

List Br. Vasc. Pl. (1958) 160, 2–5

***Salicornia* L. (*Salicornia pusilla* J. Woods, *S. ramosissima* J. Woods, *S. europaea* L., *S. obscura* P.W. Ball & Tutin, *S. nitens* P.W. Ball & Tutin, *S. fragilis* P.W. Ball & Tutin and *S. dolichostachya* Moss)**

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Salicornia L. (Chenopodiaceae) is a genus of annual, apparently leafless halophytic herbs that have articulated, succulent stems. A combination of inbreeding, which allows the development of locally differentiated populations, and considerable phenotypic plasticity has created great taxonomic complexity. Taxonomic difficulties have been compounded by very reduced morphology and the inadequacy of dried material in representing a succulent growth form. Although numerous species aggregates, species and microsomes have been described over the last 250 years in attempts to represent the observed variation, there is still no satisfactory taxonomic treatment and it is frequently impossible to assign published information specifically to taxa within *Salicornia*. Recent commentaries, with different perspectives on the taxonomic problems, are provided by Dalby (1989), Ingrouille (1989) and Rose (1989). This account reviews material referable to all of the taxa recognized provisionally by Stace (1997): *Salicornia pusilla* J. Woods, *S. europaea* L. agg. (*S. ramosissima* J. Woods, *S. europaea* L. and *S. obscura* P.W. Ball & Tutin) and *S. procumbens* Smith agg. (*S. nitens* P.W. Ball & Tutin, *S. fragilis* P.W. Ball & Tutin and *S. dolichostachya* Moss). It is possible that only three species (*S. pusilla*, *S. europaea* agg. and *S. procumbens* agg.) should be recognized (Stace 1997), corresponding with the Sections Pusillae, *Salicornia* & *Dolichostachyae* of Scott (1977). We also include relevant information for closely related putative species within the same complex world-wide.

In *Salicornia*, the main stem and its opposite branches are composed of short, cylindrical or clavate internodes, each with a succulent, photosynthetic covering, conferring the articulated appearance. The

root system tends to be superficial, often penetrating less than 10–20 cm into the sediment; the main root axis produces few branches in small individuals but larger plants develop several highly branched, woody main roots that originate from near the base of the stem. A pair of opposite, connate, highly reduced leaves constitute no more than a rim at each stem node. At the lower internodes the succulent covering may atrophy, leaving the base of the stem and some branches narrow, wiry and with ridge-like nodes. The arrangement of lateral branches is regularly decussate and in large plants may be of the 4th order; the uppermost primary branches make an angle usually less than 45° with the main stem and may be straight or curved upwards. At maturity, every branch terminates in a fleshy spike of contiguous, fertile segments; segments have convex or more or less cylindrical sides and each bears an opposite pair of (1–) 3-flowered cymes. The spike, with its decussately arranged dichasial cymes, may be distinctly tapered; it may be tinged red at maturity. The number of fertile segments per spike is variable but shows discontinuities, sometimes associated with species, resulting in modes of 2–4 (–12) or 3–12 (–22) or (4–) 6–30 fertile segments per spike.

Each cyme consists of a central flower and (usually) two lateral flowers, deeply embedded in fleshy tissue at the proximal end of a segment and subtended by a rim-like upgrowth (which may have a scarious edge) of the segment below. Within a cyme, the florets are usually arranged in a triangle with the central one distinctly distal; the laterals may be either smaller than the central floret or almost as large. The 3 (–4) minute lobes of the perianth are connate almost to their apex, usually forming a tri-radiate slit through which the stigmas and anthers or pollen may emerge; they become hard or spongy in fruit. Each flower has 1 (anterior) –2, rarely 0, stamens. The anther length may be 0.6–1 mm (with dehiscence after exertion) or 0.2–0.5 mm (with dehiscence before exertion or when not exerted). Styles 2 or style bifid bearing in all 3 plumose stigmatic lobes *c.* 0.5–0.7 mm in length, or

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*Abbreviated references are used for many standard works; see *Journal of Ecology* (1975), 63, 335–344. Nomenclature of vascular plants follows *Flora Europaea* and Stace (1997) for British plants, where authorities are not cited.

exceeding 1 mm in some tetraploids. The deeply embedded ovary is unilocular with a solitary basal ovule. The ovoid, flattened seed has a horse-shoe shaped embryo enclosed by a thin, membranous testa bearing hooked hairs (few or numerous, long or short, sometimes mucilaginous) or is sometimes glabrous. Seed mass 0.2–0.8 mg (see VIII C). Putative British species have been characterized as follows:

S. pusilla (one-flowered glasswort). Mostly erect to 25 cm, simple to much branched and bushy. Branches more or less straight. Yellowish-green, becoming brownish or pinkish-yellow, often with pink tips to the branches. Terminal spike short, up to c. 6 mm, with only 2–4 fertile segments. Lower fertile segments 1–1.5 mm long and 1–1.5 mm wide at the narrowest point. Cymes one-flowered. Flowers almost circular with a single stamen. Fertile segments disarticulating shortly before the seeds are ripe.

S. europaea (common glasswort). Erect to 35 cm, fairly richly branched. Lowest branches may be nearly as long as the main stem. Dark green becoming yellow-green and ultimately flushed pink or red. Terminal spike 10–50 (–60) mm. Fertile segments with distinctly convex sides, the lower ones 2.5–4 mm long and 3–4.5 mm wide at the narrowest point. Central flower distinctly larger than the two laterals.

S. obscura (glaucous glasswort). (Perhaps a variant of *S. europaea*). Usually erect to 40 cm, typically with primary branches only; branches curving upward distally; lowest branches not more than half as long as the main stem. Dull glaucous green with a matt surface becoming dull yellow. Segments with an inconspicuous scarious border up to 0.1 mm wide. Terminal spike 10–40 (–45) mm, and lower fertile segments 2.5–4.5 mm long and 2.8–4 (–5) mm wide at the narrowest point, similar to *S. europaea*.

S. ramosissima (purple glasswort). (Perhaps a variant of *S. europaea*). Erect or prostrate, to 40 cm, simple to much branched. Segments with a conspicuous, broad, scarious border c. 0.2 mm wide. Dark green becoming deep purplish-red. Branches more or less straight. Terminal spike (5–) 10–30 (–40) mm and lower fertile segments 1.9–3.5 mm long and 2–4 mm wide at the narrowest point. Central flower rounded-rhombic to almost circular.

S. nitens (shining glasswort). Typically erect to 25 cm with primary branches only. Plant smooth, shining, somewhat translucent, green or yellowish green becoming light brownish purple/orange. Sterile segments conspicuously swollen near the top. Terminal spike 12–40 mm with lower fertile segments (1.8–) 2–3 (–3.5) mm long and 1.8–3.5 mm wide at the narrowest point.

S. fragilis (yellow glasswort). Erect to 40 cm, usually primary branches only, the lowest normally less than one quarter the length of the main stem. Dull green becoming dull yellowish-green. Terminal spike (15–) 25–80 (–100) mm, distinctly tapering. Lower fertile segments more or less cylindrical, 3–5 mm long and 3–6 mm wide.

S. dolichostachya (long-spiked glasswort). Erect to procumbent, 10–45 cm. Much branched and bushy, the lowest branches about as long as the main stem. Dark green becoming paler or dull yellow/brownish. Terminal spike (25–) 50–100 (–200) mm, distinctly tapering. Lower fertile segments more or less cylindrical, 3–6 mm long and 3–6 mm wide.

Patterns of variation suggest that individuals exist as members of local, perhaps unique, inbreeding populations and characterization of the populations is more tractable than that of individuals. World-wide there are c. 13 species (Scott 1977) with innumerable variants. Variation within and between taxa is expressed in morphology, chromosome number, life-history characteristics, enzyme electrotypes and DNA polymorphisms. Numerical analysis of morphological variation in the field failed to support a distinction between the diploid species *S. europaea* and *S. ramosissima* (Ingrouille & Pearson 1987), although Jefferies & Gottlieb (1982) had found consistent differences at loci coding for six enzymes. Morphological variation in tetraploids of the *S. dolichostachya* group provided evidence for at least two taxa, one of which correlated with *S. fragilis* (Ingrouille *et al.* 1990). Wolff & Jefferies (1987a) used a combination of cytological, electrophoretic and morphometric characters to distinguish three groups of populations from Hudson Bay, the Atlantic coast and James Bay of North America. Transplant experiments between upper and lower levels of a salt marsh in north Norfolk, England, indicated genetically fixed differences in growth phenology between local populations (Jefferies *et al.* 1981). Subsequently, a detailed demographic analysis of reciprocal transplant experiments has shown clear losses of fitness in populations transplanted away from their local, indigenous microhabitats on the marsh and clear selection against alien populations at transplant sites (Davy & Smith 1985, 1988; Smith 1985). Analysis of ribosomal DNA polymorphism (RFLP) has confirmed the existence of genetically distinct forms but their distribution was correlated with elevation in the marsh tidal frame rather than with morphological characteristics (Davy *et al.* 1990; Noble 1990; Noble *et al.* 1992). Luque *et al.* (1995) have detected DNA polymorphism between three Spanish populations of *Salicornia* using a RAPD technique.

Succulent plants of mainly moist, saline habitats, particularly coastal salt marshes; they also grow in inland saline areas.

I. Geographical and altitudinal distribution

The composite distribution of all taxa of *Salicornia* in Britain (Fig. 1) faithfully reflects the availability of salt-marsh habitats around the whole coastline. *Salicornia* is largely absent from British inland salt marshes, despite apparently suitable habitats (Lee 1977), but it occurs in at least one, at Northwich, Cheshire. Some records are not assigned to individual species, or even species aggregates, and so the constituent taxa are more or less

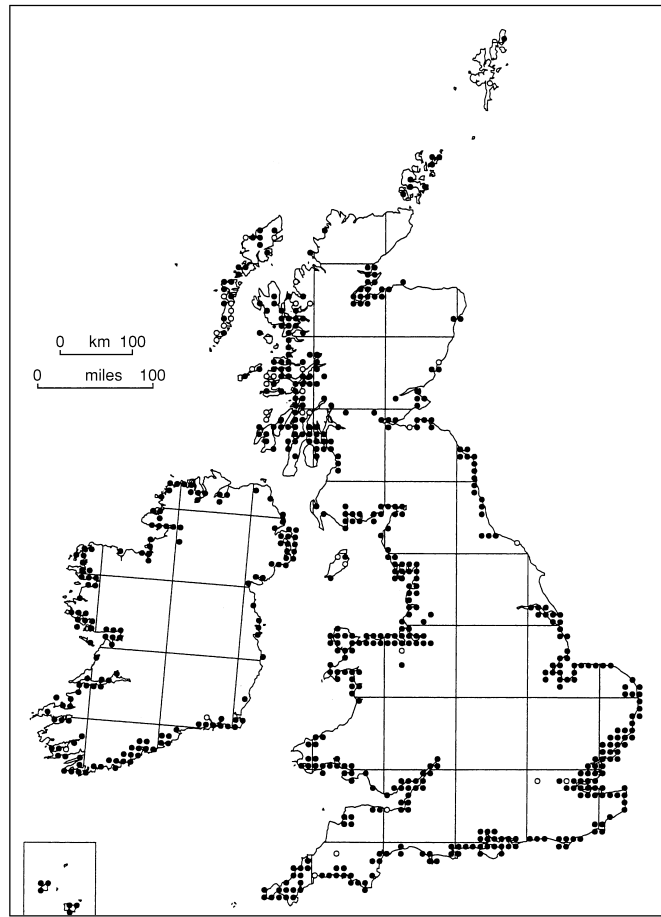


Fig. 1 The composite distribution of all taxa of the genus *Salicornia* in the British Isles. (O) Pre-1950; (●) 1950 onwards. Each dot represents at least one record in a 10-km square of the National Grid. Mapped by Mrs J. M. Croft, Centre for Ecology and Hydrology, using Dr A. Morton's DMAP programme, mainly from records collected by members of the Botanical Society of the British Isles.

under-recorded. The *S. europaea* agg. is the most widely distributed form (Fig. 2a); *S. europaea* and *S. ramosissima* both occupy most of its range, whereas records of *S. obscura* are confined to a few locations, mainly in East Anglia and on the Bristol Channel (Fig. 2b–d). The tetraploid *S. procumbens* agg. (Fig. 3a) is apparently less abundant than *S. europaea* agg., especially in Scotland, Ireland and south-west England, although it is undoubtedly under-recorded; the reasonably distinctive *S. dolichostachya* (Fig. 3b) is the most widely recorded of its constituent taxa and *S. fragilis* (Fig. 3c) also occurs around much of the English and Irish coasts, whereas *S. nitens* (Fig. 3d) appears to be very sparsely distributed on a latitudinal range from the Isle of Wight to Orkney. The highly distinctive *S. pusilla*, with its single-flowered cymes, is confined to coastal marshes in the south and east of Britain, from the Humber around to S. Wales and the southern coast of Ireland (Fig. 4).

Salicornia is found around much of the coastline of Europe from the Arctic to the Mediterranean, as well as on the shores of both the Black Sea and Caspian Sea; it is also present sporadically where inland salines occur across Europe (Atl. Fl. Eur.; Fig. 5). Much of this distribution can be tentatively attributed to the *S. europaea* agg. (Fig. 6). Members of the *S. procumbens* group are

recorded from the coasts of the Beye More inlet of the Barents Sea, the North Sea, the English Channel, the Atlantic coasts of France and Portugal, and the Mediterranean coast of France (Fig. 7). Outside Britain, *S. pusilla* occurs only on the northern and western coasts of France (Fig. 8).

From Europe and the North African coast, the distribution of *Salicornia* extends through the near East and Caucasus and central Asia, including much of The Russian Federation, where it forms enormous thickets on solonchaks in steppes and deserts (Fl. URSS 6); it is found again at the coast near Vladivostok, around Sakhalin, and on the Japanese islands of Hokkaido, Honshu and Shikoku (Vergl. Chor.; Hultén 1970). Recently *Salicornia* has been discovered in Saudi Arabia, in salt marshes on the Arabian Gulf coast and in the sabkha of Al-Aushaziya, some 400 km from the coast (Al-Turki 1992, 1997). Three (Tolkén 1967) or four (O'Callaghan 1992) species of *Salicornia* occur around the coast of southern Africa (Tanzania, Madagascar, Mozambique and South Africa). One of these, *S. uniflora* Tolkén, is analogous with *S. pusilla* in having single-flowered cymes (Tolkén 1967). *S. europaea* (s.l.) is distributed along the Atlantic coast of N. America and the St. Lawrence seaway. Plants from populations in this complex in arctic coastal marshes around

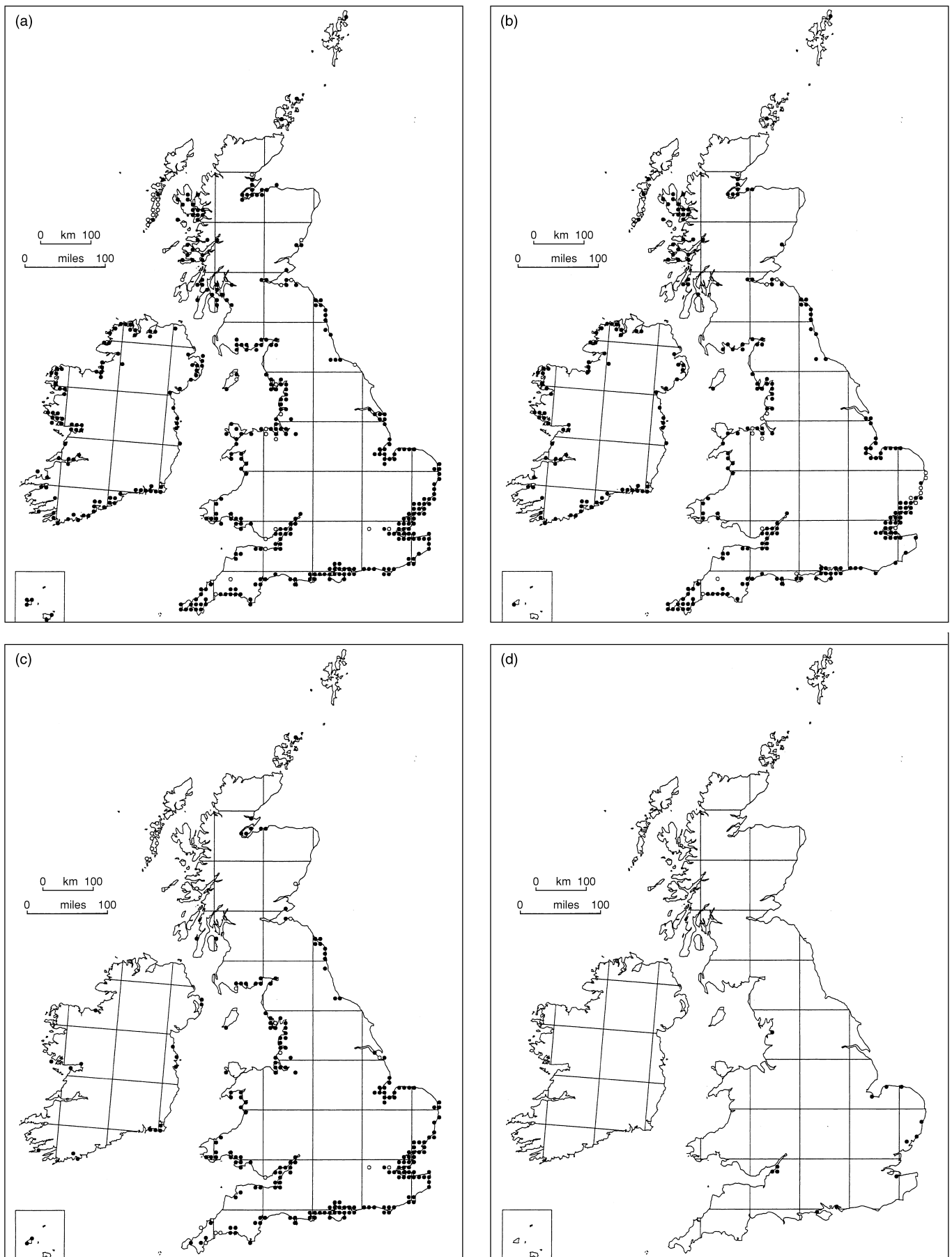


Fig. 2 The distribution of *Salicornia europaea* agg. in the British Isles. (O) Pre-1950; (●) 1950 onwards. Each dot represents at least one record in a 10-km square of the National Grid. Mapped by Mrs J. M. Croft (see Fig. 1). (a) *S. europaea* agg., (b) *S. europaea*, (c) *S. ramosissima*, and (d) *S. obscura*.

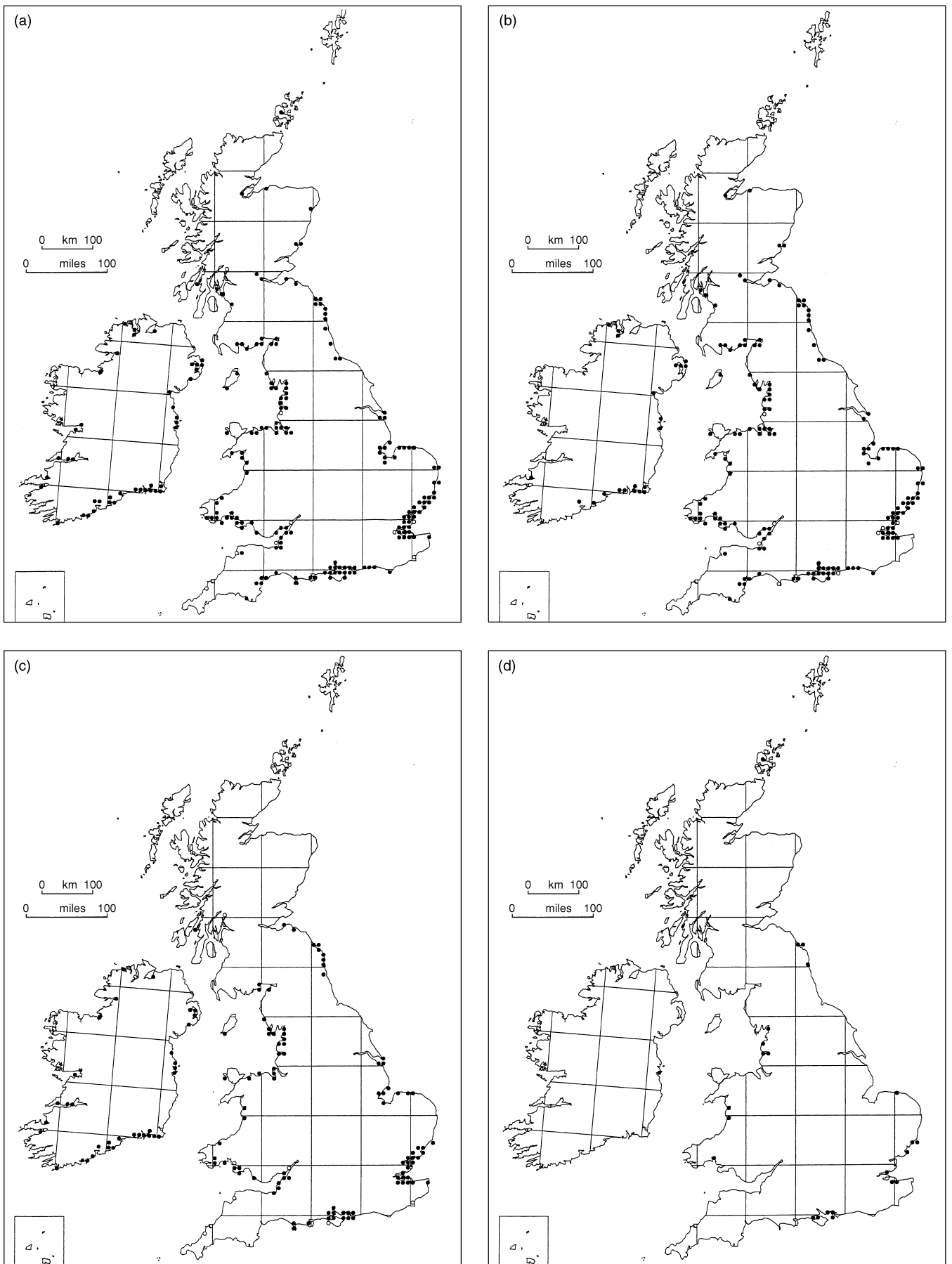


Fig. 3 The distribution of *Salicornia procumbens* agg. in the British Isles. (O) Pre-1950; (●) 1950 onwards. Each dot represents at least one record in a 10-km square of the National Grid. Mapped by Mrs J. M. Croft (see Fig. 1). (a) *S. procumbens* agg., (b) *S. dolichostachya*, (c) *S. fragilis*, and (d) *S. nitens*.

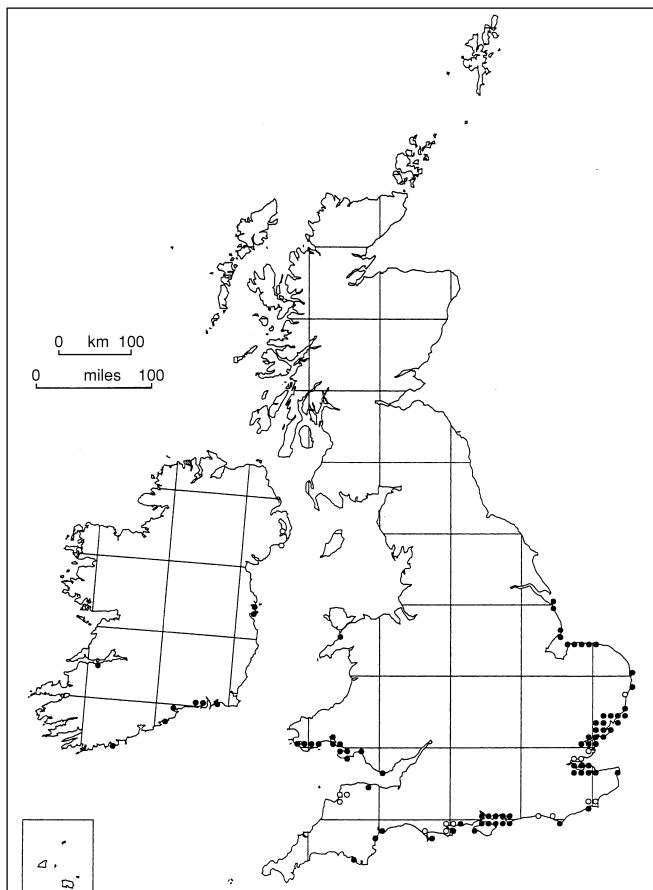


Fig. 4 The distribution of *Salicornia pusilla* in the British Isles. (O) Pre-1950; (●) 1950 onwards. Each dot represents at least one record in a 10-km square of the National Grid. Mapped by Mrs J. M. Croft (see Fig. 1).

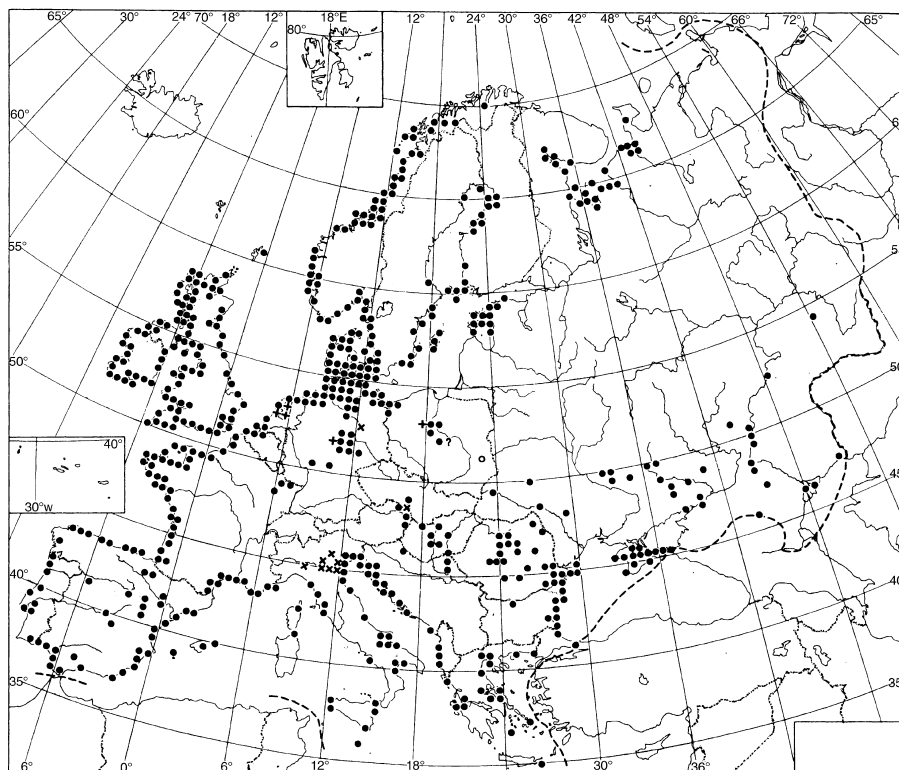


Fig. 5 The distribution of the genus *Salicornia* in Europe. Each dot (●) represents at least one record in a 50-km square. (+) extinct; (x) probably extinct. Reproduced from Atl. Fl. Eur., vol. 5 by permission of the Committee for Mapping the Flora of Europe and Societas Biologica Fennica Vanamo.

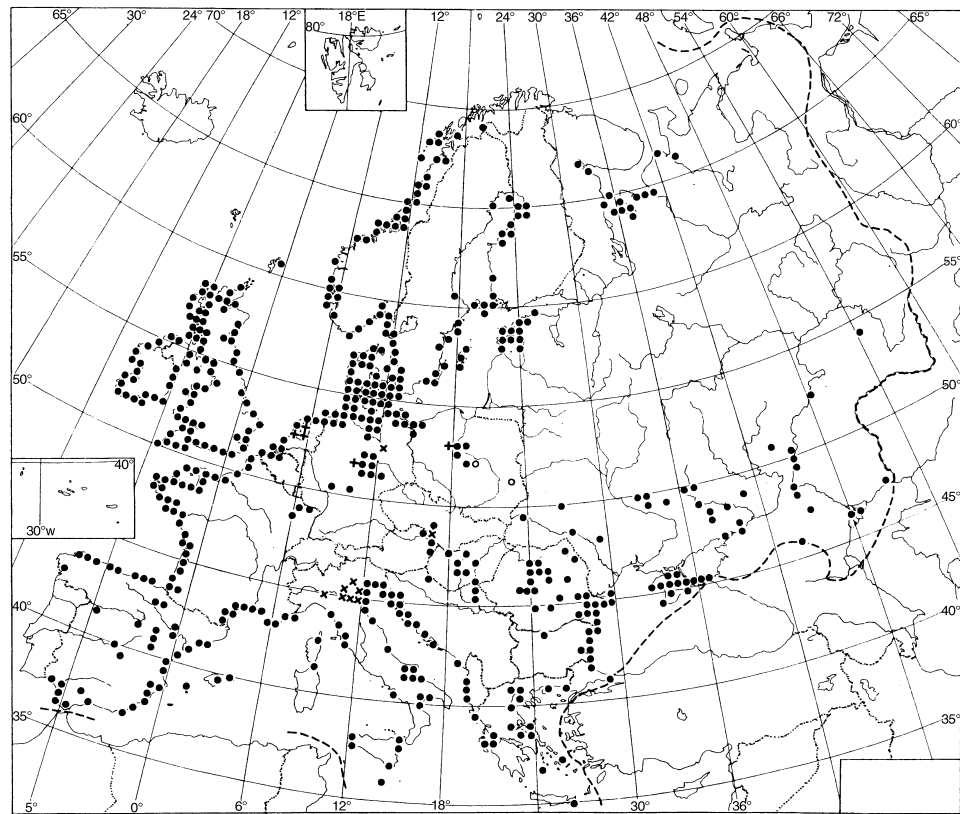


Fig. 6 The distribution of *Salicornia europaea* agg. in Europe. Each dot (●) represents at least one record in a 50-km square. (+) extinct; (×) probably extinct. Reproduced from *Atl. Fl. Eur.*, vol. 5 by permission of the Committee for Mapping the Flora of Europe and Societas Biologica Fennica Vanamo.

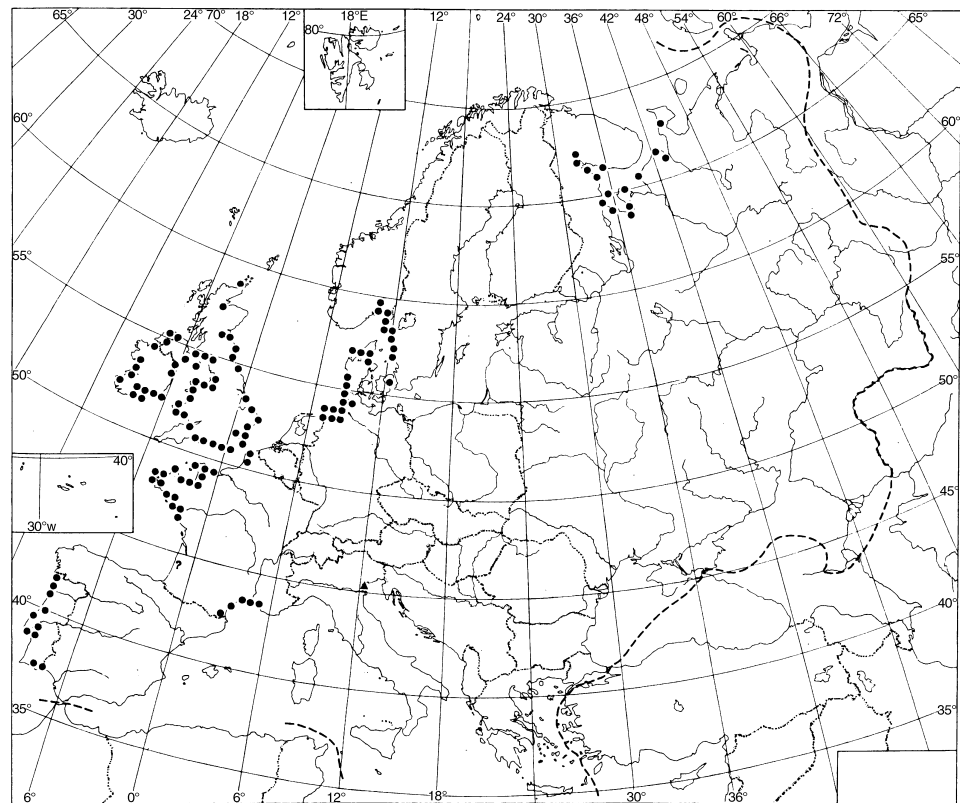


Fig. 7 The distribution of *Salicornia procumbens* agg. in Europe. Each dot represents at least one record in a 50-km square. (●) *S. dolichostachya*, *S. fragilis* and *S. nitens*; (▲) *S. veneta*. Reproduced from *Atl. Fl. Eur.*, vol. 5 by permission of the Committee for Mapping the Flora of Europe and Societas Biologica Fennica Vanamo.

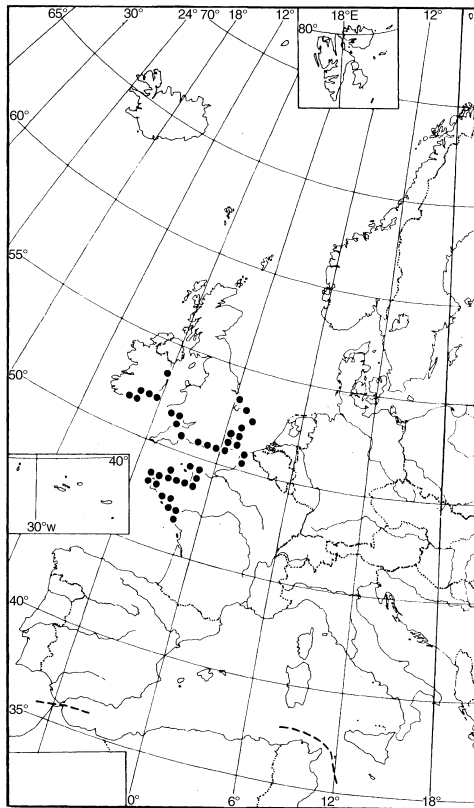


Fig. 8 The distribution of *Salicornia pusilla* in Europe. Each dot (●) represents at least one record in a 50-km square. Reproduced from *Atl. Fl. Eur.*, vol. 5 by permission of the Committee for Mapping the Flora of Europe and Societas Biologica Fennica Vanamo.

Hudson Bay have been distinguished as *S. borealis* Wolff & Jefferies and *S. maritima* Wolff & Jefferies (Wolff & Jefferies 1987b). The form widely distributed in the prairies and salt flats of western North America is generally referred to *S. europaea* ssp. *rubra* (Nelson) Breitung. *Salicornia* (s.s.) is absent from Australia, although there are perennial members of the tribe Salicornieae in five other genera (Wilson 1980). Similarly, it is absent from South America, as all species referred to *Salicornia* there are perennial (i.e., strictly *Sarcocornia* or *Arthrocnemum*) (Costa & Davy 1992).

The altitude of the vast majority of British *Salicornia* populations is below the level of the highest tides. The inland site at Northwich, Cheshire is at 10 m. However, populations in the sabkha of Al-Aushaziya, Saudi Arabia, are at 650 m and *S. rubra* in Montana, USA reaches 1277 m.

II. Habitat

(A) CLIMATIC AND TOPOGRAPHICAL LIMITATIONS

Salicornia has very wide climatic tolerances: subarctic to subtropical and oceanic to continental. Its tolerance of water stress (see VII E) and its annual life history presumably contribute to its ability to survive extreme conditions in adverse seasons. The northern limit of

Salicornia corresponds with the 10 °C July isotherm; populations at this range limit are virtually confined to low, south-facing slopes, where temperatures may be as much as 7 °C higher than the north-facing aspect (Jefferies *et al.* 1983). It is generally limited to unshaded sites with relatively high daily radiant energy availability during the growing season.

Individual populations and taxa of *Salicornia* may be very sensitive to elevational variations associated with microtopography on the gradient from land to sea of tidal salt marshes. Populations low in the tidal frame need to be more tolerant of prolonged submergence, tidal scour and waterlogging, whereas those at high elevations may experience hypersalinity in summer (Jefferies *et al.* 1979). In Norfolk, England, *S. dolichostachya* is among the vascular plants that occurs lowest in the tidal frame, where it experiences more than 600 tidal submergences per annum (Smith 1985; Davy & Smith 1988). Rozema, van der List *et al.* (1987) record it occurring mainly below the mean High Water Level in the Netherlands. *Salicornia europaea* in Norfolk is characteristic of large areas of low marsh, whereas *S. ramosissima* is more typical of pans and interfluges of the upper marsh at slightly higher elevation; *S. pusilla* is restricted to low hummocks and the landward margin, the highest parts of the tidal frame, where it is often inundated only by spring tides (Davy & Smith 1988; Noble *et al.* 1992). Similarly, Rozema, van der List *et al.* (1987) reported that *S. europaea* agg. (*S. brachystachya* (Meyer) König) occurs above Mean High Water Level.

(B) SUBSTRATUM

Various forms of *Salicornia* in intertidal habitats grow on a wide range of marine sediments, ranging from gravels and shelly sands, through silts to fine clays. In inland salines, the substrates can also vary from fine clays to coarse sands, depending on their origin. Although *Salicornia* is an early colonist of soft, unconsolidated sediments, the densest stands tend to be on firm silts and clays (Adam 1981).

Salicornia is invariably associated with saline, brackish or alkaline substrates. The ionic composition of coastal salt marsh substrates generally reflects the ionic balance of seawater, dominated by sodium chloride, but actual concentrations can vary greatly, depending on complex tidal cycles, local evapotranspiration, precipitation and any supply of fresh groundwater. The concentration of Na⁺ ions in the interstitial water from coastal marsh sediments fluctuates greatly, both seasonally and from year to year (Jefferies 1977; Jefferies *et al.* 1979; Smith 1985). In mid-summer, when successive spring high tides fail to cover the upper marsh and evapotranspiration exceeds rainfall, Na⁺ concentrations in the interstitial water may exceed 1 M in the upper marsh; conversely, near the winter solstice, the value is typically 0.2–0.3 M. The water content of the sediment shows the inverse trend, with low values in summer. Such saline substrata inevitably have exceptionally low water potentials.

During hot, dry summers the water potential (ψ_w) of the upper layers of the sediment can fall rapidly to below -5.0 MPa (-50 bars); in cooler, wetter summers ψ_w potential remains barely below that of sea water, c. -2.3 MPa (Jefferies *et al.* 1979). There are many reports of hypersaline soil conditions in sites dominated by *S. europaea*. For instance, Tsuda (1961) recorded up to 8.2% NaCl in the soil solution in Japan (cf. 3.5% total salts in seawater). Salinities in an Ohio salt pan (Ungar *et al.* 1979), measured as electrical conductivity, reached 143 mS cm^{-1} (approximately equivalent to -5.1 MPa ψ_w). Crusts of crystallizing salts are commonly seen at the sediment surface in dry weather. In inland salines, a variety of ions other than Na^+ and Cl^- may predominate.

In coastal marshes, the substrates of *Salicornia* span the tidal range and are often waterlogged for much or all of the time, depending on elevation and drainage conditions. The saturated sediments are typically hypoxic and may develop low redox potentials, even in the surface layers, with concomitantly high levels of potentially toxic reduced ions such as S^{2-} and Mn^{2+} (Ingold & Havill 1984; Singer & Havill 1985). See VII (E).

III. Communities

The classification of salt marsh vegetation in the British National Vegetation Classification (Rodwell 2000) is based substantially on the work of Adam (1978, 1981) who made a phytosociological analysis of relevés from salt marshes all round the British coast. The only community dominated by *Salicornia* is the 'Annual *Salicornia* salt marsh' (SM8) or Salicornietum europaea. Its constant species are at least one of the taxa of *Salicornia*, which can be of greatly varying density, in a generally open, ephemeral community. Sometimes there are no other species. There is often an algal mat over the substrate surface; in some areas turf furoids (*Fucus vesiculosus* ead *caespitosus*) may be abundant. Scattered plants of *Puccinellia maritima*, *Suaeda maritima* and *Spartina anglica* may occur, with occasional individuals of *Atriplex portulacoides* and *Aster tripolium* (including var. *discoideus*). *Sarcocornia perennis* may be present as a rare species. In 81 samples, the mean total cover was 53%, the mean vegetation height was 7 cm and the mean number of species was three. Within the low marsh, where it characteristically pioneers the colonization of mud flats, the Salicornietum may occur as a distinct zone (from a few metres to several hundred metres wide) or in a mosaic with Spartinetum townsendii or Puccinellietum maritimae (Adam 1981). Extensive pure stands of *Salicornia* may occur in shallow, poorly drained pans and depressions in higher parts of the marsh.

Salicornia is a constant species in two other communities (SM10 and SM11). 'Transitional low-marsh vegetation with *Puccinellia maritima*, annual *Salicornia* species and *Suaeda maritima*' (SM10) is species-poor and always dominated by complementary proportions of the three constants. It is widespread on lower

marshes, where it may be a pioneer community on sandy substrates; on heavily grazed lower marshes with a hummocky *Puccinellia maritima* community, it tends to occupy the hummock tops, whereas in muddier marshes of south-east England it is found in slight depressions within a variety of other communities. It is also widespread on the sides of large creeks where it occupies a distinct zone above the Salicornietum europaea. 'Aster tripolium var. *discoideus* salt marsh' (SM11) or Asteretum tripolii also occurs as an extensive zone on the lower marsh or on creek sides at varying levels in the marsh, with a maximum development at about 350 tidal submergences per year. In addition, 'Zostera noltii stands' (SM1) at their upper elevational limits may grade into Salicornietum. Another essentially annual community, 'Suaeda maritima salt marsh' (SM9) or Suaedetum maritimae can also grade into Salicornietum on the lower marsh. 'Spartina anglica salt marsh' (SM6) or Spartinetum townsendii colonizes marshes at the same elevation as Salicornietum and has now replaced much of it.

The seeds of *Salicornia* are widely distributed on salt marshes and so it is a variable or minor component of many other communities, where it may find ephemeral niches within the matrix of perennial species: 'Spartina maritima salt marsh' (SM4); 'Arthrocnemum perenne (*Sarcocornia perennis*) stands' (SM7); 'Rayed Aster tripolium on salt marshes' (SM12); 'Puccinellia maritima salt marsh' (SM13) or Puccinellietum maritimae (in both the 'Limonium vulgare-Armeria maritima subcommunity' or General Salt Marsh, as well as the 'Puccinellia maritima-Spartina maritima subcommunity'); 'Halimione (*Atriplex*) portulacoides salt marsh' (SM14); 'Juncus maritimus-Triglochin maritima salt marsh' (SM15); 'Festuca rubra salt marsh' or Juncetum gerardi (SM16); 'Artemisia maritima salt marsh' or Artemisietum maritimae (SM17); 'Suaeda vera-Limonium binervosum salt marsh' (SM21) of the north Norfolk coast; 'Halimione (*Atriplex*) portulacoides-Frankenia laevis salt marsh' (SM22); 'Spergularia marina-Puccinellia distans salt marsh' (SM23); 'Suaeda vera salt marsh' (SM25); 'Inula crithmoides on salt marshes' (SM26).

Adam 1981 described the vegetation of British salt marshes in terms of 49 'noda'. *Salicornia* occurred in 34 of these noda and in association with 44 other species of angiosperm, each of which occurred with a frequency greater than 81% in at least one of the 49 noda.

Salicornia can have an important role as a salt-marsh pioneer, as it is frequently the first higher plant to colonize intertidal mud and sand flats. Carey & Oliver (1918) first described accretion around *S. ramosissima* plants to form ephemeral hummocks on a sand bank in the Bouche d'Erquy, Brittany, France. These, however, did not make a permanent contribution to the relief of the marsh, unlike those of the perennial *Sarcocornia perennis*. *Salicornia* species were the first colonists of sand flats after embankment removed tidal influence from the Grevelingen Estuary, in the Netherlands (Stienstra 1987). Direct observation of a naturally

developing salt marsh in the macrotidal environment of the Severn Estuary, at Berrow, Somerset, UK, chronicled succession from bare sediment, through Salicornietum, to a species-poor Phragmitetum in fewer than 90 years (Willis 2000). Nevertheless, large stands of *Salicornia* on low-lying sand and mud flats may be ephemeral and do not necessarily initiate succession.

Salicornia spp. is the character-taxon of the class Thero-Salicornietea Tx. 1954; the order Thero-Salicornietalia and alliance Thero-Salicornion Br.-Bl. 1933 em. Tx. 1950, whose eulittoral *Salicornia*-dominated communities extend from the north Atlantic and west Baltic coasts to the west coast of France and, locally, the coasts of Portugal and the north Mediterranean (Westhoff & Schouten 1979). Ellenberg (1988) recognizes low-marsh, pure stands as Salicornietum dolichstachyae. In the same order, communities of the alliance Salicornion ramosissimae Tx. 1974 comprise swards of *Puccinellia maritima* with *S. ramosissima* at higher elevations (Ellenberg 1988). The inland saline area east of the Neusiedlersee in Austria supports Salicornietum prostratae Soó 1964, a rare community dominated by *Salicornia prostrata* (*S. europaea* agg.), with subdominant *Puccinellia peisonis*, *Phragmites australis* always present and sometimes with *Suaeda pannonica* present (Mucina *et al.* 1993). Bernatksy (1905) concluded that *Salicornia* was local and uncommon in halophytic communities of central Europe because seasonal fluctuations in water level were generally too wide. *S. ramosissima* is the dominant species of the Salicornietum europaeae hungaricum of Hungary (Soó 1960) and, in the Sarcocornio perennis-Salicornietum ramosissimae, the *Salicornia* characteristic of coastal marshes in north-west Spain (Sánchez *et al.* 1996).

IV. Response to biotic factors

The lower limit of *Salicornia europaea* on tidal mud flats at the seaward margin of salt marshes may be determined by bioturbation. Gerdol & Hughes (1993), working in the estuary of the River Crouch, Essex, found that this lower limit corresponded with the upper limit of the abundant amphipod *Corophium volutator* (Pallas), at approximately mean high water neap tide level (MHWNT). Seedlings transplanted below this level were disturbed by the activity of *Corophium* but those in areas treated with insecticide to remove the *Corophium* had a doubled survivorship, similar to that of seedlings transplanted above MHWNT. The populations of *Corophium* of up to about 14 000 m⁻² were effectively able to prevent seedling establishment.

There are varied biotic relationships between *Salicornia* and algae on lower marshes. Algal mats (of *Enteromorpha linza*, *E. torta*, *E. prolifera*, *Rhizoclonium riparium* and *Ulothrix speciosa*) may contribute to mortality of *Salicornia* seedlings by pulling them from the sediment as the mats float on the incoming tide, as at Skallingen, Denmark (Jensen & Jefferies 1984).

Costa (1992) found that patches colonized by *Fucus vesiculosus* ecad *muscooides* provided favourable sites for the trapping and germination of seeds of *Salicornia*. Mortality rates of seedlings of *S. europaea* were reduced in the algal patches. Temperatures inside *Fucus* patches were 2–4 °C lower than on the adjacent mud surface on sunny spring days (Costa 1992); fucoid algae intertwined with *Salicornia* may reduce evaporation and maintain salt concentrations closer to that of sea water (Chapman 1960). *Salicornia* plants themselves may facilitate colonization by dominant, perennial halophytes in physically stressful mid- and upper marshes, by reducing evaporation from the sediment surface and limiting salinity stress (Hacker & Bertness 1999).

A study of neighbourhood effects in mixed stands of the annuals *S. europaea* and *Suaeda maritima* at Stiffkey, Norfolk, by Costa (1992) demonstrated that their coexistence was maintained mainly by the earlier germination of the smaller-seeded, slower-growing *Salicornia* and its consequent pre-emption of resources; when germinated at the same time, *Salicornia* was a poor competitor with *Suaeda*. Particularly in the low marshes of south-east England, large areas previously dominated by *Salicornia* have been invaded and replaced by *Spartina anglica*. According to Ball & Brown (1970), *Salicornia europaea* is better able than *S. dolichostachya* to withstand competition from the perennial grasses *Spartina anglica* and *Puccinellia maritima*.

Greater species diversity and increased trophic complexity of upper marshes can lead to complex biotic interactions. Proudfoot (1993) investigated a 4-species interaction close to creek banks dominated by the shrubby perennial *Atriplex portulacoides*. The microlepidopteran *Coleophora atriplicis* (Meyrick) has successive instars of case-bearing larvae that feed on salt-marsh chenopods; early in the summer larvae feed on pollen and flowers of *Atriplex portulacoides* but in late summer they may migrate to *Suaeda maritima* and *Salicornia*, where they mine and consume the developing seeds. Proudfoot (1993) showed that a cline of decreasing abundance of *Suaeda* away from creek banks was due to increasing competition from *Salicornia*; populations of *Salicornia* close to the *Atriplex* were depressed as a result of preferential seed predation by *Coleophora* larvae. Rand (1999), working on New England salt marshes, has recently shown that the presence of *S. europaea* had an adverse effect on the annual *Atriplex patula*; this effect was also mediated indirectly through a shared herbivore, in this case the chrysomelid beetle *Erynephala maritima*. Mature stands of *Salicornia* and their seeds can be an important food resource for passerine birds and geese (see IX A). On salt marshes in northern Germany, intense sheep grazing promoted communities containing *S. europaea* and its population density decreased after reduction of the grazing intensity, as *Festuca rubra* and other more competitive perennials replaced *Puccinellia maritima* (Kiehl *et al.* 1996).

Mats of tidal detritus deposited by high tides may remain long enough to kill the vegetation and create

bare patches in which *Salicornia* stands can become established (Truscott 1978). Experimental burial with wrack (tidal litter) of *Spartina alterniflora* (using a 5–10 cm thick layer) favoured germination and establishment of *S. europaea* on a Rhode Island *Spartina patens* marsh (Brewer *et al.* 1998); the success of *Salicornia* after disturbance by wrack burial was attributed to its ability to compete with *Juncus gerardii* under the more saline conditions of exposed sediments that are subject to high rates of evaporation. Here, *S. europaea* is regarded as a fugitive species of hypersaline bare patches and pans, because of its inability to compete with the dominant perennials (Bertness *et al.* 1992).

V. Responses to the environment

(A) GREGARIOUSNESS

Salicornia is generally highly gregarious but local distributions may be random or aggregated (Brereton 1971; Joenje 1978). Seedling population densities may be greater than 100 000 m⁻² in suitable habitats. Very local high-density clumps may occur where senescing mother plants have fallen over and been incorporated into surface sediments, releasing their embedded seed complements *in situ* as they decompose. Algal patches may also trap seeds and increase local density. Population density varies greatly, with the potential for strong regulation from a combination of negatively density-dependent seed production and density-independent seedling mortality (Jefferies *et al.* 1981; Davy & Smith 1985, 1988; Smith 1985; Watkinson & Davy 1985). The effects of density on seed production arise from the great morphological plasticity: at high density, individuals are unbranched with a single, terminal spike that can produce only a few seeds; at low density, the 3-dimensional branching structure can result in large individuals with hundreds of fertile terminal spikes (see VIII C). Watkinson & Davy (1985) modelled the relationship between the reproductive output per plant (N_i/N) and the density of surviving plants (N) as:

$N_i/N = \lambda(1 + aN)^{-b}$ where λ is the number of seeds produced by an isolated plant, a is the area required to produce λ seeds and b describes the effectiveness with which resources are taken up from a given area.

Mortality tends to be of the Deevey type I pattern, preponderantly before flowering (Jefferies *et al.* 1981; Beetink 1985). The mortality in young plants at high density is largely independent of density, resulting mainly from disturbance, herbivory, interspecific competition and water stress (Jefferies *et al.* 1981; McGraw & Ungar 1981; Ellison 1987a; Ungar 1987a). Even at the highest densities found in the field (> 10 000 m⁻²), populations of *S. europaea* agg. show little evidence of self-thinning, despite closely approaching combinations of mass and density where thinning would normally be predicted, according to the $-3/2$ power rule (Watkinson & Davy 1985). The fact that size inequalities within populations (expressed as Gini coefficients) did not

change with density, or with growth during the season, is another manifestation of this (Ellison 1987b). The failure of *Salicornia* to self-thin may be explained in terms of growth geometry: because it lacks leaves and its stems branch sparsely, at high densities its biomass per unit area tends to increase as a linear function with height, rather than as the cubic function that describes more conventional morphology and which is believed to underlie the $-3/2$ self-thinning rule (Ellison 1987b, 1989).

Harley & Bertness (1996) found that plants in crowded stands of *S. europaea* on a New England salt marsh were thinner and more susceptible to breakage, becoming dependent on their neighbours for mechanical support. The breaking force for individuals that had developed in isolation was much greater than for those in crowded stands; all individuals from crowded stands had collapsed and fallen over one week after experimental removal of their neighbours.

(B) PERFORMANCE IN VARIOUS HABITATS

Salicornia is confined to saline habitats and, as an annual, its performance is constrained by the length of the growing season. At its northern limit in the Canadian Arctic, where the growing season is effectively only 3 months and conditions are generally severe, individuals reach a height of 1–10 cm and produce simple branches only at the cotyledonary node, if at all (Wolff & Jefferies 1987b). In such marginal habitats, plants colonize north-facing slopes poorly, where they do not branch and can ripen little seed; most of the populations are on south-facing slopes, where many individuals branch and seed is ripened reliably (Jefferies *et al.* 1983). In temperate latitudes, such as the salt marshes of north Norfolk, the growing season is typically 7–8 months and under otherwise favourable conditions individuals can reach 40 cm, with up to 4th-order branching at the nodes. Such large individuals tend to occur in isolation, on nitrogen-rich drift lines of hyposaline estuarine marshes or on the sides of creeks in other relatively eutrophic marshes. Performance can be severely limited by summer hypersalinity in inland marshes and on the higher elevations of coastal marshes, especially at lower latitudes. The marshes and mangal of the Saudi Arabian Gulf coast potentially enjoy a 12-month growing season, allowing the development of massively branched individuals, with woody basal internodes 7 mm in diameter, that display a wide variety of morphologies; these plants can apparently persist for more than one year (Al-Turki 1992), despite their determinate growth. No seed dormancy has been detected in such populations and this is presumably an evolutionary response to a relatively benign and reliable environment (Al-Turki 1992).

There have been few reliable measurements of net primary production. Jefferies (1972) estimated the annual net productivity of *Salicornia* spp. on the marshes of the north Norfolk coast at 876 g m⁻² year⁻¹, on the basis of frequent measurements of total standing

crop. Similarly, annual net aerial primary production of *S. ramosissima* on the Cantabrian coast (north Spain) was estimated as 486 g m⁻² year⁻¹ by Benito & Onaindia (1991) using Smalley's method.

Species or populations characteristic of low marsh, where hypersalinity is unlikely and a moderate supply of nitrogen from seawater is assured (e.g. *S. europaea* and *S. dolichostachya*), tend to have faster growth rates than those of species abundant at higher elevations (e.g. *S. ramosissima*) (Jefferies 1977; Jefferies *et al.* 1981). There are numerous differences in demographic performance associated with the elevation of populations, or species, in the tidal frame (e.g. Beefink 1985; Davy & Smith 1985, 1988).

(C) EFFECT OF FROST, DROUGHT ETC.

Freezing is less of a hazard in the habitats generally affected by *Salicornia* than in non-saline habitats with the same climate, because of depression of the freezing point by high concentrations of solutes in both soils and plants. In addition, coastal locations are generally buffered, by proximity to the thermal capacity of the sea, from the lowest extremes of temperature experienced inland at similar latitude. Nevertheless, cohorts of seedlings that have germinated between December and March may be killed by exceptionally hard frosts on the north Norfolk coast; later germinating cohorts are rarely damaged. Seedlings may also be removed by ice scour. Autumn frosts hasten the senescence and collapse of plants, thus releasing the seeds into the sediment. The seeds overwintering in the surface sediments appear to be extremely tolerant of low temperatures, even those prevailing in the arctic. The annual distribution of frost is undoubtedly one of the determinants of the length of the growing season (cf. V B). As a halophyte, *Salicornia* is tolerant of exceptionally low water potentials in its root environment, whether they arise from salinity, drought or a combination of both (see VI E).

Hydraulic forces generated by tidal flow, perhaps associated with scouring of the sediment and wave action, can be a major source of mortality for *Salicornia* seedlings at lower elevations on a salt marsh (Wiehe 1935). *Salicornia* is very susceptible to marine pollution from oil spills or refinery effluent and is killed quickly by a single spillage (Baker 1979). *Salicornia ramosissima* in a polluted estuarine marsh in south-west Spain accumulated high concentrations of As, Cr, Cu, Fe, Mn, Ni, Pb, Ti and Zn without apparent harm (Luque *et al.* 1999).

VI. Structure and physiology

(A) MORPHOLOGY

Each succulent, photosynthetic 'segment' is an internode separating consecutive pairs of oppositely arranged, but very reduced, leaves or scale leaves. In older, mainly basal, segments the outer tissues wither, leaving brown,

non-succulent stems. The morphological nature of the photosynthetic tissue associated with each internode has been controversial. Fahn & Arzee (1959) regarded it as entirely cortical in origin, attributing all photosynthesis to the stem. Duval-Jouve (1868) considered the outer cortex of each segment to be foliar in origin, a sheath being formed from the fused bases of the leaves immediately above. This 'foliar sheath' theory of the succulent cortex of *Salicornia* was given credence by de Fraine (1912) in a classical morphological study (using several species of *Salicornia*) on development at the shoot apex and of the vascular system. It was also supported by Halket (1928) after studying an abnormal plant of *S. europaea* in which the terminal parts of some leaves were clearly separated from the stem. Evidence from other succulent chenopods agrees (James & Kyhos 1961).

The vascular anatomy of a segment is well known (de Fraine 1912; Fahn & Arzee 1959; Ellison *et al.* 1993). A transverse section of the stem, taken mid-way within a segment, shows a central ring of eight primary vascular bundles enclosed by pericycle cells and an endodermis, or 'limiting layer', surrounded by a layer of water storage cells and then by a layer of photosynthetic cells. Between the inner (water storage) and outer (photosynthetic) layers lies vascular tissue originating at the distal end of the segment. Whilst it is agreed that this vascular tissue is foliar in origin, the true nature of the tissues it serves (water storing cells to the inside and photosynthetic cells towards the outside) is controversial: these non-vascular tissues are considered to be foliar by de Fraine (1912) but cortical by Fahn & Arzee (1959). At each node, two of the eight vascular bundles diverge as leaf traces opposite each other. Each leaf trace divides into three: the central trace curves upwards to supply the much reduced leaf tip whilst the lateral pair curve downwards between the water storage and palisade layers of the foliar sheath or cortex to form a closed network of anastomosing vascular tissue (Fahn & Arzee 1959). In curving downwards there is also effectively a rotation of each bundle of the lateral pair so that the phloem is outermost as in the leaf tip itself (de Fraine 1912). Above the node, two of the six surviving vascular bundles bifurcate, restoring the total to eight. Ellison *et al.* (1993) determined, by serial sectioning, changes in the mean diameters of vessel members of the primary vascular traces between consecutive nodes: hydraulic constrictions in *S. europaea* occur two nodes below the morphological emergence of a branch, differing in this respect from those in trees and palms.

The bulk of the mature stem originates from a secondary meristem immediately surrounding the system of primary bundles. Anomalous secondary thickening, widespread among members of the Chenopodiaceae, results in a concentric series of collateral vascular bundles embedded in a lignified ground tissue; the precise behaviour of the cambium during the formation of these bundles is disputed. The outer side of the vascular cambium is inactive except where it forms

aerenchyma. Aerenchyma is present, particularly in *S. europaea* and *S. ramosissima*, in the lower regions of the stem and the upper part of the main root. It is surrounded by a thin layer of cork which is very readily torn off in cutting sections. In some cases aerenchyma of a special kind is present: the aerenchyma cells are drawn out at each end and appear to be covered with large 'pores' which are actually the result of cutting across tubular outgrowths connecting the loosely arranged cells (de Fraine 1912). Broad and short tracheid-like cells (Fahn & Arzee 1959; Fahn 1974), 'steroids' and 'spiral cells' (de Fraine 1912) are found among the palisade cells in both vegetative and reproductive shoots. Their function is unknown and taxonomic significance uncertain (Ball & Tutin 1959).

Among halophytes, *S. europaea* has an exceptionally high shoot to root (dry mass) ratio of about 10 : 1 (Cooper 1982). The root is diarch with a well marked endodermis and aerating tissue consisting of large intercellular spaces bridged by trabeculae. Although the presence of aerenchyma is generally associated with tolerance to flooding, in *Salicornia* this ability may be more related to superficial rooting and metabolic adaptations (Pearson & Havill 1988). The root has anomalous secondary thickening, as in the stem.

Stomata are most numerous towards the distal end of segments. They are arranged with their long axes at right angles to the axis of the stem. A stomatal density of $49 \pm 2 \text{ mm}^{-2}$ ($n = 30$) has been recorded for *S. europaea*. Dalby (1962) measured stomatal volumes (calculated as that of a sphere from a diameter equal to that of the stoma length) ranging from 3 to $16 \times 10^3 \mu\text{m}^3$ in diploids to $8\text{--}39 \times 10^3 \mu\text{m}^3$ in tetraploids, with a changeover value around $13 \times 10^3 \mu\text{m}^3$ (= 29.17 μm for length of stoma). Ball & Brown (1970) reported the length of stomatal guard cells as (20–)24–28(–31) μm in *S. europaea* and (27–)29–36(–42) μm in *S. dolichostachya*.

Branching patterns are highly plastic and greatly affected by plant density; crowding reduces the degree of branching in both monospecific (Jefferies *et al.* 1981; Jensen & Jefferies 1984; Smith 1985; Ellison & Niklas 1988) and mixed (Costa 1992) stands. *S. europaea* s.l. growing early in a succession were bushy, profusely branched and the younger internodes were much shorter than older ones; plants in late succession were unbranched, etiolated and had internodes of equal size (Ellison & Niklas 1988; see VI E).

There has been a plethora of morphometric studies of *Salicornia* (e.g. Langlois 1961a,b; Wilkon-Michalska 1985; Ungar 1987a), mainly in attempts to determine the morphological characteristics of subtaxa and local populations. Recent studies have applied numerical methods to morphometric data (Huiskes *et al.* 1985a; Ingrouille & Pearson 1987; Ingrouille *et al.* 1990).

(B) MYCORRHIZA

Endotrophic mycorrhiza in the roots of *S. europaea* ('*S. herbacea*') was first reported by Klecka & Vukolov

(1937) in Czechoslovakia. Rozema *et al.* (1986) recorded between 0.1 and 1% colonization of root length with AM mycorrhiza in *S. europaea* ('*S. brachystachya*') on a Dutch middle marsh; *S. dolichostachya* on a low marsh showed 0.1–30% root colonization, external hyphae and a low incidence of spores. *S. europaea* at two inland salt marshes in north Germany had extensive root colonization (extra- and intraradical hyphae), with vesicles and arbuscules, whereas specimens from a marsh on the Baltic coast had only 3% colonization, with sparse vesicles and arbuscules (Hildebrandt *et al.* 2001). Spores present at high densities in soils at the inland sites were mainly identifiable as *Glomus geosporum* (Nicolson & Gerdemann) Walker, using RFLP analysis of the ITS region of the rDNA of individual spores after amplification by PCR (Hildebrandt *et al.* 2001).

The main colonist of *Salicornia* at all elevations on Stiffkey salt marshes, Norfolk, is a previously unrecorded but distinct 'fine endophyte' AM fungus, possibly *Glomus tenuis* (Greenhall) Hall (Davy *et al.* 2000). It was also present in *Aster tripolium*, along with a conventional AM fungus.

(C) PERENNATION: REPRODUCTION

Therophyte. In Britain *Salicornia* is a summer annual that perennates entirely as a seed bank in salt marsh sediments. Seeds are shed between September and late November. The sediment seed bank therefore increases rapidly from a minimum in late summer to a maximum in December and January. More than 95% of seeds are concentrated in the upper 5 mm of the sediment. Mean seed bank maxima at various elevations on the marshes at Stiffkey range from 50 000 to 100 000 m^{-2} , although local densities may be higher (Smith 1985; Davy & Smith 1988). When shed, the seeds are mostly innately dormant but the proportion of dormant seeds declines to less than about 5% by February. The relatively few seeds that have not germinated by May have further dormancy enforced by increasing sediment salinity. In September, any seeds remaining after 1 year appear to have lost viability, as judged by tetrazolium vital staining. Similarly, there appears to be no significant persistence of seeds from one year to the next in Danish marshes (Jensen & Jefferies 1984).

In contrast, persistent seed banks of *S. europaea* s.l. have been reported under more severe and less predictable conditions. Jefferies *et al.* (1983) found a seed bank in sediments of an arctic, coastal marsh, although the viability of the seeds was not certain. Substantial seed banks throughout the year, with a minimum of 38 900 m^{-2} in August and a maximum of 128 000 m^{-2} in November, were characteristic of an inland saline in Ohio, USA; in this population, which shows seed dimorphism (see VIII C, D), only the small (lateral) seeds persisted in the seed bank after the winter and this reserve played a significant role in maintaining the population in this highly stressful habitat (Ungar &

Riehl 1980; Philipupillai & Ungar 1984; Ungar 1987a,b). The representation of *S. europaea* in the sediment seed bank may be disproportionately large in comparison with the species composition of the vegetation, especially in grazed marshes (Ungar & Woodell 1996).

Lee *et al.* (1992) have developed a method of mass propagation of *S. bigelovii* clones by *in vitro* culture of shoot tips (in the presence of 1-naphthaleneacetic acid and N-(phenylmethyl)-1H-purine-6-amine) that is useful in its development as a crop (see IX A) and for experimentation.

(D) CHROMOSOMES

The taxonomic intractability of *Salicornia* is reflected in the varied chromosome numbers reported for a range of taxa (Wulff 1936, 1937; König 1939; Ludwig 1950; Hambler 1954; Nannfeldt 1955; Ball & Tutin 1959; Dalby 1962; Ferguson 1964a; Contandriopoulos 1968; Ball & Brown 1970; Parriaud 1971; Castroviejo & Coello 1980; Smith 1985; Wolff & Jefferies 1987b; Al-Turki 1992). The basic chromosome number for the genus is $x = 9$ and British material may be either diploid ($2n = 18$) or tetraploid ($2n = 36$). Aneuploid numbers reported by Wulff (1936, 1937) and Hambler (1954) are regarded as suspect (Dalby 1962). A triploid type ($2n = 27$) has been reported from Italy (Cristofolini & Chiapella 1970). The chromosomes of *Salicornia* are small, ranging from about 0.6–1.8 μm in length but with some variation in shape (Dalby 1962).

Recent systematic treatments (Ball & Tutin 1959; Ball 1964; Ferguson 1964a,b; Ball & Brown 1970; Dalby 1989; Stace 1997) use ploidy level in the delineation of species: *S. pusilla*, *S. ramosissima* and *S. europaea* s.s. are considered diploid and *S. dolichostachya*, *S. fragilis* and *S. nitens* are defined as tetraploid. Material from the field that is referred to *S. europaea* and *S. ramosissima* on morphological criteria cannot always be reconciled with this. Tetraploid types are more frequent than diploids in open, low marsh, pioneer situations (e.g. Ball & Brown 1970). Upright forms more often tend to be diploid and prostrate forms more often tetraploid (e.g. Parriaud 1971).

Diploid and tetraploid cytotypes may differ in the size of pollen, stomatal guard cells and seeds (Dalby 1962), in fertile segment shape, number of fertile segments in the terminal spike, length of anthers (Ball & Brown 1970) and in the distance between the apex of the middle floret and the apex of the segment (Ingrouille *et al.* 1990).

(E) PHYSIOLOGICAL DATA

Salinity tolerance

As a halophyte, *Salicornia* is able to maintain low water potentials in its tissues by accumulating solutes. There are many reports of the accumulation of high concentrations of inorganic ions, mainly sodium and

chloride in a variety of taxa (e.g. Albert 1975; Grouzis *et al.* 1977; Gorham *et al.* 1980; Cooper 1982; Riehl & Ungar 1982; Ayala *et al.* 1996). *Salicornia* has a relatively high ratio of Na : K, typical of dicotyledonous halophytes (Gorham *et al.* 1980; Rozema 1991). These high concentrations of inorganic ions are accumulated predominantly in the cell vacuoles; there is some evidence that pinocytosis is instrumental in ion accumulation in the vacuoles of shoot cells (Kurkova & Balnokina 1994). As in other halophytic chenopods, high concentrations of compatible organic solutes (mainly the form of the methylated quaternary ammonium compound, glycinebetaine) are maintained in the cytoplasm (Stewart *et al.* 1979; Gorham *et al.* 1980; Briens & Larher 1982). This asymmetric distribution of solutes protects metabolic activity from the potentially toxic effects of high concentrations of inorganic ions.

Optimal growth generally occurs at external salinities equivalent to less than half that of seawater, depending on other environmental conditions. Halket (1915) first showed a response of growth to salt. Seedlings of *S. ramosissima* on intact sods taken from a salt marsh grew taller when watered with 1% sea-salt solution (equivalent to c. 170 mM NaCl) than when there was no salt or when concentrations were higher (2–5%). In water culture, the greatest growth in height and branch length of *S. dolichostachya* ('*S. oliveri* Moss') was obtained in the presence of 2% (340 mM) NaCl; salt concentrations of 3–5% (520–860 mM) were progressively detrimental to growth. Plants of this species grew very poorly and failed to flower when grown without salt. Langlois (1967, 1971a) found that a daily, 90-minute immersion of seedlings of *S. europaea* ('*S. stricta* Dumort.') in nutrient solution containing 10 g L⁻¹ NaCl (170 mM) gave growth more similar to that seen in the field than treatments with no immersion or two immersions a day. Cooper (1982) reported that *S. europaea* gave its maximum yield in the saline treatments of growth experiments, applied as weekly waterings with 340 mM NaCl. The North American form *S. bigelovii* Torr. shows optimal growth at 200 mM NaCl (Ayala *et al.* 1996). Even *in vitro* callus cultures of *S. europaea* have been reported to accrue dry mass maximally in the presence of 0.75–1.0% (129–170 mM) NaCl (von Hedenström & Breckle 1974), although it is not clear what proportion of this dry mass was accounted for by accumulation of inorganic salts. In a comparison of relative growth rates under standardized glasshouse conditions with 15 salt marsh species, *Salicornia* was amongst the most salt-tolerant, both under flooded and well-drained conditions (Rozema *et al.* 1985). Rozema, van der List *et al.* (1987) found that dry mass was increased in *S. europaea* ('*S. brachystachya* Meyer') and *S. dolichostachya* by treatment with 250 mM NaCl on a clay substrate; however, growth was reduced by this salinity on a sandy substrate and *S. dolichostachya* was the more adversely affected.

The effects of salinity and inundation by seawater on different aspects of metabolism have been studied in

various segregates of *Salicornia*: protein accumulation (Langlois 1969, 1971a), sugar movement (Langlois 1971b) and plasma-membrane ATPase activity (Ayala *et al.* 1996)

Tolerance of flooding and sediment hypoxia

As expected of plants that include forms capable of colonizing the lowest parts of tidal marshes, *Salicornia* is extremely tolerant of regular flooding. Nevertheless, growth of *S. europaea* is reduced by cultivation under continuous waterlogging, in comparison with free drainage at the same salinity (Breton 1971; Cooper 1982). A combination of waterlogging and non-saline conditions results in very poor growth and survival (Cooper 1982; Keiffer *et al.* 1994).

Salicornia may avoid root hypoxia by relatively shallow rooting, despite poorly developed aerenchyma. Schat *et al.* (1987) found that experimental deoxygenation of the root environment reduced relative growth rate and the elongation rate of roots, but no effects were detected on CO₂ exchange or inorganic nutrient uptake; neither was there any difference in response between *S. dolichostachya* from the lower marsh and *S. ramosissima* from the upper marsh. Nevertheless *Salicornia* is tolerant of toxic reduced substances resulting from chemical transitions at low sediment redox potentials, including those of sulphate to sulphide and manganic to manganous ions. Ingold & Havill (1984) found that the addition of 100 µM sulphide to a sealed water-culture system did not have an adverse effect on the growth and root development of *S. europaea*, unlike three other salt marsh species examined; *S. europaea* was also the only vascular plant rooted in sulphide-containing sediments on a lower marsh. Havill *et al.* (1985) similarly did not detect any adverse effects of this concentration of sulphide on its growth and metabolism. Experiments by van Diggelen *et al.* (1987) indicate that the growth of neither *S. europaea* ('*S. brachystachya*') nor *S. dolichostachya* from The Netherlands was affected by sulphide concentrations of up to 500 µM. On the other hand, Pearson & Havill (1988) were able to distinguish between the responses of the species: root alcohol dehydrogenase (ADH) activity of *S. europaea* was little affected by culture in sulphide-containing (100 µM) nutrient solution, whereas the corresponding ADH activities of *S. dolichostachya* and *S. fragilis* were increased more than 7- and 14-fold, respectively, compared with non-sulphide treated controls.

Similarly, *S. europaea* was the most tolerant, of eight salt marsh halophytes examined, to Mn²⁺ in saline culture solution, its growth being unaffected up to a concentration of 10 mM (Cooper 1984). Presumably high concentrations of Na⁺ ameliorate the toxicity of Mn²⁺, because Singer & Havill (1985) reported that root and shoot growth was inhibited by concentrations above 0.5 mM Mn²⁺ after 6 weeks in Hoagland (non-saline) culture solution.

Water relations

Water is conserved by low transpirational losses associated with the absence of leaves and is stored in succulent tissues. The water content of stems (succulence) varies with external conditions; that in *S. europaea* ('*S. stricta*') main stems in the Orne estuary of northern France ranged from about 700–1100% of dry mass (Langlois 1968a). Likewise, tissue water potentials depend on external salinity and the accumulation of solutes through osmoregulation but they can become very low without resulting in death. Langlois (1968a) recorded solute (osmotic) potentials no lower than –2.67 MPa for *S. europaea* in the Orne estuary. Material from a coastal salt marsh at Seal Beach, California had a water potential (ψ_w) of -4.23 ± 0.24 MPa, with a component solute potential (ψ_s) of -5.32 ± 0.10 MPa (Kuramoto & Brest 1979). Tsuda (1961) reported an extreme solute potential of expressed sap as –7.6 MPa, with sodium chloride content contributing –7.2 MPa of this, under extremely hypersaline conditions in Japan. Riehl & Ungar (1982) recorded midsummer tissue ψ_w as low as –9 MPa in an inland saline in Ohio, USA. Momonoki & Kamirura (1994) reported an increase in the osmolality of stem and branch sap from about 650 mOsm kg⁻¹–2600 mOsm kg⁻¹ (approximately equivalent to ψ_w of –3 to –13 MPa) during the growing season, in plants growing at the edge of Lake Notoro-ko, Japan. The NaCl concentration required for incipient plasmolysis of epidermal cells rose from 1.6 to 2.2% during the growing season (Momonoki *et al.* 1994) and these values were high in comparison with other halophytes. Rozema, van der List *et al.* (1987) detected a diurnal cycle in *S. europaea* ('*S. brachystachya*'), with 2.7% increase in stem thickness during the dark and shrinkage during the day.

Gas exchange

As expected, stomatal conductance decreased with increasing external salinity in *S. bigelovii*, producing a concomitant decrease in the rate of transpiration (Ayala & O'Leary 1995). Carbon dioxide fixation is by the C3 pathway, with a $\delta^{13}\text{C}$ ratio of –26.62 determined for *S. europaea* (Carolin *et al.* 1982). Guy *et al.* (1986) reported a range of $\delta^{13}\text{C}$ ratio (–29 to –23) in *S. rubra* (*S. europaea* ssp. *rubra*), with less negative values at higher salinity reflecting differences in long-term water-use efficiency. Low activities of PEP carboxylase, without fluctuations due to endogenous rhythms, have been reported (Kuramoto & Brest 1979). Net photosynthetic rates have been shown to decrease slowly with lowering of external water potential; CO₂ uptake in the absence of salt was 7.59 ± 0.64 mg dm⁻² h⁻¹ on a leaf area basis (14.22 ± 1.66 mg g⁻¹ h⁻¹ on a dry mass basis) and this was reduced to 4.75 ± 0.12 mg dm⁻² h⁻¹ (8.47 ± 1.30 mg g⁻¹ h⁻¹) after equilibration for 72 h at seawater salinity (Kuramoto & Brest 1979). Dark respiration declined similarly. Schat *et al.* (1987) found

that net photosynthetic and dark respiration rates (on a fresh mass basis) declined with increasing plant fresh mass. They also observed mid-day stomatal closure, exceptionally, in certain individuals of *S. ramosissima* under hypoxic stress.

Response to inorganic nutrients

Salicornia plants growing on salt-marsh sediments, *in situ* or on cores removed for experiments, typically respond to additions of nitrogen and phosphorus only in the absence of significant competition from perennial species (e.g., Pigott 1969). In sand culture, growth of *S. europaea* and *S. ramosissima* responds to increasing nitrate concentration up to at least 1 mM (Jefferies 1977). Addition of inorganic nitrogen and phosphorus to lower marsh plots on the north Norfolk coast significantly increased shoot frequency over 5 years but did not have any effect on higher marsh plots; at the end of the experiment there was significantly greater *Salicornia* biomass in nutrient treated lower-marsh plots, particularly those that had received nitrate (Jefferies & Perkins 1977). Regular additions of nitrate- or ammonium-N within a single growing season can markedly stimulate biomass accumulation and, especially, seed production (Jefferies *et al.* 1979). Similarly, at the limits of its distribution on the shores of Hudson Bay, seed production of *S. europaea* agg. was increased greatly by experimental addition of sodium nitrate (Jefferies *et al.* 1983). *S. europaea* demonstrated the ability to accumulate nitrogen with increasing external nitrate availability (Costa 1992). Total concentrations of N in shoots of *S. dolichostachya* range from 1.0 to 1.35% (dry mass) in the field (Pigott 1969) to 6.5% in nitrogen-rich hydroponic culture (Schat *et al.* 1987).

Induction of flowering

The conditions that promote flowering are poorly understood. In cultivation, plants typically flower precociously at a few weeks old, thus terminating vegetative growth and limiting the capacity for seed production. Langlois (1968b) suggests that the high radiant flux densities found in its natural environment are necessary to prevent precocious flowering. *S. europaea* plants from both Britain (Costa 1992) and the Netherlands (Joenje 1978) have shown a minimum threshold size for successful seed production. This can lead to oscillatory population dynamics where increasing numbers of individuals fail to reach the threshold size as density increases or environmental factors limit growth.

Response to shade

Growth and branching vary enormously, depending on population density (especially at low elevation in marsh zonation, or in early successional sites) and the presence of other species (especially higher in the zonation, or in later successional sites). Branching

responses appear to be mediated substantially by light availability. A computer simulation of the 3-dimensional branching patterns in *S. europaea* generated forms that corresponded well with those found at different stages in a salt marsh succession, by simultaneously maximizing light interception and minimizing total bending moment (Ellison & Niklas 1988).

(F) BIOCHEMICAL DATA

The distinctive violet-red colouration of many forms of *Salicornia* is mainly due to the presence of a betacyanin pigment, betanidin-5-O-[2-O-(β -D-glucopyranosyl uronic acid)]- β -D-glucopyranoside (Chiji 1976). The reddish stems of *S. europaea* also contain two 2,3-unsubstituted chromones, identified as 6,7-methylenedioxychromone and 6,7-dimethoxychromone, respectively (Chiji *et al.* 1978; Arakawa *et al.* 1983). Arakawa *et al.* (1982) determined the structure of two new isoflavones (2'-hydroxy-6, 7-methylenedioxyisoflavone and 2', 7-dihydroxy-6-methoxyisoflavone) and one flavanone (—)-(2*S*)-2'-hydroxy-6, 7-methylenedioxyflavanone, from *S. europaea* in Japan. Geslin & Verbist (1985) found that flavonoids represent 1.2% of the dry mass of *S. europaea* and isolated eight flavonoids, of which the most abundant was (malonyl-6'' β -D-glucoside)-3-quercetol. Borkowski & Drost (1965) identified two distinctive alkaloids from *S. europaea* ('*S. herbacea*'), salicornin and salihherbin.

Weete *et al.* (1970) found differences between shoot, root and seed tissues of *S. bigelovii* in the relative distribution of paraffin hydrocarbons (chain lengths C₂₁ to C₃₃) and total fatty acids (chain lengths C₁₄ to C₂₄); there were also substantial differences between two populations in both hydrocarbons and fatty acids. *Salicornia europaea* seeds are rich in oil, containing 26–30% total lipids; the di-unsaturated linoleic acid accounted for 70% of the fatty acid content (Austenfeld 1986, 1988). Seed oil of *Salicornia* (SOS-7), a form selected for cultivation as an oil-seed crop, has been analysed in great detail (El-Shami & El-Negoumy 1993; El-Mallah *et al.* 1994). Its fatty acid composition is likewise dominated by linoleic acid (66.9%), with 17.5% oleic acid, only 1.4% linolenic acid and traces of stearic and palmitic acid; 22 different triglycerides were detected by HPLC. In common with other members of the Chenopodiaceae, the photosynthetic tissues of *Salicornia* contain a remarkable diversity of sterol biosynthetic capacity. Eight different 24- α -ethylsterols have been identified, with spinasterol and stigmasterol most abundant; *S. europaea* apparently differs from *S. bigelovii* in lacking isofucosterol (Salt & Adler 1985). According to El-Mallah *et al.* (1994) the seeds of SOS-7 also contain a range of tocopherols (mainly alpha and gamma), sterols (mainly 7-stigmastenol and sitosterol) and sterylglucosides (mainly B-sitosterol and campestigmasterol).

Hagène (1958) reported that early in the growing season, the ascorbic acid content of *S. pusilla* ('*S. disarticulata*') was consistent at about 250 mg 100 g⁻¹ but

in the autumn the concentration was correlated with the total hours of sunshine on the day of collection and the previous two or three days. The cell walls of *S. ramosissima* are rich in arabinose, galacturonic acid, glucose and proteins, and contain 0.7% ferulic acid and 3.8% acetic acid (Renard *et al.* 1993).

Ion transport within *Salicornia* at nodes and at the parting points of lateral roots from the main stem may be facilitated by acetylcholinesterase activity (Momonoki *et al.* 1996). There are several reports of the distributions of ions and elements in different tissues and organs of *S. europaea* agg. (Gorham *et al.* 1980; Austenfeld 1986).

Nitrogen content depends on the material, its age and environmental conditions (Langlois & Ungar 1976). Under various submergence treatments, main stems and branches of young plants of inland origin (referred to *S. ramosissima*) accumulated total N of 3.0–4.3% (dry mass), representing 1.8–3.0% as protein N and 1.0–2.1% as soluble N; corresponding values for *S. europaea* ('*S. stricta* Dumort.') of coastal origin were total N 4.7–5.5%, protein N 1.0–4.7% and soluble N 0.4–4.5%. Mature plants had generally lower nitrogen concentrations. Patterns of serological and electrophoretic variation in seed proteins (Cristofolini 1968; Cristofolini & Chiapella 1970) in 13 Italian populations corresponded neither with each other nor with those for morphology or geographical and ecological distributions. Schat *et al.* (1987) reported total phosphorus concentrations equivalent to 0.51–0.53% (dry mass) for *S. ramosissima* and 0.42–0.59% for *S. dolichostachya*.

VII. Phenology

The life cycle of *Salicornia* is typically summer-annual, although in subtropical environments plants can persist for more than a year. Germination tends to coincide with low sediment salinities, in winter in Britain (Smith 1985) and from February to June in Ohio salt pans (Ungar *et al.* 1979). The germination period can be protracted in mild winters: at Stiffkey in Norfolk, seedlings are occasionally found as early as November but are most abundant from early January to late April. Characteristically lower-marsh populations, such as *S. dolichostachya* and *S. europaea*, tend to germinate earlier than upper marsh ones, e.g. *S. ramosissima* and *S. pusilla* (Jefferies *et al.* 1981; Smith 1985).

Vegetative growth proceeds by the addition of new stem segments and, except at very high population densities, lateral branches develop. In lower marsh populations growth is usually continuous, whereas higher marsh populations often show slow growth in the period when hypersaline conditions can occur, when spring tides fail to cover the marsh surface around the summer solstice. In late July or August, vegetative growth is terminated by the production of fertile segments at the ends of all branches. Benito & Onaindia (1991) found that the standing crop of *S. ramosissima* peaked in early September in a Cantabrian salt marsh (north Spain);

the highest rate of increase in standing live crop was in July.

In Britain, flowering occurs mainly from mid-August to mid-September but flowers may be seen from late July until well into October. *Salicornia europaea* ('*S. stricta*')-type flowers a fortnight earlier than *S. ramosissima*-type (Dalby 1955). Populations flower first on the seaward edge of the marsh at Stiffkey, Norfolk, where *S. dolichostachya* flowers earliest; *S. pusilla*, found characteristically on the drier, upper interfluvies, is the last to flower (Smith 1985). Neotenuous flowering of plants has been observed by Langlois (1968b) in *S. europaea* ('*S. stricta*') grown in artificial culture. Seeds reach maturity from mid-September onwards and fall out of the dead or dying parent plant although some may remain *in situ* for germination the following spring (Ball & Brown 1970).

VIII. Floral and seed characters

(A) FLORAL BIOLOGY

Flowers are normally bisexual but plants in the field or in cultivation may exceptionally have unisexual flowers as a result of male or female organs failing to develop (Ferguson 1964b). Some populations are undoubtedly cleistogamous, their anthers dehiscing before exertion, or failing to exert (e.g. Ball & Tutin 1959). Chasmogamous flowers are usually weakly protogynous but the stigmas are persistent and often seen in contact with dehiscing anthers such that self pollination is easily possible (Knuth, Poll. 3) and is probably the norm (Dalby 1962; Ferguson 1964b). Pollen may also fall onto the stigmas of flowers immediately below on the same plant. Ferguson (1964b) found that in tetraploid plants resembling *S. lutescens* and *S. dolichostachya*, both in the field and in cultivation, either the stigmas protruded just before the undeveloped anthers were exerted or the anthers and stigmas emerged together.

The pollen grains are almost spherical, differing from other chenopodiaceous pollen only in size and details of sculpturing (Al-Turki 1992). Dalby (1962) detected large quantities of wind-borne chenopodiaceous pollen under circumstances where it is reasonable to assume that it must have come from *Salicornia*. This indicates that outbreeding is potentially possible. Pollen grain diameter in *S. europaea* is (20–)24–28(–31) μm ; in *S. dolichostachya* it is (27–)31–34(–42) μm (Ball & Brown 1970). Dalby (1962) recorded smaller pollen-grain volumes in diploids ($2\text{--}12 \times 1000 \mu\text{m}^3$) than in tetraploids ($6\text{--}19 \times 1000 \mu\text{m}^3$) with the changeover at $c. 10.5 \times 1000 \mu\text{m}^3$ (= 27.2 μm diameter). By mounting fresh pollen grains in acetocarmine and considering those which took up the stain deeply to be fertile, 90–100% of pollen grains were generally found to be fertile, whether taken from diploid or tetraploid individuals. Some tetraploid individuals showed exceptionally low pollen fertility.

'Bagging' experiments with plants on several British salt marshes have demonstrated self compatibility, with only a slight depression of seed-set associated with enclosure of the shoots in polythene bags (Dalby 1962). There is no evidence of apomixis. Excision of the stigmas from protogynous flowers of *S. europaea* resulted in failure to set seed in 16 flowers out of 17; the single seed set may have resulted from pollination before excision of the stigma (Dalby 1962).

Despite a capacity for wind pollination, the floral biology of *Salicornia* apparently favours the production of inbred lines, which may be regarded as microspecies or locally differentiated populations, with gene exchange at low frequency between them. Noble *et al.* (1992) typed the nuclear rDNA (using RFLP analysis) in 38 maternal plants from Stiffkey in Norfolk and 2112 of their progeny and found no instance of progeny differing from their maternal type. The method was capable of discriminating 1% of a different DNA type within a sample and so any out-breeding must have been at a lower frequency than 1%. This strong tendency to inbreeding undoubtedly contributes to the taxonomic complexity of the group.

(B) HYBRIDS

Uncertainty regarding the delimitation of species within *Salicornia* makes the identification of hybrids even more uncertain. A putative hybrid *S. pusilla* × *S. ramosissima* has cymes with different numbers of flowers (1, 2 or 3) on the same individual (Hyb. Br. Isl.). Such plants are not uncommon on the higher parts of the salt marsh at Stiffkey, Norfolk. Four other putative crosses from British material are listed by Stace (Hyb. Br. Isl.).

(C) SEED PRODUCTION AND DISPERSAL

A fertile segment produces a maximum of 6 seeds (2 cymes with 3 flowers each), except in *S. pusilla*, where only 2 seeds per fertile segment can be produced. The fecundity of individual plants is strongly and negatively density-dependent, as it reflects the highly plastic number and the length of fertile branches produced. Hence seed production per unit ground area may remain approximately constant over a 20-fold range of plant density, or greater. Plants at very high density, with a single fertile segment, may produce 6 seeds or fewer; isolated individuals potentially may produce more than 1000, depending on growth conditions. At typical field densities (300–30 000 m⁻² mature plants) between 300 and 10 seeds may be produced on average per individual (Jefferies *et al.* 1981; Jensen & Jefferies 1984; Smith 1985; Davy & Smith 1988).

The proportion of flowers that set seed declines at high density but individual seed mass can increase with the resulting redistribution of resources (Smith 1985). Dalby (1962) reported that diploids tend to have smaller seeds (1–1.8 mm) than tetraploids (1.2–2.7 mm) and

this has been supported by comparisons of particular taxa: *S. ramosissima* ('*S. appressa* Dumort.') has smaller seeds than *S. fragilis* ('*S. stricta* Dumort.') on the Normandy coast of France (Binet & Langlois 1962); *S. europaea* ('*S. brachystachya* Meyer') has smaller seeds than *S. nitens* ('*S. emerici* Duval-Jouve') on the Mediterranean coast of France (Knoerr 1968) and *S. europaea* has smaller seeds (1.0–1.7 mm) than *S. dolichostachya* (1.5–2.3 mm) in the Dee Estuary (Ball & Brown 1970).

Similarly, within cymes the mean mass of central (median) seeds is greater than that of the lateral ones (König 1960; Dalby 1962; Ungar 1979). The magnitude of this seed dimorphism is extremely variable. In a range of nine populations from the north Norfolk coast, Smith (1985) found mean masses of central (median) seeds of 0.25–0.57 mg and corresponding mean masses of lateral seeds of 0.20–0.50 mg; only *S. dolichostachya* did not have significantly heavier central seeds. In contrast, Ungar (1979) found that in North American *S. europaea* the central seeds (0.78 ± 0.1 mg) and the lateral ones (0.24 ± 0.4 mg) did not overlap in mass range. The composition (see VI F) as well as the concentration of nutrient reserves is the same in both small, lateral (mean air-dry mass 0.25 ± 0.01 mg) and large, median (mean air-dry mass 0.31 ± 0.01 mg) seeds of *S. europaea* (Austenfeld 1988).

Approximately 50% of the seeds fall within 100 mm of the parent plants (Ellison 1987b) but small, fairly consistent numbers spread up to 400 mm and a few can disperse considerable distances (Smith 1985). Rand (2000) found that numbers of *S. europaea* seeds caught by sticky traps correlated well with the sizes of the corresponding germinable seed banks, at sites of different elevations across a New England salt marsh. Separate *Salicornia* seeds have little buoyancy. Hilton (1975) reported that fresh seeds of *S. dolichostachya* sank immediately and air-dried seeds sank within a few minutes; sinking rates in seawater at 9 °C were 12.5–15 mm s⁻¹. Koutstaal *et al.* (1987) reported that 50% of *Salicornia* seeds sank within 2 h and all sank within a day. Submerged seeds may be rolled along the sediment surface by tidal currents but are apt to be trapped by depressions, sessile algae and perennial vegetation (Breteron 1971; Hilton 1975; Costa 1992). The testa is covered with mucilaginous and hooked hairs (Fig. 9), which assist in anchoring the seed to the sediment surface. Germinating seedlings that do not establish immediately are buoyed up by the expanding cotyledons (Petch & Swann 1968) and are likely to be carried away by tidal currents. Floating seedlings of *S. dolichostachya* can remain alive, without further growth, and able to establish for up to 3 months; this provides a potential for long-distance transport not afforded by ungerminated, shed seeds (Hilton 1975). In *S. pusilla* the disarticulated fertile segments retain their seeds and may float in sea water for 3 months (Dalby 1963); they are characteristically deposited on high points and the strand line

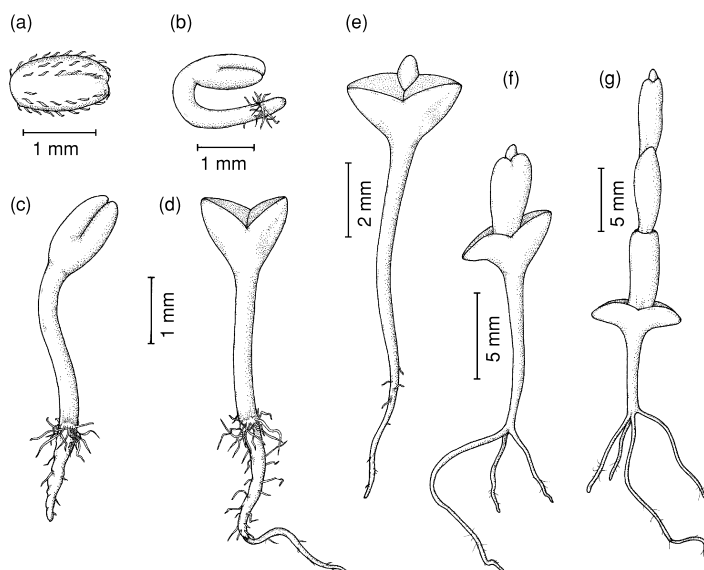


Fig. 9 Germination and seedling development in *Salicornia europaea* agg. (a) seed, (b) germination, and (c–g) developing seedling.

where the seeds germinate *in situ*. The central seeds of dimorphic *S. europaea* (*S. patula*) found in Mediterranean environments are dispersed attached to a persistent perianth, which also aids buoyancy (Berger 1985). Such floating seeds have also been noted in Norfolk, UK (Petch & Swann 1968).

(D) VIABILITY OF SEEDS: GERMINATION

The germinability of *Salicornia* seeds is generally high: collections from diverse populations have achieved 90–100% germination within a few days under laboratory conditions (Langlois 1961b; Smith 1985; Al-Turki 1992). Viability has been reported to be high after several weeks of dry storage at room temperature (Langlois 1961b; Al-Turki 1992), although this is not a realistic simulation of over-wintering conditions in British salt marshes. On salt marshes in north Norfolk seeds released into the sediment seed bank early in the autumn tend to be innately dormant. This dormancy can be broken by up to 5 weeks of chilling at *c.* 3 °C in the imbibed state, which promotes both the amount and rate of germination; seeds released later in the autumn require less chilling, suggesting that the requirement has been fulfilled partially by declining field temperatures (Smith 1985). Cold stratification to relieve seed dormancy has been widely reported in populations of *Salicornia* species (Langlois 1966; Grouzis 1973; Grouzis *et al.* 1976; Ungar 1977). Air-drying of fresh seed and pre-treatment with high salinity (equivalent to seawater) may also break dormancy (Smith 1985; Huiskes *et al.* 1985b; Keiffer & Ungar 1997).

Once the requirements for breaking dormancy have been satisfied, diurnally fluctuating temperature regimes between 5/15 and 20/30 °C appear to have little effect on overall germination but germination is faster at higher temperatures (Huiskes *et al.* 1985b; Smith 1985; Al-Turki 1992). Continuous low temperatures

inhibit germination (Huiskes *et al.* 1985b), which leads to conditional dormancy in the field in winter. Light appears to stimulate germination, at least in certain populations of *S. dolichostachya* (*'S. emeric'*), *S. pusilla* (*'S. disarticulata'*) and *S. europaea* (*'S. patula'* and *'S. stricta'*) (Langlois 1966; Grouzis *et al.* 1976; Berger 1985). *Salicornia* seeds, like those of most halophytes (Ungar 1978), germinate best at low salinity: Langlois (1961b, 1966) recorded up to 100% germination in rain-water and Lötschert (1970) reported that *S. europaea* (*'S. stricta ssp. typica'*) germinated best in pure water; Grouzis (1973) found progressive inhibition in *S. dolichostachya* (*'S. emeric'*) with increasing salinity, starting from *c.* 8.5 mM NaCl; Berger (1985) reported an optimum salinity of 34 mM NaCl in *'S. patula'*, whereas Huiskes *et al.* (1985b) and Smith (1985) independently found very similar germination at 0 and *c.* 50 mM NaCl in *S. europaea* and *S. dolichostachya*. Although above this concentration increasing salinity decreased the amount and rate of germination, a proportion of seeds that had been pre-treated for 10 days at 3 °C in distilled water germinated in solutions of NaCl up to 1 M, about double that of sea water (Smith 1985). Increasing salinity appears to lower the optimum temperature for germination (Langlois 1966; Rivers & Weber 1971; Huiskes *et al.* 1985b). Ungar (1977, 1978) found that application of 10^{-4} – 10^{-3} M gibberellic acid substantially alleviated the depression of germination associated with high salinity but kinetin had no effect. The effect of salinity on germination is a conditional dormancy, as ungerminated seeds from high salinity treatments are usually able to germinate when transferred to distilled water (e.g. Smith 1985; Garcia-Tiburcio & Troyo-Dieguez 1993); as in other halophytes this reversibility indicates that inhibition is due to low water potential rather than ion toxicity. Keiffer & Ungar (1997) found that subsequent germination in distilled water was stimulated by prolonged exposure to high

salinity (3–10% NaCl) in North American material of *S. europaea*.

Populations or taxa with well-developed seed dimorphism generally have different germination requirements for the larger (central) and smaller (lateral) seeds in a cyme. This probably represents a bet-hedging strategy that has evolved in less predictable environments, with readily germinable central seeds and highly dormant lateral seeds for dispersal in time. The central seeds of dimorphic *S. europaea* ('*S. patula*') from a Mediterranean environment (Camargue) had low sensitivity to salt, needed no cold pre-treatment and were relatively indifferent to light, whereas lateral ones were highly sensitive to salinity, needed pre-treatment with cold and showed a positive response to light (Grouzis *et al.* 1976; Berger 1985). Similarly, the large seeds of dimorphic *S. europaea* from an inland salt marsh in Ohio, USA were more salt tolerant and yielded higher germination percentages under salinities of 0–5% than the small ones (Ungar 1979); the small seeds were more dormant and remained in a persistent seed bank, unlike the large ones which germinated in the Spring after production (Philipipillai & Ungar 1984). Smith (1985) found no significant differences in germination behaviour between central and lateral seeds in a wide range of populations in the relatively predictable environment of a north Norfolk salt marsh, nor in initial rates of elongation of seedling radicles. Huiskes *et al.* (1985b) found that seeds of *S. europaea* ('*S. brachystachya*') and *S. dolichostachya* buried under a layer of sediment of 10 mm germinated but the seedlings failed to emerge.

Sodium chloride may be important for the establishment of seedlings. NaCl concentrations of 0.1–0.2 M stimulated hypocotyl elongation of *S. europaea* ('*S. herbacea*') especially in the dark (Kawasaki *et al.* 1978). In *S. bigelovii* seedlings, the cotyledons failed to expand and growth was impaired, because water movement into plants was inhibited by lack of inorganic solutes (Stumpf *et al.* 1986).

(E) SEEDLING MORPHOLOGY

The seedling (Fig. 9) normally has two fleshy cotyledons and a short, thick hypocotyl. Seedlings with three cotyledons occur regularly at low frequency. The cotyledons are fused laterally towards the base to form a cotyledonary tube which is united with the hypocotyl and forms a succulent 'cortex' around it. The cotyledons have no palisade layer but aqueous tissue is well marked. The arrangement of vascular strands in the cotyledons is the same as that described for mature vegetative segments, the hypocotyl having a double series of bundles (de Fraine 1912). Transition from stem to root takes place high in the hypocotyl and is of the van Tieghem Type III (de Fraine 1912). Seedlings from one parent plant usually resemble each other closely but differ from those of other parent plants grown in similar conditions in cotyledon size and shape, presence or absence of pigmentation (betacyanin) in the

hypocotyl and the number and origin of primary branches (Dalby 1955).

The lower limit of establishment of *Salicornia* on salt marshes often appears to be set by the time necessary for the seedlings to penetrate the sediment and develop a ring of root hairs, in order to become fully anchored. Wiehe (1935) suggested a threshold period of tidal exposure of 2–3 days for rooting sufficient to resist tidal action on the low part of an estuarine marsh. The more rapid radicle growth in *S. dolichostachya* than in *S. europaea* may give the former an establishment advantage and account for its predominance at the lowest levels of marshes (Ball & Brown 1970).

IX. Herbivory and disease

(A) ANIMAL FEEDERS AND PARASITES

Nematoda

Heteroderinae: *Cactodera salina* Baldwin, Mundo-Ocampo & McClure has adverse effects on oilseed crops of *S. bigelovii* at Sonoro, Mexico (Baldwin *et al.* 1997).

Hemiptera

Miridae: *Orthotylus rubidus* (Fieber in Puton) can have two generations on *Salicornia* that is not regularly submerged by the tide; the larvae are found June–August and adults July–October (Southwood & Leston, *Land and Water Bugs*).

Cicadellidae: *Macrostoteles sordidipennis* (Stål) [= *M. salinus* (Reuter)] has been found on *Salicornia* in France (Ribaut 1952) and has also been recorded in Britain, although not on *Salicornia* (Kloet & Hincks 1964).

Lepidoptera

Coleophoridae: Larvae of *Coleophora salicorniae* Wocke typically feed on small plants of *Salicornia* colonizing well-drained patches in mixed vegetation. They bore into the tissues, eating the seeds, and then cut off the stem tip as a case, attaching it to another stem to continue feeding (Emmet 1979); they have been recorded generally on *S. europaea* agg. (Emmet 1980) and specifically on *S. europaea*, *S. ramosissima* and *S. fragilis* (Heal 1982, 1983). Females of *Coleophora atriplicis* Meyrick oviposit in July on the flowers of *Atriplex portulacoides*. The larvae build silk-lined cases and feed successively on pollen, developing embryos and seeds until diapause in October or November. In autumn, they also migrate to adjacent *S. ramosissima* plants, where they bore into the seeds and can have considerable impact on reproductive output (Proudfoot 1993). In Rhode Island (USA) salt marshes, the spring generation larvae of the bivoltine *Coleophora caespitiella* Zeller feed on *Juncus gerardii*, whilst the autumnal generation feeds on *S. europaea*, consuming up to 25%

of the seeds (Ellison 1991). This species has been recorded in Britain but apparently not on *Salicornia* (Emmet 1979).

Gelechiidae: Eggs of *Scrobipalpa salinella* (Zeller) have been found on *Salicornia* in Britain (Emmet 1979) and the larvae feed on *S. europaea* in central Europe (Povolny 1980). Povolny also recorded larvae of *Scrobipalpa instabilella* (Douglas) and *S. nitentella* (Fuchs) on *Salicornia europaea*, and those of *S. obsoletella* (Fischer von Roslerstamm) on *Salicornia* spp.

Coleoptera

Chrysomelidae: *Cassida nobilis* L. and *C. vittata* de Vill. feed on *Salicornia* spp. (Walsh & Dibb 1954). *Erynephala maritima* Lac. is a significant herbivore of *S. europaea* on New England salt marshes (Ellison 1987a; Rand 1999). Larvae of *Metachroma* sp. have been reported to kill *Salicornia* seedlings in the USA (Stanghellini *et al.* 1988).

Curculionidae: *Baris scolopacea* Germar is found on *Salicornia* (Walsh & Dibb 1954); Hoffmann (1954) specified the presence of adults on *S. europaea*.

Diptera

Cecidomyiidae: Larvae of the gall midge *Baldratia salicorniae* Kieffer inhabit the internodes of *S. europaea* (Buhr, Gallen). *Baldratia jaxarctica* Fedotova has recently been described from *S. europaea* in Kazakhstan (Fedotova 1992).

Ephydriidae: *Clanoneurum cimiciforme* (Haliday) larvae feed on *Salicornia* (Uffen & Chandler 1978).

Acarina

Eriophyiidae: *Eriophyes salicorniae* Nalepa larvae and adults cause witches' brooms on *S. europaea* (Davis *et al.* 1982).

Aves

Twite (*Carduelis flavirostris*), linnets (*C. cannabina*) and shore-larks (*Eremophila alpestris*) feed on readily disarticulating spikes of *Salicornia* (Petch & Swann 1968). Mallard (*Ananas platyrhynchos*), pintail (*A. acuta*), teal (*A. crecca*), wigeon (*A. penelope*), shoveller (*Spatula clypea*), redshank (*Tringa totanus*), chaffinch (*Fringilla coelebs*) and thrush (*Turdus* sp.) are all known to feed on the seeds (Hilton 1975). Brown & Atkinson (1996) record that *Suaeda*/*Salicornia* salt marshes are amongst the communities most used by wintering coastal passerines, particularly twite and skylark (*Alauda arvensis*). Mature plants of *S. europaea* agg. containing seeds form much of the diet of dark-bellied brent geese (*Branta bernicla bernicla*) on the north Norfolk coast in autumn (Summers *et al.* 1993). Rowcliffe *et al.* (1998) reported a strong aggregative response to this preferred food. *Salicornia europaea* on

New England salt marshes is relatively unpalatable to Canada geese (*Branta canadensis*), whilst *S. bigelovii* has a positive chemical defence mechanism, including a pungent odour, against being eaten by this species (Buchsbaum *et al.* 1984); in *S. europaea* there is an increase in the percentage of phenolic substances, thought to render the plants unpalatable to Canada geese, from May to September (Buchsbaum & Valiela 1987).

Mammalia

Testas of *Salicornia* seeds have been reported in the faecal pellets of rabbits (*Oryctolagus cuniculus*) on a salt marsh; yellow-necked fieldmice (*Apodemus flavicollis*) sought out and consumed stored seed in preference to potatoes, carrots and apples (Hilton 1975).

Domestic animals and Man

Salicornia bigelovii has been grown as an oil-seed and forage crop in arid environments, as it may be irrigated with seawater or other saline waters. It can yield 10–20 t ha⁻¹ of seed, containing 28% oil and 31% protein with only 5–7% fibre and ash (Glenn *et al.* 1991, 1999). It is acceptable as the forage component of diets fed to goats (Glenn *et al.* 1992) and a by-product of oil extraction, *Salicornia* meal, may be used as an ingredient in broiler chicken diets (Attia *et al.* 1997).

Salicornia has a long history of human consumption as a vegetable and in pickles (Chevalier 1922). In Britain it has long been collected as samphire for eating.

(B) PLANT PARASITES

Booth *et al.* (1988) provide a review of fungal records, world-wide, on *Salicornia europaea* agg. and a detailed analysis of fungal assemblages on populations in sulphate-dominated, alkaline lakes in Manitoba and Saskatchewan, Canada. Sixty-five species of fungi have been reported from its rhizosphere and 80 taxa from the root and stem surfaces, seeds, moribund plants and dead material. Except where otherwise attributed, the following summary is from this source. Rhizosphere fungi are not included.

Zygomycotina

Mucorales: *Mortierella* (1 sp.), *Mucor* (1 sp.).

Ascomycotina

Chaetomium (1 sp.), *Didymosphaeria* (1 sp.), *Hypoxylon* (1 sp.), *Leptosphaeria* (1 sp.), *Mycosphaerella* (1 sp.), *Pleospora* (8 spp.), *Protomyces* (1 sp.).

Basidiomycotina

In Britain, the rust *Uromyces salicorniae* de Bary is found uncommonly on leaves and stems of *S. europaea*

and *S. ramosissima*; aecia are mostly on young plants in May (Ellis & Ellis 1985).

Deuteromycotina

Stagnosporopsis salicorniae (P. Magnus) Died. occurs on lower part of stems of *S. europaea* in July; scattered pycnidia are visible (Ellis & Ellis 1985). Records from Booth *et al.* (1988): *Acremonium* (7 spp.), *Alternaria* (9 spp.), *Arthrinium* (1 sp.), *Ascochyta* (2 spp.), *Aspergillus* (1 sp.), *Aureobasidium* (1 sp.), *Botrytis* (1 sp.), *Camarosporium* (3 spp.), *Cladosporium* (4 spp.), *Coniella* (1 sp.), *Coniothyrium* (1 sp.), *Dendryphiella* (2 spp.), *Diplodina* (1 sp.), *Doratomyces* (1 sp.), *Drechslera* (2 spp.), *Epicoccum* (1 sp.), *Fusarium* (4 spp.), *Gliocladium* (1 sp.), *Gliomastix* (1 sp.), *Monodictys* (1 sp.), *Papulaspora* (1 sp.), *Penicillium* spp., *Phoma* (2 spp.), *Phomopsis* (1 sp.), *Scopulariopsis* (1 sp.), *Scytalidium* (1 sp.), *Septoria* (1 sp.), *Stagonospora* (1 sp.), *Stemphylium* (3 spp.), *Trichocladium* (1 sp.), *Trichoderma* (2 spp.), *Tubercularia* (1 sp.).

An indigenous, Mexican, soil-borne fungus, *Macrophomina phaseolina*, infects roots and causes mortality in *S. bigelovii* (Stanghellini *et al.* 1992).

(C) PLANT DISEASES

See (B) above.

X. History

Salicornia is recorded from Flandrian deposits of the East Anglian Fenland. At Littleport, where it is accompanied by *Suaeda maritima*, it is in deposits close to the margin of the Fen Clay that were laid down in a marine transgression culminating about 2000 BC. At Saddlebow it has been found in deposits from the subsequent marine transgression in Roman times (Godw. Hist.).

The vernacular name 'samphire' is derived from 'sampere', an early English name from the French 'herbe de St. Pierre' (Wilson 1980). The common name 'glasswort' arose from the use of its soda-rich ashes in early glass making. William Turner's *Herball* (part iii) refers to it as 'saltwurt' and 'glaswede' in 1568; the name *Salicornia* originates from the 'Pemptades' of Dodonaeus in 1583 (First Rec.). Linnaeus described the genus *Salicornia* (*Species Plantarum* edn 2, 1763) to include all succulent and apparently leafless chenopodiaceous plants. Scott (1977) has provided an historical survey of subsequent taxonomic revisions resulting in its restriction to annual species. Pioneering taxonomic work on *Salicornia* was undertaken by Woods (1851), Dumortier (1868), Duval-Jouve (1868) and Moss (1911, 1912).

XI. Conservation

British and other European habitats supporting low marsh and mud-flat stands of *Salicornia* have been

given legal status and protection as 'Special Areas of Conservation' under a Habitats Directive of the European Union.

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