

# Biological Flora of Britain and Ireland: *Silene uniflora*<sup>†</sup>

No. 306

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#### Abstract

1. This account presents information on all aspects of the biology of *Silene uniflora* Roth (*S. maritima* With., *S. vulgaris* Garcke subsp. *maritima* (With.) Á. & D. Löve), Sea Campion, that are relevant to understanding its ecological characteristics and behaviour. The main topics are presented within the standard framework of the *Biological Flora of Britain and Ireland*: 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. *Silene uniflora* is a mat-like perennial herb that in Britain and Ireland is primarily distributed in coastal habitats, notably on sea cliffs and shingle banks but also at the drift line and rarely on sand; it also has populations on mountains and heavy metal mine waste tips. All of these substrates tend to be oligotrophic, loose-textured and freely draining, and often with adverse ion concentrations. It is found in suitable habitats around much of the Atlantic and Baltic coasts of Europe.
3. Its breeding system is gynodioecious and gynomonoecious (some individuals bearing female flowers only, some bearing hermaphrodite flowers only and others with both types of flower). The proportions of the three types of individual vary considerably between populations, but hermaphrodite flowers tend to predominate. The showy, white, nectar-producing flowers are produced continuously over the entire summer and are pollinated mainly by long-tongued Hymenoptera and night-flying moths but autogamous selfing is also frequent.
4. *Silene uniflora* and its close relative *S. vulgaris* were the subject of a classic, decadal study involving genetical and transplant experiments that was seminal in the development of 'experimental taxonomy'. More recently, attention has focused on the rapid evolution of Zn-tolerant populations of *S. uniflora* growing on mine spoil and contaminated river gravels. It has also become a model organism for the study of sexually transmitted, castrating fungal diseases in plants (notably of the genus *Microbotryum*).

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<sup>‡</sup>Nomenclature of vascular plants follows Stace (2019) and, for non-British species, *Flora Europaea*.

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## KEYWORDS

coastal plant communities, experimental taxonomy, germination, gynodioecy/gynomonocoe, insect pollination, metallophyte, *Microbotryum*, zinc tolerance

Sea Campion. Caryophyllaceae, subfamily Caryophylloideae. *Silene uniflora* Roth is a long-lived, mat-like perennial herb, with leafy shoots remaining green at the base and overwintering just above ground level.

Main tap-root producing secondary roots that vary from descending nearly vertically to a shallower spreading system. Stems procumbent to ascending, (5)10–30(60) cm, with short internodes, lower parts giving rise to new shoots to form loose or compact tufts; prostrate stems sometimes rooting adventitiously at nodes. Leaves entire, non-petiolate, opposite, decussate, glaucous and usually glabrous; laminae variable in shape and size, from narrowly oblanceolate, elliptic to linear, (10)15–30(50) × (1)3–6(10) mm. In coastal populations, leaf margin often ciliolate. Flowering stems mostly with three flowers, but varying from a single terminal one rarely to seven, in a little-branched dichasial cyme (unequal development of the pair of lateral branches not uncommon). Bracts herbaceous, sometimes with a scarios margin, narrowly lanceolate, channelled. Pedicels often elongated. Flowers 20–25 mm diameter, erect, perfectly actinomorphic. Sepals 5, joined for most of their length; calyx campanulate to urceolate or subglobose, inflated with anastomosing purplish veins, 14–21 mm long, varying in diameter from inflated (13 mm) to cylindrical (8 mm); teeth c. 3 mm. Petals white or slightly purplish, 5, free, with erect narrow claw mostly 12–16 mm long; laminae of petals normally 10–13 mm long, often overlapping and fairly deeply bilobed, hiding the calyx mouth. Corona (a crown-like ring of appendages between the petals and stamens), at the throat of the corolla, represented by two small but distinct scales or flaps per petal. Stamens normally 10, but some may be represented by vestiges only. The usually white filaments arise from the carpophore (the internode between the calyx and corolla, 3.0–4.2 mm). Anthers 1.5–2.5 mm, often purple (with anthocyanin). Styles 3(–5), free to the base. Ovary 1-celled, but septate at base. Capsules 5–10 × 4–8 mm, subglobose and papery, enclosed in the calyx, with a wide mouth and six strongly recurved teeth. Seeds blackish, rounded-reniform, 1.2–2.0 × 1.0–1.3 mm, tubercled or ‘armadillo’ (with flat plates). Air-dry mass of seed c. 1.4 mg. This information is largely derived from Marsden-Jones and Turrill (1957), who provide extensive details of variation in flower and seed structure in many populations (both British and from elsewhere), Clapham et al. (1987) and Sell and Murrell (2018).

The close relationship between *Silene vulgaris* (Moench) Garcke and *S. uniflora* has long been recognized, but the latter was afforded specific rank by Roth (1794). Following Withering (1796), British floras referred it to *S. maritima* for nearly 200 years (Babington, 1881; Clapham et al., 1962; Hooker, 1884). However, Clapham et al. (1987) and the first edition of *Flora Europaea* (Chater & Walters, 1964) demoted it again to one of eight subspecies of *S. vulgaris*. Subsequently, in the second edition of *Flora Europaea* (Chater et al., 1993), *S.*

*uniflora* was restored to specific rank, with four subspecies: subsp. *uniflora*, subsp. *thorei* (Dufour) Jalas, subsp. *prostrata* (Gaudin) Chater & Walters and subsp. *glareosa* (Jordan) Chater & Walters; of these, only subsp. *uniflora* occurs in Britain. The basis for this treatment is described by Chater and Walters (1990), who refer to five of 14 characters given by Marsden-Jones and Turrill (1957) of value ‘for diagnostic purposes’. These features are winter habit, inflorescence, flower shape, corona and teeth of the capsule. Although, unlike subsp. *uniflora*, subsp. *prostrata* and *glareosa* are hemicryptophytes, they have the other four diagnostic characters of *S. uniflora*. Subspecies *prostrata* and subsp. *glareosa* have inclined, slightly zygomorphic flowers and distinctive leaf shape, subsp. *prostrata* occurring on mountain rocks in S. Europe and subsp. *glareosa* usually on calcareous screes from the Pyrenees to the E. Carpathians. Subsp. *thorei*, with erect, actinomorphic flowers, is wholly maritime, on coastal sands of W. France (and now extinct in N. Spain). Currently, only three subspecies are recognized by Plants of the World Online (2024): subsp. *uniflora*, subsp. *thorei* (Dufour) Jalas and subsp. *petraea* (C. Hartm.) Jonsell & H.C. Prent. The last of these, featuring small-flowered, procumbent plants with few-flowered inflorescences, is endemic to the islands of Öland and Gotland in the Baltic.

*Silene uniflora* and *S. vulgaris* were the subject of a remarkable, seminal study in the development of ‘experimental taxonomy’, elaborated in Marsden-Jones and Turrill (1957). The considerable similarity between the two species has led to some confusion, especially in the older literature. *Silene uniflora* has quite often been referred to as *S. vulgaris* under the earlier names of the latter of *S. cucubalus* Wibel and *S. inflata* Sm., especially in plants growing on metalliferous soils. Distinguishing features of *S. uniflora* and *S. vulgaris* include, in the former, distinct coronal scales, herbaceous bracts and recurved teeth on the capsule, contrasted with small coronal scales, scarios bracts and erect teeth on the capsule in *S. vulgaris*. Many distinctive characters are tabulated by Baker and Dalby (1980). Both seed morphology (testa ornamentation and seed shape) and allozymes show a separation between *Silene vulgaris* and *S. uniflora*, and support the taxonomic treatment of ‘*petraea*’ as a subspecies of *Silene uniflora* (Runyeon & Prentice, 1997b).

*Silene* as currently circumscribed is a diverse genus of more than 700 species with an intricate taxonomic history. A recent large-scale analysis of its molecular phylogeny (Jafari et al., 2020) places *S. vulgaris* (and therefore presumably *S. uniflora*) in subgenus *Behenantha*, section *Behenantha*.

Studies of genetic variation in *S. uniflora* were pioneered by the early allozyme study of Baker et al. (1975), who failed to find any association between habitat and gene frequency. Subsequent work has focused on its genetic differentiation from *S. vulgaris* (see Sections 8.2 and 10), using morphometrics (Runyeon-Lager & Prentice, 2000), allozyme variation (Prentice & Giles, 1993; Runyeon

& Prentice, 1996, 1997a, 1997b) and plastid DNA markers (Prentice et al., 2011).

*Silene uniflora* is a showy, native, perennial herb, widespread on coastal shingle, sands and cliffs around Britain and Ireland but is also very localized inland on mountains and waste from metal mining.

## 1 | GEOGRAPHICAL AND ALTITUDINAL DISTRIBUTION

In Britain, *Silene uniflora* is widely and primarily distributed in coastal habitats, notably on sea cliffs and shingle banks but also at the drift line and rarely on sand (Figure 1). It is especially widespread on coasts of south-west England, western Wales, western Scotland, the Hebrides, western Ireland and throughout the Orkney and Shetland archipelagos. It is less common on the eastern coast of England, where it has not been recorded from substantial lengths of coastline. Besides its coastal sites, it occurs very rarely as a native inland in northern England, Wales, Scotland and Ireland. Relict populations from Late-glacial times are present in north and west Britain on rocks of base status (Baker, 1974; Baker & Dalby, 1980), including a few populations that follow a palaeo coastline in the Yorkshire Dales near to Ingleborough (K. Walker, pers. comm.). *Silene uniflora* also occurs in man-made inland habitats in Britain, including metalliferous mine and smelting wastes, colliery spoil, ash-tips and railway lines. In western and central Wales, it has extensively colonized shingle and gravel banks along the Rivers Ystwyth and Rheidol, in proximity to old lead/zinc and silver mine workings. It is also present, for example, on zinc mine waste in North Wales, on metalliferous slags in South Wales and the Mendips and on copper mine waste in Cornwall and south-west Ireland (Baker & Dalby, 1980). Elsewhere it occurs as a garden escape on pavements, walls, roadsides and railway ballast, and as a casual on refuse tips.

In Europe, *S. uniflora* has a wide distribution on coastal sites and also occurs in mountainous regions of central and southern Europe (Figure 2). It is present in coastal sites from Norway to Denmark, Belgium, France, Spain and Portugal as well as the Azores. It occurs in Iceland in coastal sites and also here on higher ground substantially inland (Grøntved, 1942). Around the Gulf of Bothnia, it is well distributed on the coast of Sweden and Finland (Hultén, 1971). In the Mediterranean, it is present in Italy, Sardinia, Corsica and Sicily. Inland, often montane, sites include Switzerland, Germany, Austria, Czechoslovakia, Poland, Romania and Yugoslavia (Chater et al., 1993). The distribution of *S. uniflora* is classified as Sub-oceanic Boreo-temperate by Preston and Hill (1997). It extends over some 34° of latitude from about 70° N in N. Norway and N. Russia to 36° N in Sicily.

The coastal populations of *S. uniflora* occur from just above sea level usually, to about 25 m asl, but some cliff sites are much higher. On shingle banks it is often at 4–12 m asl. Inland populations are frequently at considerably greater altitudes (Figure 3). Pearman (2023) records an upper limit of 1035 m at Stob Coire nan Lochan, Glencoe in the Scottish Highlands. Older records range from c. 250 m on the

Mendips to c. 610 m on Red Gill, Styhead Pass and Hart Crag in the Pennines in England; in Wales up to 760 m on Cader Idris; in Scotland to 970 m; and in Ireland at 430 m in Kerry, 460 m in Donegal and 690 m in Galway (Wilson, 1956). In Norway, it is reported up to 1000 m (Lid, 1963).

## 2 | HABITAT

### 2.1 | Climatic and topographical limitations

Examination of the 'climate space' occupied by *Silene uniflora* in Britain and Ireland, defined by the January and July mean temperatures of the hectads (10×10 km) in which it has been recorded, reveals a broad tolerance of temperature (Figure 4). This distribution is nevertheless clearly skewed towards milder winters (average January temperature of 4.4°C where present, compared with 3.6°C where absent) and cooler summers (average July temperature of 14.7°C where present and 15.4°C where absent). This likely reflects its predominantly coastal distribution. Its extensive geographic distribution in Europe further suggests that it is not limited by temperature there, as it must experience high temperatures in Spain and Portugal, and distinctly low temperatures in northern sites such as Iceland and northern Scandinavia, not to mention at high altitudes in the Scottish Highlands and Norway.

The mean annual precipitation in the hectads in which it occurs is 1263 mm (Hill et al., 2004), which is slightly above average for species in the PLANTATT database. However, rainfall varies considerably over the range of the plant; it is less common in the drier east than in the wetter west of Britain, but this may relate to the greater number of suitable coastal habitats on the west rather than rainfall.

Being low-growing, it is very tolerant of wind, which often reaches high velocity on coastal sites. As regards aspect, it again appears to have wide tolerance. It is more common on the crest and landward slope than the seaward slope of shingle banks (Marsden-Jones & Turrill, 1957, p. 23), but this may be largely associated with more stable conditions and higher organic content to landward. *Silene uniflora* is mainly a plant of open habitats, both coastal and inland, with high light flux. Even where it occurs in scrub of *Prunus spinosa*, the latter is low-growing and sparse, with little shade cast. Hill et al. (2004) quote an Ellenberg Value for light (L, adjusted for the British flora) of 8 for *S. uniflora* on a scale of 1–9 (i.e. 'light-loving plant rarely found where relative illumination in summer is less than 40%').

### 2.2 | Substratum

Typically, *Silene uniflora* grows on soils which are loose, well-aerated and well-drained, being absent from distinctly wet sites. Its Ellenberg Value for moisture (F, adjusted for the British flora; Hill et al., 2004) is 6 on a scale of 1–12 (i.e. moist soil but not wet). Soil texture varies considerably from pebbles to fine sand. On cliffs, *S.*

Native	GB	IR
2000–19	836	268
1987–99	770	194
1970–86	455	49
1930–69	722	136
pre-1930	170	54

Alien	GB	IR
2000–19	48	1
1987–99	6	0
1970–86	4	0
1930–69	7	0
pre-1930	4	0

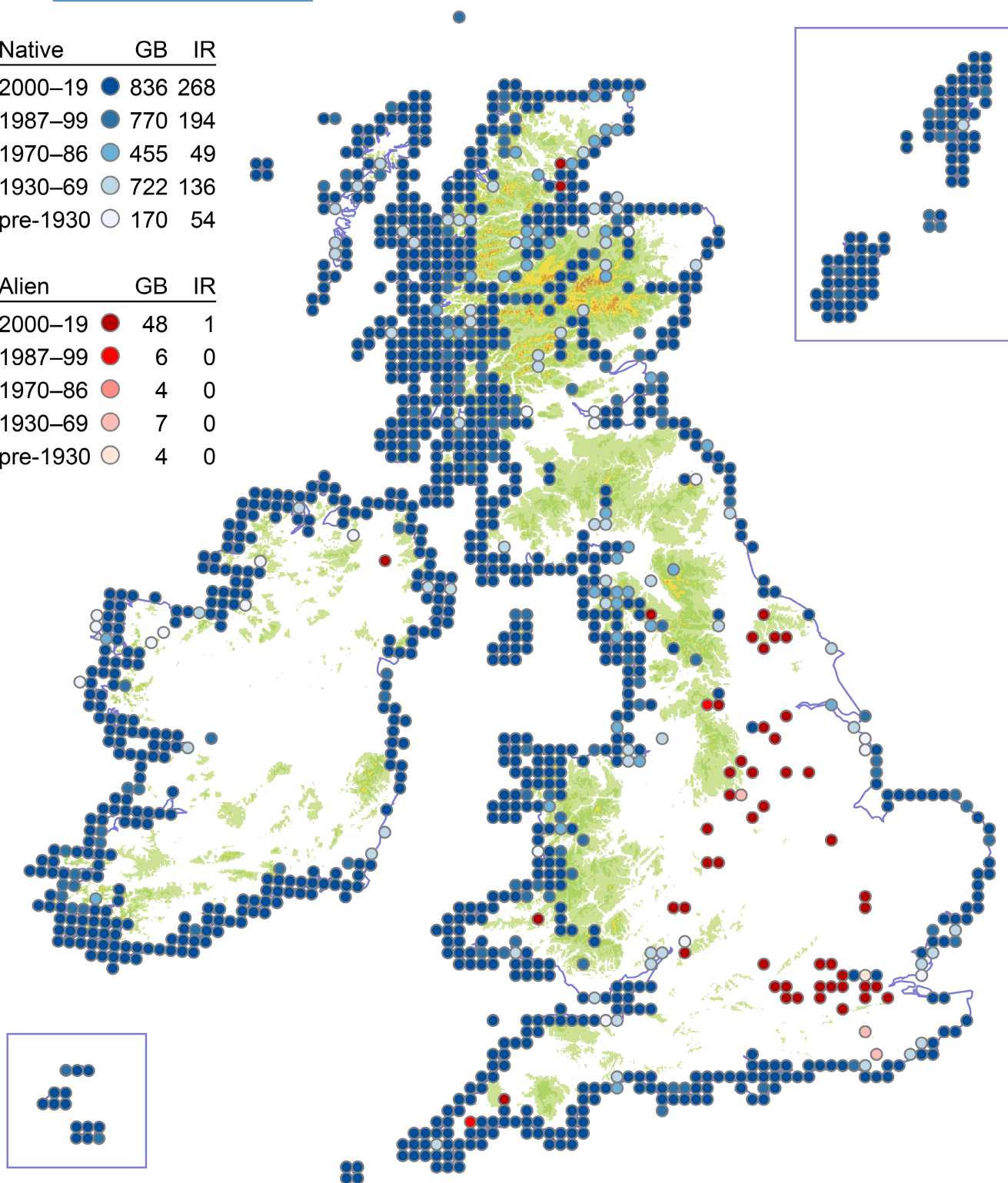


FIGURE 1 The distribution of *Silene uniflora* in the British Isles. Each dot represents at least one record in a 10-km<sup>2</sup> of the National Grid. Native (blue symbols) and alien (red symbols) distributions are distinguished. From Strohm et al. (2023).

*uniflora* grows on both lime-rich and lime-poor soils, derived from grits, shales, slates, granites, sandstones, marls and limestones (Marsden-Jones & Turrill, 1957, p. 26). On maritime cliffs in West Cornwall, *S. uniflora* occurs on many soil types, including gneiss,

hornblende schist and serpentine, with pH ranging from 4.2 to 7.7 (Malloch, 1971). This corresponds with an Ellenberg Value for pH (*R*, adjusted for the British flora; Hill et al., 2004) of 6 on a scale of 1–9 representing increasing pH. The water content of the



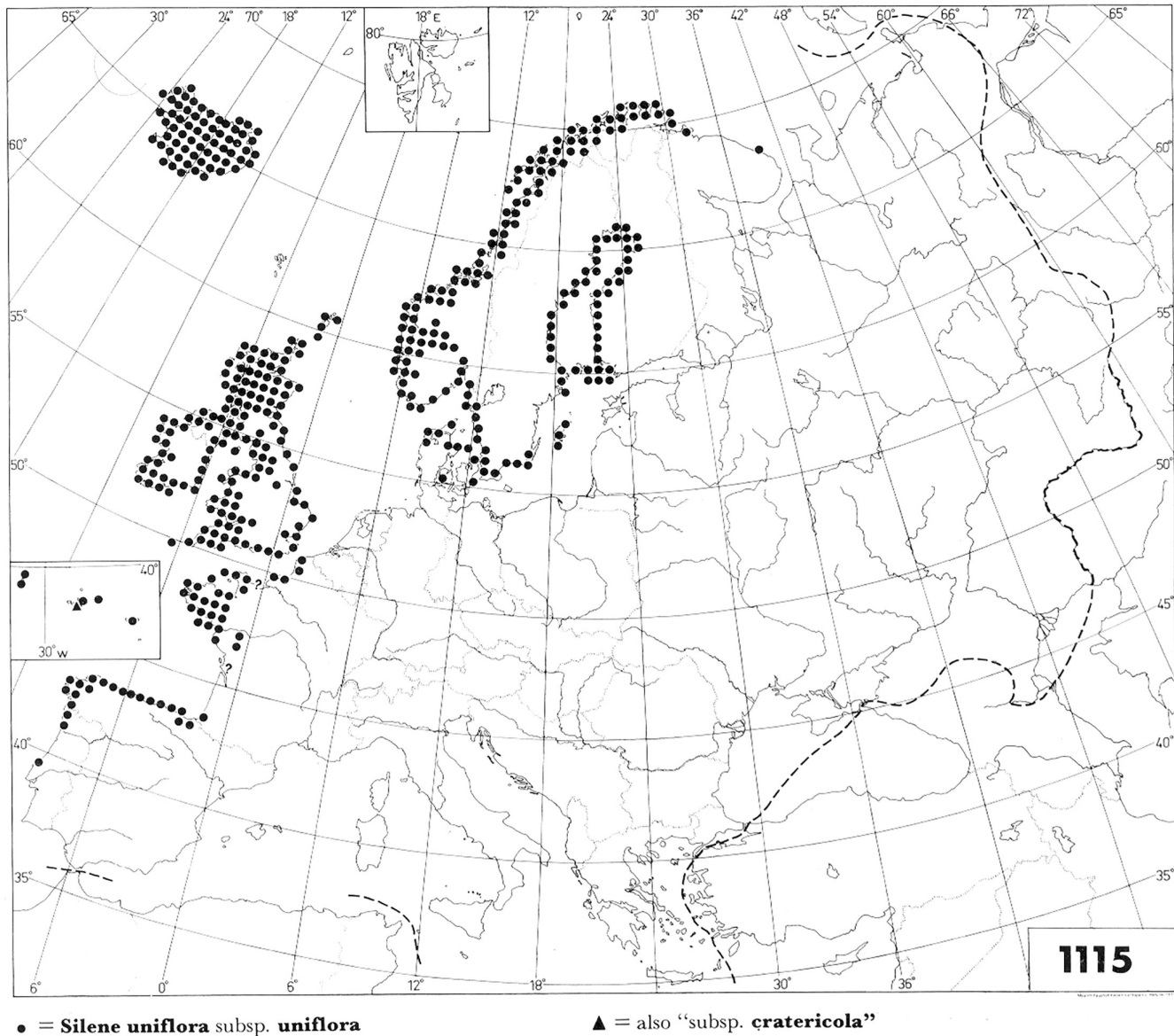


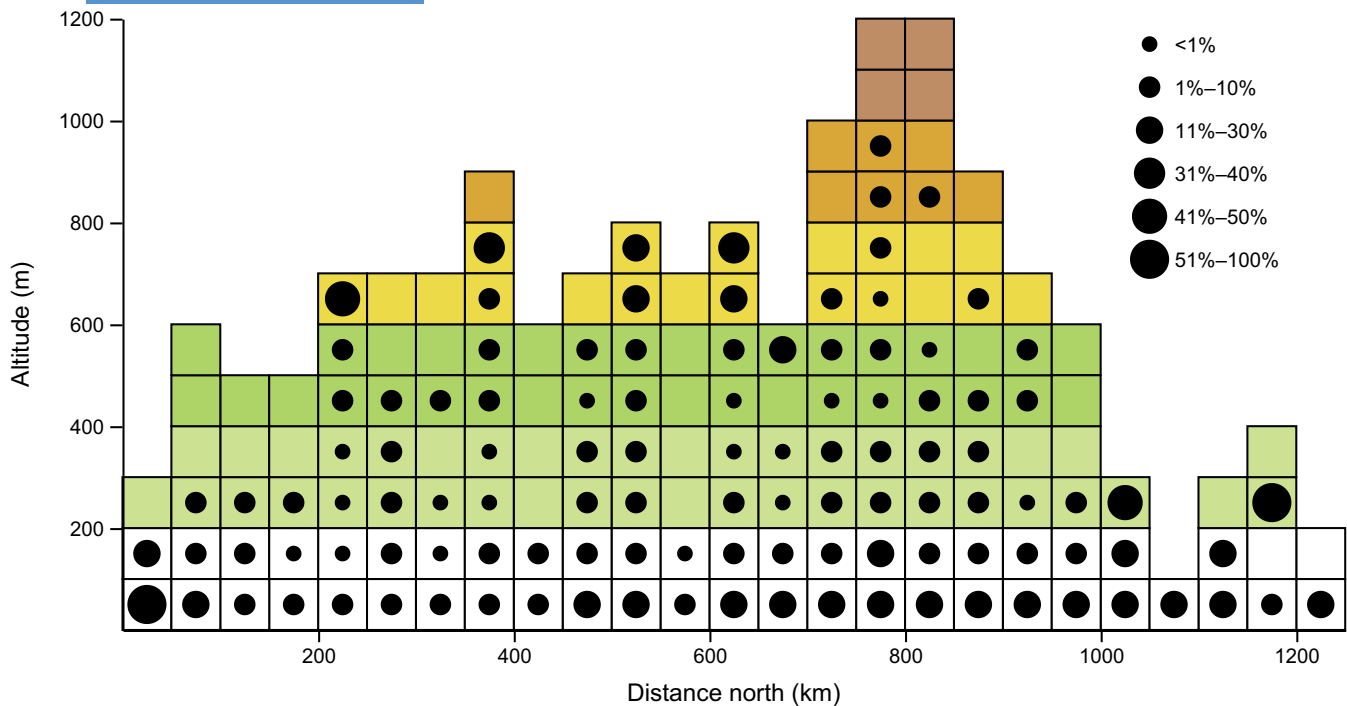
FIGURE 2 The European distribution of *Silene uniflora* (●) on a 50-km<sup>2</sup> basis. Reproduced from Atlas Florae Europaeae, vol. 7, by permission of the Committee for the mapping of the Flora of Europe and Societas Biologica Fennica Vanamo.

Cornish cliff soils varies considerably, for example, 16–133 g/100 g DW, as also does the organic content, for example, 11–43 g/100 g DW. Values for K in these soils bearing *S. uniflora* range from 0.7 to 2.0 mEq/100 g DW, for Ca from 1.9 to 9.9 mEq/100 g DW and H<sub>2</sub>PO<sub>4</sub> from 0.018 to 0.28 mEq/100 g DW (Malloch, 1971). On coastal cliffs and shingle banks, *S. uniflora* grows successfully on sites heavily manured by sea birds with high levels of N and P (Evans & Davy, 2001; Malloch, 1971; Sobey & Kenworthy, 1979). At Orford Ness, Suffolk, water-extractable concentrations of NO<sub>3</sub><sup>-</sup>, PO<sub>4</sub><sup>3-</sup>, Ca<sup>2+</sup> and Mg<sup>2+</sup> in the shingle were greatly enhanced at the sites of abandoned gull nests in comparison with non-nest sites (Evans & Davy, 2001). The Ellenberg Value for nitrogen, actually an estimate of soil fertility (N, adjusted for the British flora; Hill et al., 2004) is 4 on a scale 1–9 (i.e. low to intermediate fertility). Most of the soils supporting *S. uniflora* are affected by salinity,

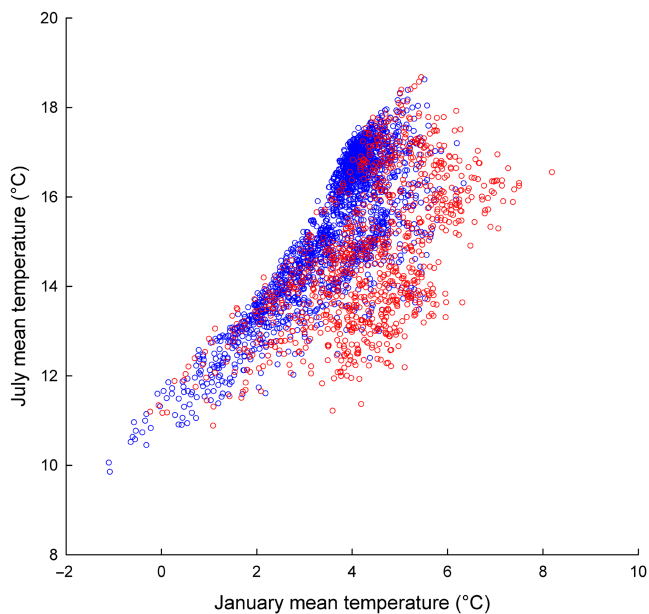
mainly through salt spray rather than more severe direct tidal influence. This is reflected in an Ellenberg Value for salt (S, adjusted for the British flora; Hill et al., 2004) of 3+ on a scale 0–9 (i.e. coastal but subject, at most, to very occasional tidal inundation). Elsewhere its soils may have ionic imbalances that would normally be regarded as adverse and it is particularly tolerant of high levels of lead, zinc and copper in mine waste and other metal-contaminated areas (see Section 6.5).

### 3 | COMMUNITIES

*Silene uniflora* is associated with a wide range of vegetation in its coastal sites but a more specialized flora inland, especially on heavy metal contaminated areas.



**FIGURE 3** The distribution of *Silene uniflora* within 50km latitudinal by 100m altitudinal bands in Britain (not including Ireland). The plot shows the proportion of all available tetrads ( $2 \times 2$  km) in each latitude/altitude cell in which the species has been recorded in the BSBI database. From Stroh et al. (2023).



**FIGURE 4** 'Climate space' occupied by *Silene uniflora* as represented by mean January and July temperatures in hectads of the British and Irish National grids. Red symbols represent hectads where *S. uniflora* is present; blue symbols those where it is absent. Climate data (downloaded from Hill et al., 2004) and distribution data (downloaded from Stroh et al., 2023) both supplied by Kevin Walker and BSBI.

On maritime cliffs, *S. uniflora* is an important component in many community types (Malloch, 1971; Rodwell, 2000), with total vegetation cover ranging from low values (e.g. 20%) to completely closed

vegetation (100%). In West Cornwall, *S. uniflora* grows in cliff bluebell communities, described by Malloch (1971) in the new association Endymio-Armerietum and by Rodwell (2000) in the National Vegetation Classification (NVC) as the *Festuca rubra-Hyacinthoides non-scripta* maritime bluebell community (MC12). This vegetation is a lush carpet of *Festuca rubra*, *Hyacinthoides non-scripta* with *Holcus lanatus*, scattered *Rumex acetosa* and many other species. In the *Armeria maritima* sub-community, *S. uniflora* is a constant species and also attains moderately high Domin values in the grassy sward, where there are small amounts of associated maritime species, including *Beta vulgaris* subsp. *maritima*, *Cochlearia danica* and *Spergularia rupicola*. *S. uniflora* has a lower frequency and cover in the *Ranunculus ficaria* (*Ficaria verna*) subcommunity, where bluebell is strongly dominant, but *Festuca rubra*, *Holcus lanatus* and *Dactylis glomerata* are also constant contributors to the ungrazed sward. The maritime bluebell community is typically found on deep, moist and fertile soils (hornblende schists), where the maritime influence may limit the spread of potentially dominant grasses such as *Arrhenatherum elatius* (Rodwell, 2000). This community is well represented in the Lizard and Land's End and is more sparsely distributed on the west coast of England and Wales northwards to Skye.

Also represented in West Cornwall as well as on the south coast and the west coast northwards to the Mull of Galloway, and on the Burren, Ireland (Malloch & Okusanya, 1979), is the MC1 *Crithmum maritimum-Spergularia rupicola* maritime rock-crevice community (Malloch, 1971; Rodwell, 2000), which is characterized by skeletal soils and the strong influence of salt spray. Here *S. uniflora* occurs with low frequency (I-II) in all three subcommunities where its

associates include the two dominants, and variously *Armeria maritima*, *Catapodium marinum*, *Limbarda crithmoides*, *Plantago coronopus*, *P. maritima* and *Tripolium pannonicum*. This community is replaced north of Galloway (Scotland), extending to Shetland, by the *Armeria maritima*–*Ligusticum scoticum* maritime rock-crevice community (MC2, Rodwell, 2000), as the most maritime vascular plant community. As in MC1, the vegetation is low-growing, with very open cover and *S. uniflora* attains higher frequency (III). There is no single dominant, *Armeria maritima*, *Festuca rubra* and *Ligusticum scoticum* all being abundant in particular stands. This community occurs on all rock types, with pH about 7, and is also found on some spray-drenched shingle beaches. Associates of *S. uniflora* here include, besides the dominants, *Plantago maritima*, *Rhodiola rosea*, *Tripleurospermum maritimum* and the moss *Schistidium maritimum*. In northern Scotland, around the coast from Islay to Aberdeen, *S. uniflora* is a fairly frequent (II) component of the MC3 *Rhodiola rosea*–*Armeria maritima* cliff ledge community (Rodwell, 2000); here, and in later mentioned NVC cliff communities, the often-fragmentary stands, with robust plants, are on rock ledges inaccessible to grazing animals. On the south coast of England, *S. uniflora* is similarly frequent in the *Beta vulgaris* subsp. *maritima* sub-community of MC4 *Brassica oleracea* maritime cliff ledge community. Mainly on the south coast of England and the west coasts of England and Scotland, *S. uniflora* achieves low to moderate frequency (I–II) in the four subcommunities in the species-diverse MC5 *Armeria maritima*–*Cerastium diffusum* subsp. *diffusum* maritime therophyte community. Here in quickly draining very shallow soils, in short open turf, it is typically associated with, for example, *Aira praecox*, *Anthyllis vulneraria*, *Arenaria serpyllifolia* and *Catapodium marinum*. Although generally infrequent in the MC6 *Atriplex prostrata*–*Beta vulgaris* subsp. *maritima* sea-bird cliff community in south and western England, *S. uniflora* in some places occurs in fair abundance. Notwithstanding the enrichment of the soil with nutrients by guano, intense disturbance by sea birds and high maritime influence are strong influences on this vegetation (Rodwell, 2000). Similarly, on the Pembrokeshire island of Skokholm, it is found in many of the puffin colonies, being often co-dominant with *Agrostis capillaris*. Here also it grows in the heavily manured nesting grounds of Lesser black-backed gulls (Goodman & Gilham, 1954). Furthermore, it is locally frequent in gull-affected sites on the north-east Scottish coast (Sobey & Kenworthy, 1979) and on the shingle spit at Orfordness, Suffolk (Evans & Davy, 2001).

*Silene uniflora* is also found in all types of maritime grassland recognized in the NVC (Rodwell, 2000). It occurs in MC8 *Festuca rubra*–*Armeria maritima* maritime grassland, which is well represented on the south and south-west coasts of England, and in Wales and Scotland. It is a constant in the *Anthyllis vulneraria* subcommunity, which has *A. vulneraria* and *Festuca rubra* as co-dominants; *Armeria maritima* and *Agrostis stolonifera* are also constant. Other associates include *Holcus lanatus*, *Plantago maritima*, *Lotus corniculatus*, *Sedum anglicum* and *Sonchus oleraceus*, to yield a colourful community in the flowering season. *S. uniflora* occurs with low frequency in the six other subcommunities described. *Silene uniflora* also persists at generally low frequency in the complete cover of the MC9 *Festuca*

*rubra*–*Holcus lanatus* maritime grassland, which occupies less maritime positions in coastal cliffs, mainly in Scotland and the west coast of the British Isles (Rodwell, 2000). It is a preferential occasional species in the *Dactylis glomerata* subcommunity, along with *Anthyllis vulneraria*. Although *Festuca rubra* is generally dominant, *D. glomerata*, *Daucus carota* subsp. *gummifer*, *Holcus mollis*, *Rumex acetosa* and *Scilla verna* are constants; other typical associates are *Lotus corniculatus* and *Hypochoeris radicata*. In the *Primula vulgaris* subcommunity of MC9, *F. rubra* dominates, *H. lanatus* is abundant and *Dactylis glomerata*, *Primula vulgaris* and *Rumex acetosa* are constants. In this subcommunity *Geranium sanguineum*, in association with *S. uniflora*, is a notable component on the base-rich serpentine soil of cliffs at the Lizard, Cornwall, where distinctive members of the vegetation include *Brachypodium sylvaticum*, *Filipendula vulgaris* and *Polygala vulgaris* (Malloch, 1971). In Ireland a *S. uniflora*–*Geranium sanguineum* community, quite similar in composition to that at the Lizard, was recognized by Braun-Blanquet and Tüxen (1952). *Silene uniflora* is a relatively minor component of the *Armeria maritima* subcommunity of the MC10 *Festuca rubra*–*Plantago* spp. maritime grassland, mainly in Scotland, where *Plantago coronopus*, *P. lanceolata* and *P. maritima* have high constancy (Rodwell, 2000). It is found at low frequency in all three subcommunities of the MC11 *Festuca rubra*–*Daucus carota* subsp. *gummifer* grassland commonly on chalk and limestone cliffs mainly on the south coast of England and Wales. Important associates here include *Bromus hordeaceus* subsp. *feronii*, *Ononis repens* and *Poterium sanguisorba*. In south-west England, *S. uniflora* is one the obviously maritime plants occasionally found in the *Dactylis glomerata* subcommunity of the W22 *Prunus spinosa*–*Rubus fruticosus* scrub community (Rodwell, 1991a). This coastal sea-cliff scrub has wind-pruned *P. spinosa* about 1 m tall, with some *Ulex europaeus*, in an open patchy canopy. Grasses are conspicuous here with a few maritime species, for example, *Armeria maritima*. In coastal sites around Britain supporting the MG11 *Festuca rubra*–*Agrostis stolonifera*–*Potentilla anserina* grassland, *Atriplex prostrata* subcommunity, *S. uniflora* may be present at modest frequency (Rodwell, 1992). In addition, occasional plants of *S. uniflora* may be found in the *Armeria maritima* subcommunity of the H7 *Calluna vulgaris*–*Scilla verna* heath community on maritime cliffs with base-poor soils on the west coast of Britain (Rodwell, 1991b).

*Silene uniflora* is a frequent member of the vegetation which develops on shingle banks which are described as its habitat *par excellence* by Marsden-Jones and Turrill (1957); this vegetation is present on the coast from north Norfolk to southern England and more fragmentarily on the west coast of Britain. These shingle banks are just beyond the reach of all but the most exceptional tides. The commonest vegetation is classified as SD1 *Rumex crispus*–*Glaucium flavum* shingle community, with these two species constant (Rodwell, 2000). Two subcommunities are recognized, the more open and diverse kind designated 'Typical' and the *Lathyrus japonicus* subcommunity which is largely confined to the south-east coast, but with a few stands in the south-west. *Silene uniflora* is regarded as common in the former subcommunity but is similarly frequent in the latter (II). It is one of the most frequent

occasional plants that, although scattered, can become locally abundant (Rodwell, 2000). The major species of these subcommunities contrast considerably with those of maritime cliffs, with some showy plants, for example, *Crambe maritima* and *Glaucium flavum* being widespread and grasses rather poorly represented in the 'Typical' sub-community. Other common associates are *Beta vulgaris* subsp. *maritima* and *Honckenya peploides*. Striking stands are permanent features of beaches and spits, for example, Orford Ness, Dungeness, Chesil Beach. In the *Lathyrus japonicus* subcommunity, *Crambe maritima* and *G. flavum* are less prominent, but *L. japonicus* forms quite extensive patches. Grasses, notably *Holcus lanatus* and *Arrhenatherum elatius*, are more frequent here in the somewhat less varied flora. With increase in stability, dominance may pass to *A. elatius*, *Festuca rubra* and *S. uniflora*, the shingle hemicyptophytes being excluded. The *Arrhenatherum*–*Silene* association is well developed at Orford Ness and Dungeness. On the Orford shingles, *S. uniflora* is abundant in both pioneer and established communities, its mat-like form stabilizing mobile shingle, giving a micro-environment favourable to other plants, and so shaping vegetation patterns (Randall & Fuller, 2001). The greater stability given by clumps of *S. uniflora* leads to colonization by lichens including *Cladonia* spp. and a range of bryophytes including *Hypnum* spp. and at Shingle Street, Suffolk the local *Rhynchostegium megapolitanum* (Lambley & Hodgetts, 2001). Scattered individuals of *S. uniflora* may be found on the drift line of beaches in the community SD2 *Honckenya peploides*–*Cakile maritima* strandline (Rodwell, 2000). Also, it is one of the many maritime species that may occur in small quantity associated with drift litter deposition at the upper reaches of salt marshes, in the SM28 *Elymus* (*Elytrigia*) *repens* salt-marsh community.

Inland sites of *S. uniflora* include metalliferous mine and smelting wastes, disused railway lines, colliery spoil, ballast sand and ash-tips (Baker & Dalby, 1980) with a wide range of ruderal and other species. On old lead mine workings at Priddy and Charterhouse, Somerset, associates include *Arenaria serpyllifolia*, *Festuca rubra*, *Holcus lanatus*, *Plantago lanceolata*, *Rumex acetosa* and *Sabulina verna* (Marsden-Jones & Turrill, 1957). Near Charterhouse and Shipham, Somerset, old calamine workings support *S. uniflora* in association with *Noccaea caerulea*, as also at Cwmsymlog lead mine, Cardiganshire and on zinc mine wastes near Betws-y-Coed, North Wales (Baker, 1974). In South Wales at Llyn-y-fan-fach, Black Mountains and on Pen-y-Fan, Breconshire, *S. uniflora* occurs with arctic-alpine species such as *Galium boreale* and *Huperzia selago* and near Dolgellau, Merionethshire, it grows in copper-enriched soil with *Armeria maritima* and *Sabulina verna* (Baker, 1974). In Scotland, *S. uniflora* occurs inland in a number of sites, including Morvern, Argyll, at about 490 m, where it is associated with *Arenaria norvegica* subsp. *norvegica* on a base-rich lithosol (Baker, 1974). It also occurs with *Arenaria norvegica* on peridotite on Ruinsval on Rum, serpentine on the Keen of Hamar and Sobul on Unst and Beinn Iadain in Morvern (K. Walker, pers. comm.). On the extensive debris of the serpentine of the barrens of the Keen of Hamar, Unst, Shetland, *S. uniflora* contributes to the sparse vegetation which includes *Agrostis stolonifera*, *Thymus*

*drucei* and the rare *Cerastium nigrescens* var. *nigrescens* (Proctor & Woodell, 1971). The infertility here is compounded by phosphorus deficiency and low levels of potassium and nitrogen. In the montane serpentine outcrop site (600 m) at Blackwater, Banffshire, Scotland, where debris is lacking over most of the area, the vegetation cover is greater and an associate here of *S. uniflora* is *Sabulina verna* (Proctor & Woodell, 1971).

In France, three coastal associations containing *S. uniflora* are characterized by Géhu and Géhu (1969). The Euphorbio-Ammophiletum *arenariae* association extends from Finistere along much of the Channel coast. Besides *Euphorbia paralias* and *Ammophila arenaria*, important components of this vegetation include *Crambe maritima*, *Crithmum maritimum*, *Elytrigia juncea*, *Glaucium flavum* and *Honckenya peploides*. In the sub-association, Crithmo-Crambetum-Silenetosum *maritimae* (of the Crithmo-Crambetum *maritimae* association), developed on shingle banks, substantial amounts of *S. uniflora* are accompanied by, for example, *Beta vulgaris* subsp. *maritima*, *Geranium purpureum* subsp. *forsteri* and *Rumex crispus*. The Honckenietum *peplidis* association is well represented on the shores of the Atlantic coast of France and extends as far south as Portugal. *Silene uniflora* grows with, for example, *Atriplex hastata*, *A. laciniata*, *Cakile maritima*, *Crambe maritima* and *Elymus obtusiusculus* besides *Honckenya peploides*. In Norway (Skogen, 1965) and in the Faroes (Ostenfeld, 1908), the coastal vegetation is similar to that of *Armeria maritima*–*Ligusticum scoticum* maritime rock-crevice community (MC2). In Iceland, shingle areas bear *S. uniflora* in association with, for example, *Leymus arenarius* and the arctic-boreal *Mertensia maritima* (Doody, 2001); the latter was formerly in shingle sites in northern Denmark supporting *S. uniflora* (Vestergaard, 2001).

#### 4 | RESPONSE TO BIOTIC FACTORS

It is likely that the distribution and abundance of *Silene uniflora* is broadly limited by interspecific competition. Its habitats, characterized by combinations of poor water retention, low nutrient supply, salinity and toxic heavy metal ions, can be regarded as refugia from intense competition from species able to exploit more congenial conditions. Nevertheless, although important as a pioneer on shingle and often in sparse vegetation (see Section 5.1), it can be a strong competitor, particularly in coastal habitats; it persists in many seral stages, even when plant cover is complete. It can grow strongly when plant cover is complete, for instance producing tall shoots on shingle when associated with *Arrhenatherum elatius*, but maintaining a more prostrate habit when cover is complete but lower growing. *S. uniflora* plays a role in stabilizing coastal shingle and can facilitate the establishment of other species thus promoting successional development (see Section 5.1).

Grazing is not a feature at most sites or in the communities occupied by *S. uniflora*, with a likely inference that animal activity would have adverse effects. It is reported that during a drought, sheep deserted their parched pastures to graze on *S. uniflora* on



Chesil Bank, Dorset, which suggests that although not preferred it is palatable when fodder is scarce elsewhere (Oliver, 1912). Rabbits may consume the flowers down to the ovary, apparently leaving the leaves untouched but denuding areas of shingle of bloom, as at Blakeney Point, Norfolk (Rowan, 1913). It is not clear how widespread this may be but there is the potential for greatly reduced reproductive output locally. Castrating fungal 'smuts' of the genus *Microbotryum* are of wide occurrence and may considerably reduce seed set (see Section 9.3). A severe attack of the smut results in complete sterility (Marsden-Jones & Turrill, 1957, p. 267).

Although many insects, most notably the larvae of noctuid moths, feed on *Silene uniflora*, damage to the plant does not usually seem to be considerable (see Section 9.1).

## 5 | RESPONSE TO ENVIRONMENT

### 5.1 | Gregariousness

Plants of *Silene uniflora* can occur as single individuals or may form small or large patches. In many of its coastal habitats, it is often present in open vegetation rather than a closed sward. Indeed it may be a pioneer on shingle, where, associated with thin *Arrhenatherum elatius*, it forms a partial cover. On some shingle beaches, there is a linear patterning resulting from a series of ridges and low areas, with the finer mixture of the shingle matrix on the ridges serving as a trap for seed (Randall & Sneddon, 2001). With temporal succession landwards, *S. uniflora* shows larger tufts aggregated in patches, some as large as, for example, 5 m<sup>2</sup>, at the inland margins of the shingle system. The important role of *S. uniflora* in seral progression on shingle in a number of coastal sites in Britain is discussed by Randall and Sneddon (2001). At Orford Ness, Suffolk, *S. uniflora* is considered to be the major species shaping overall vegetation patterns (Randall & Fuller, 2001). The stabilizing effects of the tufts of *S. uniflora*, with their horizontally spreading, prostrate stems that root adventitiously at the nodes, combined with the humus from their dead remains, result in conditions favourable to many other plants. On inland sites with metalliferous and mine wastes, vegetation is generally sparse, *S. uniflora* forming scattered but often substantial tufts. Pettersson (1997) found no disadvantage for seed set in solitary plants in comparison with clumped ones for subsp. *petraea* (see Section 8.1).

### 5.2 | Performance in various habitats

The 'Transplant Committee' of the British Ecological Society established a pioneering, long-term transplant experiment on four contrasting soil types at Potterne, Wiltshire in 1928. They monitored the performance of nine species, including *Silene uniflora*, for 10 years (Marsden-Jones & Turrill, 1930). Initially *S. uniflora* grew best on the local soil (a sandy silt, derived from the Upper Greensand), but in the

longer term, all plants on this substrate died. Subsequently those on imported chalky sand were deemed best and those on an imported calcareous clay worst; on clay, the stems became decidedly woody with sparse leaves (Marsden-Jones & Turrill, 1938).

Considerable differences in heights of flowering stems of *S. uniflora* from many localities in the field are recorded by Marsden-Jones and Turrill (1957), plants on mine waste tending to be the shortest. Stem lengths may be substantially greater under cultivated conditions (35 cm) than in the wild (24 cm), whereas no difference was found in this respect in *S. vulgaris*. The contrasting behaviour in *S. uniflora* may be partly associated with degree of exposure or soil factors. On the Pembrokeshire island of Skokholm, *S. uniflora* was reported to reach its greatest luxuriance on moist untrodden soil percolated by cliff flushes (Goodman & Gilham, 1954). Here too it was found to be very tolerant of heavy manuring, growing in the nesting grounds of lesser black-backed gulls and associated with puffin colonies. At Orford Ness, Suffolk, the cover of *S. uniflora* was significantly greater in 1-m quadrats centred on abandoned gull nest sites than on nearby non-nest sites, the greatly increased nutrient status (particularly N and P) of nest sites still being evident a year after abandonment (Evans & Davy, 2001).

Variation in vegetative characteristics between populations of *S. uniflora* was not considered high by Marsden-Jones and Turrill (1957). Nevertheless, they reported a narrow-leaved form on Chesil Beach, Dorset, and that plants on shingle have entirely or mostly armadillo seed, whereas those of cliffs and inland sites usually have tubercled seed. A detailed study of morphological variation by Baker and Dalby (1980) showed, however, significant divergence in populations in qualitative and quantitative vegetative and floral characters. Length/width ratios of the leaves differed significantly between populations, plants from metal-contaminated soils having long, narrow leaves whereas those of coastal and arctic-alpine plants were shorter, wider and fleshier. Differences were also shown in growth habits. Physiological differences in population on metalliferous soil and other sites are considered in 6.5.

### 5.3 | Effect of frost, drought, etc.

*Silene uniflora* appears to be highly tolerant of low temperatures, as it is known at high altitudes and latitude, although there may be some stem die-back under severely cold conditions (see Section 6.3). In some of its coastal sites, it experiences considerable differences in day and night temperatures. In the Mediterranean, it may sometimes be exposed to very high temperatures.

No evidence has been found of *S. uniflora* suffering from drought. On the contrary, when growing on shingle, it appears to have a copious supply of water even when other habitats are severely droughted (Davy et al., 2001; Oliver, 1912; Tansley, 1939). After a prolonged drought in 1911, when mainland grass was completely parched in September, sheep grazed in 'considerable quantities' of 'fresh succulent' *S. uniflora* on Chesil Beach (Bank), Dorset (Oliver, 1912, with photograph dated 25 September 1911).



Wind damage, even in exposed sites, seems minimal; in wind-swept areas, shoots lie close to the ground.

## 6 | STRUCTURE AND PHYSIOLOGY

### 6.1 | Morphology

The anatomy of *Silene uniflora* has been compared comprehensively with that of the closely related *S. vulgaris* as part of the long-term study led by Marsden-Jones and Turrill (1957): Hungerbühler (1956) dealt with leaf and stem anatomy; Pratt (1932) documented the vascular anatomy of the flowers; and Millner (1934) similarly described root anatomy.

Root systems vary with soil types. In sandy soil, the main tap-root has about seven secondaries from the top of the crown spreading horizontally (Marsden-Jones & Turrill, 1957). In loose shingle, the tap-root is usually over 0.7 m long, with secondary branches at an acute angle.

Stems of the cushion-like tufts are usually prostrate but ascending towards their ends. Compact tufts are formed of much-branched stems with short internodes, with leaves close together. In permanent pasture, plants may have a 'strict' habit, with slender wiry stems and erect leaves hiding the internodes (Marsden-Jones & Turrill, 1957). The opposite and decussate leaves are amphistomatous, with stomata of the diacytic (caryophyllaceous) type. In plants from Sizewell Beach, Suffolk, UK stomatal density was  $123.4 \pm 36.2/\text{mm}^2$  ( $n=20$ , mean  $\pm$  SD) on the adaxial (upper) leaf surface and  $106.6 \pm 21.0/\text{mm}^2$  on the abaxial surface, with pore lengths of  $27.3 \pm 7.2 \mu\text{m}$  and  $41.4 \pm 11.6 \mu\text{m}$ , respectively. The stomatal index  $(S/(E+S)) \times 100$ , where  $E$  is the number of epidermal cells per unit area and  $S$  the number of stomata in the same area, was  $28.4 \pm 3.1$  on the axial surface and  $28.4 \pm 2.9$  on the abaxial surface, higher than the values of many shingle species (Davy et al., 2001). Hungerbühler (1956) quotes stomatal frequencies of 80–160/ $\text{mm}^2$  for different specimens, with the guard cells slightly sunken below the epidermal surface (unlike *S. vulgaris*).

### 6.2 | Mycorrhiza

As in a number of other British species of *Silene*, *S. uniflora* appears to be entirely non-mycorrhizal (Harley & Harley, 1987).

### 6.3 | Perennation: Reproduction

*Silene uniflora* is a long-lived perennial, with a chamaephyte life form, the surviving buds being close to the ground. Normally the plant remains green during the winter, bearing dormant buds which grow out in the following spring. However, under severe cold and strong winds, some shoots may be killed and there is die-back towards the centre of a tuft, with growth the following year from buds near to

the rootstock (Marsden-Jones & Turrill, 1957). Plants usually persist for a substantial number of years.

Flowering occurs in 1-year-old plants and subsequently annually, for an average at least 5 years. Seeds sown in September 2023 and overwintered as seedlings in an unheated glasshouse in Norfolk, United Kingdom, started flowering less than 6 months later in April 2024 (personal observation). Severe infection by fungi of the genus *Microbotryum* (see Section 9.3) may considerably reduce seed production in *S. uniflora*.

### 6.4 | Chromosomes

All of the many specimens of *S. uniflora* examined by Marsden-Jones and Turrill (1957) had  $2n=24$ . Subsequently, Cobon and Murray (1983a) noted that the karyotype was very uniform, with 24 metacentric or sub-metacentric chromosomes, and found no differentiation between populations from coastal and heavy metal-contaminated sites. Similarly, no differences have been found between the chromosomes of serpentine and non-serpentine plants of *S. uniflora* (Proctor & Woodell, 1975). Meiosis in reciprocal crosses between plants from coastal and metal-contaminated habitats revealed no cryptic structural hybridity (Cobon & Murray, 1983a). On the other hand, populations of *S. uniflora* do have unstable numbers of B-chromosomes (Cobon & Murray, 1983b). B-chromosomes, which were small ( $0.8 \mu\text{m}$ ), telocentric and apparently euchromatic, were found in seven out of 39 British populations, all seven from the Norfolk coast. Cloned plants that had been subjected to stress by the addition of NaCl to their nutrient solution did not show any change in the number or distribution of B-chromosomes, and there was no evidence that their presence had any adaptive significance.

### 6.5 | Physiological data

#### 6.5.1 | Growth, photosynthesis and respiration

A study of the influence of growth temperature on the underlying components of relative growth rate (RGR) included *Silene uniflora*, as a representative slow-growing plant of an infertile habitat (Loveys et al., 2002). Notwithstanding its designation, *S. uniflora* showed a moderately high RGR in growth cabinets using hydroponic culture (Table 1). RGR was remarkably constant over the temperature range 18–28°C; however, its components revealed that this stability masked a more than halving of the unit leaf rate (i.e. rate of increase in mass per unit leaf area) with increasing temperature that was largely compensated by a proportionate increase in specific leaf area (i.e. leaf area per unit leaf mass). Ögren and Sundin (1996) also classified *Silene uniflora* as a slow-growing sun plant, taking the relatively long time of  $47.3 \pm 0.8$  (SE) min to reach 90% of its final photosynthetic rate and  $13.2 \pm 2.7$  mins to reach 90% of its final  $\text{CO}_2$  use efficiency on transition from low to high light.

**TABLE 1** Summary of effects of temperature on the growth of *Silene uniflora*. LMR, leaf mass ratio; RGR, relative growth rate; SLA, specific leaf area; ULA, unit leaf rate (net assimilation rate). From Loveys et al. (2002).

	Growth temperature (°C)		
	18	23	28
RGR mg/g/day	168	160	160
SLA m <sup>2</sup> /kg	14.9±0.5	22.6±0.6	25.8±0.5
LMR g/g	0.65±0.05	0.62±0.01	0.69±0.01
ULR g/m <sup>2</sup> /day	17.2	13.2	8.1

Much of what is known about the physiology of respiration and photosynthesis is derived from studies of thermal acclimation. Loveys et al. (2003) compared the long-term thermal acclimation of respiration in many of the same species used by Loveys et al. (2002) at the same three temperatures. In *S. uniflora*, root respiration increased with temperature but leaf respiration peaked at the intermediate temperature (23°C). They also tested the extent which pre-existing leaves and roots could acclimate to a cooler temperature, by transferring plants grown at 25 to 15°C. Respiration rates were predictably much lower at the lower temperature: leaf respiration was reported as 35.7 ± 4.5 (SE) nmol CO<sub>2</sub>/g/s at 15°C and 67.6 ± 5 at 25°C; corresponding values for root respiration were 39.1 ± 6.2 and 51.2 ± 1.6 nmol O<sub>2</sub>/g/s. Atkinson et al. (2007) found that increasing the nitrogen concentration in solution culture from 25 to 2000 µmol/L not only greatly increased root nitrogen concentrations but also substantially increased root respiration rates, whether the plants had been warm-grown or cold-acclimated.

A more detailed analysis of the acclimation of photosynthesis and respiration of numerous species in different functional groups (Campbell et al., 2007) reported values for a wide range of traits for *S. uniflora*, measured after short- and long-term exposure to temperatures the range 7–28°C in growth chambers: photosynthetic carbon assimilation under saturating light; photosynthetic carbon assimilation under growth light,  $F_v/F_m$  (variable over maximal chlorophyll fluorescence), leaf dark respiration, stomatal conductance, intercellular concentration of CO<sub>2</sub>, LMA (i.e. leaf dry mass per unit leaf area), total leaf nitrogen, total non-structural carbohydrates. Relative values were given for various proteins: COX (cytochrome oxidase), AOX (alternative oxidase) ATPase, PSII (photosystem II protein) and Rubisco (Ribulose biphosphate carboxylase/oxygenase). Notably, photosynthesis measured at saturating light ( $A_{sat}$ ) and 21°C was in the range 7.59–13.79 µmol CO<sub>2</sub>/m<sup>2</sup>/s, depending on prior growth temperature. On the basis of a coupled energy balance–gas exchange model (Beerling & Woodward, 1997) and reasonable assumptions, Davy et al. (2001) predicted a maximum potential photosynthetic rate of 17.5 µmol CO<sub>2</sub>/m<sup>2</sup>/s. Thus, the photosynthetic measurements of Campbell et al. (2007) achieved 79% of a theoretical maximum. Their values of  $F_v/F_m$  in the range 0.80–0.85 indicated that there was no accompanying stress

on Photosystem II. Leaf dark respiration under the same conditions varied from 0.46 to 2.16 µmol CO<sub>2</sub>/m<sup>2</sup>/s. Measurements of photosynthesis and respiration made at the full range of growth temperatures were also given. The traits of *S. uniflora* do not appear exceptional within the group of forbs studied (including also *Achillea millefolium*, *A. ptarmica*, *Arabidopsis thaliana*, *Plantago major*, *P. euryphylla* and *Silene dioica*) and Campbell et al. (2007) concluded there were striking similarities in the degree and biochemical underpinning of acclimation of respiration and photosynthesis in the three functional groups, despite considerable differences in traits between them.

## 6.5.2 | Water relations

As would be expected from its habitats, *Silene uniflora* is relatively drought tolerant. Although evaluated as useful for planting on 'green roofs', it could not survive in the complete absence of watering, like all other candidates except CAM species (Nagase & Dunnett, 2010). The coupled energy balance–gas exchange model (Beerling & Woodward, 1997) employed by Davy et al. (2001) estimated that *S. uniflora* had a maximum water vapour conductance of 798 mmol/m<sup>2</sup>/s, with an associated transpiration rate of 7.6 mmol/m<sup>2</sup>/s and water use efficiency of 2.3 mmol CO<sub>2</sub>/mol water. These values were typical for a range shingle species investigated.

## 6.5.3 | Inorganic nutrition

*Silene uniflora* is normally regarded as a slow-growing plant of soils deficient in nitrogen and phosphorus (see Section 2.2). However, when amply supplied with nutrients in solution culture, it can achieve a RGR of 168 mg/g/day (Loveys et al., 2002; Table 1), which is well above average for values in a wide comparison of British species (Grime & Hunt, 1975). Moreover, it responded to increasing external nitrogen concentration over nearly three orders of magnitude in an experiment of Atkinson et al. (2007). It is likely that its growth is limited by other factors in more fertile habitats (see Section 2.2) and where there are not such limitations, it is excluded by more competitive species.

Although a calcicole herb of alvar limestone *Silene uniflora* subsp. *petraea* produced only marginally more biomass on a calcareous soil than on an acid one in a pot-culture experiment (Zohlen & Tyler, 2004). Critically, it was able to maintain a similar total phosphorus content on the inherently P-deficient calcareous soil at 59.8 ± 1.8 (SE) µmol/g DW to that on the acid soil (58.4 ± 5.5 µmol/g), unlike the calcifuge herbs in the experiment. This was also the case for its inorganic P content (17.5 ± 0.8 µmol/g) on the calcareous soil and 17.2 ± 0.9 µmol/g on the acid soil. Its calcium content on the calcareous soil (627 ± 1 µmol/g) was higher than on the acid one (364 ± 17 µmol/g), but it avoided the excessive Ca uptake on the calcareous soil shown by the calcifuge herbs.

### 6.5.4 | Salinity tolerance

Seed germination shows considerable tolerance of salinity (see Section 8.4). Appreciable concentrations of stress metabolites (15  $\mu\text{mol/g}$  FW proline, 5  $\mu\text{mol/g}$  FW glycine betaine and 10  $\mu\text{mol/g}$  FW reducing sugars) were reported in *S. uniflora* growing on sand dunes by Smirnoff and Stewart (1985). As the dune sands were not particularly saline and the plants accumulated only 25  $\mu\text{mol/g}$  FW of chloride ions, it was not clear whether this was an osmoregulatory response to the salt in sea spray or to other stresses expected on dunes, such as those due to water deficit or heat.

### 6.5.5 | Heavy metal tolerance

Many inland populations of *Silene uniflora* are associated with metalliferous mine wastes (Baker, 1978a; Price & Abrahams, 1994) or serpentine (Proctor & Woodell, 1971) soils that are contaminated or enriched with high concentrations of heavy metals. Baker (1978a) compared zinc tolerance in populations from mines with that in populations from coastal or arctic-alpine settings in long-term water culture experiments. Tolerant and non-tolerant populations differed in their patterns of zinc uptake and transport. All mine populations showed some degree of restricted transport of Zn from root to shoot and some accumulated it in the roots. Overall, the root/shoot concentration ratio was strongly correlated with the logarithm of pseudo-total soil Zn concentration, whereas the Zn content of the shoots was negatively correlated with it. Baker (1978b) extended this work to investigate the effects of a high zinc and calcium environment. The total Zn content of tolerant plants was little affected by elevated Ca but was decreased significantly in the non-tolerant ones. At higher calcium concentrations, total Zn uptake by tolerant plants was significantly greater than by non-tolerant ones, but the populations did not differ in their Ca uptake. There was evidence that Zn transport was decreased by high Ca uptake in both populations, suggesting a role for Ca in ameliorating Zn toxicity. Furthermore, the uptake and transport of phosphorus (Baker, 1978c) was greater in tolerant populations than non-tolerant ones. Tolerant populations were higher yielding at low P concentrations, showed less phosphate response and proved to be more efficient in their P uptake and transport than non-tolerant ones. The capacity to evolve tolerance extends also to copper, as demonstrated by Price and Abrahams (1994) for a population in the anomalous vegetation of a topogenous mire exposed to seepage from mining activities in N. Wales. Corroboration of zinc and copper tolerance in mine-tip populations of *S. uniflora* is provided by molecular evolutionary studies of such adaptation (Papadopulos et al., 2021; Wood et al., 2023) discussed in Section 10.

In contrast to other heavy metals, Proctor (1971) found little evidence of tolerance to elevated concentrations of nickel and chromium in *S. uniflora* plants from a serpentine site (Keen of Hamar, Unst, Shetland); when grown alongside plants from a non-serpentine site (Lizard Head, Cornwall, with mica-schist soil) on the serpentine soil, the plants from the two populations were similarly stunted in comparison with a commercial potting compost. Shewry and Peterson (1975)

recorded mean tissue concentrations from Hamar of  $328 \pm 105$  (SD) and  $22 \pm 19$  ppm for Ni and Cr, respectively, with the tissue concentrations of the two elements being significantly correlated ( $r=0.584$ ,  $p<0.01$ ) in the sample of 20 plants. However, Ni concentrations in *Silene acaulis* were fivefold higher than in *S. uniflora* at the same site.

Effects of the imbalance between calcium and magnesium in serpentine soils were addressed by Shewry and Peterson (1976). Shoot tissue of *S. uniflora* from Hamar had a mean Ca/Mg ratio of  $1.40 \pm 0.45$  (SD). A bulk sample from the Nikka Vord chromite mine tip on Unst, had an even more adverse Ca/Mg ratio of 0.86. However, its congener *S. acaulis* had a mean ratio of  $0.27 \pm 0.7$ , suggesting that *S. uniflora* is more able to accumulate Ca selectively in a high Mg environment.

## 6.6 | Biochemical data

Buzón-Durán et al. (2023) investigated bioactive components present in hydromethanolic extracts of *Silene uniflora*. The main phytochemicals identified were 4-O-methyl-myoinositol (52.5%), saturated fatty acid vinyl esters (8.7%), mainly myristic acid vinyl ester and palmitic acid vinyl ester and cyclotetracosane (3.7%). They found that the extracts of *S. uniflora* were effective against the fungal pathogens *Botrytis cinerea* Pers. and *Colletotrichum nymphaeae* (Pass.) Aa in strawberries.

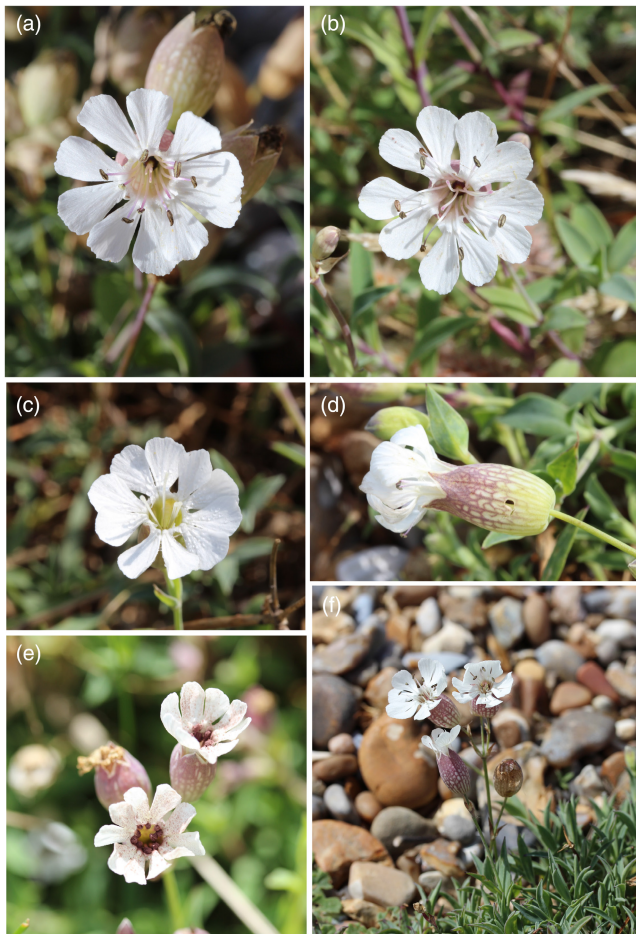
## 7 | PHENOLOGY

In Britain and Ireland, *S. uniflora* is apparent (i.e. has been recorded) throughout the year, its leaves remaining continuously visible; flowering and fruiting are spread over the whole summer from May to October (Stroh et al., 2023). Seed production follows flowering within a few weeks throughout the summer and autumn. This extended reproductive phenology is regarded as a distinguishing feature from *S. vulgaris*, in which flowering and fruiting occur over a more limited period (Marsden-Jones & Turrill, 1957). *S. uniflora* subsp. *petraea* in the alvar environment of Oland showed a similarly long flowering season but with evidence of bimodality, the mid-summer depression probably being enforced by drought (Pettersson, 1994). Larger plants started flowering earlier in the season than small ones and, notwithstanding substantial consequential losses to seed predation by noctuid moth caterpillars, they contributed a larger proportion of total seed production than the late-flowering, small plants. Flowering there is terminated by the first frosts in September or October (Runyeon & Prentice, 1997a).

## 8 | FLORAL AND SEED CHARACTERS

### 8.1 | Floral biology

*Silene uniflora* is gynodioecious (with some individuals bearing female flowers only and others bearing hermaphrodite flowers only) and gynomonocious (with both female and hermaphrodite



**FIGURE 5** Flowers of *Silene uniflora*: (a) hermaphrodite flower showing first whorl of stamens; (b) hermaphrodite flower showing second whorl of stamens; (c) female-only flower; (d) perforation of calyx and corolla by nectar robbing; (e) emasculation of flowers by anther 'smut' (*Microbotryum* sp.); (f) dichasial arrangement of flowers. Dunwich beach, Suffolk, UK. Photographs: A.J. Davy.

flowers on the same individual) (Figure 5). The proportions of the three types of individual vary considerably from population to population. Marsden-Jones and Turrill (1957) reported 86.8% hermaphrodite, 7.2% female and 5.0% hermaphrodite/female as averages from 591 plants across a wide range of populations. They also noted that the progeny from a hermaphrodite individual that had been self-pollinated frequently changed sexual status when monitored for 5 years. The flowers are actinomorphic and erect, their white petals highly visible by day and night. Female flowers result from early abortion of the anthers (Baker, 1966; Marsden-Jones & Turrill, 1957; Salisbury, 1912); whether on a hermaphrodite/female plant or a female plant, they are smaller than hermaphrodite flowers and frequently have thicker stigmas. The hermaphrodite flowers are protandrous, with two successive whorls of five stamens emerging, their filaments elongating and anthers dehiscing. At the female stage, the stigmas elongate and diverge, occupying the centre of the flower above the stamens. At anthesis stamens and stigmas are arranged symmetrically around the ovary axis. Pollen is accessible to all visiting insects and nectar, secreted

**TABLE 2** Insects recorded taking pollen or nectar on *Silene uniflora* in southern England. From Marsden-Jones and Turrill (1957). Nomenclature updated using Chandler (1998), Fitton et al. (1978) and Agassiz et al. (2013).

Diptera	Lepidoptera: Rhopalocera
<i>Bellardia</i> sp.	<i>Pieris rapae</i> (L.)
<i>Calliphora vomitoria</i> (L.)	Lepidoptera: Heterocera
<i>Chloromyia formosa</i> (Scop.)	<i>Abrostola tripartita</i> (Hufn.)
<i>Coelopa frigida</i> (Fab.)	<i>Apamea crenata</i> (Hufn.)
<i>Delia pruinosa</i> (Zett.)	<i>Apamea monoglypha</i> (Hufn.)
<i>Empis livida</i> L.	<i>Autographa gamma</i> (L.)
<i>Episyrphus balteatus</i> (de Geer)	<i>Autographa jota</i> (L.)
<i>Hylemya</i> sp.	<i>Autographa pulchrina</i> (Haw.)
<i>Meliscaeva auricollis</i> (Meig.)	<i>Diachrysia chrysis</i> (L.)
<i>Platycheirus albimanus</i> (Fab.)	<i>Evergestis forficalis</i> (L.)
<i>Platycheirus manicatus</i> (Meig.)	<i>Hada plebeja</i> (L.)
<i>Platycheirus peltatus</i> (Meig.)	<i>Hadena bicruris</i> (Hufn.)
<i>Rhingia campestris</i> Meig.	<i>Hadena perplexa</i> (D. & S.)
<i>Scathophaga stercoraria</i> (L.)	<i>Mamestra brassicae</i> (L.)
<i>Syrirta pipiens</i> (L.)	<i>Polychrysia moneta</i> (Fab.)
Hymenoptera	<i>Sideris rivularis</i> (Fab.)
<i>Andrena angustior</i> (Kirby)	<i>Udea lutealis</i> (Hübner)
<i>Andrena haemorrhoea</i> (Fab.)	<i>Udea olivalis</i> (D. & S.)
<i>Andrena ovata</i> (Kirby)	<i>Xanthorhoe fluctuata</i> (L.)
<i>Apis mellifera</i> L.	Coleoptera
<i>Bombus hortorum</i> (L.)	<i>Hypera arator</i> (L.)
<i>Bombus lapidarius</i> (L.)	<i>Psilothrix cyaneus</i> (Oliv.)
<i>Bombus lucorum</i> (L.)	
<i>Bombus pascuorum</i> (Scop.)	
<i>Bombus pratorum</i> (L.)	
<i>Bombus terrestris</i> (L.)	
<i>Chrysis ignita</i> (L.)	
<i>Halictus rubicundus</i> (Christ)	
<i>Hylaeus hyalinatus</i> Smith	
<i>Lasioglossum albipes</i> (Fab.)	
<i>Lasioglossum leucopus</i> (Kirby)	
<i>Lasioglossum minutissimum</i> (Kirby)	
<i>Lasioglossum morio</i> (Fab.)	
<i>Lasioglossum smeathmanellum</i> (Kirby)	
<i>Osmia aurulenta</i> (Panz.)	

from tissue at the base of the filaments, to Lepidoptera (mainly crepuscular moths) and long-tongued Hymenoptera; 'robbers' may also perforate the calyx to obtain nectar. Insects captured taking pollen or nectar are summarized in Table 2 (Marsden-Jones & Turrill, 1957); it is possible that climate change since this list was



compiled will have affected the pollinators visiting *S. uniflora* but more recent data are not available. Moths whose larvae will subsequently feed on the developing seeds typically also pollinate the flowers at the time of oviposition, thus securing their food supply (Pettersson, 1992a; see Section 9.1).

Warren and James (2008) used *Silene uniflora* clones with flower stems of different lengths and thicknesses to test the hypothesis that flowers wave to attract insects. There was heritable variation in these estimates of floral mobility. Overall, medium length, thin flower stalks were visited more frequently and by more insect species, leading to the suggestion of an evolutionary trade-off between waving to attract attention and not being too mobile to prevent effective pollination.

Self-pollination has been shown to play an important role in the absence of insect visitors (Marsden-Jones & Turrill, 1957).

## 8.2 | Hybrids

Although fully fertile hybrids of intermediate morphology can be readily produced in experimental crossing of *S. uniflora* and *S. vulgaris* (Marsden-Jones & Turrill, 1957), natural hybrids in Britain are uncommon (Stace et al., 2015), attributed to the different distributions of the parents (Marsden-Jones & Turrill, 1957). *S. uniflora* subsp. *petraea* and *S. vulgaris* are sympatric on the Baltic island of Öland, the former in ecologically distinct limestone habitats ('alvar') and the latter as a widespread weed; they hybridize in intermediate habitats. On the basis of allozyme data, Runyeon and Prentice (1996) found high levels of interspecific gene flow between the two species but concluded that the genetic integrity of *S. uniflora* was not at risk from genetic contamination, because of separation by habitat preferences and flowering phenology. Subsequent work has revealed further likely post-zygotic barriers to introgression (Andersson et al., 2008; see Section 8.4). Examination of morphometric characters across a hybrid zone (Runyeon-Lager & Prentice, 2000) revealed clinal variation in individual characters but, nevertheless, all plants could be assigned to one or other of the parental species. Mosaic variation in plastid DNA and allozyme markers in the European ranges of *S. uniflora* and *S. vulgaris* is evidence for ancient hybridisations, prior to their post-glacial range expansions (Prentice et al., 2011).

Heaslip (1951) claimed to have produced viable seed from artificial crosses between *Silene latifolia* and *S. uniflora* (as *S. maritima*), but no naturally occurring hybrid has been reported from the British Isles (Stace et al., 2015), or indeed elsewhere, despite both species being widely distributed. As her seed was commercially sourced in the USA, it is possible that there was taxonomic confusion with *S. vulgaris*.

## 8.3 | Seed production and dispersal

The mean number of ovules per ovary was 92 (range 37–182) for plants of wild origin grown under uniform conditions in an experimental garden (Marsden-Jones & Turrill, 1957). Estimates of the

number of seeds produced per capsule made nearly 30 years apart on open-pollinated samples from different populations corresponded closely at 51 and  $53.6 \pm 21.4$ , SD. Plants selfed or crossed under controlled conditions yielded consistently fewer seeds per capsule than open-pollinated ones, possibly because of the unnatural conditions. Overall, plants were estimated to produce c. 45 capsules per year over a typical reproductive life of 5 years, suggesting a total output of c. 12,000 seeds. In an alvar population of subsp. *petraea* seed production was greatly reduced in late-flowering plants (Pettersson, 1994). This population produced 64–77 ovules per flower and 28–40 seeds per fruit (late-early flowering, respectively). Pettersson (1997) found that for subsp. *petraea*, there was no effect of plant size or density on fruit-set per flower, contrary to expectation. The number of ovules per ovary and the number of seeds per capsule declined with increasing plant density, meaning that seed production per plant was largely determined by plant size. Therefore, the number of seeds set was slightly higher for widely scattered plants than for clumped ones and this was the case for both gender morphs.

Mean seed mass has been reported as 1.37 mg (Marsden-Jones & Turrill, 1957). This is slightly lighter than the equivalent mass they report for *S. vulgaris* (1.49 mg), making *S. uniflora* seemingly an exception to the significant trend for shingle species to have heavier seeds than their non-shingle congeners (Davy et al., 2001). However, the individual seed mass of subsp. *petraea* is apparently lighter, at 0.63 mg in late-flowering plants and 0.67 mg in early-flowering plants, the difference due to flowering time itself being significant (Pettersson, 1994). A seed with a typical 'armadillo' testa is shown in Figure 6.

Seed dispersal is mainly by the wind, with seeds being shaken from the capsule. However, broken-off infructescences retaining seeds within their capsules (or within the persistent calyces) can be blown considerable distances along the shore, especially on shingle beaches (Marsden-Jones & Turrill, 1957).

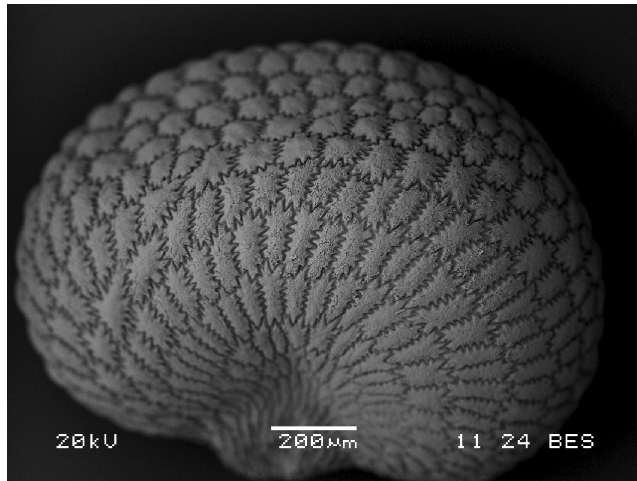
## 8.4 | Viability of seeds: Germination

Autumn germination is common, and seeds can sometimes germinate within the capsule or the bladder, membranous calyx; the radicles penetrate these structures into the underlying substrate, while the cotyledons are supported above it (Marsden-Jones & Turrill, 1957). This may have adaptive value for the establishment of small seeds on coarse, shingle substrates (Davy et al., 2001).

Marsden-Jones and Turrill (1957) reported 92%–96% germination for seeds sown on soil in a glasshouse (c. 16°C) in the spring after collection from Chesil Beach, Dorset, UK. Seeds from the same site collected some 27 years later began germinating 3–4 days after sowing and yielded 75%–100% germination on moist filter paper in Petri dishes (15–18°C). No seeds 25 years old or older germinated but the storage conditions were not specified.

Seeds collected from a shingle-beach population at Sizewell, Suffolk and stored dry, at room temperature for a few weeks were



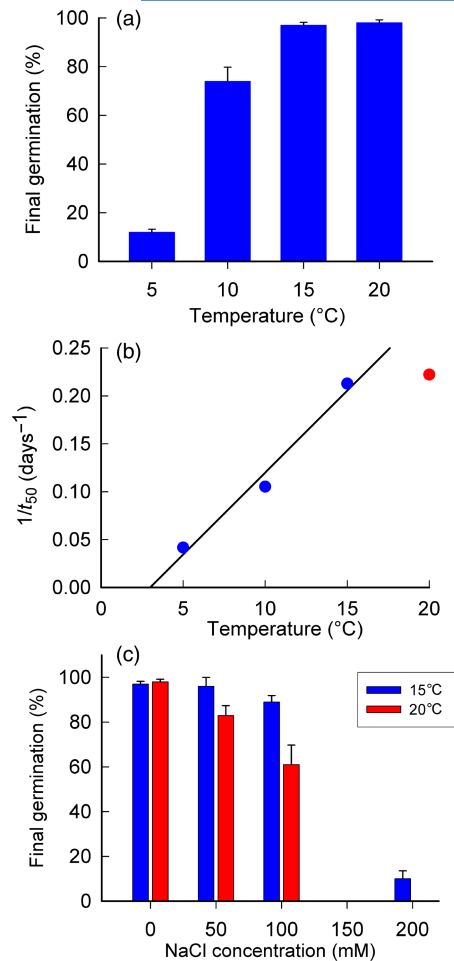


**FIGURE 6** Scanning electron microscope image of a seed of *Silene uniflora* showing the testa with 'armadillo' plates. Seed collected from Dunwich beach, Suffolk, UK. Photograph: R. Evans-Gowing.

tested under different environmental conditions. There was 98% germination at constant 20°C and diurnally alternating light flux (12h/day); germination was only slightly lower at 15°C but was reduced progressively to 12% at 5°C (Figure 7a). The rate of germination (the reciprocal of the time to 50% of final germination;  $1/t_{50}$ ) was dependent on temperature, and extrapolation of a regression over the linear range (5–15°C) yielded a base temperature for germination of 3.0°C (Figure 7b). As might be expected for a coastal plant, germination tests at a range of NaCl concentrations indicated considerable salinity tolerance; there was relatively little inhibition of germination up to a salinity of 100mM NaCl, although inhibition was greater at 20°C than at 15°C; when seeds were treated with 200mM NaCl (approximately equivalent to half the salinity of seawater), there was only 10% germination at 15°C and none at 20°C (Figure 7c). There was no significant difference in the germination behaviour of seeds in diurnally alternating light and continuous darkness.

In a broad screening of coastal species to salinity (under laboratory condition of c. 20°C and north-facing natural light), Woodell (1985) reported similar results for *S. uniflora*, with 91% germination in freshwater, only 4% in half-strength seawater (reported as equivalent to 300mM NaCl) and none at higher concentrations. However, when the ungerminated seeds were transferred to freshwater after 18 days under saline conditions, they showed high germinability: 84% of seeds germinated after previous exposure to 3/2 strength seawater (c. 900mM NaCl). This shows that salinity effects on *S. uniflora* germination are substantially due to reversible, osmotically enforced inhibition rather than ion toxicity.

Andersson et al. (2008) reported strong paternal effects on seed germination characteristics in crossing experiments between *S. uniflora* subsp. *petraea* and *S. vulgaris*. The latter species had higher



**FIGURE 7** Germination of *Silene uniflora* after 6 months' dry storage at room temperature. (a) Final germination (%) at constant temperature after 47 days (vertical bars represent  $\pm 1$  SE). (b) Rate of germination ( $1/t_{50}$ ) in response to temperature; temperatures in the ascending linear range (blue symbols, 5–15°C) were included in a linear regression to derive the basal temperature for germination ( $y = 0.0171x - 0.0512$ ,  $r^2 = 0.979$ ); the red symbol (20°C) was above this range. (c) Final germination (%) after 39 days in response to NaCl concentration at constant temperatures of 15 and 20°C (vertical bars represent  $\pm 1$  SE). Tests were carried out on filter paper in five replicate Petri dishes (sealed with Parafilm) with 20 seeds each per replicate. Dishes were kept in incubators with illumination from warm-white fluorescent tubes for 12h/day. Data of R. Symes.

germinability (88.4%) than the former (59.1%) and a lower median time to germination (7.4 vs. 29.4 days) but in both respects seeds resulting from interspecific crosses tended to the characteristics of the pollen parent.

## 8.5 | Seedling morphology

Germination is epigeal (Figure 8). The radicle ruptures the testa and, on emerging, produces an 'appressorium' of root hairs that then



**FIGURE 8** Stages in the germination of seeds of *Silene uniflora*: (a) imbibed seed; (b) radicle emergence; (c) radicle with an 'appressorium' of root hairs; (d) elongated radicle densely clothed with root hairs; (e) emergence of the cotyledons; (f) seedling with horizontal cotyledons; (g) seedlings at 2 months old. Photographs: (a–f) R.D. Payet; (g) A.J. Davy.

come to clothe it densely as it elongates. The pair of green, elongate cotyledons then emerge and separate to assume a horizontal alignment as they expand. The first pair of spatulate, tapering true leaves develop from the plumule, with successive decussate pairs added as the primary stem elongates. Pairs of branches develop subsequently in the axils of the cotyledons and early true leaves.

## 9 | HERBIVORY AND DISEASE

### 9.1 | Animal feeders or parasites

Sheep (Oliver, 1912) and rabbits (Rowan, 1913) will graze *S. uniflora* where they have access to it (see Section 4). Feeding by the snails *Cornu aspersum* (O. F. Müller) and *Cepaea nemoralis* (L.), not to

mention various species of slug can devastate seedlings in cultivation, but it is not known whether they have significant effects in the field (A.J. Davy, personal observation).

A substantial number of insects is known to feed on the plant (Table 3). Larvae of noctuid moths, especially *Hadena* spp., are important feeders. Both *Hadena confusa* (Hufnagel) and the Anthomyiid fly *Delia pruinosa* (Zetterstedt) lay eggs in the flowers of the endemic *S. uniflora* subsp. *petraea* on Öland; larvae of both consume the developing seeds but the moth caterpillars also predate any larvae of *D. pruinosa* that they encounter (Pettersson, 1992a). Ovipositing female flies prefer non-pollinated flowers to older, pollinated ones but then depend on pollination by the moth to assure a food supply for their larvae. Although the eggs are usually laid singly in flowers, the caterpillars of *H. confusa* are mobile and consume 20–30 seed capsules each (Pettersson, 1992b).

TABLE 3 Insect feeders recorded on *Silene uniflora* retrieved from the Biological Records Centre (2020), with additional records from Ellis (2001–2024). Nomenclature updated using Blackman (2010) and Agassiz et al. (2013).

Order	Family	Insect feeder	Insect stage	Feeding mode	Plant parts used
Coleoptera	Coccinellidae	<i>Subcoccinella vigintiquattuorpuntata</i> (L.)	L+A	P	Leaves. Larvae may feed only on mildews.
Coleoptera	Chrysomelidae	<i>Ochrosis ventralis</i> (Illiger)	A	P	Leaves
Diptera	Agromyzidae	<i>Liriomyza strigata</i> (Meigen)	L	M	Leaves
Diptera	Anthomyiidae	<i>Delia pruinosa</i> (Zetterstedt)	L	B	Seeds
Diptera	Anthomyiidae	<i>Pegomya hyoscamii</i> (Panzer)	L	M	Leaves
Diptera	Cecidomyiidae	<i>Contarinia cucubali</i> Kieffer	L	P, G	Leaves
Diptera	Cecidomyiidae	<i>Dasineura subterranea</i> (Kieffer)	L	P, G	Vegetative buds
Diptera	Cecidomyiidae	<i>Jaapiella floriperda</i> (F. Löw)	L	P, G	Flowers
Diptera	Cecidomyiidae	<i>Jaapiella inflatae</i> (Rübsaamen)	L	P	Inquiline in <i>J. floriperda</i> galls
Hemiptera	Aphididae	<i>Brachycolus cucubali</i> (Passerini)	L+A	P, R	Flower buds; leaves
Hemiptera	Aphididae	<i>Brachycaudus lychnidis</i> (L.)	L+A	P	Stems, leaves, flowers
Hemiptera	Aphididae	<i>Brachycaudus populi</i> (del Guercio)	L+A	P	Stems, leaves, flowers
Hemiptera	Aphididae	<i>Macrosiphum penfroense</i> Stroyan	L+A	P	Leaves, flowers
Hemiptera	Pseudococcidae	<i>Atrococcus luffi</i> (Newstead)	L+A	P	Scales on roots
Lepidoptera	Geometridae	<i>Charissa obscurata</i> ([D.& S.])	L	P	
Lepidoptera	Geometridae	<i>Eupithecia venosata</i> (F.)	L	P	Fruits; seeds; flowers
Lepidoptera	Geometridae	<i>Scopula emutaria</i> (Hübner)	L	P	
Lepidoptera	Lasiocampidae	<i>Malacosoma castrensis</i> (L.)	L	P	
Lepidoptera	Noctuidae	<i>Acronicta cinerea</i> (Hufnagel)	L	P	
Lepidoptera	Noctuidae	<i>Apamea oblonga</i> (Haworth)	A	P	Nectar
Lepidoptera	Noctuidae	<i>Aporophyla australis</i> (Boisduval)	L	P	Leaves
Lepidoptera	Noctuidae	<i>Conisania andalusica</i> (Denis & Schiffermuller)	L	P, B	Roots, leaves and stems
Lepidoptera	Noctuidae	<i>Hadena albimacula</i> (Borkhausen)	L	P	Seeds/ fruits
Lepidoptera	Noctuidae	<i>Hadena bicurris</i> (Hufnagel)	L	P	Fruits/seeds
Lepidoptera	Noctuidae	<i>Hadena caesia</i> (Denis & Schiffermuller)	L	P	Fruits/seeds; flowers; flower buds; vegetative buds; roots
Lepidoptera	Noctuidae	<i>Hadena confusa</i> (Hufnagel)	L	P	Fruits/seeds
Lepidoptera	Noctuidae	<i>Hadena perplexa</i> (Denis & Schiffermuller)	L	P	Fruits/seeds; flowers
Lepidoptera	Noctuidae	<i>Polymixis xanthomista</i> (Hübner)	L	P	Fruits/seeds; flowers
Lepidoptera	Noctuidae	<i>Sideridis reticulata</i> (Goeze)	L	P	Fruits/seeds; leaves
Lepidoptera	Noctuidae	<i>Sideridis rivularis</i> (F.)	L	P	Fruits/seeds; leaves
Lepidoptera	Coleophoridae	<i>Coleophora lithargyrinella</i> Zeller	L	P, M, C	Leaves
Lepidoptera	Gelechiidae	<i>Caryocolum vicinella</i> (Douglas)	L	P, M?, W	Shoots; leaves
Lepidoptera	Tortricidae	<i>Philedonides lunana</i> (Thunberg)	L	R	Leaves
Thysanoptera	Aeolothripidae	<i>Aeolothrips tenuicornis</i> Bagnall	L+A	Predator	Feed on mite/thrip larvae in flowers

Note: Insect stage: A, adult; L, larva. Feeding: B, boring; C, case-forming; G, galling; M, mining; P, phytophagous; R, rolling; W, webbing.

Leaf galls may be formed by the Hemipteran *Hayhurstia cucubali* and the gall midges *Jaapiella* spp. The pale red larvae of *Jaapiella floriperda* were associated with hypertrophied, discoloured flowers, while the white jumping larvae of *Contarinia cucubali* were observed

in galls formed from terminal leaf-buds, and those of *Dasineura subterranea* were in swollen buds formed from leaves exposed at sand level, all at Blakeney Point, Norfolk, United Kingdom (Bagnall & Heslop-Harrison, 1924; Table 3).



## 9.2 | Plant parasites

See Section 9.3.

## 9.3 | Plant diseases

### 9.3.1 | Basidiomycota

#### *Pucciniomycotina*

Two rust fungi *Puccinia behenis* Otth. and *Uromyces behenis* (DC.) Unger are found on *Silene uniflora* (Ellis & Ellis, 1997; Wilson & Henderson, 1966). *P. behenis* is scarce (British Mycological Society, 2024) but also inconspicuous and therefore possibly overlooked. It forms uredinia and telia, but its life cycle has never been confirmed as aecia have not been recognized. It is assumed to be a heteroecious species (Klenke & Scholler, 2015) possibly with aecia on *Bupleurum*—Tranzschel (1940) reports a strong association between *P. behenis* on *Silene repens* and aecia on *Bupleurum scorzonrifolium*, and postulates that aecia on perennial *Bupleurum* spp. are sometimes *P. behenis* and sometimes *P. bupleuri*. But this does not seem to have been tested by inoculation. *U. behenis* is more frequent on *S. uniflora* (British Mycological Society, 2024). Its aecia are conspicuous with white margins and yellow spores on purplish spots on leaves, often but not always on the lower surface. The telia are blackish-brown to black (Ellis & Ellis, 1997), hypophyllous and on stems. *U. behenis* has a reduced cycle and the uredinia are unknown, though Wilson and Henderson (1966) say they are aecidioid, that is, like the aecia.

Anther 'smuts' are also in the Pucciniomycotina and actually more closely related to rusts; they have been widely reported on *Silene uniflora* from May to October, the violet spore mass produced in the anthers of infected flowers being easily detected (British Mycological Society, 2024; Ellis & Ellis, 1997). Recent advances in molecular analysis have revealed strong host specificity in anther smuts, and two cryptic species parasitise natural populations of *S. uniflora*, *Microbotryum silenes-inflatae* (DC. Ex Liro) G. Deml & Oberw. and *M. lagerheimii* Denchev (Chung et al., 2012; Smith et al., 2020). *Microbotryum* attacks only the anthers in *S. uniflora*, replacing the pollen with its spore mass. In southern England, the two species of *Microbotryum* can occur together (Chung et al., 2012) and each individually has been found at the same site as the smut *Thecaphora melandrii*—see below (Smith et al., 2020). The only records confirmed by molecular analysis for Scotland are for *M. silenes-inflatae* in the Outer Hebrides, where it has been found at 12 locations between 2008 and 2016 (Smith, 2017; Smith et al., 2017). Maternal half-sib families of seeds were collected from individual *S. uniflora* plants and then 30–50 individual plants per family were inoculated with four pathogen genotypes, two from each of the two *Microbotryum* species; this showed that resistance to the two *Microbotryum* species is strongly correlated among the host populations (Chung et al., 2012). *Microbotryum lagerheimii* from *S. uniflora* in the United Kingdom was found to be

genetically differentiated from that on an alternative host, *S. vulgaris*, in the Alps and Pyrenees; four different genetic clusters of *M. silenes-inflatae* co-occurred in the Alps, the United Kingdom and the Pyrenees, and infected both *S. vulgaris* and *S. uniflora* (Abbate et al., 2018). These *Microbotryum* species appeared to be maintained by different environmental niches (elevation, temperature and precipitation), rather than by host specialization or allopatry.

#### *Ustilaginomycotina*

One true smut, *Thecaphora melandrii* (Syd.) Vánky & M.Lutz, was first discovered in Britain only in 2019, on *S. uniflora* in southern England (Smith et al., 2020). It differs from *Microbotryum* in affecting all the parts of the flowers except the calyx, which become swollen and eventually replaced by the spore mass. The flowers generally do not open, but the buds look swollen and misshapen. The smut is systemic, and all the flowers on a plant are usually affected. The spores are formed in loose balls (which break up when mounted in water), in contrast to *Microbotryum* spp. which have solitary spores. Both *T. melandrii* and *Microbotryum* have been found in the same populations of *S. uniflora* (Smith et al., 2020).

### 9.3.2 | Deuteromycota

#### *Coelomycetes*

*Diplosporonema delastreii* (Lacroix) Höhn. ex Petrak is reported on *S. uniflora* as being common from July to October; the acervuli are yellowish, about 0.15 mm diameter, the conidia being hyaline with one or two septa (Ellis & Ellis, 1997).

## 10 | HISTORY

Seeds of *Silene uniflora* have been found in deposits from the Anglian glacial stage (c. 480,000 years BP), and from one Early Weichselian (c. 70,000–50,000 years BP) and five Late Weichselian (50,000–15,000 years BP) sites (Godwin, 1975). In contrast, there is only one record from an interglacial stage (the Ipswichian, c. 125,000–90,000 BP). For many records of the *S. vulgaris* aggregate, it is not possible to be confident about distinguishing fossil seeds from those of *S. vulgaris* s.s. but W.B. Turrill was prepared to accept all specimens submitted to him as *S. uniflora*, largely on the basis of their 'armadillo' seed coats (see Section 8.5); one, from Ponders End in the Lea Valley, N. London, was confirmed by the presence of a fruit capsule (Reid, 1949) and Godwin (1975) reaffirmed his view that there appeared to be a consensus of experienced opinion that *S. uniflora* is represented in the Lea Valley 'Arctic bed' deposits (c. 28,000 radiocarbon years BP). There is a single record from the Late Flandrian, a Roman site at Finsbury Circus, London. Godwin (1975) remarked on the extraordinary abundance of the *S. vulgaris* agg. at the height of the Weichselian glaciation, where it has been associated with fresh soils, open habitats, salinity and a severe periglacial climate. Hence, there is every likelihood that *S. uniflora* is a periglacial survivor in Britain.

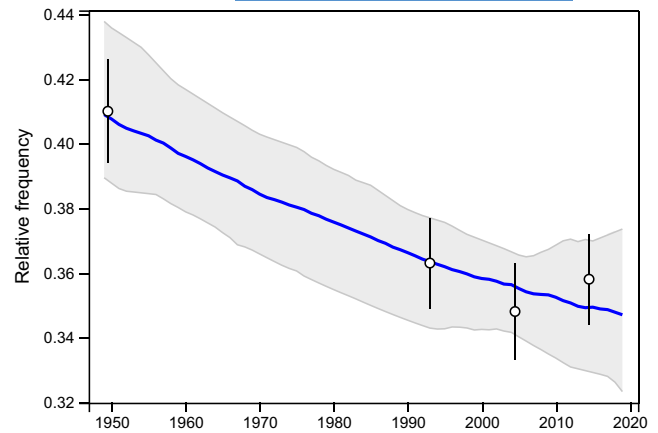
Neither allozyme nor distributional data supported a recent origin for *S. uniflora* subsp. *petraea* as a hybrid between *S. vulgaris* and *S. uniflora* subsp. *uniflora*, although an older hybrid origin could not be ruled out (Runyeon & Prentice, 1997a). It is likely that the two subspecies of *S. uniflora* colonized open habitats in Sweden during the late glacial or early postglacial, whereas *S. vulgaris* followed the spread of agriculture. Large-scale geographic patterns of allozyme alleles and plastid haplotypes across Europe (Prentice et al., 2011) were consistent with there having been repeated episodes of interspecific hybridization between *S. uniflora* and *S. vulgaris* that pre-dated a largely allopatric range expansion of the two species during the postglacial period.

Papadopoulos et al. (2021) reconstructed the evolutionary history of Zn tolerance in *S. uniflora* using reduced representation sequencing (ddRAD). They investigated populations from four mine sites in England (Priddy Pools, Somerset), Wales (Grogwynion, W. Wales and Swansea) and Ireland (Ross Island, County Kerry) that had been worked at various times between the 16th and 20th centuries (with evidence of mining from the Bronze Age and Roman era, respectively, for Kerry and Somerset) and compared them with their nearest counterpart coastal populations. The mine and coastal population pairs revealed three independent colonizations of mines from different coastal sites. Furthermore, there had been parallel evolution of zinc tolerance, without gene flow spreading adaptive alleles between mine populations. They identified genes with functions linked to physiological differences between the putative tolerant and non-tolerant ecotypes, although genetic differentiation at specific loci was only partially shared between mine populations. The results were consistent with a complex, polygenic genetic architecture underpinning rapid adaptation over about 250 years. Subsequently, by using coastal relatives to approximate the ancestral state, Wood et al. (2023) showed that genes displaying beneficial patterns of phenotypic plasticity in ancestral populations were overrepresented in the highly parallel gene sets of tolerant Zn-populations, indicating that ancestral plasticity facilitates such repeated adaptation to novel environments.

According to Pearman (2017), the first British record of *Silene uniflora* was in 1571 from the Isle of Wight, where it was described as 'Lychnis marina, Anglica ... in aggeribus maritimis Vectis Insulae Angliae' in the *Stirpium Adversaria Nova*, by P. Pena & M. de L'Obel (p. 148). In 1597, Gerard's *Herball, or general history of Plantes* recorded that 'Lychnis marina Anglica ... groweth by the sea-side in Lancashire at a place called Lytham, five miles from Wygan'. A later record from 1640 in the *Theatricum Botanicum ...* of J. Parkinson was 'By Hurst Castle neare the Isle of Wight'. The Latin binomial *Silene maritima* is found in the 3rd edition of William Withering's *A Botanical Arrangement of British Plants* (Withering, 1796). However, the currently accepted name, *S. uniflora*, has precedence, having been published 2 years earlier by Roth (1794).

## 11 | CONSERVATION AND MANAGEMENT

*Silene uniflora* has been designated a species of least concern in Red Lists for Great Britain (Dines et al., 2005), England (Stroh et al., 2014.),



**FIGURE 9** Smoothed time trend in the frequency of *Silene uniflora* at a 10-km scale in Britain, based on FREquency SCALing Local ('Frescalo') modelling of records in four date classes since 1930 that adjusts for recording effort. The filled white circles and black bars are the Frescalo-estimated means and standard deviations of the species' relative frequency in each time period, plotted at the median of the relevant BSBI date-class. The smoothed trend is estimated by fitting 100 generalized additive models to data resampled from the Frescalo means and standard deviations; the blue line is the median of these model fits, while the grey ribbon is its 90% uncertainty interval. From Stroh et al. (2023).

Wales (Dines, 2008) and Ireland (Wyse Jackson et al., 2016). Models adjusted for recording effort suggest that there has been a moderate decline in its relative frequency in Britain at a 10-km scale since 1930, but its distribution has remained relatively stable since the 1980s (Figure 9); at the same time, it is likely that recent more intensive recording has improved knowledge of its coastal range in Ireland and northern Scotland, however (Stroh et al., 2023).

The main threat to *S. uniflora* is likely to come from loss of its main habitat of coastal shingle. The threats to shingle structures have been myriad, not least from the extraction of aggregate, and economic development ranging from nuclear power stations and port facilities to tourism. As a substrate shingle is inherently unstable and vulnerable not only to the forces of tides and currents but also to the engineering works that seek to defend against them (Walmsley & Davy, 2001). Above all, such coastal habitats will be increasingly vulnerable to the inevitable effects of sea-level rise and increased storminess associated with climate warming (Mossman et al., 2015). There is also concern for the metallophyte populations. Sites in west Wales have diminished with various restoration activities at some of the mine sites and the work of the river authorities. In particular, at the classic Rhandirmwyn site, it has become difficult to locate appreciable numbers of plants (A.J.M. Baker, personal observation). This may be the result of natural leaching of the heavy metals and closing-up of the turf (possibly exacerbated by increased deposition of nutrients favouring more competitive species).

## AUTHOR CONTRIBUTIONS

Arthur J. Willis and Alan J. M. Baker initiated and partially drafted the account. Following Arthur's death in 2006, Anthony J. Davy was



invited to assume the lead role, carrying out relevant field and laboratory investigations, while completing and substantially updating the account. Alan commented on and approved the manuscript.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest. Anthony J. Davy is the Editor of the *Biological Flora* series in the Journal of Ecology but took no part in the peer review or decision-making processes for this manuscript.

## PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14341>.

## DATA AVAILABILITY STATEMENT

This paper largely reviews existing literature. Germination data used for Figure 7 are available on Dryad: <https://doi.org/10.5061/dryad.b8gtht7mk> (Davy & Baker, 2024).

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