A Century of Evolution in *Spartina anglica*

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I. SUMMARY

This review describes the origin and spread of the salt marsh grass *Spartina anglica*, the first specimen of which was collected from Lymington, Hampshire in 1892, and presents new material relating to its ecology and evolution. Using electrophoretically detectable variation, we confirm the strong circumstantial evidence that *S. anglica* originated by

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chromosome doubling of the sterile hybrid between the Old World species *Spartina maritima* and the North American *Spartina alterniflora*. In addition, extensive analysis of isoenzyme and seed protein phenotypes indicates that *S. anglica* is almost totally lacking in genetic variation. This may result from a narrow genetic base following a single origin or from a multiple origin from the uniform parents. It is likely to be maintained by the extensive clonal spread of most populations from a few, often deliberately introduced, founders and by preferential pairing at meiosis between identical homologous chromosomes preventing recombination between the component genomes.

The implications of these findings are manifold. For example, the genetic uniformity of the species may help to explain why it has a relatively narrow ecological amplitude. A simple multiple-regression model incorporating largely physical, tide-related variables indicates that the distributional limits of *Spartina* in metres above Ordnance Datum are predicted remarkably well by tidal range, with variation in fetch, estuary area and position on the estuarine gradient significantly improving the prediction (generating equations explaining more than 90% of the variation in both the upper and lower limits). That the niche of the species can be so well defined is most probably due to its recent evolution and its lack of genetic differentiation as well as the predominance of physical, as opposed to biological, factors limiting its downshore spread.

The species' genetic uniformity, coupled with its frequent occurrence as dense, monospecific stands, may also account for the recent rapid spread in several populations of the ergot fungus, *Claviceps purpurea*. For example, in Poole Harbour, Dorset, the average level of infected inflorescences rose from 36% in 1983 to more than 85% in 1988.

Spartina anglica is, unusually among temperate grasses, a C_4 species (one of only eight such species in Britain), and the implications of this method of carbon fixation in a species whose biomass production and possible northward spread may be limited by early spring and summer temperatures is considered, particularly in relation to projected climatic warming. The short-term causes and consequences of die-back in the southern parts of the plant's range are described, including the changes in low water tidal channels accompanying the invasion and subsequent decline of *Spartina* in a south coast harbour.

In a section describing the species' interaction with other species we discuss the effects of *Spartina*'s invasion on aerial and benthic invertebrates and on overwintering wading birds, particularly the dunlin, *Calidris alpina*, the decline in numbers of which correlates with the spread of the grass in British estuaries. Soil conditions, grazing and temperature are important factors affecting the competitive interaction of *S. anglica* with *Puccinellia maritima*, the latter invading *S. anglica* swards more rapidly in sandier, grazed marshes in more northern latitudes.

The consequences of the genetic bottleneck that occurred during the speciation process and the relative youth of *S. anglica* in evolutionary terms are emphasized throughout by comparing the species with *P. maritima*. The greater variation, population differentiation and niche breadth of the latter species are particularly evident.

Finally, we look forward to the changes which may occur with global warming and rising sea levels and how they may affect the second century of the species' evolution.

II. INTRODUCTION

The perennial salt marsh grass *Spartina anglica* C.E. Hubbard has become the textbook example of allopolyploid speciation and successful invasion by a new species (Fig. 1). First recorded from Lymington, Hampshire, in 1892, it now occurs in temperate zones throughout the world, mainly because it has been widely planted to stabilize tidal mud flats. It has profoundly altered the ecology of mud flats and salt marshes over many thousands of hectares.

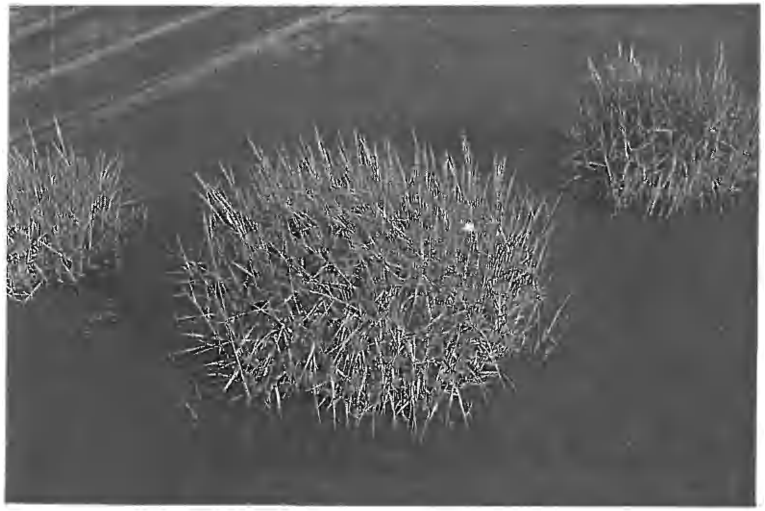

Fig. 1. *S. anglica.*

The first one hundred years of the "Spartina story" (Lambert, 1964) have produced an extensive literature—a bibliography with more than 480 references was compiled by J.C.E. Hubbard more than 25 years ago (Hubbard, 1965, unpublished). In this contribution we do not attempt a comprehensive review of that literature, but highlight the important landmarks in the study of the species. These include its discovery and spread in the early part of the century, the detective work in the late 1950s and early 1960s on its origins, the extensive research during the same period on its ecology, particularly in southern England where *S. anglica*-dominated marshes were already showing extensive die-back, and the demonstration in 1975 that the species utilizes the C_4 photosynthetic pathway. These findings are discussed in the light of recent significant advances in several research areas. Among the most illuminating of these are biochemical confirmation of the species' origins and the evidence of a narrow genetic base. The latter is particularly relevant in considering the development of the species' niche, its interaction with other species, especially pathogens, and its future evolution.

The following sections bring together these recent findings and attempt to demonstrate that *S. anglica* continues to provide a rare and fascinating opportunity to gain insight into the early stages of species evolution. In examining this continuing and dynamic process we also look forward to the possibility of cycles of invasion and decline, of northward spread under global warming, and of changing relationships with pathogens and competitors.

III. THE HISTORY OF *SPARTINA ANGLICA*

A. The Discovery and Spread of *Spartina* × *townsendii*[*]

In 1879, H. and J. Groves described a plant growing on mud flats at Hythe, Hampshire ". . . which, by the majority of characters given in British works, would be *S. alterniflora* rather than *S. stricta* [= *S. maritima*], yet which we now consider to be the latter". By 1880, however, the Groves had revised their opinion that the plant was a form

of *Spartina stricta* and wrote that it ". . . occupies so intermediate a position between that species and *S. alterniflora*, that it appears desirable not to include it in either". The Groves (1880, 1882) named this plant *Spartina townsendi* (spelt initially with one "i"; the second was added by other authors and is now the accepted spelling) in honour of Frederick Townsend, author of the *Flora of Hampshire* (Britten, 1906).

There is some dispute as to how long these forms of *Spartina* had been at Hythe before the Groves described them as a new species. According to Hubbard (1965a), the Groves collected the plants on which they based their descriptions in 1877. Hubbard states, however, that a Mr R.S. Hill had collected specimens of the same plant at Hythe in 1870, but that the plant was thought to be a luxuriant form of *Spartina maritima*. Sutherland and Eastwood (1916) also gave 1870 as the first date of collection of *S.* × *townsendii* based on a specimen in the Warner Herbarium, University of Southampton. They suggest, moreover, that descriptions of *Spartina alterniflora* from near Southampton given by Sowerby in his "*Grasses of Great Britain*", published in 1861, are very close to those of *S.* × *townsendii* published by the Groves. The earliest confirmed date for the discovery of *S.* × *townsendii*, however, remains 1870.

The plant spread relatively slowly at first and had not reached Cracknore Hard (2 miles north of Hythe) by 1883 (Stapf, 1908), but was recorded from Southampton in 1887 (Stapf, 1913). Stapf (1913), however, describes how ". . . towards the end of the eighties, something occurred that favoured the spreading of the grass". Marchant (1967) correlates this with the formation of the seed-bearing amphidiploid *S. anglica*. Indeed, the first confirmed record for *S. anglica* is from 1892 at Lymington, Hampshire. After this date it often becomes difficult to know whether records are referring to *S.* × *townsendii* or *S. anglica* as the distinction between the two was not recognized until 1957 (see footnote p.4). Goodman *et al.* (1969) state that sterile material features largely, though not exclusively, in collections from 1892 to 1910, such as those from Yarmouth, Isle of Wight (1893), Poole Harbour (1905), and Lymington (1893 and 1907).

After 1910 it is likely that as *S. anglica* was deliberately introduced into other parts of the British Isles for coastal protection and land reclamation (see below). *Spartina* × *townsendii* was also introduced into some areas due to mixed collections of both species being made, especially as many collections were made from Poole Harbour where *S.* × *townsendii* was still present in several sites in the 1960s (Hubbard, 1965a). *Spartina* × *townsendii* is still present as substantial swards at Hythe and has been found on the landward edge of *S. anglica* swards in Norfolk (Swann, 1965), Poole Harbour (Hubbard, 1965a) and the

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[*] *Note on nomenclature*: For many years it was thought that there was only one form of the hybrid between *S. maritima* and *S. alterniflora*, namely the fertile amphidiploid. In 1957, however, C.E. Hubbard showed that there still existed the F1 hybrid between *S. maritima* and *S. alterniflora*. He stated that this form was the one described by the Groves, and, therefore, the name "*townsendii*" should only be applied to the initial hybrid rather than its amphidiploid derivative. This left the amphidiploid without a name. Hubbard (1968) invalidly published the name *S. anglica* for the amphidiploid, although later (in Heywood, 1978, p. 364) he published a valid diagnosis, so legitimizing the name. The term "*S. anglica* agg." will be used in this article when referring specifically to both forms together.

Bristol Channel (Holland, 1982). The preference of *S.* × *townsendii* for these higher, more stable habitats also occurs in Holland (Drok, 1979). Hubbard and Stebbings (1967) estimated that the total area covered by *S.* × *townsendii* in Britain was only 20 ha compared with about 12 000 ha of *S. anglica*.

As in the British Isles, *S. anglica* has been used overseas for land reclamation and coastal defence, and it seems inevitable that some *S.* × *townsendii* has been introduced along with it, especially when the material had been taken as cuttings from Poole Harbour. *Spartina* × *townsendii* has been recorded from Holland on the basis of cytological data (Drok, 1979, 1983) and may also occur in New Zealand. The presence of *S.* × *townsendii* there is based on the fact that much "*S. anglica*" in New Zealand produces no seed (Allan, 1930; observations of C. E. Hubbard in Ranwell, 1967); however, the erratic nature of seed set in *S. anglica* (see below) makes this a poor diagnostic character.

The other confirmed site for *S.* × *townsendii* is in the extreme south west of France and north east of Spain around Hendaye and San Sebastian, although it has only just been recognized as such. In 1892 Neyraut collected an unusual form of *Spartina* at Hendaye and these plants were named *S.* × *neyrautii* by Foucaud in 1894 (Mobberley, 1956). This species has long been regarded as a hybrid between *S. maritima* and *S. alterniflora* and recent evidence from isozyme studies has confirmed this (see below). Under the International Code of Botanical Nomenclature, therefore, *S.* × *neyrautii* must be regarded as a synonym of *S.* × *townsendii* as it was the later of the two names to be published (Raybould *et al.*, 1990). Although *S.* × *townsendii* occurred in several locations in this area, extensive land reclamation reduced it to a single site near San Sebastian Airport (Hubbard *et al.*, 1978).

Another complication when considering the distribution of *S.* × *townsendii* is the occurrence of polyhaploids derived from *S. anglica*. Marchant (1967) described a seedling of *S. anglica* that was morphologically very close to *S.* × *townsendii* rather than its *S. anglica* parent. A chromosome count of this plant gave $2n = 61$, which was exactly half the number of the parent clone (Marchant, 1968). This seedling was produced presumably by the development of an unfertilized egg cell (agamospermy), and its similarity to *S.* × *townsendii* is to be expected as homologous chromosomes in *S. anglica* are identical and chromosome pairing is predominantly as bivalents (see below). *Spartina anglica* gametes, therefore, will be very similar genetically to *S.* × *townsendii*. Marchant (1975) has suggested that *S.* × *townsendii* in some parts of the country may be secondarily derived from *S. anglica* by polyhaploidy. The occurrence of dwarf, densely tillering forms of *S. anglica* that have been described from the Bristol Channel and the Dovey Estuary (Chater and Jones, 1951; Chater, 1965), from areas north of Dublin (Boyle, 1976a), south west Holland (Drok, 1979, 1983) and New Zealand (Allan, 1930; Bascand, 1970) may represent polyhaploid clones; careful cytological examinations are required, however, to confirm this suggestion.

B. The Discovery and Spread of *Spartina anglica*

As stated above, the first record for *S. anglica* is from Lymington in 1892 and after this date there is uncertainty as to whether records refer to the sterile F1 or the amphidiploid. The exact place and date of the origin is unknown. Although the rate of spread in the 1890s and 1900s was rapid, suggesting spread by seed, Goodman *et al.*, (1969) believe that in many areas the F1 was predominant. Whatever the proportions, by 1899 either *S. anglica* or *S.* × *townsendii* had begun to colonize Poole Harbour in the west and Chichester Harbour in the east, and many intervening areas (Stapf, 1908). On the north coast of the Isle of Wight there were populations at Yarmouth by 1893, on the River Medina in 1895, and on several marshes between Ryde and Cowes in 1907 (Stapf, 1908). Back on the mainland, Christchurch Harbour was beginning to be colonized by 1913 (Oliver, 1920) and Pagham Harbour by 1918 (Oliver, 1925). Oliver (1925) also gives a record from the mouth of the River Rother at Rye. The colonization of salt marshes between Poole and Rye probably represents the extent of completely natural spread of *S. anglica* in the British Isles, although extensive secondary natural spread following deliberate introductions has occurred (e.g. Goodman *et al.*, 1959).

Spartina anglica also spread to the north coast of France by natural means (or by accidental spread through shipping activity; there is no record of *S. anglica* ever having been deliberately introduced into France (Ranwell, 1967)). The first records are from Reville, on the north east tip of the Cotentin Peninsula, and Carentan at the mouth of the River Vire in 1906; slightly further east, the species was found at Sallenelles on the River Orne just north of Caen in 1918 (Oliver, 1925). By 1926 there were 1000 ha of *S. anglica* at Carentan (Oliver, 1926).

The other area where *S. anglica* has been very successful in France is on the marshes at the mouth of the River Seine. The first record is from Tancarville in 1915 and from Harve and Deauville in 1922 (Oliver, 1925). Oliver (1926) says that the rate of spread of *S. anglica* on the Seine marshes was the fastest he had ever seen, and Senay (1934) estimated that the plant covered 1000 ha. *Spartina anglica* seems to have colonized many of the estuaries on the northern coast of France and

Ranwell (1967) estimated that there were between 4000 and 8000 ha of *Spartina* by the mid-1960s.

The distribution of *S. anglica*, both in the British Isles and around the world, has been radically altered by deliberate introductions of the species. In the 1900s it was realised that *S. anglica* was very efficient at stabilizing bare mud flats (Stapf, 1907). This led to its utilization by private landowners as a method of reclaiming mud flats for agriculture and by coastal defence authorities for coastal protection. Many introductions of the species have been made around Great Britain and they have been thoroughly catalogued by Goodman *et al.* (1959) and Hubbard and Stebbings (1967). The first record of deliberate planting of *S. anglica* is from the Beaulieu Estuary in 1898, and this was followed by north Norfolk in 1907 and the Lincolnshire Wash in 1910. Most of the planting, however, was carried out in the 1920s (e.g. Bryce, 1936) with major efforts (utilizing 2000 or more cuttings (Ranwell, 1967)) in the Thames and Blackwater Estuaries, the Exe, the Severn Estuary (especially on the Somerset coast), the Dee, and the Humber. The east coast plantings were very successful, and during the 1930s virtually every estuary in Essex and southern Suffolk was either planted with *Spartina* or was colonized as the result of natural spread from the introduced material (Goodman *et al.,* 1959). The other major population of *S. anglica* on the east coast is in the Wash with further smaller populations as far north as Udale Bay in the Cromarty Firth (Smith, 1982). The plant has also been introduced successfully on the west coast. Hubbard and Stebbings (1967) record that the estuaries of the Severn, the Burry, the Dovey, the Mawddach, the Dee, the Ribble, and the Wyre all have populations of *S. anglica* in excess of 100 ha. Numerous other estuaries and salt marshes between these major sites have *S. anglica* populations, with the furthest north being the Isle of Harris in the Outer Hebrides.

Goodman *et al.* (1959), Hubbard and Stebbings (1967) and Ranwell (1967) all estimated the total area of *S. anglica* in Great Britain to be about 12 000 ha. This has been revised recently by Charman (1990) to 10 000 ha, though Charman points out that part of the disparity may lie in differing estimation procedures. What is clear, nevertheless, is that there have been significant changes in the distribution of *S. anglica* since 1967. Charman records a 44% reduction in cover on the east coast, an 11% reduction on the south coast, and a 40% increase on the west coast. The south and east coast populations of *S. anglica* are some of the oldest, whilst those on the west coast are much younger. Indeed, Charman reports that 20 new *S. anglica* populations have become established on the west coast since Hubbard and Stebbings' survey. This is evidence that *S. anglica* populations undergo a change from invasion and sward formation to regression (often termed "die-back"). Reasons for this are discussed in later sections. The current distribution of *S. anglica* in Great Britain is shown in Fig. 2.

In Ireland, *S. anglica* was first introduced on the south coast in the River Lee in 1925 (Cummins, 1930). Further introductions were made on the west coast in the Shannon and Fergus in 1928, 1931 and 1932

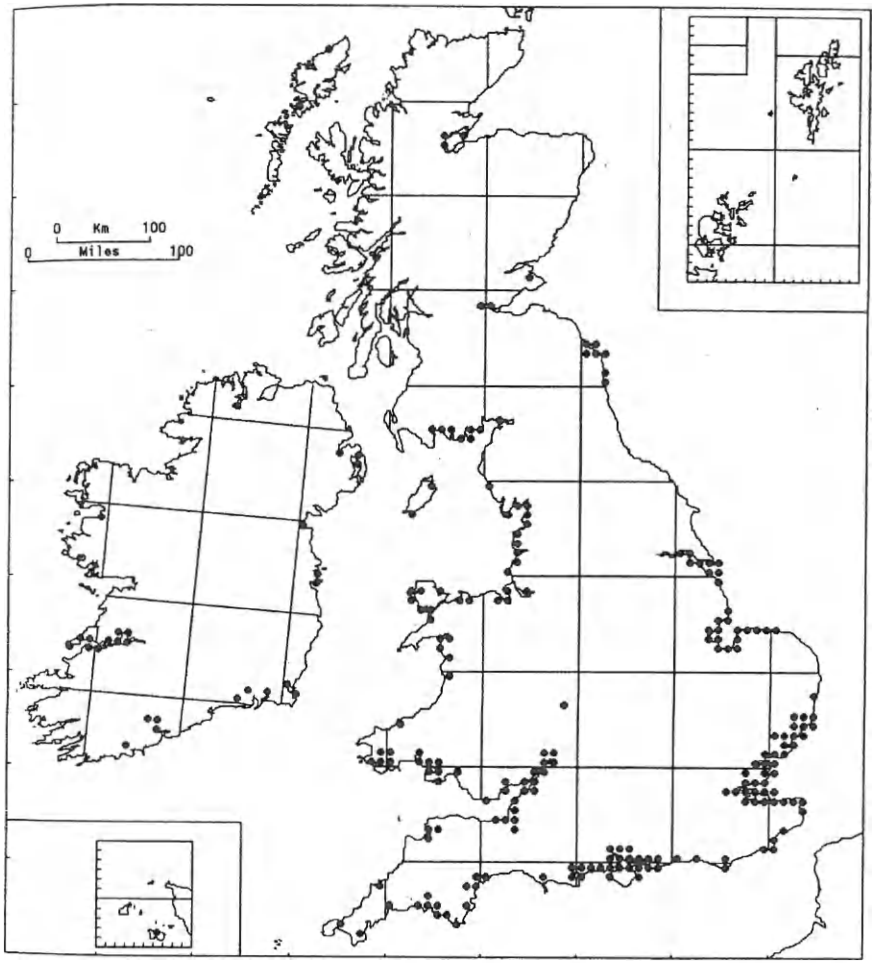

Fig. 2. The distribution of *S. anglica* (including records of *Spartina* × *townsendii*) in the British Isles (GB-204, Ir-27, Ch.Is-1). Map supplied by the Biological Records Centre, ITE, Monks Wood.

(Praeger, 1932). On the east coast, introductions were made in the Dublin Bay area in 1932 (Boyle, 1976a) and in Belfast Lough in 1929 (Praeger, 1932). Ranwell (1967) estimated that there were between 200 and 400 ha of *S. anglica* in Ireland.

Spartina anglica has now been successfully introduced into many areas outside the British Isles, notably Holland (4000–5000 ha), Germany (400–800 ha) and Denmark (500 ha), with smaller introductions in Australia and New Zealand (Ranwell, 1967). The most remarkable spread has been that following the introduction of the species to China. The descendents of only 21 individuals, survivors of a batch of 35 sent as seed in thermos flasks by D. S. Ranwell in 1963, have spread, mainly by planting, along almost the entire Chinese coast to occupy, by 1980, more than 36 000 ha (Chung, 1990). *Spartina anglica*'s present geographical range is from 57.5 °N to 48 °N in Europe, 46 °S to 35 °S in New Zealand and Australia (Ranwell, 1967), and from 41 °N to 21 °N in China (Chung, 1990).

Unsuccessful introductions of *S. anglica* have been made on the eastern seaboard of the USA, in the Caribbean and the Guianas, India and South Africa. Ranwell (1967) has suggested that winter temperature may be the crucial factor in whether establishment is successful; the species is damaged by frost, and warm winter temperatures are said to impede development. It is worth remembering, however, that *S. anglica* survived for nearly 2 years in British Guiana and was only exterminated after it was overrun by a native *Spartina* species, *Spartina brasiliensis* (Lambert, 1964).

To conclude, it is interesting to note the role of Poole Harbour in the spread of *S. anglica*, especially in the light of the scarcity of genetic variation in the species (see below). Hubbard (1965a) estimated that between 1924 and 1936 over 175 000 cuttings were exported from material derived from Poole Harbour, and of these 46 000 were planted in the British Isles. This figure does not include numerous batches of seed from this material that were also dispatched. This must represent a severe genetic bottleneck for the species.

IV. THE ORIGIN OF *SPARTINA ANGLICA*

A. Early Ideas on the Origin

Despite the fact that the Groves' descriptions of *S.* × *townsendii* had emphasized that the plant had many morphological characters intermediate between those of *S. maritima* and *S. alterniflora*, it is surprising how little the possibility of a hybrid origin is considered in the early literature. Most authors tried to fit the new form into previously

decribed taxa. Boswell (in Groves and Groves 1882) suggested that the plant might be "true" *Spartina glabra*, and Townsend (1883) thought that the plant was a variety of *S. maritima*. Corbière and Chevalier, writing in 1906 about the appearance of *Spartina* in Normandy, claimed that *S. anglica* could not be a hybrid as it had fertile pollen and seeds, and because *S. alterniflora* did not occur in northern France (Oliver, 1925); they thought the plant to be *S. glabra* var. *pilosa*.

Many of the early explanations of the appearance of the *S. anglica* agg. were based on the possibility of a direct introduction of foreign *Spartina* taxa, usually one of the numerous named varieties in the *S. alterniflora*/*S. glabra* complex. This is probably more a reflection of the confused state of the taxonomy of *S. alterniflora* at that time than to any great resemblance of the *S. anglica* agg. to the published descriptions of other taxa (see Mobberley (1956) for a review of the ideas on the taxonomy of *S. alterniflora*). The introduction of a foreign species theory was disposed of by Stapf (1908), who found that no species of *Spartina* exactly matched the forms that had first appeared at Hythe. Stapf proposed that the most plausible alternative was that the *S. anglica* agg. had arisen by hybridization between *S. maritima* and *S. alterniflora*, given the intermediate morphology of the plants and their similarity to "*S.* × *neyrautii*" which had arisen in the only other location where *S. maritima* and *S. alterniflora* co-existed (Stapf, 1908).

This idea rapidly became accepted, although the uniformity of seed progenies of *S. anglica* created problems because if the species was a hybrid, segregation of parental traits would be expected. The situation was summed up by Oliver (1925) who wrote:

> If it [*S. anglica*] is a hybrid, then it should betray its hybrid constitution. In one respect it does this, viz. in the extreme vegetative vigour which it displays. A vigorous constitution of this kind is not unusual in a first cross; what is surprising is that not only is this vigour maintained through many seed generations but that the plant should remain substantially uniform. There is no evidence of segregation, which is to be expected in an ordinary hybrid.

Oliver goes on to say that the lack of segregation may not necessarily be a problem and appears to propose the possibility that the characteristics of *S. anglica* could be explained by allopolyploidy:

> This circumstance [lack of segregation], which at first sight seems to negative the hybrid theory, does not however absolutely close the door to it, because there exists a class of hybrids characterized by perfect stability. But it would be premature to assert that *S. townsendii* belonged to this class, without the production of evidence.

Huskins (1930a,b) finally provided this evidence when he made chromosome counts on *S. anglica* and its putative parents, and found them to be in perfect agreement with the theory of an allopolyploid origin. Although Huskins' figures have proved to be inaccurate (see below), the publication of his papers firmly established allopolyploidy as the prevailing theory to account for the origin of *S. anglica*, and this theory has never been in serious doubt.

There is now a wealth of evidence to show that *S.* × *townsendii* is a hybrid between *S. maritima* and *S. alterniflora*, and that chromosome doubling in *S.* × *townsendii*, either in somatic tissue or by the fusion of unreduced gametes, produced *S. anglica*. This evidence can be split broadly in four categories: morphological, historical, cytological and biochemical.

B. Evidence for the Origin

1. *Morphological Evidence*

As noted in a previous section, when the Groves first described *S.* × *townsendii* they thought that the plant was *S. alterniflora* but then decided that it was *S. maritima* (Groves and Groves, 1879), before eventually deciding that the plant was neither of these species. The reasons for thinking initially that the plants were *S. alterniflora* were that the specimens were too tall to be *S. maritima* and that the panicles consisted of four to six spikes rather than the two usually present in *S. maritima*. In addition, the spikes were longer and had more spikelets than usual for *S. maritima*. The Groves thought, however, that these were unreliable characters for distinguishing between *S. alterniflora* and *S. maritima*. The decision to assign the forms found at Hythe to *S. maritima* was based on them having leaves distinctly articulated with the leaf sheaths and flag leaves that did not overtop the spikes, both characters of *S. maritima*. *Spartina alterniflora*, on the other hand, has leaves that are more continuous with the sheaths and flag leaves that always extend beyond the spikes.

It can be seen from the early confusion that *S.* × *townsendii* has many characteristics in common with both *S. maritima* and *S. alterniflora*, tending towards *S. alterniflora* in inflorescence structure, and towards *S. maritima* in foliage characters. These hybrid characteristics are borne out by the data of Marchant (1967) and Hubbard (1968). Other characteristics given as evidence of hybrid origin are the prolific rhizome production, as in *S. alterniflora*, and the dense tillering, as in *S. maritima*. The morphological evidence is, therefore, consistent with *S.* × *townsendii* being a hybrid between *S. alterniflora* and *S. maritima*.

This being the case, we may ask whether the morphology of *S. anglica* is consistent with it being the product of chromosome doubling in *S.* × *townsendii*. The failure to distinguish between the two for over 50 years shows that they have many features in common. In most respects apart from height, however, *S. anglica* is larger than *S.* × *townsendii* (Marchant, 1967; Hubbard, 1968). *Spartina anglica* leaves tend to be longer and wider, the ligules are longer, and the spikes are longer as are the spikelets. This is suggestive of the so-called "gigas" morphology of increased size of plant organs resulting from increased cell size due to polyploidy. Marchant (1967) also found that the volume of pollen grains of *S. anglica* is twice that of *S.* × *townsendii*, a strong indication that chromosome doubling in *S.* × *townsendii* gave rise to *S. anglica*. Thus, the morphological data are entirely consistent with the classical theory.

2. *Historical Evidence*

From information on the historical distribution of *S. alterniflora* and *S. maritima* it can be shown that the two species co-existed in Southampton Water immediately prior to the discovery of *S.* × *townsendii*.

Spartina maritima occurs from Britain and the Low Countries in the north, through France, Spain and Portugal, and into the Mediterranean; further south the plant occurs in rather isolated populations down the west coast of Africa from Morocco to the Cape of Good Hope. *Spartina maritima* is usually thought of as a native of the British Isles. Throughout northern Europe, however, it shows a lack of vigour in comparison with specimens from Spain and Africa. This led Chevalier (1923) to suggest that it may only be native to Africa and was introduced into northern Europe by shipping.

The first record for *S. maritima* in Britain is from northern Kent in 1629 (Hubbard, 1965b). Bromfield (1836) recorded it from the mouth of the River Itchen and Hythe, and Townsend (1883) described it as being "rather common" in Hampshire. By the 1900s the species had been recorded from Lincolnshire to north Kent on the east coast, and from Chichester to the Exe on the south coast (Stapf, 1908). This probably represented the greatest limit of *S. maritima* in Britain and by the 1930s it was becoming quite rare. Hall (1934) records that it had been "practically exterminated" in Hampshire, and in a recent survey the only location for the plant on the south coast was Hayling Island (Raybould *et al.*, 1991b). The pattern is similar on the east coast, where since 1950 the plant appears to have been lost from Lincolnshire, Norfolk and Kent and now occurs only on high level salt marshes in Essex and southern Suffolk (Raybould *et al.*, 1991c).

There appear to be several reasons for the decline of *S. maritima*. On the south coast many habitats have been destroyed through land reclamation for agriculture or industrial development; this is especially so in Southampton Water (Marchant, 1967; Raybould *et al.*, 1991b). On the east coast, although some populations may have been lost through land reclamation, the major factors have been erosion and successional change, the invasion of high-level *S. maritima* habitats by *Halimione portulacoides* being a particularly common cause of its decline (Raybould *et al.*, 1991b). It has often been assumed that the spread of *S. anglica* has been important in the decline of *S. maritima*. These species rarely co-occur, however, and the spread of *S. anglica* and the decline of *S. maritima* are probably two independent indicators of ecological, sedimentary and sea level changes, rather than cause and effect.

Spartina alterniflora is a native of the eastern seaboard of North America where it grows in large monospecific swards from Newfoundland in the north to the Gulf of Mexico in the south. The species is also recorded from tropical South America, although some botanists consider these records refer to the closely related species *S. glabra* Muhl. *Spartina alterniflora* was probably introduced into Southampton Water from the USA by shipping. Bromfield (1836) suggests that the species may have been in the River Itchen since 1816. Townsend (1883) records that in 1879 it was "abundant by the Itchen from the sea upwards to beyond Southton [Southampton]". Stapf (1908) also recorded that the plant was abundant in the Itchen and Southampton Water. The range of the species extended ultimately from Lymington in the west to the mouth of the River Meon in the east (Hall, 1934).

As is the case with *S. maritima, S. alterniflora* has undergone a major decrease in distribution since the turn of the century. Industrial development has played a large part in this regression, although some populations were lost due to being overrun by *S. anglica* (Marchant, 1967). Since 1963 the species has existed at only one site, at Marchwood on the west shore of Southampton Water (Marchant and Goodman, 1969).

From the records available, there appear to be two places where *S. maritima* and *S. alterniflora* occurred together, namely at the mouth of the Itchen and at Hythe. Bromfield (1836) wrote that where the Itchen entered Southampton Water "*Sp. stricta* grows close to patches of *Sp. alterniflora*". Townsend (1883) also recorded both species from this location. Townsend also reported *S. alterniflora* and *S. maritima* as growing together at Hythe, and the Groves (1879) found specimens of *S.* × *townsendii* growing amongst stands of *S. alterniflora*.

If it is assumed that *S. maritima* was growing at the mouth of the Itchen when *S. alterniflora* was first introduced, then the species could have existed together for over 50 years before the discovery of *S.* × *townsendii*. Historical records show, therefore, that the origin of the *S. anglica* agg. through hybridization was feasible.

3. *Cytological Evidence*

The first work on the cytology of the *S. anglica* complex was by Huskins (1930a,b). Using mitotic cells from root tip meristems, he found *S. maritima* had $2n = 56$, *S. alterniflora* $2n = 70$ and *S. anglica* $2n = 126$. These counts fit exactly with the theory that *S. anglica* is the amphidiploid derivative of the other two species. Huskins used plants of *S. alterniflora* from New York State rather than British material, which left him open to the criticism that he may have examined a different cytotype from the one involved in the origin of *S. anglica* (Marchant, 1963). Nevertheless, the results seemed so conclusive that for nearly 30 years the question of the origin of *S. anglica* was not re-examined.

The work of Hubbard (1957) in pointing out that an F1 hybrid existed at one time probably sparked a new interest in the cytology of the *S. anglica* complex. Boyle and Kavanagh (1961) counted $2n = 126$ for *S. anglica* from Ireland, although they later corrected this to $2n = 124$ by the re-interpretation of multivalents (Boyle, 1973).

Marchant (1963) showed that Huskins' counts were inaccurate, and gave counts for *S. maritima* of $2n = 60$, for *S. alterniflora* of $2n = 62$, and for *S. anglica* a range from $2n = 120$ to 124. He also found sterile plants at Hythe with $2n = 62$ and these were designated *S.* × *townsendii*. These counts were in good, though not in perfect agreement with the classical theory.

Marchant (1968) gives a detailed account of the cytology of the complex. *Spartina maritima* almost always forms 30 bivalents at meiosis and all mitotic cells had $2n = 60$. In *S. alterniflora* from Britain, Marchant found some inconstancy in chromosome number in some tillers. In one tiller there was a range from $2n = 61$ to $2n = 66$ with a mode of 62. Meiotic counts were always $n = 31$ with a maximum of two multivalents per cell, suggesting a polysomic constitution of $6x + 2$. Marchant (1970) also counted *S. alterniflora* material from North America and found $2n = 62$ in all cases. This ended speculation that *S. alterniflora* existed as two chromosome races of $2n = 8x = 56$ and $2n = 10x = 70$ (until the 1960s it was thought that the genus *Spartina* had a basic number of 7 rather than 10).

In *S.* × *townsendii* Marchant (1968) found some variation in chromosome number within tillers, with a mode of 62. As with *S. alterniflora*, he suggested that the variation had a physiological basis as plants that had weak growth had most variation. Meiosis was shown to be complex with numerous univalents and multivalents at metaphase I (Fig. 3). Trivalents were the most common multiples, although quadrivalents and other arrangements occurred, and usually less than half of the chromosomes were left unpaired. Chiasma frequencies ranged from 0.53 to 0.75

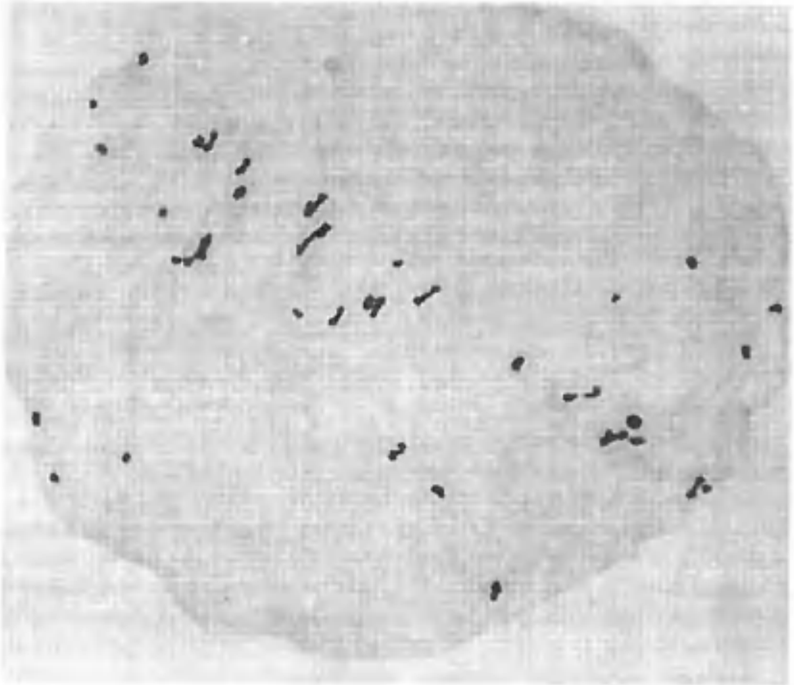

Fig. 3. Metaphase 1 at meiosis in *Spartina* × *townsendii* ($2n = 6_{III} + 15_{II} + 14_{I} = 62$).

per paired chromosome, and from 17.4 to 31.3 per cell, depending on univalent frequency. The highest pairing was in plants with the "dwarf brown" phenotype first described from the Dovey Estuary and the Bristol Channel by Chater and Jones (1951).

Marchant found a range of chromosome numbers in *S. anglica* from $2n = 120 - 127$, with the great majority of clones having 120, 122 or 124. All clones showed almost regular meiotic pairing (Fig. 4) with a high chiasma frequency of 0.74–0.86 per paired chromosome. Univalents occurred up to a maximum of ten per cell in aneusomatous plants due to some chromosomes having no homologue with which to pair. Quadrivalents occurred up to a maximum of five per cell, and trivalents to a lesser extent.

Marchant also described possible backcrosses of *S. anglica* to a parental species. Two unusual clones were found in Southampton Water. One clone gave a count of $2n = ca\ 90$ at meiosis, with a maximum of 16 univalents and only rare multivalents. There was relatively little lagging at anaphase, and the second division was more or less regular, giving tetrads that appeared normal. Seed set in the clone was described as "abundant". The other clone gave counts of $2n = ca\ 76$ from mitotic cells. At meiosis up to 19 univalents were found with few multivalents. At anaphase laggards were common with as many as 11 univalents being excluded from daughter nuclei. Tetrads were irregular but seed was set occasionally. Both these clones resembled *S. alterniflora* in morphology (Marchant, 1967) and possibly represent a backcross of *S. anglica* to this parent. The genome relationships elucidated by Marchant's work are shown in Fig. 5, and strongly support the theory of the origin as outlined previously.

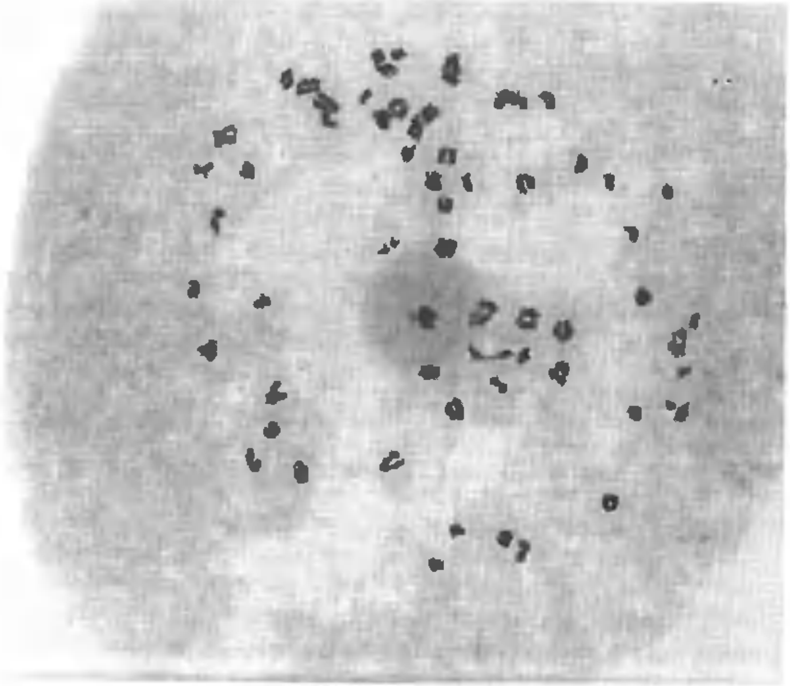

Fig. 4. Diakinesis at meoisis in *S. anglica* ($2n = 61_{II} + 2_{I} = 124$).

Despite the very strong evidence, from several sources, some doubts still remained over the origin of *S. anglica*. First, it had not proved possible to resynthesize the species from the putative parents. Marchant (1964) attempted to cross *S. maritima* and *S. alterniflora* by bagging

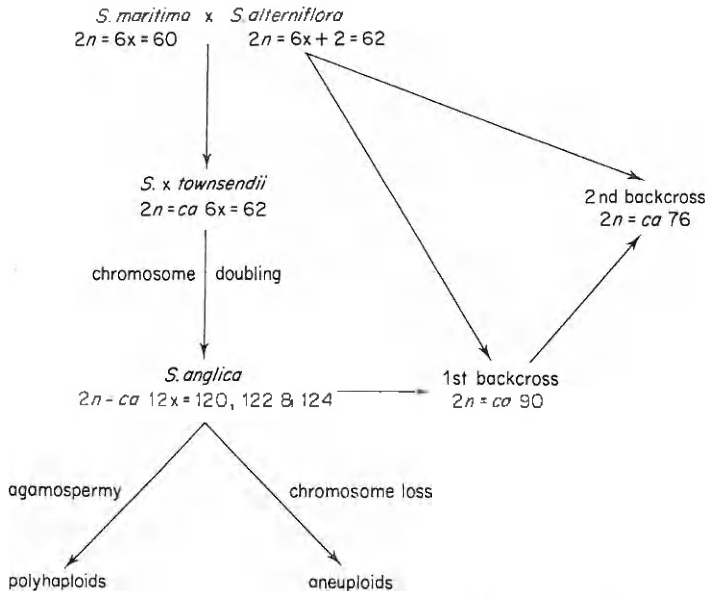

Fig. 5. Genome relationships in *Spartina* (based on Marchant, 1968).

flowering heads together and by placing pots in which the species were growing adjacent to each other.

In neither set of experiments was seed set on either species. Marchant (1964) also used colchicine in an attempt to double the chromosome number of *S.* × *townsendii* to produce *S. anglica*. Treatments included immersion of tiller and rhizome apices in colchicine solution, application of colchicine-containing agar blocks to growing points, and injection of colchicine solution inside the leaf sheath enclosing the flowering spikes. In no instance was chromosome doubling induced. Also, Raybould (1989) found that the pollen of both *S. alterniflora* and *S. maritima* grown in a glasshouse was completely sterile on the basis of the fluoroscein diacetate test (Heslop-Harrison *et al.*, 1984), so that experiments to resynthesize *S.* × *townsendii* could not be performed. A second doubt was raised by the revised chromosome counts presented by Marchant. The counts of Huskins meant the possibility that *S. anglica* could have arisen directly from either *S. alterniflora* or *S. maritima* through autopolyploidy could be discounted. The new counts made by Marchant, in which the chromosome numbers of both *S. maritima* and *S. alterniflora* are roughly half those of *S. anglica*, meant that autopolyploidy must be considered.

The available evidence was largely against an autopolyploid origin. First, the karyotype of *S. anglica* appeared to be a combination of the karyotypes of *S. maritima* and *S. alterniflora* (Marchant, 1968). The chromosomes of *Spartina* are, however, very small and Marchant could not unequivocally confirm an allopolyploid origin on the basis of chromosome morphology. Secondly, the chiasma frequency in both putative parents is high (Marchant, 1968) and thus an autopolyploid produced from either of these species might be expected to have a high frequency of multivalents. *Spartina anglica* forms multivalents rarely (see Fig. 4, for example) and so the case for alloployploidy seemed strong. There are several cases documented, however, where autopolyploids form only bivalents. This phenomenon has been observed, for example, in *Lotus corniculatus* (Dawson, 1941), *Tolmeia menziesii* (Soltis and Soltis, 1988), the fern genera *Asplenium* and *Adiantum* (Lovis, 1964; Vida, 1970; Manton *et al.*, 1970) and in several artificially produced autotetraploid crops (Timmis and Rees, 1971; Armstrong, 1971; de Wet and Harlan, 1972). Thus, autopolyploidy could not be rejected completely.

4. *Biochemical Evidence*

The evidence that finally confirmed the allopolyploid origin came from isozyme electrophoresis. In newly formed allopolyploids the component diploid genomes are often expressed entirely (Gottlieb, 1982). Thus an allopolyploid species would have isozyme phenotypes that are the product of the addition of parental polypeptide subunits, resulting in all the parental bands being present, plus possible new hybrid bands in multimeric enzymes (Roose and Gottlieb, 1976). In newly formed autotetraploids it is assumed that no bands could be present that were not present in the parental species, and this is borne out by the evidence available (Crawford and Smith, 1984; Soltis and Soltis, 1988). It has recently been shown (Gray 1986; Raybould 1987, 1989; Gray *et al.*, 1990a; Raybould *et al.*, 1991b) that British material of *S. maritima* and *S. alterniflora* possess unique bands in several isozyme systems and that *S.* × *townsendii* contains all of these bands (see Fig. 6). In addition, *S.* × *townsendii* showed several novel hybrid bands in systems where multimeric enzymes are formed. In all systems *S. anglica* had phenotypes identical to *S.* × *townsendii*. This evidence completely confirmed the allopolyploid origin of *S. anglica*. Guenegou *et al.* (1988) found similar results using French material, although certain features of this work suggest that the genotypes of the parental material they examined were not those involved in the origin of *S. anglica*. For example, in superoxide dismutase they found that both *S. alterniflora* and *S.*

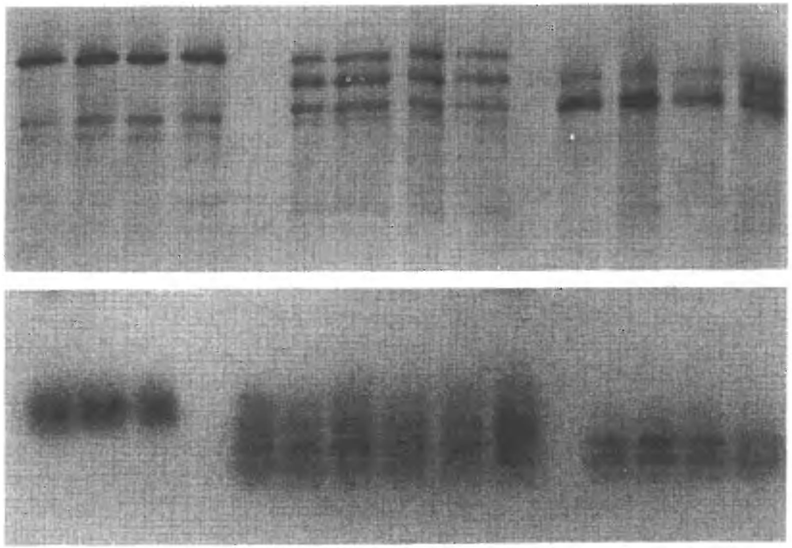

Fig. 6. Isozyme phenotypes in *Spartina* demonstrating that *S. anglica* phenotypes are those expected if the species is an allopolyploid derivative of *S. alterniflora* and *S. maritima*. a (Upper): Esterase (1–4 *S. maritima*, 5–6 *S.* × *townsendii*, 7–8 *S. anglica*, 9–11 *S. alterniflora*, 12 *S. glabra*) b. (Lower): Phosphoglucose isomerase (1–3 *S. alterniflora*, 4–9 *S. anglica*, (10–13 *S. maritima*) (with permission from Raybould *et al.*, 1991a).

maritima had bands that were not present in *S. anglica*, whereas Raybould *et al.* found that in British material of the parental species all of the parental bands in this system are found in the hybrids. A similar position occurred with acid phosphatases. Guenegou *et al.* also found esterase phenotypes with non-parental bands, which, since most esterase enzymes are monomeric (Gottlieb, 1981), further suggests that their material was not involved in the origin of *S. anglica*.

C. "*Spartina* × *neyrautii*"

The evidence reviewed in the preceeding sections confirms beyond reasonable doubt the nature of the origin of *S. anglica*. There is, however, further evidence from a plant known as *S.* × *neyrautii*. In south west France there was also an accidental introduction of *S. alterniflora*. It was discovered by Loiseleur in the Ardour Estuary near Bayonne in 1803. By the early 1900s it had spread along the coast for about 25 miles from Capbreton to the Bidassoa Estuary (Stapf, 1908). *S. maritima* is native to this area (Mobberley, 1956). In 1892, Neyraut collected an unusual form of *Spartina* from Hendaye (Mobberley, 1956) and the status of this plant and similar types found in the area caused much confusion. When Neyraut discovered the plant he though it to be identical to *S.* × *townsendii* (Chevalier, 1923). In 1894 Foucaud described it as a hybrid between *S. maritima* and *S. alterniflora* (Stapf, 1908), but named it *S.* × *neyrautii* as he believed it had certain differences from *S.* × *townsendii*. The hybrid nature of *S.* × *neyrautii* was confirmed by Marchant (1977), who found that it had the same chromosome number and meiotic behaviour as *S.* × *townsendii* and also very similar morphology. Raybould *et al.* (1991a) confirmed that the plant is a *S. maritima* x *S. alterniflora* hybrid using isozyme phenotypes, and showed that *S.* × *neyrautii* must be considered as a synonym of *S.* × *townsendii*. The fact that *S.* × *townsendii* has been discovered in the only two places where the distributions of *S. alterniflora* and *S. maritima* are known to have overlapped is a further confirmation of the nature of its origin.

D. Problems Over the Origin

Two questions remain to be answered over the origins of the *S. anglica* agg. First, did *S. anglica sensu stricto* arise more than once, and second, do the two independent origins of *S.* × *townsendii* represent reciprocal hybridizations, as suggested by Arber (1934). The first question has been addressed by Raybould *et al.*, (1991a). They found that *S. anglica* has extremely low levels of genetic variation at isozyme loci (see below), suggesting a single origin. The parental species and *S.* × *townsendii*, however, also show little variation and so a multiple origin from uniform parents cannot be discounted. Further research using more sensitive methods of detecting genetic variation (such as "genetic fingerprinting") may resolve this problem. There is no available information on the second question. A possible solution, however, may be a study of the inheritance of chloroplast or mitochondrial markers, which have been used recently to demonstrate reciprocal origins for *Tragopogon* species in the USA (Soltis and Soltis, 1989).

V. VARIATION IN *SPARTINA ANGLICA*

A. Sources of Genetic Variation in *Spartina anglica*

The available evidence on the levels of genetic variation in British populations of the parental species of *S. anglica* is limited to an isozyme survey by Raybould *et al.* (1991b). This found that the single extant population of *S. alterniflora* was monomorphic, and, although there was some evidence of variation in *S. maritima*, British material of this species also appeared to be largely monomorphic with isozyme variation limited to two comparatively rare forms of the enzymes shikimic acid dehydrogenase and glutamate oxalacetate transaminase.

As indicated earlier, this lack of significant levels of isozyme polymorphism in the parental species means that it is not possible to distinguish between single or multiple occurrences of either the original hybridization event which produced *S.* × *townsendii* or the subsequent chromosome doubling which produced *S. anglica* (as has been done with other allopolyploid species such as *Senecio cambrensis* (Abbott and Ashton, 1989), *Tragopogon* (Roose and Gottleib, 1976) and *Plagiomnium medium* (Wyatt *et al.*, 1988)). However, the lack of enzyme polymorphism in the parental species does at least suggest that even if multiple events have occurred, they are likely to have resulted in genetically identical forms of *S. anglica*.

Since the original formation of the species, the generation of variation in *S. anglica* may have occurred in a number of ways apart from conventional mutation. One possible source of variation is through backcrossing and subsequent introgression with one of the parental species. Some evidence of the type of chromosomal polymorphism that might be associated with such events exists (see Section IV above). Two further potential sources of variation are chromosomal in origin. In an allopolyploid species such as *S. anglica*, in which chromosome doubling has restored fertility, pairing at metaphase I of meiosis often only occurs between homologous chromosomes, i.e. equivalent chromosomes from the same parental genome. This phenomenon, known as preferential pairing, has been extensively studied in polyploids such as wheat (e.g. Riley and Chapman, 1958). Strict preferential pairing maintains the variation between the parental genomes in the form of fixed heterozygosity (e.g. Aung and Evans, 1987). In contrast, if homeologous pairing, i.e. pairing between the equivalent chromosome from different parental genomes, occurs, recombination between the parental genomes is possible. Homeologous pairing—even at relatively low frequencies—could lead to the gradual release of genetic variation from recombination between the parental genomes.

A second chromosomal source of variation is through aneuploidy (i.e. the gain or loss of chromosomes) as the result of either unbalanced segregation at meiosis or somatic events. In general, plant species, especially high polyploids such as *S. anglica*, are relatively tolerant of the resulting unbalanced chromosome dosage that results from aneuploidy, at least through the vegetative stages of their life cycle. However, the resulting complications at meiosis normally lead to at least some level of reduced sexual fertility. This is not a problem in species which, like *S. anglica*, propagate extensively by asexual means (Gibbs *et al.*, 1978).

B. Evidence for Genetic Variation in *Spartina anglica*

1. Morphological Variation

Although many authors have reported field observations of morphological variation in *S. anglica*, it has only recently been systematically studied. Some evidence of phenotypic variation comes from plants which appear "distinct" under field conditions, for example the "brown dwarf" type identified by Chater and Jones (1951). Marchant (1968) has shown that many dwarf forms have a chromosome number of $2n = 62$, suggesting that they have a polyhaploid origin. Some other "distinct" types have been shown to revert to typical *S. anglica* morphology when brought into artificial cultivation (Raybould, 1989).

Spartina anglica has also been observed to display zonal variation in morphology across some salt marshes. For example, Marks and Mullins (1984) and Marks and Truscott (1985) have reported the zonation of *S. anglica* on the salt marshes of the southern shore of the Ribble estuary, in north west England. They recognized four zones on the basis of shoot density and vegetative vigour. Zonation of *S. anglica* has also been extensively studied on the salt marshes of the north shore of the Dee estuary in Cheshire. Taylor and Burrows (1968) identified differences in time of flowering, seed production, rates of tillering and number of overwintering shoots across this marsh. If these zonal differences are genetic in origin and the result of adaptive differentiation in response to different environmentally induced selection pressures across the marsh, extremely rapid microevolution must have occurred since the original colonization of the Cheshire marshes on the Dee in 1945. However, genetic variation cannot be inferred from such observed zonal differentiation alone since any genetic effects will be confounded with age effects and a range of environmental effects.

Material from the Dee estuary salt marsh has been subjected to careful study in a series of common garden experiments. Plants derived from single tillers, from distinct zones showed significant differences even after 2 years of cultivation under common environmental conditions (Hill, 1990). In addition, plants transplanted into the zones from which they originated showed significantly greater rates of survival than plants transplanted between zones. This appears to indicate that there may be a genetic component to the observed zonal differentiation across the Dee estuary salt marsh. However, the unambiguous resolution of such morphological variation into its genetic and non-genetic components in such a phenotypically plastic species as *S. anglica* poses a number of major experimental problems. Since individual clones may be long-lived, there is considerable potential for carry-over effects into clonal trials under common garden conditions. Carry-over effects may arise in several ways. For example, differences in the nutritional status of the clones can produce effects, as in the differences in salt tolerance among clonal lines of *Puccinellia maritima* which were found to be caused by variation in the salt concentration of the soils from which the clones were sampled rather than by differences in genotype (Gray and Scott, 1977). Carry-over effects may also occur in perennials from differences in clone age, older ramets being less able to change their phenotypes in response to environmental change (Breese *et al.*, 1965). Different levels of viral infection, to which long-lived clonal plants are especially prone, may also lead to non-genetic differences in gross morphology, yield and competitive ability (Silander, 1985)—although its effects on growth are unknown, a leaf mottling virus, spartina mottle virus, was identified by Jones (1980) and isolated from plants in several populations. Unfortunately, the differences in morphological variation in *S. anglica* populations, both zonally in the Dee and Ribble estuaries, and within and between complementary zones on different salt marshes (Thompson, 1990), are largely of the type which could arise from differences in clonal age or viral infection levels. Although there is no direct evidence of such effects, plants from the lower zones, which are usually younger, are generally more vigorous and have greater phenotypic plasticity (Thompson, 1989, 1990; Thompson *et al.*, 1990, 1991 a,b,c. Thompson *et al.* (1990, 1991a,b,c), on the basis of further common garden, reciprocal transplant and genotype/environment experiments, suggest that most of the variation is due to age-related decline in vigour, and thus to somatic rather than genetic differences between populations.

The only way to resolve this variation into its genetic and environmental components would be to carry out an appropriately designed trial of seed progenies (using the type of experimental designs summarized in Lawrence (1984)). This has not proved possible in *S. anglica* because of the unpredictable pattern of seed set in recent seasons, the problems of controlled germination of seed, and the difficulties of growing such a large, vigorous, rhizomatous salt marsh perennial grass in a fully randomized field trial. Ideally, seed progenies produced under glasshouse conditions should be used, to avoid environmental differences during seed maturation, which can cause carry-over effects (e.g. Funk *et al.*, 1962; Nelson *et al.*, 1970). Even strong short-term environmental stimuli at the seedling stage can influence the phenotype of that plant's seed progeny (Hague and Jones, 1987).

2. *Biochemical Variation*

Although high levels of seed protein variation and extensive isozyme polymorphism are features of many higher plant populations (e.g. Gepts, 1990; Hamrick and Godt, 1990), an extensive study of protein variation in *S. anglica* conducted by Raybould *et al.* (1990b) found no evidence of seed protein variation, and found only a single GOT isozyme variant in a survey of 12 different enzyme systems. In contrast, the polyploid grass *P. maritima* was found to be highly polymorphic for every isozyme system studied in the population coexisting with monomorphic *S. anglica* on the Dee estuary salt marshes (Raybould *et al.*, 1991a) (Fig. 7), and in several other populations (Gray *et al.*, 1979). It

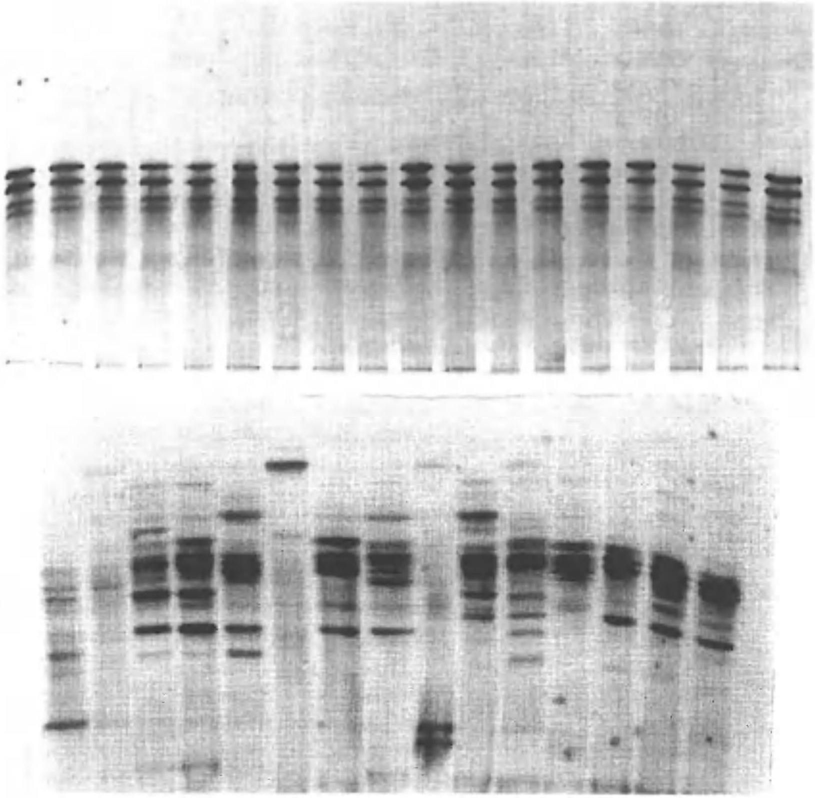

Fig. 7. Comparison of the variation in esterase isozymes in clones of (a) (Upper): *S. anglica* and (b) (Lower): *P. maritima* collected along the same 300 m transect on the Dee estuary (with permission from Raybould *et al.*, 1991a).

appears, therefore, that at the protein level *S. anglica* has extremely low levels of genetic variation. The single GOT variant identified by Raybould *et al.* (1991a) was characterized by the loss of several GOT bands which correlated with a small reduction in chromosome number, suggesting an aneuploid origin. The variant appeared to be largely confined to Poole Harbour and showed considerable variation in frequency between creeks. Its sporadic distribution elsewhere may reflect either a series of sampling events, as Poole material has been distributed throughout Britain, or alternatively a series of independent aneuploid origins.

Of course, a lack of electrophoretically detectable variation does not conclusively signify an absence of genetic variation. Isozyme markers may show lower levels of variation than quantitative traits, as in *Hordeum murinum* (Giles, 1984) and *Xanthium strumarium* (Moran and Marshall, 1978; Moran *et al.*, 1981). In general, however, seed proteins tend to be more variable than isozymes, probably because of fewer functional constraints on seed protein structures (Gillespie and Blagrove, 1975; Righetti *et al.*, 1977). For example, Doll and Brown (1979) estimated that hordeins were 10–30 times as variable as isozymes in barley. The completely invariate protein profiles of *S. anglica* seeds are therefore strong indicators of genetic uniformity in the species—particularly as we assume the seeds to be produced sexually, whereas common garden trials use vegetative tillers which could be entirely clonal. The general conclusion that can be drawn from the existing information is that, apart from the sporadic occurrence of chromosome variation resulting from aneuploidy, polyhaploidy and back-crossing (see above), there is little unambiguous evidence of genetic variation in *S. anglica*. This is what one might expect from both its origin and the pattern of its subsequent spread, since British material of both parental species shows little evidence of variation; the original hybridization event and the subsequent chromosome doubling appear to have occurred at very low frequency, possibly only once, and the process of small-scale clonal sampling and subsequent multiplication which has been used to plant out new sites would have dramatically reduced any variation which might have been present. Finally, conventional mutation is unlikely to have led to the generation of significant levels of genetic variation over such a short evolutionary timescale.

3. Genetic Variation in Other Clonal Salt Marsh Grasses

The lack of genetic variation in *S. anglica* which is likely to be a major factor in the future evolutionary success of the species, is in contrast to at least some other clonal salt marsh grasses. Genetic differentiation, some of adaptive significance, has been demonstrated in *P. maritima* using clonal and seed progeny trials and isozyme studies (Gray, 1985a, Gray *et al.*, 1979, Gray and Scott, 1980), as has genetic variation in salt tolerance in salt marsh *Festuca rubra* using clonal and seed progeny material (Rhebergen and Nelisson, 1985). Perhaps more significantly, Silander (1984, 1985; Silander and Antonovics, 1979) provided evidence for adaptive genetic variation in North Carolina populations of the related *Spartina patens*, which, although based on trials of clonal material, was supported by isozyme variation. Indeed, clonal plants generally are found to possess genetic variation, most having multiclonal populations with most clones restricted to one or a few populations and rarely being widespread (Ellstrand and Roose, 1987).

VI. THE ECOLOGY OF *SPARTINA ANGLICA*

A. Rates and Pattern of Spread and Dispersal

As detailed above, *S. anglica* was successfully introduced to coastal and estuarine mudflats throughout the world, especially during the 1920s and 1930s. Natural dispersal of seed, usually in entire spikelets, over long distances may have occurred by tidal currents, shipping, or on the feet of wading birds (as suggested by Hardaker (1942) as the means by which it reached an inland site on the Droitwich Canal (Goodman *et al.*, 1969)). The rate of spread at individual sites has varied greatly but in many areas has involved the rapid spread from transplants or other propagating units to form a continuous sward. This process has acquired a terminology (Hubbard, 1965a), young plants derived from seedlings or plant fragments expanding into more or less circular "tussocks" which fuse to form "clumps", often of irregular outline, with clumps finally coalescing to form a "sward". Caldwell (1957) noted a pattern of concentric rings of different shoot density distribution in expanding tussocks (which she termed "auxoclones"), growing without competition on open mudflats. The rings are produced annually by the peripheral growth of rhizomes but are not detectable in all expanding tussocks.

The formation of swards is not always a rapid or continuous process. Many of the early transplants failed or appeared to be held at the tussock phase. The known reasons for failure include inappropriate site conditions (too unstable, too sandy) and frost, particularly at the northern edge of the species' range; the death of transplants by frost has been recorded from Scotland (J. Bryce, unpublished), the north Netherlands (Kamps, 1962), north Germany (Konig, 1948) and China (Chung, 1990). The very slow spread in some areas may have been due to the introduction of only *S.* × *townsendii* plants, which are both less vigorous vegetatively and unable to spread by seedlings. This is believed to account for the slow expansion of populations in several Australian and New Zealand marshes (Ranwell, 1967).

Even where the fertile amphidiploid has been introduced and has become successfully established, the rate of spread may be remarkably discontinuous. Particularly characteristic of western and northern sites in Britain is a pattern where initial colonization, whether slow or rapid, is followed by a long period of around 20, 30 or even 40 years during which there is little or no expansion in area of the tussocks or swards. This is then followed by a sudden burst of population growth. Gray *et al.*, (1990a) have documented such a pattern in the Conwy estuary in North Wales, where the rapid colonization of a large mudflat in the upper estuary occurred in the early 1970s, adjacent to a sward which had not grown much in area for almost 20 years. Deadman (1984) records a similar rapid expansion between the mid-1960s (the Hubbard and Stebbings (1967) estimate) and 1982 in several other Welsh estuaries to which the plant had been introduced in the 1930s. In Morecambe Bay there has been rapid colonization in recent years of parts of the River Kent estuary, where only isolated clumps were present up to 1982 (R. Scott, pers. comm.; Whiteside, 1984). Further north, in the Cromarty Firth (57.5 °N), the populations at Dingwall Bay, planted in 1932, had not increased much in size by 1955 but were expanding by around 2 m per year (with a maximum of 8 m in 1976) during the 1970s (Smith, 1982). Similarly, at nearby Udale Bay, populations established in 1948 expanded in area from 1358 m^2 in 1970 to 4228 m^2 a decade later (Smith, 1982).

The causes of this pattern are unknown, but evidence from several sites indicates that sudden spread is marked by a successful phase of seedling establishment, lasting only 1 or 2 years, followed by expansion of the more-or-less evenly aged tussocks to eventually form a sward. These events require the coincidence of high seed production and suitable conditions both for seedling establishment and subsequent tussock expansion. It is not clear which of these conditions is most frequently absent in sites where *S. anglica* is failing to spread. Although the species is noted for the unpredictable production, viability and germination of its seeds (Hubbard, 1970; and below), it is equally clear that in some areas changes in the sedimentary regime have preceded the expansion of the population. For example, the tidal flats recently colonized in Morecambe Bay became notably muddier, due to a change in position of the River Kent low-water channel, before they were invaded.

In some areas, colonization of the tidal flats below an existing sward occurs by the successful establishment of plant fragments. This may follow uprooting by storms, as at Bridgwater Bay (Ranwell, 1964a), or by grazing animals, as at Udale Bay (Smith, 1982). Both plant fragments and seedlings may occur as propagating units in the same area (Chater and Jones, 1957; Taylor and Burrows, 1968). Under suitable conditions, seedlings may occur at densities up to 13 000 m^{-2} on bare mud and up to 9750 m^{-2} in the sward, where most die, the sward being maintained by rhizome formation and tillering (Goodman, 1960; Goodman *et al.*, 1969). The factors affecting seedling establishment on bare mud have been studied experimentally by Groenendijk (1986), who demonstrated a critical interaction between mudflat elevation, and hence hydrodynamic stability, and seed burial depth in determining seedling emergence and growth. Seeds buried between 1 and 3 cm had the greatest chance of establishing as seedlings, those nearer the surface being lost through desiccation or sediment movement, and deeper buried seeds deteriorating rapidly in viability. The lower elevational limits of *S. anglica* in Groenendijk's study area (the Oosterschelde in the south west Netherlands) were controlled mainly by wave action uprooting seedlings, supporting Morley's (1973) suggestion that this is a major limiting factor.

Seed production in *S. anglica* is extremely variable, both temporally and spatially. Goodman *et al.*, (1969) recorded 92% seed-set at Lymington in 1954, followed by 18% the next year. Taylor and Burrows (1968) found both seasonal (15%, 38% and 64% in successive years) and tussock to tussock variation in the Dee estuary. Detailed studies of the Ribble estuary marshes have revealed zonal variation in filled spikelet production, Marks and Truscott (1985) recording in 1978 2.3%, 77.1%, 16.9% and 3.7% in successive zones from the pioneer to the upper limit of *S. anglica*. However, less than 5% of the filled spikelets produced seed which germinated. Mullins and Marks (1987) recorded values ranging from 3.1 to 6.8%, from 6.7 to 25.8%, from 2.1 to 4.5% and from 4.0 to 5.7% over three years in the comparable zones of a nearby marsh. Although filled spikelet production in Poole Harbour populations averaged 27% in 1984, no seed germinated, and viable seed production has been exceptionally low in every year since 1983 (Gray *et al.*, 1990b).

It is not surprising that seed does not set in most years since seed production may involve the breakdown of a self-incompatibility system. Raybould (1989) used the petri-dish method of Lundqvist (1961) to examine cross-pollination of *S. anglica* from geographically widely separated populations. In all cases, growth of the pollen was arrested rapidly and the pollen tubes had the typical curled appearance found in a "weak" self-incompatibility reaction (*sensu* Shivanna *et al.*, 1982). Grasses have a two-locus self-incompatibility system, and in polyploid grasses only one allele needs to be matched at each locus in the pollen and stigma for a self-incompatibility reaction to result (Fearon *et al.*, 1984a,b,c). As *S. anglica* is a duodecaploid with a very narrow genetic base, it is extremely unlikely, that there are any cross-compatible genotypes within the species. When seed is produced, it is only in inflorescences which appear relatively early in the year. Inflorescences emerging after August on the Ribble marshes all failed to produce mature filled seed, irrespective of their position on the marsh (Mullins and Marks, 1987; Marks and Mullins, 1984). The delayed development of inflorescences in the higher parts of the marsh was thus a major factor in the much lower proportion of seed produced in this zone. The conditions under which the self-incompatibility system may break down, sporadically producing large numbers of viable seed, are unknown. The occasional production of seed in glasshouse-cultivated plants suggests that higher than average temperatures and humidity may be a factor. High temperatures are known to lead to a breakdown in self-incompatibility in other species, for example *Trifolium repens* (Chen and Gibson, 1973) and *Lilium longiflorum* (Ascher and Peloquin, 1966). Additionally, Stapf (1913) noted that high seed set occurred following a hot, dry summer in 1911.

In summary, the natural spread of *S. anglica* populations characteristically comprises two phases: the initial invasion and establishment of seedlings on open mudflats, and the subsequent radial expansion of tussocks to form clumps and ultimately a sward. Seedling establishment is a rare event in most populations and often follows many years of purely clonal expansion. This may be when mudflat conditions reach a threshhold of sediment type or stability or following a year in which, unusually, there is high seed production (or when both circumstances coincide). In the 1970s and 1980s there appears to have been a sudden expansion of several populations in estuaries in the west and north of Britain to which the plant may have been introduced in the 1930s and 1940s. Of the factors related to tidal submergence which may limit the seaward spread of populations, the tidal uprooting of seedlings is known to be particularly effective.

B. Growth and Production

The annual cycle of growth in *S. anglica* comprises the production in leaf axils in November of overwintering buds which then grow fast and flower in the long days of summer and early autumn, the flowering culms dying as a new generation of buds is formed the following November (Goodman *et al.*, 1969). Rhizomes develop during the winter, in response to short days (Goodman 1960). Flowering extends from July to November and even, in mild winters, into the following year.

Spartina anglica swards occur across a wide range of sediments ranging from clays, fine silts and organic muds to more sandy substrata and even shingle where it is regularly inundated by the tide. They also experience a wide range of sediment accretion rates, generally varying from 3 mm year^{-1} to as much as 8–10 cm year^{-1} (Bird and Ranwell, 1964; Ranwell, 1964a; Lee and Partridge, 1983), but extremely high annual rates recorded for short periods in actively growing swards include 17 cm at Bridgwater Bay, England (Ranwell, 1964a), 20 cm at Sloedam, the Netherlands (Verhoeven, 1951), and 24 cm and 26 cm at Qidong and Rudong, respectively, in China (Chung, 1990).

This range of conditions is reflected in the variation in productivity. Estimates of above-ground standing crop from British marshes include an average of around 825 g m^{-2} (dry weight) on high marshes and a range from 418 g m^{-2} to 1232 g m^{-2} at Bridgwater Bay (Ranwell, 1961, 1964b), an average of 1145 g m^{-2} (Dunn *et al.*, 1981), from the Ribble estuary marshes, and a range of values from 400–500 g m^{-2} for Seafield Bay in Essex (Long *et al.*, 1990). Estimates of above-ground net primary production range from 475–700 g m^{-2} year^{-1} at Seafield Bay to 1600–1850 g m^{-2} year^{-1} in the Ribble (Scott *et al.*, 1990; Scott in Marks and Truscott, 1985). Groenendijk (1984) reported an annual above-ground net primary production of 1162–1649 g m^{-2} in a Dutch salt marsh. All these figures are considerably lower than those reported for *S. alterniflora* marshes in North America (e.g. Turner, 1976) where maximum values of 4 800 g m^{-2} of annual above-ground net productivity may be reached in tall creek-edge stands (Gallagher *et al.*, 1980). In one of very few studies of below-ground biomass in *S. anglica*, Dunn (1981) and Long *et al.*, (1990) have shown that, although there is much year-to-year variation, on average 75% of the biomass was below ground, with rhizomes accounting for around half the below-ground total, and that peak below-ground biomass was reached in the early winter. They also estimated that gross primary production, which takes account of the turnover of shoots, roots and rhizomes between samples, in the Seafield Bay marsh was around 4500 g m^{-2} year^{-1}, some three times the estimate of net production. Perhaps the most interesting aspect of the growth of *S. anglica* is the late annual development and temperature dependence which stem essentially from its utilization of the C_4 photosynthetic pathway. The species is one of a small number of C_4 species in the British flora (eight known, of which at least three are introductions—Long (1983)) and is exceptional among them in being a dominant component of large areas of vegetation (Long *et al.*, 1975). The C_4 species, in which the first product of photosynthetic CO_2 fixation is oxaloacetate, in contrast to phosphoglycerate in C_3 species, mostly occur in tropical and subtropical regions and are rare in cool, temperate climates. The "Kranz" leaf anatomy (numerous chloroplasts in the bundle sheath cells) and low CO_2 compensation point (the ambient concentration of CO_2 at which the net flux of CO_2 at the leaf surface in the light is zero) typically found in C_4 species was reported for *S. anglica* in 1975 (seemingly independently by Long *et al.* (1975) and Mallott *et al.* (1975)). Further work by S. P. Long and his colleagues has established that *S. anglica* shows at least partial adaptation to cooler climates, being able to tolerate, and maintain photosynthesis at, lower air temperatures than nearly all other C_4 species (Dunn *et al.*, 1981; Long and Woolhouse, 1978; Long and Incoll; 1979, Long, 1983; Thomas and Long 1978). Although at optimum temperatures C_4 species exhibit greater nitrogen and water-use efficiency than comparable C_3 species, a factor which may be important in the high tolerance of salinity in *S. anglica* and its relatives, their photosynthetic rates are generally inferior at 16 °C, and at 7–9 °C photosynthetic CO_2 assimilation ceases. In *S. anglica*, however, photosynthetic rates of individual leaves equal those of the C_3 species *P. maritima* at 5 °C and 10 °C and exceed them above 10 °C, reaching to 50% higher at 25 °C. (Similar results have been obtained from one of the other temperate perennial C_4 species, *Cyperus longus* (Jones *et al.*, 1981.))

Despite this partial adaptation, demonstrated in the laboratory in plants grown at temperatures above 12 °C, detailed field studies in south east England have shown that, whilst some leaf growth may occur throughout the year, significant canopy development does not begin until the mean air temperature exceeds 9 °C (Dunn, 1981; Dunn *et al.*, 1981; Long, 1983). This is revealed in the contrast in growth pattern with *P. maritima* shown in Fig. 8. *P. maritima* shows an increase in shoot weight in March, when air temperatures rise above 5 °C, growth peaking in June and July, whereas *S. anglica* does not show an increase until June, when temperatures exceed 9 °C, and peaks in October. Despite this, both species have a similar net primary production, that in *S. anglica* being produced over a shorter and later period (Hussey and Long, 1982). Indeed, Long (1983) concludes that adaptation of *S. anglica*, and other C_4 perennials, to cool climates has been through their ability to grow and reproduce during the relatively short part of the year when average temperatures rise above 9–10 °C, as well as the partial adaptation of CO_2-assimilatory capacity to low temperatures.

This feature of the growth of *S. anglica* may be reflected in the zonal pattern of seed production in more northerly populations, described above, where the later flowering of the high marsh plants was attributed by Mullins and Marks (1987) to the delay of tiller development by depressed spring and early summer soil temperatures in this zone (Marks and Mullins, 1990). Detailed studies of the tiller dynamics of the

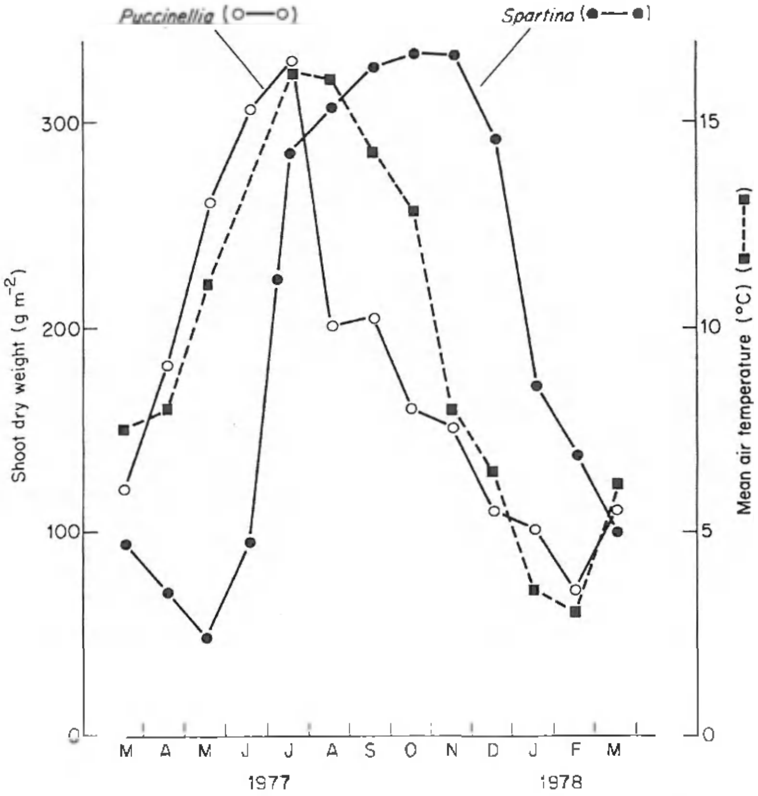

Fig. 8. The dry weights of living shoot material in monotypic stands of *S. anglica* and *P. maritima* in northeast Essex; also shown is mean air temperature. Modified from Long (1983).

Dee estuary population lend support to this idea. Taylor and Burrows (1968) report earlier and more vigorous shoot production in lower marsh populations, as do Hill (1990), Thompson (1989), and Thompson *et al.* (1991a,b), who show that shoot production also continues later in the pioneer zone and that there are clear zonal differences in tiller demography. The more vigorous growth in the pioneer zone is marked by higher tiller production and the greater proportion of tillers which flower within a year. Thompson *et al.* (1991a) also reports markedly later flowering in a population of *S. anglica* in the Cromarty Firth, a similar trend of later flowering in northern populations having been observed for *S. alterniflora* on the east coast of the USA (Somers and Grant, 1981).

The contrast in seasonal growth and production between *S. anglica* and *P. maritima* consequent upon their utilization of different photosynthetic pathways suggests that the outcome of their competitive interaction will be strongly influenced by climate, and particularly spring and early summer temperatures and the length of the growing season. Although confounded by variation in sediment type and grazing, there is evidence that the ability of *P. maritima* to replace *S. anglica* on the northern Dutch marshes of the Waddensea area is related to its relatively early seasonal development, and thus shading of young *S. anglica* shoots (Scholten and Rozema, 1990). In the south Netherlands Delta area, dense monospecific swards of *S. anglica* are currently persisting or, as in southern Britain, are only slowly being invaded by *P. maritima* and other species. The rate at which *S. anglica* is being replaced by *P. maritima* and other species, notably *Aster tripolium* and *Suaeda maritima*, in the north Ribble marshes (Hill, 1987), and the decreasing upper limit to *S. anglica* swards with increasing latitude (described below), are also indicators of climatic effects on the species' growth and competitive ability.

Recently, Long (1990; Long *et al.*, 1990) has examined the intriguing consequences of projected climatic changes, due to the accumulation of so-called greenhouse gases, on the primary productivity of *S. anglica* and *P. maritima* using a simple analytical model. The model, which predicts primary production from light interception and conversion efficiencies, suggests that production in both species will increase, but for different reasons. The C_3 species may be expected to increase primary production principally by increased conversion efficiency in a high CO_2 environment through reduced photorespiratory losses. However, of greatest significance in the C_4 species is the effect of elevated temperatures which would enable it to increase early spring growth (reaching the point where leaf area index is sufficient to intercept 30% of the incoming radiation 50 days earlier with a 3 °C temperature increase), and thus the size and photosynthetic capacity of the canopy. This gives a predicted increase in annual production from $1.3\ \mathrm{kg\,m^{-2}}$ in 1978 to $2.1\ \mathrm{kg\,m^{-2}}$ in 2050 (Long, 1990).

Although produced relatively late and over a short period, the high and uniformly dense biomass presented by *S. anglica* swards has attracted various forms of exploitation. These include cropping for silage (Hubbard and Ranwell, 1966), paper-making (Chung, 1990), and, more recently, as a potential biofuel crop (Scott *et al.*, 1990). Although Bryce (1941) reported no diminution in yield during 3 successive years' cropping of an English south coast marsh. Scott *et al.* (1990), again working on the Ribble marshes, demonstrated a decline in yield from 16 dry tonnes $\mathrm{ha^{-1}\ year^{-1}}$ to 8 tonnes $\mathrm{ha^{-1}\ year^{-1}}$ after 3 years in autumn- and winter-harvested plots. Harvesting plots early in the season resulted in their colonization by *P. maritima*, whilst cuts in January maintained *S. anglica* cover (by increased stem density). The production of a *P. maritima*-dominated salt marsh by repeated summer and early autumn croppings on the Ribble parallels the effects of grazing, there and on other marshes. *Puccinellia maritima* replaces *S. anglica* at a greater rate in marshes grazed by sheep, the rate depending on local site conditions (Ranwell, 1961, 1964b, 1967).

C. The Niche of *Spartina anglica*

The establishment of *S. anglica* swards on mudflats throughout northern Europe has led to the view that the species is phytosociologically in some way out of equilibrium with or is a "disharmonic element" (Beeftink, 1975, p. 431) in its environment, both by blocking the "natural" succession to other communities and exhibiting extensive die-back in the longer established sites (Beeftink, 1975, 1977). As indicated above, however, examples of succession from *S. anglica* swards are fairly widespread and are increasingly being reported from studies of permanent plots (Hill, 1987). The replacement of *S. anglica* by *P. maritima* was reported from the French coast as early as 1926 (Oliver, 1926). Ranwell's (1964b) studies at Bridgwater Bay charted the invasion of swards by (usually taller) species such as *Scirpus maritimus*, *Phragmites australis* and *Elymus pycnanthus* (= *Agropyron pungens*). Under brackish conditions, *S. anglica* may be succeeded by *Juncus maritimus* and *F. rubra* (Packham and Liddle, 1970), and even in the south coast sites where it is dying back in the lower zones, the upper limit of the species may be invaded by *P. maritima* and *Halimione portulacoides* (Gray and Pearson, 1984).

Whether it is in the active sward-building phase or is dying back, *S. anglica* is now found throughout most of its range as a belt of vegetation immediately seaward of the other salt marsh communities. Although individual clumps may be found at higher elevations, particularly in low-lying areas such as creek edges or pans, and may even occur around pools within reclaimed land, the upper limit of the sward is commonly marked by a gradual but often clear transition to other perennial vegetation (Fig. 9). The boundary between *S. anglica* swards and the landward vegetation tends to be more obvious in areas of high tidal range and on more steeply sloping marshes (see, e.g., Plate 1 in Armstrong *et al.*, 1985). The upper limit of *S. anglica* is likely to be determined by its competitive interaction with the species to landward

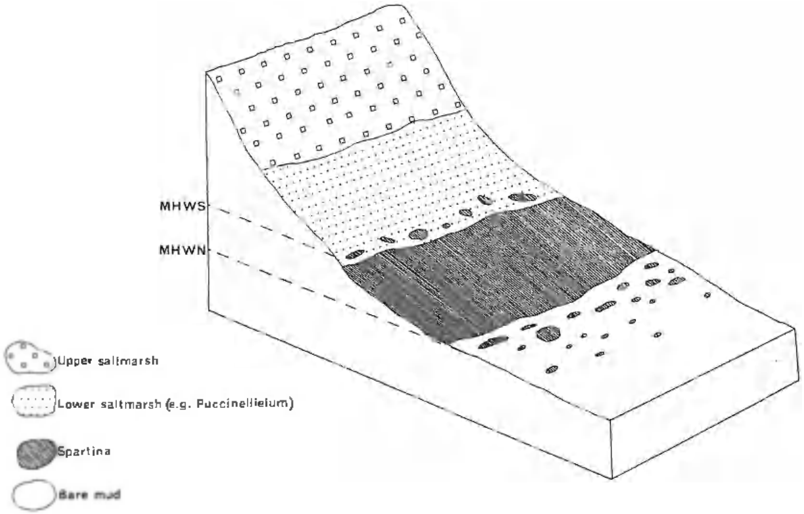

Fig. 9. Diagrammatic representation of the zone typically occupied by *S. anglica* in British salt marshes.

(listed above) under conditions which increasingly favour the competitor over *S. anglica* as mudflat levels rise due to sediment accretion. The factors related, to increasing tidal submergence which appear to determine the lower limit of individual salt marsh species will affect both the outcome of competition between *S. anglica* and the species above it, and also the lower limit of *S. anglica* itself (Gray, 1985a). In some areas, as demonstrated in a classic study of *Salicornia* species by Wiehe (1935), and by Groenendijk (1986) for *S. anglica*, the physical effects of tidal submergence are important in limiting the plant's seaward spread. The effects of frequency and periodicity of tidal submergence are also likely to be important. For example, Armstrong *et al.* (1985) showed that, in the *S. anglica* zone of an English east coast marsh, reducing conditions persisted throughout much of the soil profile and were indifferent to periods of exposure, there being phases of oxidation only near the surface and at neap tide periods. By contrast in the zones above *S. anglica* soil redox potentials were either lowered monthly during the high spring tides or there were longer periods of oxidation.

Such tide-related limiting factors were presumably important in restricting the seaward advance of pioneer species such as *P. maritima*, *Aster tripolium* and *Salicornia* species before the advent of *S. anglica*. The ability of *S. anglica* to colonize the zone below these species (and in some cases to invade upwards into the *Puccinellia* zone) stems from the suite of evolved physiological and physical attributes of the genus conferring salinity- and flooding-tolerance. These include not only the utilization of the C_4 photosynthetic pathway but also the ability to oxidize phytotoxins such as Fe(II) compounds and sulphides (Carlson and Forrest, 1982; van Diggelen, *et al.*, 1986) and the vigour and tolerance of sediment accretion, greater in the allopolyploid than its native progenitor. Together these attributes have enabled *S. anglica* to invade a zone which was formerly unoccupied, at least by perennial vegetation, and could be regarded as a vacant niche (i.e. unexploited space and resources, usually only recognized when it has been occupied—Gray, 1986).

A recent attempt to quantify the niche of *S. anglica* in terms of physical and tide-related variables is described by Gray *et al.* (unpublished). Their data set comprised measurements of the upper and lower limit of *S. anglica* along 107 levelled line transects across salt marshes in 19 estuaries in south and west Britain from Poole Harbour to Morecambe Bay. A close relationship was observed between both the upper and lower limits and the tidal range of the estuary (Fig. 10). Indeed, simple linear regressions of distribution limits against spring tidal range indicated that 88% and 86% of the variation in upper and lower limits, respectively, could be accounted for by variation in tidal range alone. Other variables which significantly improved the ability of multiple regression equations to account for the variation in distribution limits were "fetch in the direction of the transect" (a measure of exposure), "estuary area", "estuarineness" (the position of the transect along the gradient from estuary mouth to upstream tidal limit), and, in the case of upper limits, "latitude". The lower limit (LL) of *S. anglica* (in metres OD Newlyn) was best described by the equation

$$\begin{array}{lllll} LL = & -0.805\ + & 0.366\ (SR)\ + & 0.053\ (F)\ + & 0.135\ (\log_e A) \\ & (0.102) & (0.019) & (0.016) & (0.025) \\ & (R^2 = 93.7,\ S = 0.35)^* & & & \end{array}$$

where SR = spring tidal range (m), F = fetch in the direction of the transect (km) and A = estuary area (km^2). *Spartina* therefore extended further down the shore than would be predicted from tidal range effects alone on those transects with a shorter seaward fetch and in smaller estuaries.

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[*] In the equations above, the standard errors of the regression coefficients are given in brackets below each coefficient—the significance of the particular variable can be tested using Student's t computed as $t = b/SE(b)$ which is distributed as t with $N - 1 - p$ degrees of freedom, where N = the number of transects and p = the number of regressor variables in the equation. S = Residual standard deviation in metres.

The upper limit (UL) of *Spartina* was described by:

$$\begin{array}{ccccccccc} UL = & 4.74 & + & 0.483 & (SR) + & 0.068 & (F) - & 0.099 & (L) \\ & (2.29) & & (0.028) & & (0.020) & & (0.045) & \end{array}$$

$$(R^2 = 90.2,\ S = 0.50)$$

where SR = range and F = fetch, as in the equation above, and L = latitude (in degrees N expressed as a decimal).

The upper limit was similarly affected by fetch but also varied significantly with latitude: the further north the marsh, the lower down the shore relatively speaking was the upper limit of the *Spartina* sward.

Both equations accounted for more than 90% of the variation in the upper or lower limits of the species, a remarkably high proportion for a biological model. The lower limit could also be predicted in relation to its deviation from the Mean High Water Neap tides (MHWN)—tidal range again accounting for most of the variation. In general, *S. anglica* was able to extend below MHWN in estuaries with a spring tidal range of less than 7 m (Fig. 10).

The reasons advanced for the precision with which the vertical limits of *S. anglica* could be predicted were threefold (Gray *et al.*, unpublished). First, tidal range provides a good general estimator of the complex of interacting factors which are likely to be determining the limits of the species distribution, encompassing variation in turbidity and in mechanical factors such as water depth and current speed. Second, such physical factors clearly control *S. anglica* limits, particularly the lower limits, to a degree unusual in natural vegetation. In the absence of biological competitors, the species has extended seawards to the point where tide-related variables limit its further spread (Hubbard, 1969; Morley, 1973; Groenendijk, 1986). Significantly, the upper limit, where *S. anglica* may interact with a number of different species, is likely to be fixed partly by competition, and thus by biological as well as physical factors. These factors are less easy to quantify. Interestingly, the downshore movement of the upper limit which occurs with increasing latitude may reflect overall changes in competitive ability of *S. anglica* under lower temperatures and a shorter growing season. Third, the relatively recent evolution of the species and its apparent genetic uniformity (Raybould *et al.*, 1990b, and above) have precluded extensive population differentiation of the type which enables species such as *P. maritima* and *Aster tripolium* to increase their amplitude in salt marsh habitats (Gray *et al.*, 1979; Gray and Scott, 1980; Gray, 1985a, 1987). It is probable that the realised niche (*sensu* Hutchinson (1957)) of *S. anglica* is changing more rapidly than in these, and other older, species. The die-back of swards in the lower zones of marshes in the south of England and elsewhere, and the changes resulting from competitive interactions at the upper limit throughout its range, are part of this highly dynamic process as the niche of the species evolves.

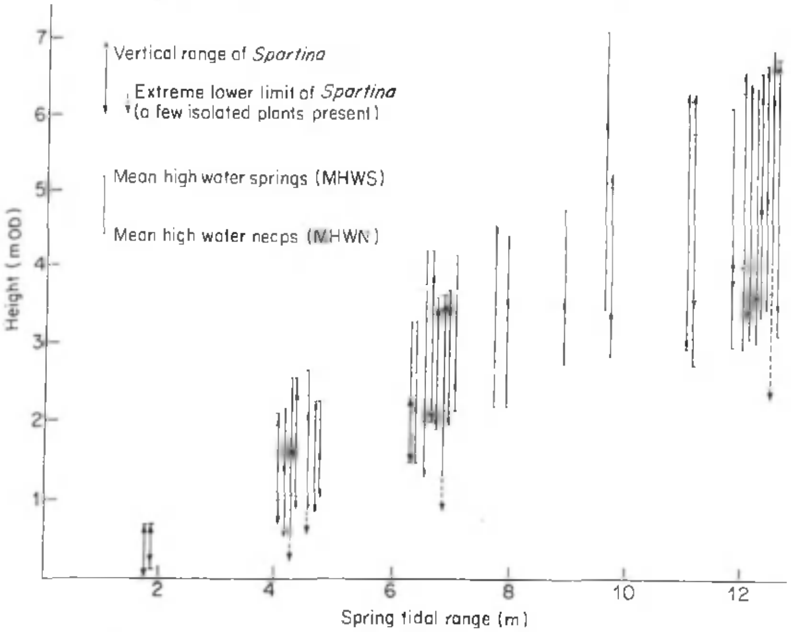

Fig. 10. Vertical range of *S. anglica* marsh and spring tidal range for 32 sites from 20 estuaries. (From left to right: Poole Harbour (two lines, the first from Ranwell *et al.*, 1964), Foryd Bay, Teign, Dovey, Mawddach, Traeth Bach, Tamar, Tavy, Milford Haven (two), Tywi, Taf, Red Wharf Bay, Conwy, Lavan Sands, Loughor, Dee, Ribble, Mersey, Shepperdine, Morecambe Bay, Severn (ten sites)).

D. Interactions with Other Species

1. *Competition with* Puccinellia maritima

As described above, the invasion of established *S. anglica* swards by other vascular plants has been observed throughout the species' range. The major perennial occupant of the lowest salt marsh zones in western Europe prior to the arrival of *S. anglica* was *P. maritima* (Adam, 1981; Dijkema, 1984). In some areas *S. anglica* has invaded former *P. maritima*-dominated vegetation, and is perceived as a threat to salt marsh pasture (Ranwell, 1972), whilst in others *P. maritima* invades and replaces *S. anglica*. The tendency for *P. maritima* to replace *S. anglica* in more northern marshes in Britain is also seen in the Netherlands, where there is a marked contrast between the Waddensea marshes in the north and those of the Delta area in the south west (Beeftink, 1977; Dijkema, 1984; Scholten and Rozema, 1990). The north/south variation in both Britain and the Netherlands is unfortunately largely confounded with variation in soil type and grazing pressure. The northern marshes are generally sandier and more heavily grazed.

Recently, Scholten and Rozema (1990, and Scholten *et al.*, 1987) have examined competition between *S. anglica* and *P. maritima* in the field and laboratory. Removal experiments in the area of the species' overlap on a Waddensea salt marsh indicated that *S. anglica* growth is suppressed by *P. maritima* at the higher levels (showing a significantly higher biomass production when *P. maritima* was removed), and *vice versa* lower down. The interacting effects of soil type (sand *vs* clay), salinity (saline, 400 mM NaCl *vs* brackish, 200 mM NaCl), and soil moisture (dry *vs* waterlogged) were analysed in a competition experiment using a replacement series design (de Wit, 1960) and the effects of nutrients and grazing were investigated by adding KNO_3 and KH_2PO_4 and by clipping. The overall results indicated that *P. maritima* was a better competitor under most conditions, gaining an advantage by early growth that pre-empts space and shades emergent *S. anglica* shoots. The advantage of *P. maritima* increased progressively with time, especially on sand. *Spartina anglica* grew better on clay than on sand, and growth on clay was better under dry conditions, whereas on sand it was better under waterlogged conditions. Saline conditions reduced growth in both species more or less equally, added nutrients had little effect on either monocultures or mixtures, and clipping almost completely suppressed the growth of young *S. anglica* shoots, whereas *P. maritima* was less affected, especially on brackish dry sand (Scholten and Rozema, 1990).

These experiments accord well with field distributions and help to explain how *P. maritima* is able to invade an *S. anglica* sward, particularly under lower spring temperatures and on sandier soils. *S. anglica* also facilitates the establishment of *P. maritima* (and other species) by the protection it provides against uprooting by tidal currents, the increased surface elevation by accretion of silt around the shoots, structural improvement of the upper layers of sediment by litter accumulation, and by radial oxygen loss from the rhizomes (Rozema *et al.*, 1985; Scholten and Rozema, 1990).

2. *The Ergot Fungus* Claviceps purpurea

In recent years, and especially during the past decade, many populations of *S. anglica* become heavily infected with *Claviceps purpurea* (Fr.) Tul., a pyrenomycete fungus which causes ergot disease. The fungus is most visible during the sclerotial phase when the sclerotia, or ergots, may be seen protruding from the inflorescence (Fig. 11). Overwintering on or below the mud surface, the ergots germinate in late spring and, via a primary infection by the sexual ascospores, the fungus can spread rapidly through the summer by means of asexual conidia extruded from infected florets in a sticky honeydew. *Claviceps* displays a certain amount of host specificity (Mantle, 1980), and Loveless (1971) suggested that the strain parasitizing *S. anglica* probably differs sufficiently to be regarded as a distinct taxon. *Spartina anglica* ergots have exceptionally high alkaloid content (0.91%), consisting of the lysergic acid derivatives ergotamine and ergotoxine (Mantle, 1969).

Although reported on *S. alterniflora* in the USA as long ago as 1895 (Eleuterius, 1970), *C. purpurea* does not appear to have been recorded in Europe before 1960, where it occurred at a low level on *S.* × *townsendii* near Dublin (Boyle, 1976b). Several records of light infections in the early 1960s are recorded before the first heavy infections, in Poole Harbour in 1971 and in Ireland in 1975 and 1976 (Boyle, 1976b;

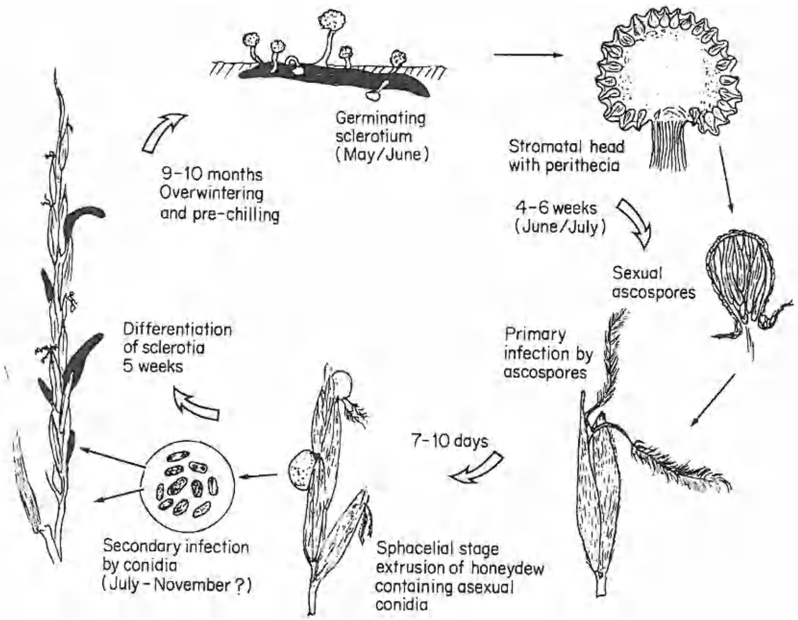

Fig. 11. Life cycle of *C. purpurea* on *S. anglica* (reproduced with permission from Gray *et al.*, 1990b).

Gray *et al.*, 1990b). By the 1980s, heavy infection was apparent in several areas including Poole Harbour, the Dee and the Ribble estuaries. In 20 "populations" (each comprising a 0.5 ha area of *S. anglica* sward) in Poole Harbour, infection rose from a mean of 36.4% of all inflorescences containing at least one ergot (or honeydew) in 1983 to a mean of 85.2% in 1988 (Gray *et al.*, 1990b). More than 90% of all flowering heads were infected in several populations. In the Ribble estuary, infection rose from less than 1% of infected inflorescences in 1981 to as high as 52% in the main sward in 1986, and similar increases were recorded in the Dee between 1986 and 1988 (Thompson in Gray *et al.*, 1990b).

These exceptionally high, even epidemic, levels of disease are relatively rare in natural plant communities (Burdon, 1987; Clarke *et al.*, 1987) and prompt at least two important questions: what are the effects of the pathogenon the host? and why are infection levels so high? The first question is difficult to resolve. Although there is a clear effect on fecundity, in that every ergotized floret reduces potential seed production by one, the extremely low levels of seed-set in most populations and the possible effects on seed production in uninfected florets make measurement of the actual effect on fecundity extremely difficult. An estimate for Poole Harbour populations in 1985 indicated that potential seed production was reduced by 16% on average, but by as much as 47% in some populations, and there were eight ergots for every filled spikelet (Gray *et al.*, 1990b). In addition, there is limited evidence that the demand of the fungus on the host's resources may lead to host damage—a significant negative relationship between mean ergot weight and number of ergots per inflorescence suggesting that developing sclerotia compete for limited nutrients. The extent of the effect is impossible to measure in field populations because it is not possible to recognize individual plants (ramets).

The uncharacteristically heavy infection in *S. anglica* is most obviously related to the fact that the species tends to occur as dense, monospecific swards, and thus resembles an agricultural crop in its vulnerability to epidemics (Burdon and Chilvers, 1982). Furthermore, the apparent genetic uniformity of *S. anglica*, its proliferation mainly by clonal expansion, and its extended period of flowering from July to November make it especially vulnerable to pathogen attack. Speculation as the the future development of the disease must take account of the species' current inability to evolve resistance, of the possible effects of unusual weather conditions which might break the cycle of infection, and of the recently discovered presence of a hyperparasite, the fungus *Fusarium heterosporum*, which is a potential agent of biological control of *Claviceps* (Gray *et al.*, 1990b).

3. *Invertebrates*

The fauna of *S. anglica* marshes has received very little attention, in contrast to that of the *S. alterniflora*-dominated marshes of North America (e.g. Teal, 1962; Daiber, 1982). Payne (1973) noted only four insect species commonly occurring in *S. anglica* swards in Poole Harbour. These were a leafhopper, *Euscelis obsoletus*, a herbivorous grasshopper, *Chorthippus albomarginatus*, an omnivorous grasshopper, *Conocephalus dorsalis*, and a predatory damsel bug, *Dolichonabis lineatus*. The first three appeared to be feeding on *S. anglica*, although *C. dorsalis* fed also on *E. obsoletus*, as did *D. lineatus*. This rather skeletal insect food-chain mirrors, but is less rich than, *S. alterniflora* marshes. Other insects found in Poole Harbour *S. anglica* marshes included three species of shorebug (Saldidae) and several spider species, including *Argiope bruennichi*.

Jackson and his colleagues (Jackson, 1984; Jackson *et al.*, 1985, 1986) also found relatively few species of macroinvertebrates in the *S. anglica* canopy of a marsh at Seafield Bay in East Anglia—13 taxa in all, and only six occurring regularly. Of these, only one, the sap-feeding spittlebug *Philaenus spumarius*, was a significant consumer of live *S. anglica* material, and the consumption of this species was a very small fraction of the plant's annual production. The total annual assimilation by all canopy invertebrates amounted to less than 0.3% of the total annual above-ground net primary production, with *P. spumarius* assimilating 0.4 g of a canopy-species total of $0.5\,\mathrm{g\,cm^{-2}\,year^{-1}}$). As in North American marshes, the assimilation of *Spartina* material was dominated by sediment-associated detritivores (assimilating more than $40\,\mathrm{g\,cm^{-2}\,year^{-1}}$), of which the dominant species was the polychaete worm *Nereis diversicolor*, accounting for more than 85% of all *S. anglica* material assimilated. Although dominated quantitatively by *N. diversicolor*, the invertebrate fauna associated with the sediments in this marsh was surprisingly rich in species, at least in the lower zones, with a total of 15 species of which 12 occurred regularly. Although this is a similar level of diversity to *S. alterniflora* marshes, Jackson *et al.* (1985) suggest that the inequitable density distributions, in which one species dominated, reflects the recent origin of *S. anglica* marshes. Observations elsewhere (Millard and Evans, 1984; S. McGrorty, pers. comm.) indicate that the benthic fauna of advancing or stable *S. anglica* marshes is generally depleted in relation to the nearby tidal flats, and that although epibenthic species may be present in *S. anglica* swards, the Seafield Bay site may not be characteristic.

Interestingly, because it is the only C_4 species present, Jackson's study of the fate of *S. anglica* in the food chain was able to exploit the differences in carbon isotope utilization between C_3 and C_4 species and the tendency for animals to reflect the $^{13}C/^{12}C$ ratio of their food sources (Teeri and Schoeller, 1979). His finding that few of the canopy species utilize *S. anglica* as a major food source may reflect the relative indigestibility of C_4 species as a whole (Caswell and Reed, 1976) or the relatively recent origin of the species. Of the annual net primary production of *S. anglica* at Seafield Bay, between 14% and 20% was assimilated by invertebrates (> 85% of that by *N. diversicolor*), mostly as detritus *in situ*, about 30% was dissipated by micro-organisms and meiofauna, and of the rest around 15–22% is exported away from the site as detritus or live material and is available for incorporation into estuarine food-chains (Jackson, 1984).

4. Spartina anglica *and the Decline of the Dunlin.* Calidris alpina

Whatever its richness and density, the invertebrate fauna of *S. anglica* swards is much less available as food to wading birds (Charadrii) than that of the nearby tidal flats. Indeed, the major threat which *S. anglica* is perceived to pose in European estuaries is its invasion of bird feeding-grounds—either the eelgrass (*Zostera* spp.) and algal (*Enteromorpha* spp.) beds utilized by herbivorous wildfowl such as the Brent goose, *Branta bernicla*, and widgeon, *Anas penelope*, or the invertebrate-rich mudflats used by waders (Doody, 1990; Nairn, 1986; Ranwell and Downing, 1959). Despite this perception, documented evidence of an effect on birds is rare, and the overwintering populations of most species of waders have remained constant or have increased in size since nationwide counts began in the early-1970s (Goss-Custard and Moser, 1988). A notable exception is the dunlin, *Calidris alpina*, the overwintering numbers of which had declined up to 1988 by almost a half since 1973/74 (Salmon and Moser, 1985).

The dunlin was among the species which fed particularly at the tide edge and on the higher parts of the flats in the Dyfi estuary and whose numbers declined during the period of *S. anglica* expansion there in the early and mid-1970s (Davis and Moss, 1984). (The other species were oystercatcher, *Haematopus ostralegus*, ringed plover, *Charadrius hiaticula*, and sanderling, *Calidris alba*.) Millard and Evans (1984) also noted that dunlin, and other flock-feeding species, prefer to feed on open mud and, unlike redshank, *Tringa totanus*, were rarely found among *S. anglica* clumps or in the sward at Lindisfarne in northern England. Goss-Custard and Moser (1988, 1990) compared the different rates of decline of dunlin numbers in different British estuaries to the changes in abundance of *S. anglica* in those estuaries during the period 1971/72 to 1985/86. Numbers had declined at the greatest rate in estuaries where *S. anglica* had expanded most during that period and, with some exception, had hardly changed in those where *S. anglica* populations were static. It is suggested that *S. anglica* both removes feeding areas and reduces feeding time, both of which would increase rates of emigration and mortality. However, as the authors point out, the decline of dunlin and the spread of *S. anglica* may have occurred independently, or may be linked by a third factor such as sedimentary or nutritional changes in the estuaries. The removal of *S. anglica* using herbicides has resulted in the return of waders, including dunlin, to formerly vegetated areas at Lindisfarne (Corkhill, 1984; Evans, 1986), but areas from which the grass had died back along the English south coast are not being exploited. This may be because these sediments are unsuitable for invertebrates to colonize or are covered with mats of algae (Tubbs, 1977).

E. Die-back, Control and Conservation

Although *S. anglica* spread rapidly in the early decades of this century and continues to spread in western and northern estuaries, the degeneration of swards along the south coast of England was noted as early as the mid-1920s. Patchy degeneration was reported from the Beaulieu estuary in 1928 and by the mid-1950s about 60 ha of *S. anglica* marsh had been lost in the Hampshire Basin (Manners, 1975). Die-back began in Poole Harbour in the mid-1920s, where *S. anglica* was first recorded in 1890, had spread to cover more than 775 ha by 1924, but had declined to around 415 ha by 1980 (Gray and Pearson, 1984). Other detailed studies of decline have been made from Langstone Harbour (Haynes and Coulson, 1982) and from Milford Haven in South Wales (Dalby, 1970; Baker, 1976; Baker *et al.*, 1990). Decline in area of *S. anglica* swards has been recorded from many English south and east coast estuaries and from some in south west Britain, from northern France and from the south west Netherlands.

Investigations into die-back, mainly carried out at Southampton University between 1953 and 1965, did not conclusively provide a proximal causative agent but clearly characterized the conditions under which die-back occurs (Goodman, 1960; Goodman and Williams, 1961; Goodman *et al.*, 1959; Sivaneson and Manners, 1972). These include badly drained, usually waterlogged, highly anaerobic soils with a high proportion of fine particles and a high sulphide content. The high organic levels which result from initial *S. anglica* decay may increase the rate of die-back by increasing the water-retaining ability of the muds. Both toxic levels of sulphide (Goodman and Williams, 1961) and anoxia in the rhizomes (Barker, 1963) have been directly implicated in the death of plants in die-back areas.

Whatever the immediate cause of die-back, its interest from a broader perspective comes from the series of physiographical and physical changes which follow the invasion of *S.anglica*, particularly the creation by rapid sediment accretion of a series of badly drained marshes, often with a concave profile. Replacing more gradually sloping mudflats, these marshes remove from circulation extremely large volumes of sediment. Depths of up to 1.8 m of accreted sediment have been recorded below *S. anglica* marshes in Poole Harbour (Hubbard and Stebbings, 1968). Thus, when die-back begins, the sediments (and presumably nutrients) released are likely to have a major impact on the intertidal area to seaward. This is illustrated by the changes in the bed levels of major navigating channels within Poole Harbour between 1849 and 1980, during which period *S. anglica* invaded and subsequently died back (Fig. 12).

Die-back can therefore be viewed as a 'natural' process in which a newly evolved species has dramatically altered the sedimentary and drainage characteristics of the marshes, and created the anaerobic, waterlogged conditions which led to its own destruction. Whether this process will occur on the generally sandier marshes in the west and north, and whether it will be a cyclic process in the south, *S. anglica* reinvading newly accreted mudflats, are extremely interesting questions (the lack of reinvasion thus far may be because mudflat levels are too low or unstable). The answers to them will determine the eventual niche which the species occupies.

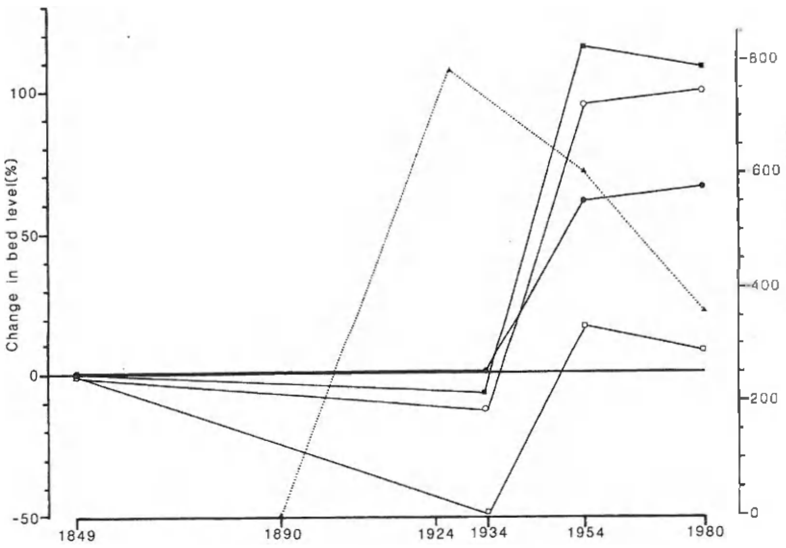

Fig. 12. The percentage change in bed levels of four major channels in Poole Harbour, Dorset, between the Admiralty Surveys of 1849 and those of 1934, 1954 and 1980. (-■- Wytch Lake, -○- Middlebere Lake, -●- Wareham Channel, -□- South Deep). Also shown is the change in area of *S. anglica* marsh (. . .▲. . .). Modified from Gray *et al.*, 1990a.

Whilst extensive die-back occurs in the south (and several local agencies responsible for sea defence contemplate replanting *S. anglica* to protect sea walls), elsewhere the continued spread of the plant has prompted attempts to control it. Of ten control programmes reviewed by Way (1987), four were to prevent encroachment onto amenity-beaches, three were to prevent colonization of bird-feeding areas, two were to preserve the floristic diversity of adjacent salt marsh, and one was to clear a harbour prior to the creation of an amenity beach. Most programmes involved a combination of physical removal (by digging or bulldozing tussocks and clumps) and herbicide spraying, either with a backpack, a tractor-mounted boom, or aerial spraying. The most commonly used herbicide has been glyphosate (Roundup®), and the most frequently recommended has been Dalapon®, a sodium salt of dichloropropionic acid. Way (1987) suggests there is a need to conduct trials using low dosages of more modern herbicides. Only partial success in controlling the plant is reported from most areas, and eradication once it has become established is extremely difficult and costly. However, providing a long-term commitment is made, *S. anglica* can usually be contained by repeated spraying.

Significantly, half of the reasons given above for controlling *S. anglica* relate to aspects of nature conservation. In deciding whether the species was harmful or not to nature conservation interests, Doody (1990) lists its beneficial effects as:

1. preventing coastal erosion and stabilizing mudflats;
2. aiding reclamation for agriculture;
3. its high productivity in the estuarine ecosystem;
4. the creation, via succession, of grazing marsh; and
5. its value for research.

Against this, he balances the harmful effects of

1. invading intertidal flats rich in invertebrates and utilized by overwintering waders and wildfowl;
2. replacing more diverse plant communities;
3. producing dense, monspecific swards which alter succession and

are replaced in ungrazed areas by equally species-poor communities; and

4. promoting agricultural reclamation, and thus the destruction of species-rich, high-level salt marsh.

On balance, Doody concludes that *S. anglica* must be regarded as a threat in estuaries of high wildlife interest, both to bird populations and to 'natural' salt marsh succession.

VII. THE FUTURE OF *SPARTINA ANGLICA*

Human intervention has played a key role in the initial speciation process which created *S. anglica* and in the subsequent success of the species through extensive planting. It is also clear that the intervention of man, both direct and indirect, is likely to have a major effect on the immediate future of *S. anglica* and on its long-term evolutionary survival. Human intervention apart, it is likely that the two main factors that will determine the long-term success of the species are its occupation of a vacant niche which exists on the seaward edge of salt marshes and its high levels of phenotypic plasticity (Thompson, 1989).

It appears likely that the species will continue to expand its total area in Britain and northern Europe to occupy much of the potential salt marsh habitat that is available to it, subject only to the continued loss of salt marsh resulting from estuarine development or rising sea levels. On the basis of current evidence, attempts to limit this spread on a large scale, or even to totally eradicate *S. anglica* by extensive treatment with herbicides, are futile. Once the species is established there appears to be little that can be done to eradicate it totally from an estuary, and the development of a management plan for salt marsh habitats and estuaries which takes account of its presence would appear to be the only economically sensible strategy. The full extent of the possible range that is available for colonization by *S. anglica* remains to be determined. The success of introductions in northern Europe and as far afield as Australia (Ranwell, 1967) and China (Chung, 1990) suggests that the species has the potential to occupy and dominate the equivalent niche on mudflats in estuarine environments throughout the cool temperate regions of the world, subject only to competition from other *Spartina* species and climatic limitations. Though the physiological evidence strongly suggests that there will be a climatically defined limit to its northern expansion through the influence of cool spring temperatures which limit early season growth (Long, 1983), there is as yet no clear information available with which to predict the extent of its southern expansion into warmer climates, although Ranwell (1967) does suggest that winter temperatures may be important.

The rate at which future expansion of *S. anglica* may take place is difficult to predict. Whilst direct human intervention has been the major factor in its long-distance dispersal within the short timescale over which it has existed, there is clear evidence that, once established, the species is able to spread efficiently and occupy an individual estuary (although there may be a significant lag phase from its original colonization to its full occupation of all the available sites). Because of the widespread planting of the species throughout the British Isles, it is not yet apparent how efficient it is at independent dispersal between estuaries through seed or clonal fragments unless the estuaries are adjacent or are linked by intermediate areas of salt marsh. However, it did spread successfully, apparently unaided, more than 150 km eastwards along the coast and more than 100 km across the English Channel from its point of origin in the early part of the century. The efficiency of such "independent dispersal" will be important in determining the rate at which the species can expand to colonize available habitats and will be a major factor in the future spread of the species from introduced sites throughout the world.

In the longer term it appears likely that the process of global warming may have a major effect on the future of *S. anglica*. There are two main consequences of global warming which may have a direct impact. The predicted rise in sea levels will result in the destruction of some coastal habitats through inundation, and although new ones will replace them, a long time may pass before new stable habitats become established (Rowntree, 1990). The second likely consequence of global warming is that *S. anglica* (in common with many other species, e.g. see Grime (1990)) may alter its geographical range and become of increasing importance in north European estuaries as temperatures increase and allow improved early season growth at northern latitudes. The likely timescale of such predicted changes in global temperature and erosion of salt marsh in the face of rising sea level will be important in determining how well *S. anglica* is able to repeatedly recolonize available habitats in the face of such dynamic changes to the environment. The success of *S. anglica* so far is due in part to its great flexibility, its highly plastic phenotype enabling it to tolerate a wide range of substrates and conditions, including high accretion rates. It is at least tempting to speculate that this flexibility may in part be due to the high levels of fixed heterozygosity which exist in such a high polyploid of hybrid origin.

Although such flexibility may account for its short-term success, the evolutionary success of the species on a much longer timescale will depend greatly on its ability to generate genetic variation. Such variations will be required to enable it to evolve adaptively in response to evolutionary pressures from pests and pathogens. Since all the current evidence suggests that the existing levels of variation are extremely low as a direct consequence of the genetic bottleneck that occurred during the speciation process (Raybould *et al.*, 1990b), *S. anglica* is faced with a major evolutionary problem. The conventional processes, such as mutation, which create suitable adaptive variation for a species, occur over a relatively long timescale, though in *S. anglica* there is some potential for the generation of variation by either the breakdown of preferential pairing or by backcrossing with one or other parental species (see above). *S. anglica* is nevertheless faced with the evolutionary risk of surviving through a period of severely reduced genetic resources. The current dominance of *S. anglica* swards by what appears to be a single genotype may be an inherently unstable situation since, like many agricultural crops, it will be vulnerable to epidemics (Burdon and Chilvers 1982). Indeed, it might be argued that the current vigour and dominance of *S. anglica* in salt marsh habitats may in part be the result of the relative absence of a natural complement of adapted herbivore, pest and disease organisms, as has been suggested, for example, to explain the vigour of *Eucalyptus* species in alien habitats (Pryor, 1976).

This temporary escape from enemies may mean that not only the *S. anglica* swards themselves but also the entire salt marsh communities which they protect from erosion, may in the long-term be vulnerable to the evolution and spread of *Spartina* pests or pathogens. The potential danger of such epidemics is well illustrated by the recent dramatic spread of ergot fungus through many UK *S. anglica* swards since the early 1960s (see Section VI above). Apart from its immediate effect, this pathogen may have a direct bearing on the evolutionary future of the species by severely limiting seed-set. The resulting reduction in sexual reproduction, though of comparatively minor significance in the short-term survival of aspecies such as *S. anglica*, which efficiently reproduces itself asexually, may drastically limit the rate at which the species can evolve to combat successfully this and any future pest and disease epidemics.

The future of *S. anglica* will therefore not only provide us with a unique opportunity to study many important ecological processes as the species and its niche develop together, but also will provide us with an important evolutionary laboratory to investigate the initial processes in the success or failure of a new species. The key elements in the second century of this ecological and evolutionary drama are likely to be the role of human intervention, both direct and indirect, and the ability of the species to respond to evolutionary pressures in the face of its current severely limited genetic variability.

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Genetic and Phenotypic Aspects of Life-history Evolution in Animals

R. H. SMITH

I. SUMMARY

Fitness is determined by survival rate and fecundity at different ages. Life-history theory is concerned with how constraints lead to optimal combinations of age-specific survival and fecundity, that is combinations which maximize fitness in a given environment. The optimization approach emphasizes constraints of resource allocation, often described as physiological trade-offs. Experimental examination of trade-offs has

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