness and length. These could be important descriptors for future studies. CCo and Cayeux 2 have long, thin leaf stalks and are 85–75% similar. In contrast, Cayeux 9, Gatteville 1 and Kerlouan 3 have very thick and/or short leaf stalks and have only 25–35% similarity with CCo.

This study showed that there is considerable genetic variation in *C. maritima*. The RAPD primers developed will enable researchers to check the level of homogeneity of the lines after a few breeding cycles. A separate race, *C. maritima* var. *pontica* described by Schulz (1919), occurs on the coasts of the Black Sea and the Sea of Azov. The genetic distance of this variety from other populations remains to be determined; the only plant grown from seeds obtained from Museum d'Histoire Naturelle in Paris appeared different at the juvenile stage, with pubescent cotyledons and first leaves (Briard, Horvais & Péron 2002).

In another study, ISSR markers were used to investigate population structure in *C. maritima* populations found on either side of the English Channel. Despite the expectation that smaller populations would contain lower levels of genetic diversity, no significant correlation between genetic diversity and total population size, and the number of plants or flowering plants was found (Bond, Daniels & Bioret 2005), possibly because gene flow between populations is high. Although four of the populations sampled had effective population sizes of < 30, it is possible that enough 'small' populations were not sampled to determine a relationship between genetic diversity and population size. Alternatively, the degree of geographical isolation between populations, especially small ones, is also vital in determining the amount of genetic variation that can be maintained as a result of gene flow. In the absence of gene flow, populations will gradually become genetically distinct. Diversity was high within all populations (eight from France including two subpopulations and nine from UK including one subpopulation), except for one (Crozon Peninsula in France) that was small and geographically isolated (see VIII C). Despite the wide geographic range, the majority of diversity (71%) was contained within populations, with no unique genotype, or even allele, identifying any population, suggesting that *C. maritima* is predominantly an outcrossing species. Plotting genetic distances with multidimensional scaling (MDS) techniques and assignment testing indicated high levels of population diversity and gene flow. Assignment testing showed that 8.7% of individuals were assigned to a population other than the one from which they were collected, indicating high levels of gene flow, through the dispersal of salt-water-tolerant seeds. Assignment testing also shows that none of the individuals was assigned to the adjacent populations, suggesting that gene flow via pollen dispersal is limited. *C. maritima* is insect pollinated, and if gene flow was only through pollen transfer, we would expect to find isolation by distance. Geographically close populations generated high pairwise *R*-values of 0.8 indicating genetic separation, a phenomenon that would not be expected if gene flow via pollen

dispersal was high. The pattern of genetic variation can also be explained by examining the direction of currents in the English Channel, the Bay of Biscay, and the localized currents (see VIII C).

Cuttings, taken from the extremities of the roots of healthy plants (technically called 'thongs'), are well adapted for cultivation and horticultural purposes (Taylor 1927; Story & Montgomery 1948). Root cutting is the most efficient propagation method for Sea-kale although both root and stem cuttings can be used for vegetative propagation (Taylor 1927; Story & Montgomery 1948) for commercial use. Shoot regeneration capacity is high in root cuttings. They should be taken up in autumn, cut into lengths of about 10 cm and laid in a heap of sand or earth until spring, when they should be planted out like the seedlings. If the root cuttings are small, it is best to grow them in a pot in a cold frame until they are established and then, they can be planted outside in spring or autumn when the seedlings are about 10 cm tall. *In vitro* morphogenesis of *C. maritima* has also been demonstrated by culturing the root tissues. The culture produced a range of organized structures of varying complexity from nodular to rootlike outgrowths, teratomas leafy shoots and embryoid-like structures (Bowes 1976). Plantlets of Sea-kale have also been produced by tissue culture of petioles of *C. maritima* after several months (Drew & Fellows 1986).

A cultural practice for growing and forcing Sea-kale was developed and used in northern France (Péron 1985; Péron & Régner 1987). The clone CCo was obtained from a sample of a rhizome fragment from a Sea-kale plant present in the departmental collection of edible plants in Ecole Nationale Supérieure d' Horticulture of Versailles and used to devise a cultural system which consists of three parts: (i) cutting production phase, (ii) field production phase and (iii) etiolated sprouting phase in a dark chamber. In the first phase, micropropagation permits rapid *in vitro* plantlet production (Péron & Régner 1987). Alternatively, cuttings are obtained and kept at low temperatures and high atmospheric humidity until transplantation in the field during the second phase, between 15 March (for root cuttings) and 15 May (for *in vitro* plantlets). The plants form one or several foliar rosettes during their growth in the field over *c.* 6–8 months. Growth stops and the leaves abscise *c.* 15 November. At this time, the plants can be transferred into a dark chamber for the third phase. After removing a part of the root biomass, plants are set in a moss peat substrate and transferred to a dark forcing chamber (15 °C, relative humidity 85%). The etiolated sprouts are edible after 28–30 days. The duration of the sprouting phase at the end of winter is shorter if the plants are left longer in the field before transfer. The best yields (*c.* 100–120 g per plant or 5.3–6.4 tonnes ha⁻¹ with a population of 53 500) are obtained early in the season *i.e.* *c.* 25 December. However, yield reduction during winter is accompanied by a concomitant decrease in sprout quality (Péron 1989). This clone and its propagation method are protected by French patent (8401984) and U.S. patent (4645031).

USES

Sea-kale is rich in vitamin C, mineral salts, sulphur and iodine (see VI F). It contains sulphur heteroside, recognized as having anti-cancer properties. Because of its high vitamin C content, it is used to prevent scurvy as well as viral infections. It has also been used as a purifier, diuretic, antiseptic and for its antifungal effects (see VI F). The leaves have been used for healing wounds, the fruits for removing worms (Boullard 2001) and the raw juice of seeds to fight gastritis and gastric ulcers. The seeds are very rich in oil (41.7%) of potential economic value (Regel 1940; Heidt 1945; Dolya *et al.* 1973) and are also used for cosmetic purposes. It is used as an ornamental plant and as a model for epigenetic studies (see X CULTIVATION). Young leaves are eaten raw or cooked like spinach (Thompson 1878; Larkcom 1980; Loewenfeld, Back & Bosanquet 1980; Launert 1981; Facciola 1990). Young shoots – raw or cooked (Thompson 1878; Uphof 1959; Hedrick 1972; Mabey 1974; Facciola 1990) – have a delicate nutty flavour with a crisp texture (Huxley 1992; Phillips & Rix 1995) and are available in spring. The shoots are usually blanched and can be cooked like asparagus (Launert 1981; Facciola 1990). When properly cooked, they retain their crispness and have a very agreeable flavour, somewhat like hazelnuts but with a slight bitterness (Facciola 1990) (see VI F). The root is eaten cooked and is rich in starch and sugars (Komarov 1968) and contains some protein. Young flower buds are eaten raw or cooked (Phillips & Rix 1995).

TAXONOMY AND PHYLOGENY

The genus *Crambe* is the second largest of the tribe Brassiceae, after *Brassica* itself (Gómez-Campo 1980; Warwick & Black 1997a), and comprises approximately 38 old-world species (Bramwell 1969; Santos-Guerra 1983, 1996; Khalilov 1991a,b). *Crambe* exhibits major disjunct distributions among four major geographical regions: Macaronesian (12 species), Mediterranean (four species), east African (three species) and Eurosiberian–southwest Asian (20 species) (Bramwell 1969; Gómez-Campo 1980; Santos-Guerra 1983, 1996; Khalilov 1991a,b).

Candolle (1821) subdivided the genus *Crambe* into three sections: sect. *Dendrocrambe* DC., sect. *Leptocrambe* DC. and sect. *Sarcocrambe* DC., primarily based on the dimensions and shape of the proximal joint of the fruits, but it closely corresponds to the geographical areas of distribution of the taxa. Sect. *Dendrocrambe* is endemic to Macaronesia, sect. *Leptocrambe* is distributed throughout the Mediterranean basin as far as the east of Africa, and sect. *Sarcocrambe* has an area of distribution that goes from the east of Europe to the steppes and mountains of Central Asia. The type species of the genus (*C. maritima* L.) was designated by Green (1925) and belonged to sect. *Sarcocrambe* (Candolle 1821) which later became the typical section, *Crambe*. Later authors, such as Prantl (1891), Schulz (1919) and Prina (2009), followed this scheme without any change, only adding new taxa.

Phylogenetic studies based on ITS regions (Francisco-Ortega *et al.* 1999, 2002) are in agreement with the findings of Prina (1999, 2000), based on morphological characters, and the generic systematics originally proposed by Candolle (1821). The phylogenetic analysis of the ITS regions of 27 species of *Crambe* and 18 related genera showed *Crambe* to be a monophyletic genus with three major monophyletic lineages with average bootstrap values of 99.75%, 91.25% and 73%, respectively. The patterns of relationships in the ITS tree are concordant with known climatic events in northern Africa and south-western Asia since the middle Miocene. The first lineage belonging to the section *Dendrocrambe* comprises those taxa endemic to the Macaronesian archipelagos; a predominant Mediterranean distribution forms the second assemblage belonging to the section *Leptocrambe*, and the third lineage, belonging to the sections *Crambe* and *Oriente-crambe*, includes all Eurosiberian–Asian taxa including *C. maritima* and a species from the highlands of east Africa (*C. kilimandscharica*). A disjunction between east Africa (*C. abyssinica*) and the Mediterranean (*C. hispanica*) occurs in the second clade, and a basal biogeographic split between east Africa and Eurasia occurs in the third clade (Francisco-Ortega *et al.* 1999).

Five major lineages were identified in the Eurasian clade. Four of these lineages included only one species each (*C. kilimandscharica*, *C. gordjagini*, *C. edentula* and *C. schugnana*). *C. maritima* was placed in the fifth and the largest lineage with 15 species, and this was strongly supported by an average bootstrap value of 95.25%. Two major groups ('*maritima*' and '*orientalis*') with average bootstrap values of 82.75% and 66% were distinguished within this lineage. All six species in the '*maritima*' group (*C. aspera*, *C. gibberosa*, *C. maritima*, *C. pinnatifida*, *C. pontica* and *C. tataria*) of the section *Crambe* have European distributions and do not occur east of the Caucasus region. In contrast, the nine species in the '*orientalis*' group have a predominantly Asian distribution. This includes two species of the section *Crambe* (*C. cordifolia* and *C. kotschyana*) and seven species of the section *Oriente-crambe* (*C. aculeolata*, *C. amabilis*, *C. cordifolia*, *C. grosheimii*, *C. koktebelica*, *C. juncea*, *C. orientalis* and *C. persica*).

An assemblage of eight genera of the subtribes Raphaniae and Brassicinae (*Brassica*, *Crambella*, *Eruca*, *Guiraoa*, *Hirschfeldia*, *Raphanus*, *Rapistrum* and *Sinapidendron*) were sister groups to *Crambe* with low levels of bootstrap support (< 50%) in the basal branches, and did not resolve relationships with *Crambe*. Both subtribes appear to be highly polyphyletic in the ITS trees (Francisco-Ortega *et al.* 1999). Phylogenetic analysis performed with 14 species of the genus *Crambe* with flavonoids as phylogenetic markers showed that *C. cordifolia*, *C. maritima* and *C. tataria* belong to the same clade and that *C. maritima* is sister to *C. tataria* as in the ITS phylogeny. The 14 species were placed in three groups which closely correspond to the three sections *Crambe*, *Dendrocrambe* and *Leptocrambe*, with the exception of *C. orientalis* (section *Crambe*) and *C. glabrata* (section *Leptocrambe*).

which were agglomerated into section *Dendrocrambe* (Aguiñagalde & Gómez-Campo 1984).

Crambe maritima L. (= *C. pontica* Steven) was originally described by Linnaeus in 1753 as one of two European species, along with *C. hispanica* L., as the Mediterranean species. *C. maritima* populations encountered on the shores of the Black Sea were named var. *pontica* (Stev. Rupr. Ex.) in 1869, according to H. Meusel in Godeau (1974). The materials from the Black Sea have also been considered by Schulz (1919), among others, to be a different taxon (*Crambe pontica* Stev. ex Rupr. or *C. maritima* L. prole *pontica* (Steven ex Rupr.) O. E. Schulz). However, no differentiating morphological traits were found between the samples from the Black Sea region and the other regions by Prina (2000).

Approximately half the members of the monophyletic tribe Brassiceae exhibit heteroarthrocarpy (Avino *et al.* 2012), including *C. maritima*. It has been debated whether heteroarthrocarpy represents an ancestral (Appel 1999) or derived (Gómez-Campo 1980) state. Phylogenetic reconstructions indicated that non-heteroarthrocarpic fruits represent the ancestral state and heteroarthrocarpy the derived state that evolved multiple times in the tribe (Hall *et al.* 2011).

XI. Conservation

Crambe maritima has shown a decline in several regions in the twentieth century (Scott & Randall 1976), but has also been found in some new sites (Briard, Horvais & Péron 2002). The decline in parts of its British range is probably because of loss of its shingle habitat due to coastal development and sea-defence works. It has also declined in other areas, notably in South Wales, possibly due to human trampling. It had 'locally rare' status in south Northumberland (VC 67) in 2012 (Groom, Young & Richards 2012), indicating that it has been recorded in three or fewer sites since 1987. It was also accorded rare status in 2012 in Cheshire (VC 58). On the other hand, this species seems to be increasing in some areas of southern England. It is much more common now on Chesil Beach than it was in the 1940s, when it was collected for culinary use. It was considered 'nationally scarce' in 1997 (recorded in 16–100 10-km squares) in Britain, but nevertheless was in the 'least concern' category in 2005 (Cheffings & Farrell 2005). It has always been very rare throughout its documented history in Northern Ireland; it is known from a single colony at Glasdrumman, north of Annalong, where in 1988, a single plant was discovered. In 1966, it was found at a new site (Portavo), where it persisted until 1975, and possibly disappeared due to human interference.

Although formerly legally protected in the Republic of Ireland under the Flora (Protection) Order, 1980, as it had been believed to be threatened with extinction in the 1960s, *C. maritima* has lost its protected status, because of the discovery of a range of new sites (Webb & Akeroyd 1991). Yet a perusal of Irish botanical literature spanning the period 1800–1970 shows that *C. maritima* has always been regarded as very rare in Ireland, the majority of populations being very small in size and transient in nature. Many of the populations

recorded during the period 1970–1999 were impermanent, very small in size, and rarely flowered and fruited. The extant populations of the species are generally small, very disjunct and very vulnerable to destruction from both natural and human threats (Mahony 2000). To date, only one accession of *C. maritima* has been collected and stored under *ex situ* conditions, but 15 different sites for collection have been identified in the priority list for the conservation of crop wild relatives (T. Curtis, unpubl. data).

The species is even rarer in France and has a 'Rare and protected plant status' in Annex 1 of the Decree of 20 January 1982, as amended 31 August 1995, and published in the Official Gazette of 17 October 1995. Many sites in France previously described in the literature have disappeared, while several new large sites have been found. A breeding programme initiated in 1992 performed a systematic search for wild populations in France, from Quiberon (south Brittany) to Dunkerque (north France near Belgium), to enlarge its genetic basis. Studies to estimate genetic variation were done to enhance the gene pool, maintain the different populations and also to help develop cultivars with desirable traits (Briard, Horvais & Péron 2002).

Apart from disturbance, decline has also been caused by several other factors such as the deterioration of Sea-kale stocks associated with vegetative multiplication that results in virus accumulation (Brown 1937), the high labour input for commercial production (Evans 1982) and low rates of germination and establishment from seed (Scott & Randall 1976). Another possible cause may have been removal of plants into cultivation at a time when this species was a more popular garden vegetable.

Vegetated shingle is one of the scarcest habitats within the British Isles, Europe and indeed the world; it is largely restricted to northern Europe, Japan and New Zealand (Walmsley & Davy 2001). Substantial permanent losses of shingle habitat have occurred both recently and historically; they have been disproportionately high in southern England primarily due to gravel extraction and building (Doody & Randall 2003). Habitat H1220, to which *C. maritima* is faithful, has increased in 10-km square occupancy across the UK slightly over the last 25 years. However, between 1994 and 2006, JNCC (2007) reported that > 25% of habitat area in the UK was in unfavourable condition.

Climate change, associated with rising sea level and coastal defence work, will affect the sediment dynamics of shingle coastline, and the fossil nature of many shingle structures suggests that there will be further decline, especially in southern England. Pye & French (1993) estimated that 200 ha of shingle vegetation should be restored in England to offset natural losses to erosion, but that the difficulties of doing this meant that habitat loss should be prevented as the options for restoration are limited. This scarcity of vegetated shingle is recognized in the UK Biodiversity Action Plan (1994). Vegetated shingle is a priority habitat for conservation, and the Habitat Action Plan for coastal shingle includes an objective to restore degraded or damaged shingle structures (UK Biodiversity Group 1999). There are 20 Local Biodiversity Action

Plans in the UK, which have reported targets for vegetated coastal shingle. Whilst most of the obvious areas (e.g. Kent, Sussex) are represented, it is difficult to make a clear link from the national plan to local plans and also to get feedback from the local plans (Houston, Rooney & Doody 2009). The Northern Ireland Habitat Action Plan for Coastal Vegetated Shingle (2005) identifies *C. maritima* as a priority species.

Early attempts to revegetate shingle arose because it was considered that substantial perennial vegetation cover would improve the stability of shingle features and reduce the need for engineered coastal protection. *Suaeda vera* was observed to be important for stabilizing shingle ridges on Blakeney Point, Norfolk (Oliver & Salisbury 1913a,b), and other species, such as *Honckenya peploides* and *Crambe maritima*, were considered to be capable of contributing to stabilization (Carey & Oliver 1918). Seeds of *Crambe maritima* and *Lathyrus japonicus* sown on shingle at Blakeney Point failed to establish self-sustaining populations (White 1967). The establishment and maintenance of a permanent flora on shingle beaches are dependent upon the mobility, matrix and moisture conditions of the beach (Scott 1963; Randall 1977; Fuller 1987).

The feasibility of restoring shingle and dune vegetation was investigated as part of the Sizewell 'B' Vegetation Restoration Project in Suffolk, UK (Walmsley & Davy 2001). Four approaches to vegetation restoration, using either sown seed or container-grown plants or the conserved natural soil seed bank, or relying on natural regeneration, were investigated. Natural regeneration and the natural soil seed-bank methods were not effective for re-establishing *Crambe maritima*. When seeds were sown, no seedling emergence occurred in the first season. After two seasons, total seedling emergence, as a percentage of the viable seed sown, was only 18% for *C. maritima*. All seedlings and established plants in all the plots were exterminated some 20 months after sowing due to burial with 15–25 cm of substrate, and none of the plants re-emerged 10 months after burial. Thus, establishment was too poor and the risk of catastrophic failure was too great on fringing shingle beaches (Walmsley & Davy 1997b). Survival of plants grown in containers and transplanted to the field was very high during the first year (Walmsley & Davy 1997b,c). Substrate composition, which was related to planting location, was the most important factor influencing plant establishment; plants were significantly larger after one season's growth in the seaward plots, which contained a higher proportion of coarse shingle (Walmsley & Davy 1997c). Container-grown plants were also better able to survive erosion or burial. Severe tidal inundation resulted in some plants being buried under up to 49 cm of material, while others were eroded by more than 30 cm 8 months after planting. *C. maritima* was able to tolerate 22 cm of erosion and burial up to a depth of 16 cm. A high percentage of plants recovered from < 10 cm erosion or burial, but greater changes in level reduced emergence rates significantly. Overall, 44% of *C. maritima* plants survived erosion or burial. Planting is best carried out soon after the high tides occurring around the spring equinox to provide the longest

possible period for establishment prior to potential disturbance by winter storms. The layout of plantings should reflect the natural distribution on the beach profile of undisturbed, reference areas of shingle. Recently planted *C. maritima* should be protected from trampling and herbivores such as rabbits (Walmsley & Davy 2001).

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References

- Aguinagalde, I. & Gómez-Campo, C. (1984) The phylogenetic significance of flavonoids in *Crambe* L. (Cruciferae). *Botanical Journal of the Linnean Society*, **89**, 277–288.
- Ancev, M. (1981) IOPB chromosome number reports. LXXXIII. (ed. A. Love). *Taxon*, **30**, 829–861.
- Appel, O. (1999) The so-called "beak" a character in the systematics of Brassicaceae? *Botanische Jahrbücher für Systematik*, **121**, 85–98.
- Appelqvist, L. (1971) Lipids in cruciferae: VIII. The fatty acid composition of seeds of some wild or partially domesticated species. *Journal of the American Oil Chemists' Society*, **48**, 740–744.
- Asen, P.A. & Andreassen, J. (1976) New vascular plant records from Aust-Agder and Vest-Agder counties south Norway Part 1. *Blyttia*, **34**, 205–210.
- Asen, P.A. & Andreassen, J. (1978) New vascular plant records from Aust-Agder and Vest-Agder counties south Norway Part 3. *Blyttia*, **36**, 95–102.
- Aune, E.I. & Frisvoll, A.A. (1984) Seakale, *Crambe maritima* found in Froan western central Norway. *Blyttia*, **42**, 165–166.
- Avino, M., Kramer, E.M., Donohue, K., Hammel, A.J. & Hall, J.C. (2012) Understanding the basis of a novel fruit type in Brassicaceae: conservation and deviation in expression patterns of six genes. *EvoDevo*, **3**, 20.
- Barbour, M.G., De Jong, T.M. & Pavlik, B.M. (1985) *Marine Beach and Dune Communities*. Chapman and Hall, New York, NY, USA.
- Baron, M. & Binet, P. (1964) Quelques aspects physiologiques de la germination des semences de *Crambe maritima* L. *Bulletin de la Société Française de Physiologie Végétale*, **10**, 263–267.
- Bauch, R. (1943) Zwei neue Pflanzenformen aus Mecklenburg. *Berichte Der Deutschen Botanischen Gesellschaft*, **61**, 132–138.
- Beck, W. (1931) Variations in the Og of plant tissues. *Plant Physiology*, **6**, 315–323.
- Beerling, D.J. & Woodward, F.I. (1997) Changes in land plant function over the Phanerozoic: reconstructions based on the fossil record. *Botanical Journal of the Linnean Society*, **124**, 137–153.
- Bird, R. (1989) *Growing from Seed*, Vol. 3 (ed. R. Bird). Thompson and Morgan, Ipswich, UK.
- Bogemans, J. & Erdet, L. (2012) *Saline Crops, from Halophyte Research to Sea Vegetable Markets*. Intellicrops bvba, Ninove, Belgium.
- Bond, J., Daniels, R. & Bioret, F. (2005) Genetic diversity in *Crambe maritima* along the English Channel: the role of ocean currents in determining population structure. *Ecography*, **28**, 374–384.
- Boullard, B. (2001) *Plantes Médicinales du Monde. Réalités et Croyances*. Estem, Paris, France.
- Bowes, B.G. (1976) *In vitro* morphogenesis of *Crambe maritima* L. *Protoplasma*, **89**, 185–188.
- Boyce, S. (1954) The salt spray community. *Ecological Monographs*, **24**, 29–67.
- Bramwell, D. (1969) The genus *Crambe* (Cruciferae) in the Canary Islands flora. *Cuadernos de Botánica Canaria*, **6**, 5–12.
- Breckle, S.-W. (2002) Salinity, halophytes and salt affected natural ecosystems. *Salinity: Environment–Plants–Molecules* (eds A. Läuchli & U. Lüttge), pp. 53–77. Kluwer, Dordrecht, The Netherlands.

- Briard, M., Horvais, A. & Péron, J.Y. (2002) Wild seakale (*Crambe maritima* L.) diversity as investigated by morphological and RAPD markers. *Scientia Horticulturae*, **95**, 1–12.
- Brown, W. (1937) A study of the deterioration of sea-kale stocks, with notes on some disease of that crop. *Journal of Pomology*, **15**, 69–85.
- Byre, A. (2001) *Crambe maritima* L. – from rare to invasive in the Oslo Fjord region. MS thesis. University of Oslo, Oslo, Norway.
- Cadée, G. (2005) Drifting branches of *Crambe maritima* L. with fruits. *Cahiers de Biologie Marine*, **46**, 217–219.
- Camus, G. (1947) Modifications histologiques provoquées par les bourgeons se développant sur des prismes de *Crambe maritima* L. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences (Paris)*, **224**, 154–156.
- deCandolle, A.P. (1821) *Crambe* L. *Regni Vegetabilis Systema Naturale*, Vol. 2, pp. 650–656. Treuttel, Würtz & Co, Paris, France.
- Carey, A.E. & Oliver, F.W. (1918) *Tidal lands: a study of shore problems*. Blackie and Son, London, UK.
- Chatto, B. (1982) *The Dry Garden*. Dent, London, UK.
- Cheffings, C.M. & Farrell, L., eds (2005) *Species Status No. 7. The Vascular Plant Red Data List for Great Britain*. Joint Nature Conservation Committee, Peterborough, UK.
- Chittendon, F. (1956) *RHS Dictionary of Plants plus Supplement*. Oxford University Press, London, UK.
- Clapham, A.R., Tutin, T.G. & Warburg, E.F. (1962) *Flora of the British Isles*, 2nd edn. Cambridge University Press, Cambridge, UK.
- Clemente-Munoz, M. & Bernejo, J.E.H. (1978) The nectar producing apparatus of the tribe brassicaceae cruciferae. *Anales del Instituto Botanico A.J.Cavinilles*, **35**, 279–296.
- Crookston, R. & Moss, D.N. (1970) The relation of carbon dioxide compensation and chlorenchymatous vascular bundle sheaths in leaves of dicots. *Plant Physiology*, **46**, 564–567.
- Darwin, C. (1857) On the action of sea-water on the germination of seeds. *Journal of the Linnean Society of London, Botany*, **1**, 130–140.
- Darwin, F. (1887) On the relation between the 'Bloom' on leaves and the distribution of the stomata. *Journal of the Linnean Society of London, Botany*, **22**, 99–116.
- Davy, A.J. & Figueroa, M.E. (1993) The colonization of strand lines. *Primary Succession on Land* (eds J. Miles & D.W.H. Walton), pp. 113–131. Blackwell, Oxford, UK.
- Davy, A.J., Willis, A.J. & Beerling, D.J. (2001) The plant environment: aspects of the ecophysiology of shingle species. *Ecology & Geomorphology of Coastal Shingle* (eds J.R. Packham, R.E. Randall, R.S.K. Barnes & A. Neal), pp. 191–201, Westbury Academic & Scientific Publishing, Yorkshire, UK.
- Daxenbichler, M.E., Spencer, G.F., Carlson, D.G., Rose, G.B., Brinker, A.M. & Powell, R.G. (1991) Glucosinolate composition of seeds from 297 species of wild plants. *Phytochemistry*, **30**, 2623–2638.
- DBIF (2015) *Database of Insects and their Food Plants*. Biological Records Centre. <http://www.brc.ac.uk/dbif/>. Accessed 1 February 2015.
- DeMars, B.G. & Boerner, R.E.J. (1996) Vesicular-arbuscular mycorrhizal development in the Brassicaceae in relation to plant life span. *Flora (Germany)*, **191**, 179–189.
- Dimmit, M.A., Wiens, J.F. & Van Devender, T.R. (2005) *Extreme Succulent Plant Diversity on Cerro Colorado near San Ignacio, Baja California Sur*. Oxford University Press, New York, NY, USA.
- Dolya, V.S., Shurupii, E.N., Podzolkova, T.V. & Kaminskii, N.A. (1973) Seed oils of some cruciferae species. *Khimiya Prirodnykh Soedinenii*, **9**, 15–18.
- Doody, J.P. & Randall, R.E. (2003) *A Guide to the Management and Restoration of Coastal Vegetated Shingle*. http://www.english-nature.org.uk/living-with-thesea/project_details/good_practice_guide/shingleCRR/shingleguide/home.htm. Accessed 1 February 2015.
- Drew, R.L.K. & Fellows, J.R. (1986) Generation of seakale (*Crambe maritima* L.) plantlets by tissue culture. *Annals of Botany*, **58**, 179–181.
- Druce, G. (1932) *The Comital Flora of the British Isles*. Buncle & Co., Arbroath, UK.
- Eklund, O. (1927) Versuche über des Keimungs- und Schwimmvermögen einiger Samen und Früchte in Ostseewasser. *Memoranda Societatis pro Fauna et Flora Fennica*, **2**, 13–29.
- Eklund, O. (1931) *Crambe maritima* in Nordbaltischen Gebiet. *Memoranda Societatis pro Fauna et Flora Fennica*, **7**, 41–51.
- Ellenberg, H., Weber, H.E., Düll, R., Wirth, V. & Werner, W. (1991) Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica*, **18**, 1–248.
- Evans, D.R. (1982) *Forcing Crops*. University Press, Bath, UK.
- Facciola, S. (1990) *Cornucopia - A Source Book of Edible Plants*. Kampong Publications, California, USA.
- Flowers, T.J., Hajibagheri, M.A. & Clipsom, N.J.W. (1986) Halophytes. *The Quarterly Review of Biology*, **61**, 313–337.
- Francisco-Ortega, J., Fuertes-Aguilar, J., Gómez-Campo, C., Santos-Guerra, A. & Jansen, R. (1999) Internal transcribed spacer sequence phylogeny of *Crambe* L. (Brassicaceae): molecular data reveal two Old World disjunctions. *Molecular Phylogenetics and Evolution*, **2**, 361–380.
- Francisco-Ortega, J., Fuertes-Aguilar, J., Seung-Chul, K., Santos-Guerra, A., Crawford, D.J. & Jansen, R.K. (2002) Phylogeny of the Macaronesian endemic *Crambe* section *Dendrocrambe* (Brassicaceae) based on internal transcribed spacer sequences of nuclear ribosomal DNA. *American Journal of Botany*, **89**, 1984–1990.
- FRDBI (2015) *The Fungal Records Database of Britain and Ireland*. British Mycological Society. <http://www.fieldmycology.net/FRDBI/assoc.asp>. Accessed 1 February 2015.
- Fuller, R.M. (1987) Vegetation establishment on shingle beaches. *Journal of Ecology*, **75**, 1077–1089.
- Fusheng, L. & Peron, J.Y. (1998) Study of the dynamics of nutritional elements in seakale (*Crambe maritima* L.) during growth. *Acta Horticulturae*, **467**, 215–226.
- Fusheng, L., Peron, J.Y. & Blanchard, N. (1998) Effect of different pre-treatments to overcome the dormancy of seakale (*Crambe maritima* L.) seeds. *Acta Horticulturae*, **467**, 233–243.
- Garnier, E., Shipley, B., Roumet, C. & Laurent, G. (2001) A standardized protocol for the determination of specific leaf area and leaf dry matter content. *Functional Ecology*, **15**, 688–695.
- Géhu, J. (1960a) La végétation des levées de galets du littoral français de la Manche. *Bulletin de la Société Botanique du Nord de la France*, **13**, 141–152.
- Géhu, J. (1960b) Un site célèbre de la côte Nord bretonne: Le Sillon de Talbert (C.-du-N.). Observations phytosociologiques et écologiques. *Bulletin du Laboratoire Maritime de Dinard*, **46**, 93–115.
- Géhu, J.M. (1964) L'excursion dans le Nord et l'Ouest de la France de la société internationale de phytosociologie. *Vegetatio*, **12**, 1–95.
- Géhu, J.M. & Géhu, J. (1959) Note phytologique concernant la station de *Crambe maritima* L. de l'anse Du Guesclin (Ille-et-Vilaine). *Bulletin du Laboratoire Maritime de Dinard*, **45**, 56–62.
- Géhu, J.M. & Géhu, J. (1969) Les associations végétales des dunes mobiles et des bordures des plages de la côte atlantique française. *Vegetatio*, **18**, 122–166.
- Géhu, J.M. & Géhu-Franck, J. (1979) Sur les végétations nord-atlantiques et baltiques à *Crambe maritima*. *Phytocoenologia*, **6**, 209–299.
- Gerdemann, J. (1968) Vesicular-arbuscular mycorrhiza and plant growth. *Annual Review of Phytopathology*, **6**, 397–418.
- Glazkova, E.A. (1998) Floristic findings on the islands of the eastern part of the Gulf of Finland. *Botanicheskii Zhurnal*, **83**, 131–133.
- Glenn, M., Chew, F.S. & Williams, P.H. (1985) Hyphal penetration of *Brassica* (Cruciferae) roots by a vesicular-arbuscular mycorrhizal fungus. *New Phytologist*, **99**, 463–472.
- Gómez-Campo, C. (1980) Morphology and morpho-taxonomy of the tribe Brassicaceae. *Brassica Crops and Wild Allies. Biology and Breeding* (eds S. Tsunoda, K. Hinata & C. Gómez-Campo), pp. 3–30. Japan Scientific Societies Press, Tokyo, Japan.
- Green, M. (1925) Standard-Species of the Linnean genera of Tetradymania. *Bulletin of Miscellaneous Information (Royal Gardens, Kew)*, **2**, 49–58.
- Groom, Q.J., Young, G. & Richards, A.J. (2012) *The Rare and Scarce Plants of South Northumberland. Rare Plant Register of South Northumberland. Version 3.0*. Botanical Society of Britain and Ireland, London, UK.
- Guppy, H. (1906) *Observations of a Naturalist in the Pacific between 1896 and 1899*. Macmillan Press, London, UK.
- Hall, J.C., Tisdale, T.E., Donohue, K. & Kramer, E.M. (2006) Developmental basis of an anatomical novelty: heteroarthrocarpy in *Cakile lanceolata* and *Eruca erucarioides* (Brassicaceae). *International Journal of Plant Sciences*, **167**, 771–789.
- Hall, J.C., Tisdale, T.E., Donohue, K., Wheeler, A., Al-Yahya, M.A. & Kramer, E.M. (2011) Convergent evolution of a complex fruit structure in the tribe Brassicaceae (Brassicaceae). *American Journal of Botany*, **98**, 1989–2003.
- Halpin, A.M.E. (1978) *Unusual Vegetables: Something New for this Year's Garden*. Rodale Press, Emmaus, PA, USA.
- Harborne, J.B. & Baxter, H. (2001) *Chemical Dictionary of Economic Plants*. John Wiley and Sons, New York, NY, USA.
- Harley, J.L. & Harley, E.L. (1987) A check-list of mycorrhiza in the British flora. *New Phytologist* (Supplement), **105**, 1–102.
- Hedrick, U. (1972) *Sturtevant's Edible Plants of the World*. Dover Publications Inc, New York, NY, USA.
- Heidt, K. (1945) Meerkohlarthen (*Crambe* spp.) als ertrageiche Öl-Gemüse und Futterpflanzen. *Pflanzenbau*, **20**, 170–176.

- Hill, M., Preston, C.D. & Roy, D.B. (2004) *PLANTATT. Attributes of British and Irish Plants: Status, Size, Life History, Geography and Habits*. Centre for Ecology and Hydrology, Huntingdon, Cambridgeshire, UK.
- Hoffmann, H. (1886) Phaenologische Beobachtungen. *Berichte Der Deutschen Botanischen Gesellschaft*, **4**, 380–399.
- Horwood, A. (1919) *British Wild Flowers in their Natural Haunts*. Gresham Publishing, London, UK.
- Houston, J.A., Rooney, P.J. & Doody, J.P. (2009) The conservation and management of coastal vegetated shingle in England: report of the meeting at Salthouse, North Norfolk, 18 September 2008. Sand Dune and Shingle Network: Occasional Paper No. 1., Liverpool Hope University Press, Liverpool, UK.
- Huxley, A. (1992) *The New RHS Dictionary of Gardening*. MacMillan Press, New York, NY, USA.
- Isermann, M. & Rooney, P. (2014) Biological Flora of the British Isles: *Eryngium maritimum*. *Journal of Ecology*, **102**, 789–821.
- Jaretsky, R. (1932) Beziehungen zwischen Chromosomenzahl und Systematik bei den Cruciferen. *Jahrbücher für Wissenschaftliche Botanik*, **76**, 485–527.
- JNCC (Joint Nature Conservation Committee) (2004) *Common Standards Monitoring Guidance for Vegetated Coastal Shingle*. Peterborough, UK. http://jncc.defra.gov.uk/pdf/csm_coastal_shingle.pdf. Accessed 13 January 2014.
- JNCC (Joint Nature Conservation Committee) (2007) *Second Report by the UK under Article 17 on the implementation of the Habitats Directive from January 2001 to December 2006*. www.jncc.gov.uk/article17 Peterborough, UK. Accessed 13 January 2014.
- Jones, W. (1925) Polarity phenomena in seakale roots. *Annals of Botany*, **39**, 359–372.
- Junghans, T. (2010) Ein bemerkenswerter Neufund des meerkohls (*Crambe maritima*) auf Borkum (Ostfriesische Inseln, Niedersachsen). *Floristische Rundbriefe*, **44**, 26–30.
- Khalilov, I.I. (1991a) The system of the genus *Crambe* (Brassicaceae). *Botanicheskii Zhurnal*, **76**, 1612–1613.
- Khalilov, I.I. (1991b) Generis *Crambe* L. (Cruciferae) sectiones tres novae. *Novosti Sistematiki Vysshikh i Nizshikh Rastenii*, **28**, 78–79.
- Knuth, P. (1908) *Handbook of Flower Pollination*. Clarendon Press, Oxford, UK.
- Komarov, V. (1968) *Flora of the USSR*. Israel Program for Scientific Translation, Jerusalem, Israel.
- Koutsikopoulos, C. & Le Cann, B. (1996) Physical processes and hydrological structures related to the Bay of Biscay anchovy. *Scientia Marina*, **60**, 9–19.
- Koyro, H.-W. & Lieth, H. (2008) *Global Water Crisis: The Potential of Cash Crop Halophytes to Reduce the Dilemma*. Mangroves and Halophytes: Restoration and Utilisation (eds H. Lieth, M.G. Sucre & B. Herzog). Springer, Dordrecht, The Netherlands.
- Lacroix, P. & Le Bail, J. (2006) *Plan de Conservation en Faveur du Chou Marin (Crambe maritima L.) en Région Pays de la Loire*. Conservatoire Botanique National de Brest, Antenne régionale des Pays de la Loire, France.
- Larkcom, J. (1980) *Salads all the Year Round*. Hamlyn Publishers, Middlesex, UK.
- Lauert, E. (1981) *Edible and Medicinal Plants*. Hamlyn Publishers, Middlesex, UK.
- Lee, J.A. & Ignaciuk, R. (1985) The physiological ecology of strandline plants. *Vegetatio*, **62**, 319–326.
- Litardière, R. & Doulat, E. (1942) Recherches caryologiques sur le *Crambe maritima* L. – Le noyau somatique et l'évolution chromosomique. *Bulletin de la Société Botanique de France*, **89**, 123–126.
- Loewenfeld, C., Back, P. & Bosanquet, P. (1980) *Britain's Wild Larder*. David & Charles Publishers, Devon, UK.
- Lysak, M.A., Cheung, K., Kutschke, M. & Bureš, P. (2007) Ancestral chromosomal blocks are triplicated in Brassicaceae species with varying chromosome number and genome size. *Plant Physiology*, **145**, 402–410.
- Mabey, R. (1974) *Food for Free*. Collins, Glasgow, UK.
- Mahony, T.O. (2000) Some comments on the flora (protection) order, 1999: Republic of Ireland. *Irish Botanical News* 10 (ed. B.S. Rushton), pp. 1–62. The Committee for Ireland, Botanical Society of the British Isles, London, UK.
- Manton, I. (1932) Introduction to the general cytology of the Cruciferae. *Annals of Botany*, **46**, 509–556.
- Martins, C. (1857) Expériences sur la persistance de la vitalité des graines flottant à la surface de la Mer. *Bulletin de la Société Botanique de France*, **4**, 324–336.
- Mayer, E. (1936) *Beiträge zur Pflanzengeographie der europäischen Sandstrand und Küstendunengebiete*. PhD thesis, University of Münster, Münster, Germany.
- Medve, R. (1983) The mycorrhizal status of the Cruciferae. *American Midland Naturalist*, **109**, 406–408.
- van der Meijden, R. (2005) *Heukels' Flora van Nederland*, 23rd edn. Wolters-Noordhoff, Groningen/Houten, The Netherlands.
- Menema, J., Quené-Boerenbrood, A.J. & Plate, C.L., eds (1985) *Atlas van de Nederlandse Flora 2. Zeldzame en vrij zeldzame planten*. Bohn, Scheltema & Holkema, Utrecht, The Netherlands.
- Molisch, H. (1912) Das Offen- und Geschlossensein der Spaltöffnungen, veranschaulicht durch ein neue Methode (Infiltrationsmethode). *Zeitschrift für Botanik*, **4**, 106–122.
- Montgomery, L., Khalaf, M., Bailey, J.P. & Gornal, K.J. (1997) Contributions to a cytological catalogue of the British and Irish flora 5. *Watsonia*, **21**, 365–368.
- Moore, W. (1959) *British Parasitic Fungi*. Cambridge University Press, Cambridge, UK.
- Munns, R. (2005) Genes and salt tolerance: bringing them together. *New Phytologist*, **167**, 645–663.
- Munns, R. & Tester, M. (2008) Mechanisms of salinity tolerance. *Annual Review of Plant Biology*, **59**, 651–681.
- Nordhagen, R. (1940) Studien über die maritime Vegetation Norwegens. I. Die Pflanzengesellschaften der Tangwälder. *Bergens Museums Årbok*, **1939–40**, 1–123.
- Oliver, F.W. & Salisbury, E.J. (1913a) The topography and vegetation of the National Trust Reserve known as Blakeney Point, Norfolk. *Transactions of the Norfolk and Norwich Naturalists' Society*, **9**, 485–542.
- Oliver, F.W. & Salisbury, E.J. (1913b) Vegetation and mobile ground as illustrated by *Suaeda fruticosa* on shingle. *Journal of Ecology*, **1**, 249–271.
- Parnell, J.A.N. (1986) Chromosome numbers of Irish plants 1. *Watsonia*, **16**, 82–83.
- Péron, J.Y. (1985) *Clone de crambé maritime (Crambe maritima L.) et procédé permettant sa multiplication végétative par culture in vitro*. Patent No. 8401984. INPI, Paris, France.
- Péron, J.Y. (1989) Physiology and cultural practices of seakale cultivated from cutting and produced like witloof. *Acta Horticulturae*, **242**, 249–258.
- Péron, J. (1990) Seakale: a new vegetable produced as etiolated sprouts. *Advances on New Crops* (eds J. Janick & J.E. Simon), pp. 419–422. Timber Press, Indianapolis, IN, USA.
- Péron, J.Y., Gouget, M. & Declercq, B. (1991) Composition nutritionnelle du crambé maritime (*Crambe maritima* L.). *Sciences des aliments*, **11**, 683–691.
- Péron, J.Y. & Régner, E. (1987) In vitro propagation of *Crambe maritima*. *Canadian Journal of Botany*, **65**, 72–75.
- Phillips, R. & Rix, M. (1991) *Perennials*, Vols 1 and 2. Pan, London, UK.
- Phillips, R. & Rix, M. (1995) *Vegetables*. Macmillan Press, London, UK.
- Plant, W. (1940) The role of growth substances in the regeneration of root cuttings. *Annals of Botany*, **4**, 607–615.
- Pompe, E. (1941) Beiträge zur Ökologie der Hiddenseer Halophyten. *Beihefte zum Botanischen Centralblatt*, **60**, 223–326.
- Prantl, K. (1891) Cruciferae. *Die Natürlichen Pflanzenfamilien*, Vol. 3 (eds A. Engler & K. Prantl), pp. 145–206. Wilhelm Engelmann, Leipzig, Germany.
- Preston, C.D., Pearman, D.A. & Dines, T.D. (2002) *New Atlas of the British and Irish flora: An Atlas of the Vascular Plants of Britain, Ireland, The Isle of Man and the Channel Islands*. Oxford University Press, Oxford, UK.
- Priestley, J.H. & Swingle, C.F. (1929) *Vegetative propagation from the standpoint of plant anatomy*. United States Department of Agriculture, Washington, USA.
- Prina, A. (1999) A taxonomic revision of *Crambe*, sect. *Leptocrambe* (Brassicaceae). *Botanical Journal of the Linnean Society*, **133**, 509–524.
- Prina, A.O. (2000) *Revisión Taxonómica del Género Crambe L. (Brassicaceae, Brassicaceae)*. Tesis doctoral inédita, Universidad Politécnica de Madrid, Madrid, Spain.
- Prina, A.O. (2009) Taxonomic review of the genus *Crambe* sect. *Crambe* (Brassicaceae, Brassicaceae). *Anales del Jardín Botánico de Madrid*, **66**, 7–24.
- Pye, K. & French, P.W. (1993) *Targets for Coastal Habitat Re-Creation*. English Nature Science No 13. English Nature, Peterborough, UK.
- Pyke, M. (1940) Observations on the distribution of vitamin B1 in some plant families. *Biochemical Journal*, **34**, 330–334.
- Quinac, A., Charrier, A., Ribaillier, D. & Péron, J.Y. (1994) Glucosinolates in etiolated sprouts of sea-kale (*Crambe maritima* L.). *Journal of the Science of Food and Agriculture*, **65**, 201–207.
- Randall, R.E. (1977) Shingle formations. *The Coastline* (ed. R.S.K. Barnes), pp. 199–213. John Wiley & Sons, London, UK.
- Randall, R.E. (2004) Management of coastal vegetated shingle in the United Kingdom. *Journal of Coastal Conservation*, **10**, 159–168.

- Rappe, G. (1984) The distribution of some lesser known thalassochorous plant species along the Belgian coast, compared with their distribution in Western Europe. *Biologisch Jaarboek [Dodonaea]*, **52**, 35–56.
- Regel, C. (1940) In Mitteleuropa wildwachsende und angebaute Ölpflanzen. *Angewandte Botanik*, **22**, 400–413.
- Ridley, H. (1930) *The Dispersal of Plants throughout the World*. Reeve, Ashford, Kent, UK.
- Rieseberg, L.H. & Soltis, D.E. (1991) Phylogenetic consequences of cytoplasmic gene flow in plants. *Evolutionary Trends in Plants*, **5**, 65–84.
- Rieseberg, L.H., Whitton, J. & Linder, C.R. (1996) Molecular marker incongruence in plant hybrid zones and phylogenetic trees. *Acta Botanica Neerlandica*, **45**, 243–262.
- Robinson, G.M. & Robinson, R. (1932) A survey of anthocyanins. II. *Biochemical Journal*, **26**, 1647–1664.
- Robinson, G.M. & Robinson, R. (1934) A survey of anthocyanins. IV. *Biochemical Journal*, **28**, 1712–1720.
- Rodwell, J.S., ed. (2000) *British Plant Communities*, Vol. 5. Cambridge University Press, Cambridge, UK.
- Rozema, J., Bijl, F., Dueck, T. & Wesselman, H. (1982) Salt-spray stimulated growth in strandline species. *Physiologia Plantarum*, **56**, 204–210.
- Ruffio-Châble, V., Chatelet, P. & Thomas, G. (2001) Developmentally aberrant plants in F1 hybrid populations of *Brassica oleracea*. *Acta Horticulturae*, **539**, 89–94.
- Santos-Guerra, A. (1983) *Vegetación y Flora de La Palma*. Interinsular Canaria, Santa Cruz de Tenerife, Spain.
- Santos-Guerra, A. (1996) *Crambe feuilleii* (Brassicaceae) Santos sp. nova for the flora of Hierro Island (Canary Islands). 2nd Symposium Fauna and Flora of the Atlantic Islands (eds Anonymous), pp. 162. Departamento de Biología, Universidad de Las Palmas de Gran Canaria, Las Palmas de Gran Canaria, Spain.
- Schulz, O.E. (1919) Cruciferae-Brassicaceae. *Das Pflanzenreich*, **70**, 228–249.
- Scott, G. (1960) *The Biology of Shingle Beach Plants with Special Reference to the Ecology of Selected Species*. PhD thesis, University of Wales, Cardiff, UK.
- Scott, G.A.M. (1963) The ecology of shingle beach plants. *Journal of Ecology*, **51**, 517–527.
- Scott, G.A.M. & Randall, R. (1976) Biological Flora of the British Isles. *Crambe maritima* L. *Journal of Ecology*, **64**, 1077–1091.
- Sellam, A., Iacomi-Vasilescu, B., Hudhomme, P. & Simoneau, P. (2007) *In vitro* antifungal activity of brassinin, camalexin and two isothiocyanates against the crucifer pathogens *Alternaria brassicicola* and *Alternaria brassicae*. *Plant Pathology*, **56**, 296–301.
- Sernander, R. (1901) *Den skandinaviska vegetationens spridningsbiologi*. T:5 Boktryckeri Aktiebolag, Uppsala, Sweden.
- Steubing, L. (1949) Beiträge zur Ökologie des Wurzelsystems von Pflanzen des flachen Sandstrands. *Zeitschrift für Naturforschung. B, Journal of chemical sciences*, **4**, 114–123.
- Storey, R. & Wyn-Jones, R.G. (1979) Responses of *Atriplex spongiosa* and *Suaeda monoica* to salinity. *Plant Physiology*, **63**, 156–162.
- Story, I.F. & Montgomery, N. (1948) Effect of heat pre-treatment on early forcing of seakale. *The Journal of Horticultural Science & Biotechnology*, **24**, 214–218.
- Stoughton, R.H. & Plant, W. (1938) Regeneration of root cuttings as influenced by plant hormones. *Nature*, **142**, 293–294.
- Straka, H. (1959) Zur Ausbreitungs- und Keimungsökologie des Meerkohls (*Crambe maritima* L.). *Schriften Naturwissenschaftliche Vereins Schleswig-Holstein*, **29**, 73–82.
- Taylor, G. (1927) Seakale cultivation. *The Journal of the Ministry of Agriculture*, **33**, 939–943.
- Thompson, B. (1878) *The Gardener's Assistant*. Blackie and Son, London, UK.
- Tommerup, I. (1984) Development of infection by a vesicular-arbuscular mycorrhizal fungus in *Brassica napus* L. and *Trifolium subterranean* L. *New Phytologist*, **98**, 487–495.
- UK Biodiversity Group (1999) *Tranche 2 Action Plans Volume V: Maritime Species and Habitats*. English Nature, Peterborough, UK.
- UK Government (1994) *Biodiversity: The UK Action Plan*. HMSO, London, UK.
- Uphof, J.C.Th. (1959) *Dictionary of Economic Plants*. H.R. Engelmann (J. Cramer), Weinheim, Germany.
- de Vos, A.C., Broekman, R., Groot, M.P. & Rozema, J. (2010) Ecophysiological response of *Crambe maritima* to airborne and soil-borne salinity. *Annals of Botany*, **105**, 925–937.
- Walmsley, C.A. (1995) *The ecology of shingle-beach vegetation in relation to its restoration*. PhD Thesis, University of East Anglia, Norwich, UK.
- Walmsley, C.A. & Davy, A.J. (1997a) Germination characteristics of shingle beach species, effect of seed ageing and their implications for vegetation restoration. *Journal of Applied Ecology*, **34**, 131–142.
- Walmsley, C.A. & Davy, A.J. (1997b) The restoration of coastal shingle vegetation; effects of substrate composition on the establishment of seedlings. *Journal of Applied Ecology*, **34**, 143–153.
- Walmsley, C.A. & Davy, A.J. (1997c) The restoration of coastal shingle vegetation; effects of substrate composition on the establishment of container-grown plants. *Journal of Applied Ecology*, **34**, 154–165.
- Walmsley, C.A. & Davy, A.J. (2001) Habitat creation and restoration of damaged shingle communities. *Ecology & Geomorphology of Coastal Shingle* (eds J.R. Packham, R.E. Randall, R.S.K. Barnes & A. Neal), pp. 409–420. Westbury Academic & Scientific Publishing, Yorkshire, UK.
- Wanntorp, H.-E. & Odegaard, F. (2005) Tre missförstadda jordloppor om förekomsten av *Psylliodes isatidis* Heikertinger, *P crambicola* Lohse och *P brisouti* Bedel i Norden Coleoptera, Chrysomelidae. *Entomologisk Tidskrift*, **126**, 191–199.
- Ward, H.M. (1908) *Trees. A Handbook of Forest Botany for the Woodlands and the Laboratory*, Vol. 4 (ed. P. Groom), Cambridge University Press, Cambridge, UK.
- Warwick, S. & Black, L.D. (1997a) Molecular phylogenies from theory to application in Brassica and allies (tribe Brassiceae, Brassicaceae). *Opera Botanica*, **132**, 159–168.
- Webb, D.A. & Akeroyd, J.R. (1991) Inconstancy of sea-shore plants. *Irish Naturalists' Journal*, **23**, 384–385.
- Westhoff, V. & Den Held, A.J. (1969) *Plantengemeenschappen in Nederland*. Thieme, Zutphen, The Netherlands.
- White, D.J.B. (1967) *An Annotated List of the Flowering Plants and Ferns on Blakeney Point, Norfolk*. National Trust, Norfolk, UK.
- Woodell, S. (1985) Salinity and seed germination patterns in coastal plants. *Vegetatio*, **61**, 223–229.
- Xiong, L. & Zhu, J.K. (2002) Salt tolerance. *The Arabidopsis Book/American Society of Plant Biologists*, **1**, e0048.