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Author(s): John D. Thompson

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The Biology of an Invasive Plant

What makes Spartina anglica so successful?

John D. Thompson

One of the most widespread and locally abundant North American, intertidal, salt-marsh plants is a species of cordgrass, *Spartina alterniflora* Loisel. The species forms dense, monospecific stands that dominate the lower portion of the intertidal zone along the eastern seaboard of North America—from southern Canada to northern Florida and, in the Gulf of Mexico, from Florida to southern Texas (Mobberley 1956). After its accidental introduction (as a result of the transport of seeds in shipping ballast) into Southampton Water on the south coast of England in the early nineteenth century, *S. alterniflora* hybridized with its European cogener, *Spartina maritima* (Curtis) Fernald. The result was the F_1 hybrid *S.* × *townsendii* H. & J. Groves, which, as a result of subsequent chromosome doubling, produced a new species, *Spartina anglica* C. E. Hubbard.

As a result of both natural dispersal and artificial introduction, this species has since spread into many estuarine salt marshes around the coastline of the British Isles. After initial

John D. Thompson is a postdoctoral research scientist at the Centre d'Ecologie Fonctionelle et Evolutive, Centre National de la Recherche Scientifique, F-34033 Montpellier Cedex, France. © 1991 American Institute of Biological Sciences.

Just a century after its origin, S. anglica is a characteristic feature of estuarine salt marshes in Great Britain

colonization of an estuary, the species characteristically becomes a dominant component of the marsh, producing extensive and dense monospecific swards. In contrast, the progenitor species have retained a limited distribution. Why, then, has *S. alterniflora* not colonized salt marshes in Britain to the extent that it has in the United States, although its derivative *S. anglica* has extensively colonized this habitat? This question creates, if not one of the mysteries alluded to by James Michener, an interesting puzzle. What attributes of *S. anglica*, in particular those not held by its parents, have made it so successful? In this article, I outline how the results from a broad spectrum of research together answer this question. I begin with a piece of history.

Just after Darwin—another origin of species

Invasive plant species are those that colonize habitats where they have never previously occurred (Mack 1985). The characteristics of such species that contribute to their successful spread have long fascinated students of natural history. The de-

tailed descriptions and discussions provided in the early works of Elton (1958) and of Baker and Stebbins (1965) ignited the interests of contemporary ecologists.

Fueled by an international recognition of the importance of alien invaders in relation to the ecology, management, and conservation of natural plant communities, much research has tried to characterize the demographic behavior and genetic constitution of invasive species. This search for generalities has shown that invasive species often have certain features that increase their fitness. However, there are enough exceptions so that no suite of characteristics can be said to be representative of invading species (Brown and Marshall 1981, Roy 1990). Furthermore, chance colonization and the occurrence of an open habitat may be primary elements facilitating the spread of an alien species (Gray 1986). Even so, to occupy that open habitat the invader must have advantageous properties not held by the pre-existing species.

An invasive species can be considered successful if it colonizes a wide geographical range, exists over a range of localized environmental conditions, and/or forms a dominant component of the habitat into which it spreads. During the last 100 years, there has been a process of invasion around the coastline of Great Britain that satisfies each of these criteria.

Until the end of the nineteenth century, low-lying intertidal estuarine mudflats around the coast of Great Britain had remained almost devoid

of higher plant life. This habitat had remained uncolonized due to the vicissitudes of a range of environmental factors related to the physical and chemical effects of long periods of tidal inundation. Then, just after Charles Darwin published his treatise on the origin of species, the species of cord grass now known as *Spartina anglica* (Figure 1) originated. This origin of a species ultimately changed the face of intertidal salt marshes in Great Britain and later in several other countries.

S. anglica is a rhizomatous, perennial grass that spreads by extensive clonal growth. Its origin is a classic example of the evolution of a new species by allopolyploidy, a process that does not require geographical isolation of populations and involves two steps. First, hybridization occurs between two diploid species, producing a diploid chromosome set made up of one copy of each chromosome from each of the two parents. As a result of the dissimilarity of the maternal and paternal chromosomes, no chromosome pairing can occur during meiosis, hence chromosomal sterility of the gametes occurs. The second step is a doubling of the chromosome content to produce two copies of each of the original parental chromosomes. The chromosomes now can form bivalent pairs during meiosis and thereby produce viable gametes. The outcome is a polyploid species that has the genetic complements of both parental species and thus the potential for increased vigor.

When *S. alterniflora* ($2n = 62$) was accidentally introduced into Southampton Water, it hybridized with the native *S. maritima* ($2n = 60$) to produce a sterile hybrid ($2n = 62$), which was first recorded in 1872. Later, this sterile hybrid species produced a fertile form ($2n = 120$–124) by chromosome doubling (Marchant 1968a).

For almost 70 years, the sterile and fertile hybrids were not recognized as distinct species and were considered under the aggregate heading of *S. × townsendii sensu lato*. Then, in the 1960s, detailed morphological and cytological invesigations (Marchant 1967, 1968a,b) confirmed that there were two hybrid species, and the fertile form, which was known to con-

Figure 1. A tussock of *Spartina anglica* growing on the exposed tidal mudflats of the Dee Estuary, Cheshire, England.

tain twice as many chromosomes as the parental species, was subsequently named *Spartina anglica*. However, the allopolyploid origin of *S. anglica* was confirmed only recently by a detailed electrophoretic investigation of isozyme variation (Gray et al. 1990), which showed that *S. anglica* contains both the isozyme complements observed in *S. alterniflora* and in *S. maritima*.

Initially, the spread of the hybrid progeny was slow. Then from approximately 1890 onward the rate of spread of cord grass out of Southampton Water and into adjacent estuaries became noticeable (Stapf 1908, 1914). This spread has been interpreted as a result of the appearance at that time (some 20 years after the sterile hybrid *S. × townsendii* was first recorded) of the fertile form, *S. anglica*, which could spread rapidly to new sites by seed dispersal.

However, it is possible that the fertile form arose immediately after the initial hybridization event. The characteristic pattern of *Spartina* colonization involves a single colonization episode lasting one or two years, followed by a period of slow clonal growth as seedlings establish, and then a burst of prolific clonal expansion due to the vegetative spread of

established tussocks (usually in the absence of further seed input to the population). Also, seed set in young, pioneer populations is low, but it often increases as the marsh develops (Marks and Truscott 1985, Thompson 1989). Hence the fertile and sterile forms may have originated at the same time.

No matter what the exact date of appearance was, it was soon realized that the grass was "wonderfully adapted to life on the mudflats" (Stapf 1908, p. 35), and had, on the south coast of England, "gained ground at first slowly and unobtrusively, then it spread all much so indeed, that it altered completely the aspect of the foreshore and the estuarine reaches of the rivers from Chichester Harbour in the East to Poole Harbour in the West" (Stapf 1914, p. 76). As a result of widespread introduction for marsh reclamation purposes and subsequent vigorous clonal growth and natural dispersal to uncolonized sites, *S. anglica* now occupies approximately 10,000 hectares of intertidal salt marsh along the coast of Britain (Charman 1990).

The colonization of individual marshes by *S. anglica* can usually be seen in three stages (Figure 2). Colonization of low-lying, bare tidal mudflats by seedlings or vegetative fragments produces a pioneer population of tussocks which, by rapid radial clonal growth, can cover the surface of a previously bare site within a few years. The sward that results usually contains few other species due to the high density of tillers of *S. anglica*. In upper marsh zones, individual tussocks of *S. anglica* often occur in a mosaic of species characteristic of mature salt marsh. These mature populations may be the result of either sward degeneration or the invasion of creeks and pans (slight depressions in the marsh surface).

S. anglica has thus successfully colonized a vacant niche, established dominant meadowlike populations, and persisted across a broad spectrum of intertidal marsh zones. The attributes of *S. anglica*, which have allowed it to become—just a century after its origin—such a characteristic feature of estuarine salt marshes in Great Britain, provide a fascinating example of the characteristics of a successful invading species.
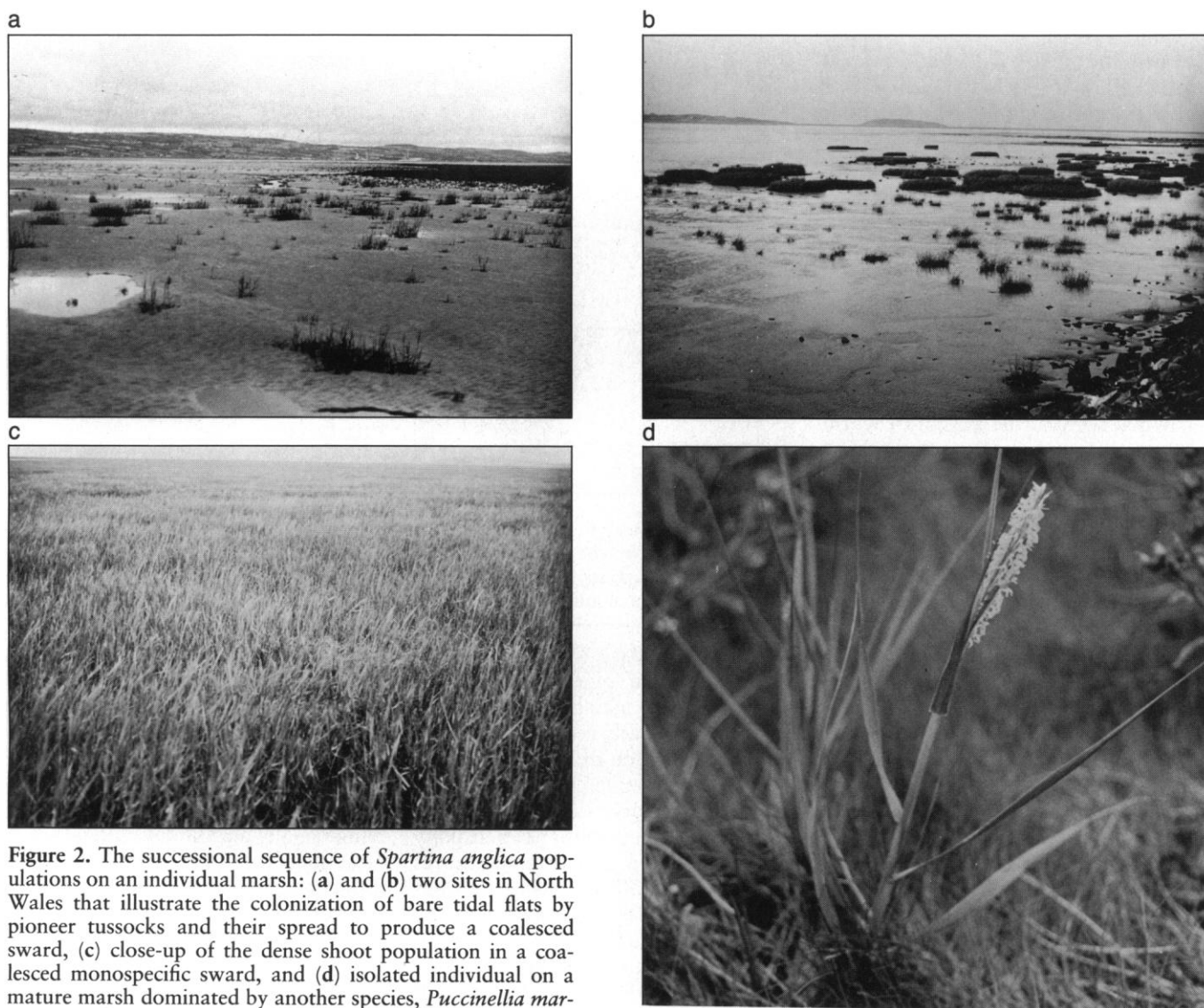
Figure 2. The successional sequence of *Spartina anglica* populations on an individual marsh: (**a**) and (**b**) two sites in North Wales that illustrate the colonization of bare tidal flats by pioneer tussocks and their spread to produce a coalesced sward, (**c**) close-up of the dense shoot population in a coalesced monospecific sward, and (**d**) isolated individual on a mature marsh dominated by another species, *Puccinellia maritima* (Huds.) Parl.

Sediment accretion: the foundation of success

S. anglica is famed for its ability to accrete large volumes of tidal sediment (Ranwell 1972). Its stout stems and fleshy leaves slow down the ebb and flow of tidal water and trap the sediment it carries, mostly in the axes of the leaves where they sheath the stem. As the aerial parts senesce, this sediment is deposited around the base of the plant and is bound together by the extensive rhizome network. In this way, a rise and consolidation of the marsh surface can occur at remarkably rapid rates, to a far greater extent than that achieved by other species or on unvegetated marsh.

On the upper and middle zones of vegetated marshland on the north-west coast of Europe, accretion rates normally range from 0.2 to 2.0 cm per year (Ranwell 1972). In the presence of an expanding colony of *S. anglica* in the Bristol Channel, where the waters are rich in silt and the tidal range (approximately 12 m) is near maximal for northwest Europe, Ranwell (1964a) reported a rate of accretion of 8–10 cm per year. Studies at two sites in Poole Harbour on the south coast of England have reported 70 cm accretion after 60 years of *S. anglica* colonization at Arne Bay (Bird and Ranwell 1964) and 100 cm of accumulated sediment in a 50-year-old marsh at Keysworth (Ranwell 1964a).

This accretion and binding of tidal sediment is greatly enhanced by the high tensile strength of the under-ground parts of this species, which also makes *S. anglica* more effective in reducing lateral cliff erosion than other salt-marsh species native to northwest Europe (Van Eerdt 1985). Furthermore, such newly accreted tidal sediment is often rich in essential macronutrients (Ranwell 1964b), hence rapid accretion will greatly enhance fertility and further stimulate colonization of the marsh surface. The species is therefore valuable for reclamation of intertidal mudflats for commercial development and foreshore protection.

The rapid clonal growth of *S. anglica* due to vigorous vegetative propagation is well known. For example, a study by Chater and Jones (1957) showed that rates of radial clonal growth can exceed 30 cm per year on

organic muds in the Dovey Estuary, causing the area covered to increase from 3.5% to 90% in two years. This rapid growth facilitates the domination of estuarine sites soon after the initial colonization or introduction (e.g., in Poole Harbour domination by *S. anglica* was completed just 25 years after the species was first recorded there; Hubbard 1965).

This rapid clonal spread is directly related to the species' rhizomatous habit (Figure 3). The rhizomes develop during winter (Goodman 1960) while the aboveground parts are not growing, so with the advent of warm spring temperatures, massive shoot production can begin. The dissemination and sprouting of rhizome fragments has also greatly enhanced the ability of *S. anglica* to establish in new sites, for example at Bridgewater Bay (Ranwell 1964b).

The ability to accrete tidal sediment and spread extensively by vegetative growth has prompted the deliberate introduction of *S. anglica* to many estuarine sites to reclaim bare marshes for commercial purposes and to protect foreshores from tidal erosion. These introductions have served to disseminate the species to regions where it might not have naturally spread. However, once introduced to a given area, it has frequently colonized additional estuaries by natural dispersal.

Photosynthesis—a C_4 species in a C_3 climate

S. anglica has a physiology consistent with it being a C_4 plant. In common with other C_4 species, the first products of its photosynthetic carbon metabolism are four-carbon compounds (Thomas and Long 1978). *S. anglica* has a low photosynthetic carbon-dioxide compensation point (i.e., the carbon-dioxide concentration in the air at which its net flux at the leaf surface in the light is zero) and a Kranz type of leaf anatomy (i.e., starch is only accumulated in chloroplasts found in the bundle sheath cells of the leaves). The chloroplasts in the bundle sheath cells also have twice the cross-sectional area and grana with fewer thylakoid stacks than those in C_3 species (Long et al. 1975). Furthermore, *S. anglica* has a low photorespiratory rate (Long and

Figure 3. A pioneer tussock of *Spartina anglica* that shows the plagiotropic rhizomes, which enable clones to spread rapidly across uncolonized mudflats.

Woolhouse 1978).

The presence of the four-carbon photosynthetic metabolism in *S. anglica* is particularly intriguing. C_4 species include some of the most vigorous and productive grasses, but their high productivity, due to enhanced rates of photosynthesis, can usually only be attained at leaf temperatures at and above 30° C. Hence any advantage gained by having this form of metabolism usually accrues only to species inhabiting climates warmer than those of the British coastal salt marshes. Indeed, the cooler conditions in temperate regions usually prevent their colonization by C_4 species.

The success of *S. anglica* is similar to other C_4 species in North America (Teeri and Stowe 1976). However, the only other C_4 species that have colonized habitats in the cool temperate climate of northwest Europe do not form dominant components of the communities they inhabit (Long 1983, Long et al. 1975). In a cool climate, could this reliance on the four-carbon photosynthetic pathway have contributed to its success?

S. anglica, like other C_4 species, above 10° C shows a rate of photosynthesis much greater than C_3 species and at or below 10° C shows a much lower rate than C_3 species (Dunn et al. 1987). However, these authors also found that a crucial feature of the metabolism of *S. anglica* is

its ability to maintain rates of photosynthesis, at 5–10° C, equivalent to those of a C_3 grass, *Lolium perenne* L., a feature not held by other C_4 species found in northwest Europe (e.g., see Long et al. 1983). Thus *S. anglica* does not appear to have been influenced by the constraints that have limited other C_4 species to climates in lower latitudes, and the benefits of its C_4 metabolism have no doubt been a considerable plus for its consequent success.

Tolerance—one of the hardy few

The rapid spread of *S. anglica* ultimately results from its ability to colonize low-lying estuarine mudflats below the level of other halophytes. Ranwell et al. (1964) reported a tolerance of tidal inundation of up to six hours duration during periods of active growth and up to nine hours at other times. Their data were collected for a natural population growing in silt-laden water. In other regions where the silt content of tidal water is less, such as in the Waihopai estuary in New Zealand (Hubbard and Partridge 1981) and under cultivation in clear seawater (Hubbard 1969), even longer periods of submergence are tolerated.

Such long periods of tidal inundation require a physiological and morphological adjustment to extremely high external concentrations of sodium and chloride ions. These ions will tend to enter the plant, causing a severe imbalance in the osmotic potential of the cytoplasm.

In *S. anglica*, these problems are overcome in several ways. First, the plant increases the outflow of ions that would become toxic if allowed to accumulate in the cytoplasm. This process is primarily carried out by two-celled salt glands (hydathodes) on both leaf surfaces. The glands actively secrete aqueous salt solutions when the plant is grown on saline substrates (Rozema et al. 1982, Skelding and Winterbotham 1939, Sutherland and Eastwood 1916). Second, the plant restricts the entry of excess quantities of toxic ions into the roots (Rozema et al. 1985a). Third, *S. anglica* accumulates concentrated solutions of proline and glycinebetaine (Storey and Wyn Jones 1978, Wyn

Jones and Storey 1978). These compounds are thought to be compatible solutes for the salt ions eliminated from the cytoplasm, and thus they help regulate the ionic balance and hence the osmotic potential of the cytoplasm and intercellular spaces. Fourth, root tissue contains a well-developed aerenchyma, which facilitates physiological performance under anaerobic conditions (Rozema et al. 1988) and diffuses gaseous oxygen, which can oxidize the harmful quantities of salt in the substrate (Rozema et al. 1985b). Finally, a spin-off from the possession of the C_4 photosynthetic pathway is the presence of a high water-use efficiency (the ratio of carbon dioxide assimilated to water transpired). This efficiency may be advantageous in conditions of high salinity; a tolerance of high salinity is a common feature of C_4 species.

C_4 species have a strong requirement for sodium, which may enhance the in vivo activity of the enzyme catalyzing the primary carboxylating stage of the four-carbon photosynthetic pathway (Schomer-Ilan and Waisel 1973). Thus sodium exclusion requires a delicate balance with the sodium requirement of the cell. Furthermore, it is necessary to ameliorate the ionic imbalance due to the accumulation of iron, manganese, and sulfide ions caused by periodic inundation with tidal water. Roots of *S. anglica* oxidize what would become toxic levels of these ions. This oxidation occurs both internally, for example the detoxification of excess sulfide ions to the sulfur dipole dimethylsulfonioproprionate (Larher et al. 1977, Stewart et al. 1979), and externally by the outward diffusion of oxygen into the interstitial solution (Rozema et al. 1985b).

But what caused the spread and greater vigor of *S. anglica* in relation to its progenitors? In the British Isles, low-lying intertidal mudflats were also open for other halophytic species, including the two parents, to colonize. *S. alterniflora* is also a C_4 grass that is physiologically adapted to the salt-marsh habitat (Smart 1982), but it has not spread in Europe. It is thus pertinent to consider whether factors intrinsic and unique to *S. anglica*, not shared by its cogeners, may have played an influential part in the success story.
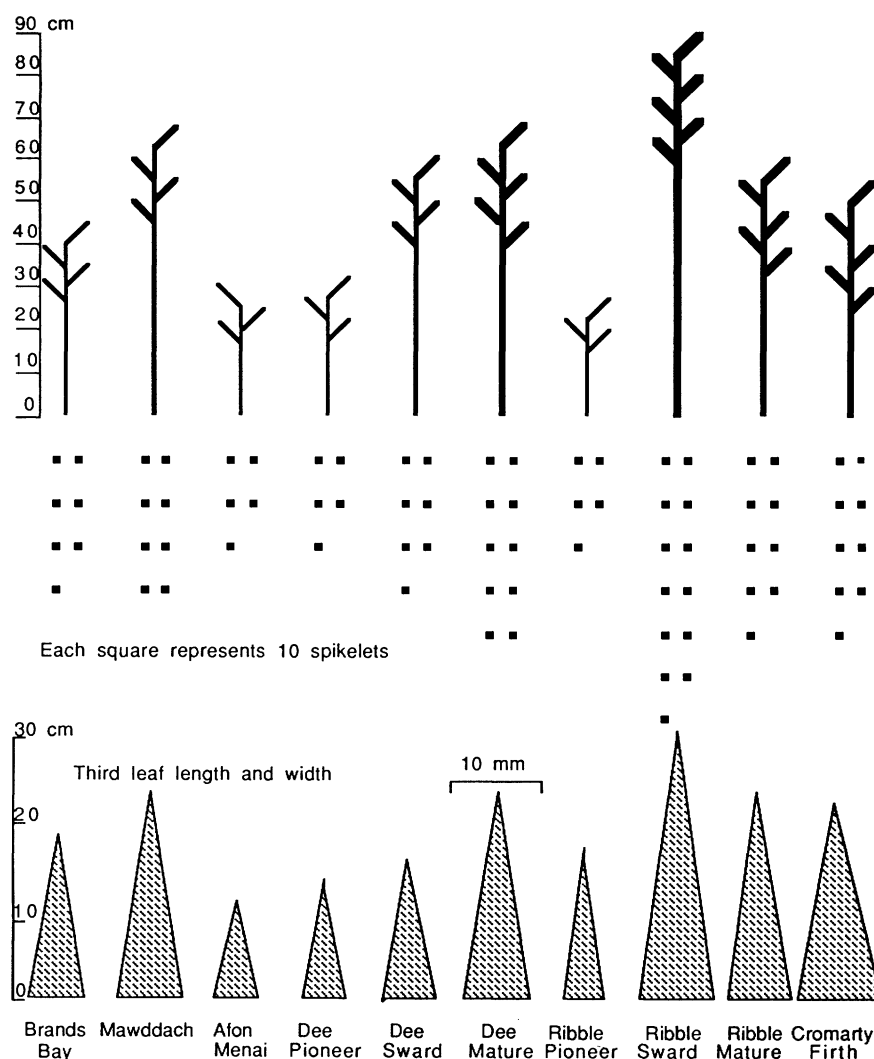

Figure 4. Diagrammatic representation of the morphological variation observed among ten natural populations of *Spartina anglica*. The figure portrays the mean value, for each of ten named populations, of culm height, the number of spikes and spikelets, culm diameter, and third-leaf length and width. (Reprinted from Thompson 1990.)

Karyotype—is big beautiful?

The origin of new species by the process of polyploidy is one of the most widespread processes of plant species evolution. The most common, naturally occurring form of polyploidy is allopolyploidy—hybridization and subsequent chromosome doubling (Stebbins 1950). Most known allopolyploids have prehistoric origins, and they have thus had the chance to undergo considerable change since their origin. The parents will also have evolved further, or become extinct, hence the exact ancestry of many allopolyploids is difficult to ascertain. In contrast, the origin of *S. anglica* has occurred under human observation, the approximate time and place of the original hybridization are known, and the parents are extant. The parents may not last long, however, because *S. alterniflora* never spread naturally out of Southampton Water, where a single population remains, and *S. maritima* has undergone considerable range contraction in this century.

Two lines of evidence suggest that allopolyploids have greater vigor and selective advantage in relation to their diploid progenitors. First, an advantage is due to the genetic diversity that results from the presence of two genomes inherited from different parent species (Stebbins 1950, 1971). This diversity provides the basis for novel physiological properties not held by the parents, which may in turn facili-

tate colonization and persistence in new habitats (De Wet 1971). Second, there is the combination of the advantage of hybridity with a "balancing" of the excessive segregation in the hybrid genome due to chromosome doubling, the so-called "balanced hybridity" (Tal 1980). The process of allopolyploidy thus involves the generation and maintainance of new and favorable gene combinations, particularly those in which adaptive fitness is increased by heterozygosity (the presence of different forms of each gene in an individual) and by epistasis (interaction between genes; Stebbins 1950).

Polyploid evolution also occurs as an increased chromosome number due to autopolyploidy (i.e., the production of a tetraploid from a cross between two plants of the same species). The increased chromosome number that this engenders may itself be responsible for a range of advantageous traits (Levin 1983), which may facilitate the ecological differentiation and relative success of the tetraploid derivatives (Lumaret 1988). Nevertheless, it is the combination of two complete genomes that seems most beneficial in the relative success of polyploid species (De Wet 1971).

Recently, studies have been undertaken to examine how the ecological success of S. anglica may have been promoted by a genetic differentiation of populations in different sites and/or the capacity of individual plants to respond to environmental variation (i.e., show phenotypic plasticity). These studies have led to a particularly intriguing issue.

A characteristic feature of natural populations of S. anglica is the greater morphological stature and seed production of plants sampled from successionally mature (high marsh) populations compared with those in pioneer (low marsh) populations in a single estuary (e.g., Marks and Truscott 1985). Furthermore, a study of morphological variation in ten populations sampled over the full latitudinal range of the species in the British Isles (Thompson 1990) has shown that pioneer populations sampled from different estuarine sites are morphologically more similar than those in adjacent zones at a different successional stage in the same estuary.

For example, consider the morphological variation between populations in the successional sequences observed on the Dee and Ribble estuaries, from pioneer through sward to mature populations (Figure 4). Also note a third pioneer population (Afon Menai in Figure 4), which was consistent with the pioneer populations in the Dee and Ribble estuaries.

Clonal material was collected from the plants measured in these ten populations and grown for two years under uniform conditions in an experimental garden (Thompson et al. 1991a). The greater stature of plants in successionally mature populations was not maintained under uniform conditions (Figure 5), and it is thus not a result of genetic differentiation of the populations. What is more, electrophoretic investigations of ma-

terial from the same ten populations have shown that for a range of enzyme systems there is practically no electrophoretically detectable protein variation (Raybould 1989).

The marked plasticity of individual plants was further observed in replicated clonal material reciprocally transplanted among three sites of an individual estuary (Thompson et al. 1991b) and over a range of controlled conditions (Thompson et al. 1991c). Together, these results indicate that the level of allelic genetic variation in this species is low and that a major factor influencing the spread of this species across different zones of the salt-marsh habitat may be the capacity of individual plants to respond to environmental variation.

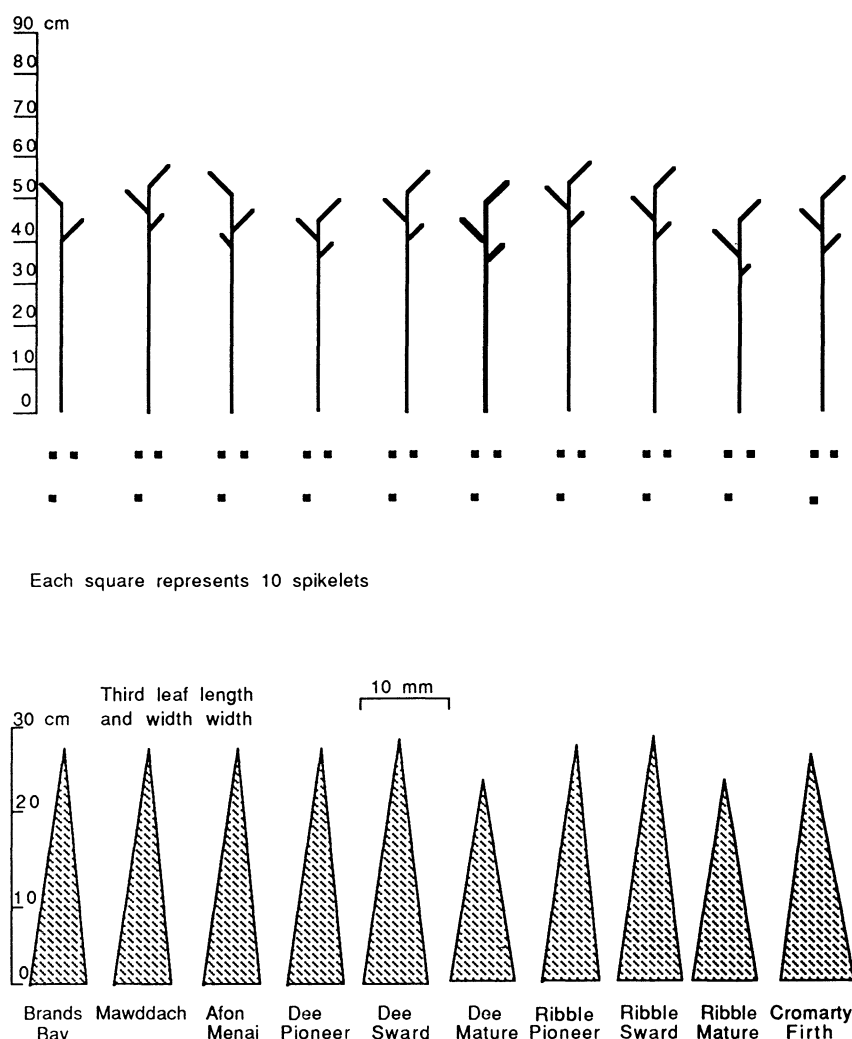Although most of the morphological variation between natural popula-

Figure 5. Diagrammatic representation of the morphological variation observed among ten populations of *Spartina anglica* grown under uniform coditions. The diagram is based on the data of Thompson et al. (1991a). For explanation see Figure 4 caption.

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tions is due to phenotypic plasticity, there does appear to be some genetically based variation. Within some populations, there is variation in the overall stature of clones that is not related to successional habitat variation. This variation can be observed in plants that have tall slender culms and long narrow leaves, that is a graceful stature, which resembles the sterile hybrid *S.* × *townsendii*. This variation has been observed in the field (Thompson 1990), under uniform conditions in an experimental garden (Thompson et al. 1991a), and over a range of experimental conditions (Thompson et al. 1991c). In each of these three studies, the observed variation was quantified statistically by pairwise character-correlation analysis and multivariate analysis. Whereas in most comparisons a significant positive correlation was found between characters, the width of culms and leaves was not correlated with their length. Hence some plants were observed to have long but narrow stems and leaves.

The low levels of genetically based variation suggest that the original hybridization may have occurred only a small number of times, perhaps only once. Furthermore, crossing-over between paired chromosomes at meiosis will tend to interchange identical chromosome segments. So progeny will tend to breed true, giving rise to a fixed heterozygosity, which does not produce new adaptive gene combinations. The increased genetic diversity of individual alloploid clones may, however, have conveyed a plasticity and tolerance of environmental variation that may have significantly influenced the spread and persistence of *S. anglica* in the face of the environmental variation that accompanies successional development in the marsh.

Another change worth watching

Although vegetative propagation may have been a primary means by which *S. anglica* colonized the open habitat that other species could not colonize, this type of reproduction may represent an Achilles' heel for long-term persistence. If genetic variation is low, *S. anglica* may yet succumb, like other monocultures, to parasite or pathogen infestation.
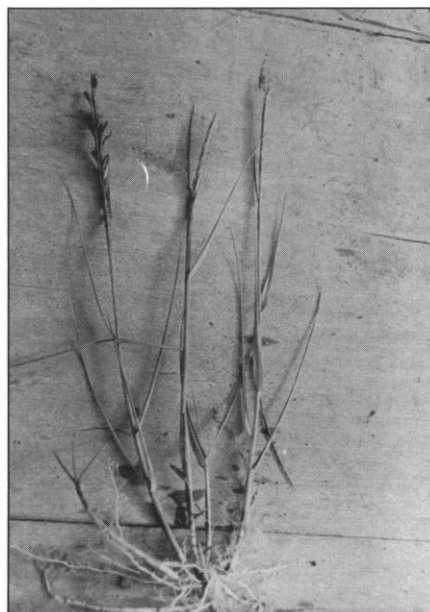

Figure 6. The occurrence of ergot infestation which, as shown here, may infect all the seed set by a plant. Spikelets without ergot on this plant also had no seed.

The last few years have seen a significant rise in the infection of fertile *S. anglica* inflorescences with the ergot fungus, *Claviceps purpurea* (Fr.) Tulasne (e.g., Thompson 1989). This fungus can effectively prevent viable seed set by infecting all the embryos in an inflorescence (Figure 6), and thereby the fungus poses a problem for future dispersal and recolonization of sites made bare by tidal erosion.

Ergot infection is not the only problem. A frequently observed feature of populations of *S. anglica* on the south coast of England is die-back (Figure 7), a reduced vigor and death of large areas of successionally mature populations due to a soft-rotting of the rhizome. The anaerobiosis and toxicity effects induced by prolonged waterlogging appear to be major influences (Goodman 1960, Goodman and Williams 1961, Goodman et al. 1959), but a definitive cause remains unknown.

Factors intrinsic to the plants themselves may also be involved, because die-back sites have been observed to be recolonized. Furthermore, mature populations consistently lack the vigor shown by successionally younger populations when vegetative fragments are transplanted to a uniform pot environment (Thompson et al. 1991a) or reciprocally transplanted among natural sites (Thompson et al. 1991b). Hence it is possible that age-related effects (some clones in mature marshes may be more than 60 years old) may be involved in the die-back of successionally mature populations—physiological senescence and/or an accumulation of deleterious somatic mutations and harmful viruses, both of which would be transmitted to all vegetatively produced tillers. Die-back also afflicts natural populations of *S. alterniflora* in the United States (Mendelssohn and McKee 1988).

Figure 7. Die-back in a previously vigorous sward of *Spartina anglica*.

Although the long-term persistence and success of *S. anglica* may not be without certain difficulties, the species is still vigorously colonizing extensive areas of tidal flats and is reinvading areas made bare by tidal activity on the northwest coasts of England and Wales. Stapf (1908, p. 35) commented that the effects of *Spartina* colonization on the salt-marsh habitat would be "a change worth watching and studying." The spread of ergot infection and the low level of genetic variation documented by recent research continue to make the success story worth watching and studying.

There are many striking examples of the rapid spread of invasive species; in some cases, a peak in luxuriance is followed by a marked decline. For example, the massive vegetative spread of what is thought to have been a single clone of *Elodea canadensis* in inland waterways in the British Isles, to the extent that it blocked ditches and rivers, was followed by a reduction such that the plant ceased to be a serious threat (Gilmour and Walters 1973). It is thus still possible that the rise of the *Spartina* empire may yet be followed by a decline and fall reminiscent of other famous empires.

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