
SM6

Spartina anglica salt-marsh community *Spartinetum townsendii* (Tansley 1939) Corillion 1953

Constant species

Spartina townsendii *sensu lato* comprises the male sterile F_1 hybrid $S. \times townsendii$ and the much commoner fertile amphidiploid from the same cross, *S. anglica*. The latter alone was recorded in our samples and is the sole constant of the community.

Rare species

Arthrocnemum perenne

Physiognomy

S. anglica always dominates as scattered tussocks, coalescing clumps or a continuous sward up to 1 m in height. The community is species-poor though the associates are somewhat varied. *Puccinellia maritima* and annual *Salicornias* occur frequently and may account for up to 50% cover and beneath them there is often an algal mat. Free-living fucoids such as *Fucus vesiculosus* ecad *caespitosus* and ecad *volubilis* may be locally abundant. $S. \times townsendii$ may be recognised within *S. anglica* swards by its denser tussocks of shorter shoots. It sometimes forms extensive swards as at Hythe and Poole (Marchant 1967) and may occur as a landward fringe to *S. anglica* (Hubbard 1965). In such cases the associates of $S. \times townsendii$ are the same as in the community as a whole.

Sub-communities

Beeftink & Géhu (1973) and Kortekaas *et al.* (1976) have characterised a variety of sub-communities within the European *Spartinetum townsendii*. Some corresponding distinction could be made within the British stands but their general species poverty, their capacity for rapid floristic change and the unchallenged dominance of *S. anglica* throughout argue for retaining a single community at national level. Sub-division may be more appropriate in detailed studies of particular marshes: a few sites, for example, have a distinctive phase with *Atriplex hastata* and *Suaeda maritima* conspicuous.

Habitat

Although scattered plants of *S. anglica* can be found in almost every salt-marsh community, the distinctive situations of the community are towards the seaward fringes of marshes, on creek sides, colonising old pans in the upper-marsh zone and, more rarely, in brackish seepage areas behind sea walls. The *Atriplex hastata*-*Suaeda maritima* phase is characteristic of tidal drift.

A wide variety of substrates is colonised, from extremely soft mud to shingle. There is some evidence of more rapid vegetative spread through finer material (Chater & Jones 1957). The pH is generally above 7.0 and loss-on-ignition varies from 0.2% to 36.3% (Adam 1976). The sediment is generally strongly reduced although there may be a narrow zone of oxidation around the roots. *S. anglica* is extremely tolerant of tidal submergence. In general, its lower limit seems to be around mean high water of neap tides, which implies about 6 hours' submersion/day at spring tides (Goodman *et al.* 1969, Dalby 1970, Morley 1973, Proctor 1980) but in exceptional situations, as in the shelter of Poole Harbour with its narrow tidal range, the community may extend down to mean low water of neap tides, with as much as 23½ hours' submersion/day at neap tides (Hubbard 1969). The lower limit of colonisation is therefore probably controlled by factors other than submersion tolerance and it appears most likely that exposure to the physical effects of wave or tidal action is responsible. Goodman *et al.* (1959) and Goodman (1960) have shown how *S. anglica* may become dwarfed by such a process where the maximum fetch is short. Such stunted plants resume normal growth under culture (Goodman *et al.* 1969) and should be distinguished from the dwarf brown mutants described from certain sites (e.g. Chater 1965). It is also possible that the nature of the substrate may influence the seaward limit of the species but data are lacking. The landward limit of extension may be controlled by the juxtaposition of existing communities up the shore. *S. anglica* can tolerate up to about 2.5‰ chloridity

(Ranwell *et al.* 1964, Proctor 1980) and this may give it more competitive advantage in the hypersaline conditions when dry weather follows high tides on the upper marsh.

The community occurs on both grazed and ungrazed marshes. Although less heavily exploited than some marsh communities, it appears to be eaten by rabbits, sheep and cattle and *S. × townsendii* may actually be encouraged or maintained by grazing (Hubbard 1965) and its growth favoured against invasion by *S. anglica* where the two species occur contiguously. Hubbard & Ranwell (1966) showed that cut and ensilaged *S. anglica* had a similar intake, digestibility and crude protein content to medium quality hay when fed *ad libitum* to Halfbred × Suffolk wethers, though they recognised that marsh physiography would usually militate against its widespread exploitation as a crop. Despite its dramatic spread, *S. anglica* rarely seems to pose a navigational hazard though its presence in coastal resorts or nature reserves may be undesirable. Some control has been achieved by helicopter spraying with dalapon (Ranwell 1967) though assiduous digging is usually necessary to ensure eradication.

Zonation and succession

S. × townsendii was first noticed around Southampton Water in the 1870s and is presumed to be a natural hybrid between the native *Spartina maritima* and the introduced *S. alterniflora* (Marchant 1967). Its slow natural spread was quickly overtaken by the much more vigorous fertile amphidiploid *S. anglica* which, in the 20 years after its first appearance in Southampton Water and The Solent probably around 1890, had colonised every estuary and salt-marsh between Chichester and Poole (see, for example, Goodman *et al.* 1959, 1969, Hubbard 1965, Ranwell 1967, Hubbard & Stebbings 1967). Widespread planting for reclamation after 1910 extended the distribution of *S. anglica* in Britain and natural spread from these centres has filled many gaps.

S. × townsendii appears to have been transmitted to a number of scattered localities by inclusion of sterile material in transplant consignments but this species probably accounted for less than 20 ha out of a total of over 12000 ha of marsh dominated by *S. townsendii* s. l. in Great Britain at the last detailed survey (Hubbard & Stebbings 1967).

Once established, the plants perennate and reproduce naturally by rhizome fragmentation, especially where the tidal run is fast, as at Bridgwater Bay (Ranwell 1964a) and, in the case of *S. anglica*, by seed, the set of which is regular though variable in quantity (Goodman *et al.* 1969). Spread from such fragments or seedlings can be rapid in *S. anglica* with clonal patches expanding and coalescing into clumps and then closing to a sward; in other cases discrete patches may persist for long periods.

In many places *S. anglica* has become established on previously bare substrates and initiated the development of new marshes. Accretion of material has been found to vary between 0.5 and 10 cm/year (Ranwell 1964a, Bird & Ranwell 1964); at the higher rates something like 500 cm/ha/year of material is deposited. Accretion rate may depend on local climate, the tidal pattern and perhaps the seasonal microflora (Ranwell 1964a) and the subsequent marsh drainage pattern may be influenced by the slope, tidal range and substrate type (Braybrooks & J. M. Lambert, unpublished). Accretion eventually raises the marsh surface to a level at which other species can theoretically compete with the *S. anglica* but, although species from *Puccinellietum maritimae* and *Juncetum gerardi* communities occur occasionally within swards, they are never particularly abundant and competition with the tall and vigorous *S. anglica* may prevent overtopping and the replacement of the community. Litter accumulation or frost action (Hubbard & Stebbings 1967, Ranwell 1972) and grazing (Ranwell 1961, Goodman *et al.* 1969) may initiate the opening up of the *S. anglica* sward and allow the spread of *Puccinellia maritima*.

On the higher parts of ungrazed marshes there is evidence of invasion by a variety of plants. At Bridgwater Bay, a short-period sub-seral alternation of *S. anglica* and *Atriplex hastata* has been observed on accumulated drift with sand (Ranwell 1961, 1964b). *A. hastata* has also invaded the upper part of a *S. anglica* marsh at Lytham on the Ribble estuary. At Keysworth in Poole Harbour, *Elymus pycnanthus* has invaded (Hubbard & Stebbings 1968). There and at Bridgwater, *Scirpus maritimus* and *Phragmites australis* have also appeared at higher levels and replaced about 50% of the *S. anglica* sward in 12 years. Ranwell (1972) has suggested that such a process is favoured by the development of less saline conditions consequent upon land-drainage seepage but this has not been widely investigated. *Halimione portulacoides* can establish itself along creek margins within *S. anglica* marshes (Goodman *et al.* 1959).

S. anglica has also become established on existing marshes. Invasion of *Zostera noltii* swards has been recorded on the south and east coasts (Goodman *et al.* 1959; Bird & Ranwell 1964; Hubbard & Stebbings 1968) and Chapman (1959) mapped such a process in North Cockle Bight at Scolt Head between 1932 and 1959. At that site, *Z. angustifolia* on very soft mud was not invaded; neither is there any evidence that *S. anglica* has anywhere replaced *Z. marina* which occurs at lower levels than *Z. noltii*. At Keysworth in Poole Harbour, a *Ruppia maritima*-*Potamogeton pectinatus* community has been replaced by *S. anglica* (Hubbard & Stebbings 1968). *S. anglica* can flourish at the same level as the *Salicornietum europaeae* and, as a result, pioneer vegetation

of this kind is now of local occurrence throughout south-east England.

The extent to which *S. anglica* invades other existing marsh communities is uncertain. Pans and creeks in vegetation higher up the marsh may be grown over and scattered plants are widespread throughout marshes, but the wholesale replacement of other communities is not well documented. Chater & Jones (1957) provide some evidence for a slow advance into *Puccinellietum maritimae* and *Juncetum gerardi* in the Dovey estuary but this is not apparent at many sites. Similarly there is little evidence as to how much invasion into *S. anglica* swards takes place from contiguous communities. On grazed marshes in the Dovey, creek levees have become colonised by *Festuca rubra* which has eventually ousted *S. anglica*; because of the frequency of creeks there, the total area of marsh affected is considerable (Chater 1973). Heavily grazed and poached upper levels of *S. anglica* have elsewhere been invaded by *Puccinellia maritima*. It is not known how far the development of a *S. anglica* community to seaward of an existing marsh complex affects the overall nature of the marsh but it might be expected that alterations in drainage would be of prime importance.

In general, *S. anglica* has consolidated its early initial spread but the patchy degeneration of sward which became known as 'die-back' was noticed as early as 1928 and in some sites has made a considerable impression. It is still mainly restricted to Channel coast marshes and its exact cause remains unknown. Pathogens and pollution have been ruled out (Goodman *et al.* 1959) and it seems possible that the process is caused by a toxic reduced inorganic ion (perhaps sulphide) produced in anaerobic waterlogged root environments (Goodman & Williams 1961). Alternatively, the switch from accretion to ablation under *S. anglica* may be responsible for its demise.

Distribution

Spartinetum townsendii is widespread around the English and Welsh coasts and is still expanding vigorously at a number of sites along the Scottish shore of the Solway. *S. × townsendii* in itself present in abundance only below Hythe in Southampton Water (Hubbard & Stebbings 1967) though there is F₁ material scattered through *S. anglica* swards from Poole to Wittering and on the Isle of Wight. This natural limit is probably set by the slow vegetative spread of the species. There are also small quantities, probably transmitted with *S. anglica* for transplant, in Norfolk, Somerset, Merioneth and

Dublin. The limit of *S. anglica* and of the association as a whole, may be related to temperature: in the northern hemisphere, really successful plantings occur south of the 13–18 °C July isotherms (Goodman *et al.* 1969). The far northern stations of the species in Argyll and Harris (Hubbard & Stebbings 1967) have not been checked but it is known that growth in these localities is very slow and seedling establishment poor because of winter storms, cold and bird damage (Shaw, *pers. comm.* in Goodman *et al.* 1969). The European distribution of the community is discussed by Beeftink (1972), Géhu (1972) and Beeftink & Géhu (1973).

Affinities

The association is easily defined floristically by the dominance of *S. anglica* and in phytosociological schemes the community has been placed in a separate class, the Spartinetea, with other communities based on *S. maritima* and *S. alterniflora*.

Floristic table SM6

<i>Spartina anglica</i>	V (5–10)
Algal mat	III (2–9)
<i>Puccinellia maritima</i>	III (1–7)
<i>Salicornia</i> agg.	III (1–7)
<i>Suaeda maritima</i>	II (1–5)
<i>Aster tripolium</i> var. <i>discoideus</i>	I (1–7)
<i>Aster tripolium</i> (rayed)	I (2–6)
<i>Aster tripolium</i>	I (1–5)
<i>Atriplex prostrata</i>	I (2–7)
<i>Limonium</i> cf. <i>L. vulgare</i>	I (1–3)
<i>Plantago maritima</i>	I (3–5)
<i>Fucus vesiculosus</i> ecad <i>caespitosus</i>	I (2–5)
<i>Fucus vesiculosus</i> ecad <i>volubilis</i>	I (2–6)
<i>Catenella repens</i>	I (2)
<i>Cochlearia anglica</i>	I (2–5)
<i>Spergularia media</i>	I (1–5)
<i>Halimione portulacoides</i>	I (2–6)
Number of samples	136
Mean number of species/sample	3 (1–10)
Mean vegetation height (cm)	34 (8–10)
Mean total cover (%)	84 (25–100)

