The decline of *Spartina alterniflora* (Poaceae) in the British Isles

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ABSTRACT

Spartina alterniflora was introduced from the U.S.A. in the 1820s. It is one of the parents of the fertile amphidiploid *Spartina anglica* and is an important resource for the study of polyploid speciation. Throughout the 20th century the distribution of *S. alterniflora* has declined and it is currently found at only one site, in Southampton Water. This study compares present and past distributions and discusses reasons for its decline, both throughout the harbour and at the one remaining site. Industrial and marine developments have resulted in loss of habitat as well as causing changes in tidal action, sediment deposition and increased pollution. These have all contributed to the decline of *Spartina alterniflora*. Competition with *Spartina anglica* has also played a role.

KEYWORDS: decline, distribution, polyploid speciation *Spartina anglica*.

INTRODUCTION

Spartina alterniflora Lois. is a perennial grass native to saltmarshes of the eastern seaboard of North America. Around 1820 it was unintentionally introduced to mudflats on the River Itchen, Hampshire (the earliest confirmed record of *S. alterniflora* is a herbarium specimen collected by Borrer from the Itchen in 1829), from where it spread throughout Southampton Water (Marchant 1967). In some areas, *S. alterniflora* grew beside *S. maritima* (Curtis) Fernald, a plant of Old World saltmarshes, which is now extinct in Southampton Water (Gray *et al.* 1999). Fertilisation of *S. alterniflora* by *S. maritima* pollen (Ferris *et al.* 1997) produced a sterile hybrid now named *Spartina* × *townsendii* Groves & J. Groves. The first record of this plant is from Hythe in 1870 (Groves & Groves 1880). Chromosome doubling in *S.* × *townsendii* formed *Spartina anglica* (Marchant 1968; Raybould *et al.* 1991a), a fertile amphidiploid species.

Spartina anglica spread naturally along the south coast of England, the Isle of Wight and the north coast of France by seed and by rhizome fragments (Oliver 1925). It was also introduced into many saltmarshes in Britain and overseas for coastal defence and land reclamation (Ranwell 1967). Its rapid spread, and in the south of England a rapid decline, raised concerns about changes to shipping channels and effects on populations of wading birds and other species occupying intertidal mudflats (Gray *et al.* 1991; Raybould 1998).

In addition to economic and nature conservation relevance, *S. anglica* has immense scientific importance. Because the species formed so recently, and because both its parental species are extant, it provides a superb opportunity to study the ecological and genetic consequences of polyploid speciation, a key process driving plant evolution. However, throughout the 20th century *S. alterniflora* has declined in Southampton Water. It is extinct in the River Itchen and River Hamble, and since the early 1960s the only remaining population of *Spartina alterniflora* in the British Isles has been at Bury Marsh, Marchwood, Southampton Water. The map in Fig. 1 shows the location of the River Hamble, River Itchen and the Marchwood site. This population is the last remnant of the *S. alterniflora* material involved in the origin of *S. anglica* and is therefore a unique resource to evolutionary biologists.

THE HISTORY OF *SPARTINA ALTERNIFLORA* IN THE BRITISH ISLES

Marchant (1967) gives a detailed account of the spread of *S. alterniflora*. At the height of its distribution, *S. alterniflora* grew as a more-or-less continuous sward on the east shore of the Itchen. There were also two smaller patches on the west shore of the Itchen. In Southampton

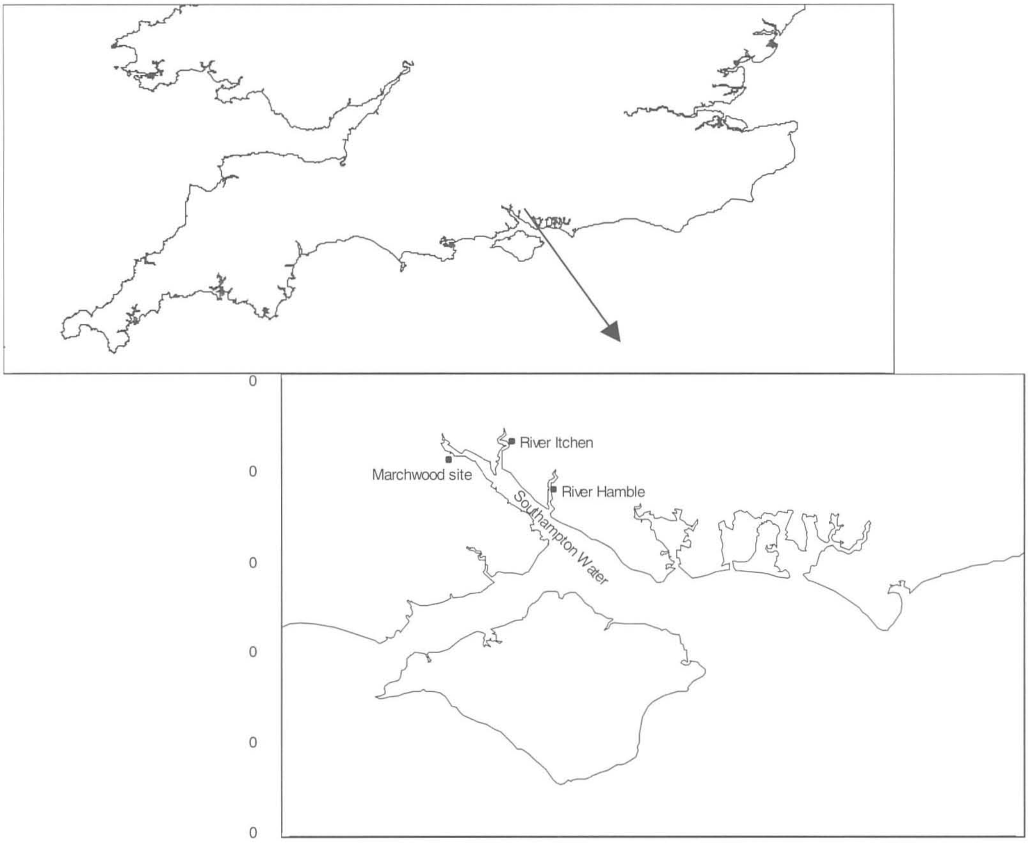


FIGURE 1. Map of southern Britain with inset of Southampton water showing the locations of the River Itchen, R. Hamble and the last remaining site for *Spartina alterniflora;* Bury Farm, Marchwood.

Water/River Test upstream of the Itchen, *S. alterniflora* occurred as several discontinuous swards from Hythe Marina to Cracknore Hard, and as a large sward on the Bury Farm marshes as far upstream as Eling Churchyard. The species also occurred on the eastern shore of the Test from Redbridge to Millbrook. Downstream of the Itchen, *S. alterniflora* grew at Hythe in a large patch about half a mile south of the pier. *S. alterniflora* was also common in the Hamble at Burlesdon, Lincegrove, Hamble-le-Rice and Warsash and occurred as far downstream as Hillhead at the mouth of the Meon.

It is likely that *S. alterniflora* spread through Southampton Water by vegetative reproduction only. Bromfield (1836) commented that *S. alterniflora* in the Itchen "seldom perfects its fruit" and Marchant (1968) states that "British" *S. alterniflora* always "fails to set seed". This is also the case in New Zealand (Partridge 1987). This may be due to low pollen fertility (Marchant 1968). It is possible that the introduced *S. alterniflora* is a single clone (Raybould *et al.* 1991b) and because some clones of *S. alterniflora* are self-incompatible (Daehler 1998) even if viable pollen is produced, self-incompatibility may prevent any seed set in "British" *S. alterniflora.*

Recession of *S. alterniflora* began around 1920 (Marchant & Goodman 1969) and by the 1930s it was extinct in the Hamble and at Hythe. By 1924, the populations at Eling and Redbridge to Millbrook were extinct. A small population at Dibden was destroyed by reclamation in 1963; this left the Bury Farm marshes at Marchwood as the final site for the *S. alterniflora* material involved in the evolution of *S. anglica.*

The main objectives of this work were to map the current distribution of *S. alterniflora* on the Bury Farm marshes and to survey areas in Southampton Water and the Rivers Test, Itchen and Hamble where *S. alterniflora* once occurred to assess why the populations had declined.

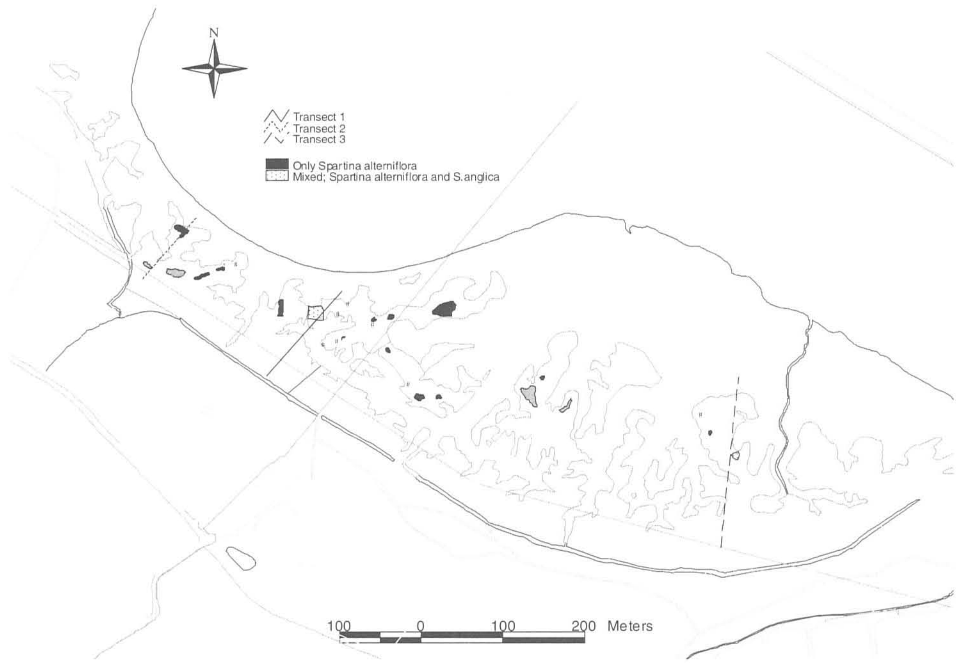


FIGURE 2: The distribution of *Spartina alterniflora* at Marchwood, Bury marsh, Southampton Water.

MATERIALS AND METHODS

BURY MARSH: MAPPING *SPARTINA ALTERNIFLORA*

Patches of *Spartina alterniflora* were identified from the morphological characters in Marchant (1964) and Hubbard (1984). Each patch was mapped using a Magellan promark X hand held GPS unit, taking measurements of dimensions and recording associated vegetation. The data were imported to ARCVIEW to create a digital map of the marsh. This survey was carried out in October/November 1999.

BURY MARSH: PHYSICAL NICHE AND ASSOCIATED VEGETATION

The topography of the marsh was surveyed in October/November 1999 using a Pentax Total Station electronic theodolyte. Transects were set up across the marsh (Fig. 2). Transect 1 was placed in the middle of the marsh and passed through several patches of *Spartina alterniflora*. Transect 2 was established to the western side of the marsh and crossed a particularly low-lying patch of *S. alterniflora* which lies at the back of the marsh near to an equally low-lying patch of *S. anglica*. Transect 3 was placed to the eastern side of the marsh where there is far less *S. alterniflora* present.

Measurements were taken at each point where the vegetation or topography changed significantly and these have been plotted onto profile diagrams. The plant species found have been related to the height (Ordnance Datum) at which they were found.

SURVEY OF PREVIOUS SITES

In addition to the above, the sites around Southampton water where *Spartina alterniflora* had been recorded previously were visited to assess possible reasons for its loss.

RESULTS

BURY MARSH: MAPPING *SPARTINA ALTERNIFLORA*

Figure 2 shows the distribution of *S. alterniflora* on the Bury Farm Marsh and the extent of the

FIGURE 3a. *Spartina alterniflora* at Bury Marsh, Marchwood. This photo shows the topography of the marsh; there is a large creek system.

FIGURE 3b. *Spartina alterniflora* growing at the front of the marsh, which is being visibly eroded.

marsh in relation to neighbouring coastal features. Figure 3a shows a view across the marsh with *S. alterniflora* in the foreground and a part of the extensive creek system in the background.

Only two patches appear to be completely mixed stands of *S. alterniflora* and *S. anglica*, although five other patches have *S. anglica* beginning to invade at the edges. The "mixed" and "pure" patches are marked in Fig. 2. It is noticeable that *S. alterniflora* is now absent from areas described as "mixed" by Marchant (1964), indicating that *S. anglica* has replaced it.

Atriplex portulacoides L., *Limonium vulgare* Miller, *Aster tripolium* L. and *Triglochin maritimum* L. are all present in the patches. *Atriplex portulacoides* and *Puccinellia maritima* (Huds.) Parl. are particularly abundant. Only one stand appears to be purely *S. alterniflora* with no other species and this is found at the front of the marsh to the north west of the map. This stand can be seen in Fig. 3b. The area in which the *S. alterniflora* is growing is visibly eroding.

Most patches of *S. alterniflora* are on high parts of the marsh in areas with high species diversity. The species tends not to occur right on the edges of deep creeks where *Atriplex portulacoides* grows in pure stands. It is also found growing in low-lying areas of the marsh.

The map in Fig. 4 shows the distribution of *S. alterniflora* at the site in 1964. This map has been created using information in Marchant's thesis (1964). The distribution shown in Marchant's map has been superimposed onto the shape of the marsh as it is today. The marsh has changed in shape and extent since the original map so this new version is a pictorial representation rather than a distribution map. It does, however, enable comparisons to be made between 1964 and the present. The abundance of *S. alterniflora* has decreased. In 1964, the eastern side of the marsh contained several mixed stands of *S. anglica* and *S. alterniflora*. These were restricted to the back of the marsh, while the front of the marsh was dominated by *S. anglica*. Now there are only a few small patches of *S. alterniflora* on the eastern side of the marsh and two of these are still mixed stands today. *Spartina alterniflora* is concentrated on the west side of the marsh. In 1964, it was

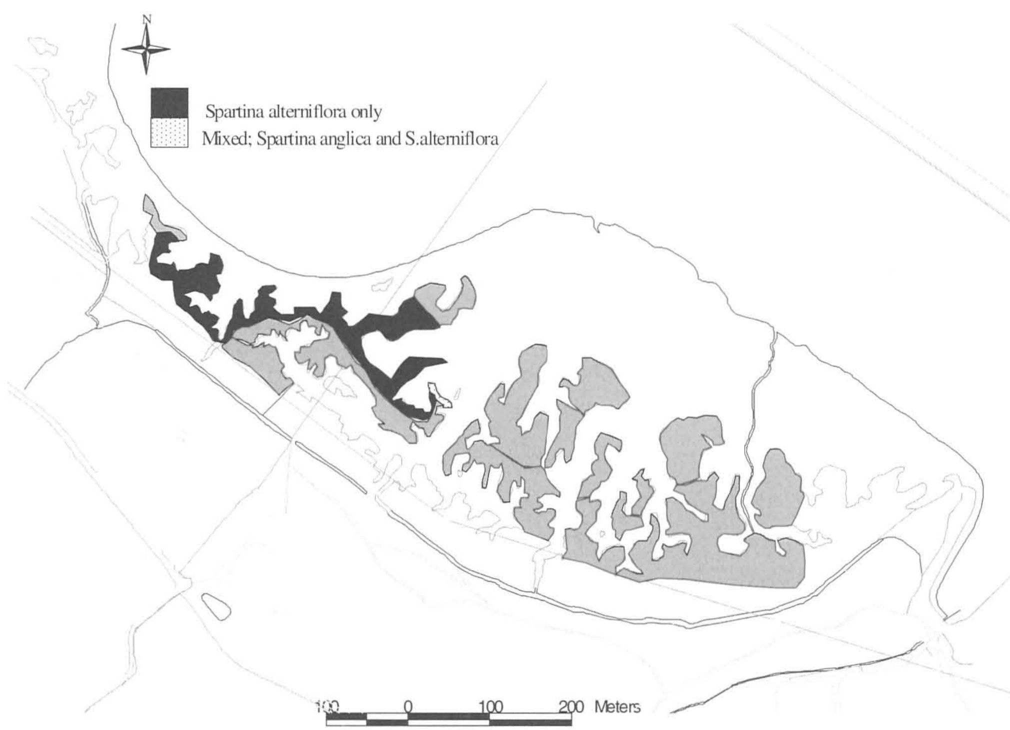


FIGURE 4. Map based on Marchant's 1964 map showing the distributions of *Spartina alterniflora*, *S. anglica* and mixed swards.

distributed throughout this part but has definitely contracted. Marchant (1964) describes some of the stands as degenerate. He noted that although the largest pure stands of *S. alterniflora* grew in the low-lying areas, these swards were less vigorous and had lower pollen fertility. On the higher sites, although other plant species are present, the individuals of *S. alterniflora* appear to be much healthier.

BURY MARSH: PHYSICAL NICHE AND ASSOCIATED VEGETATION

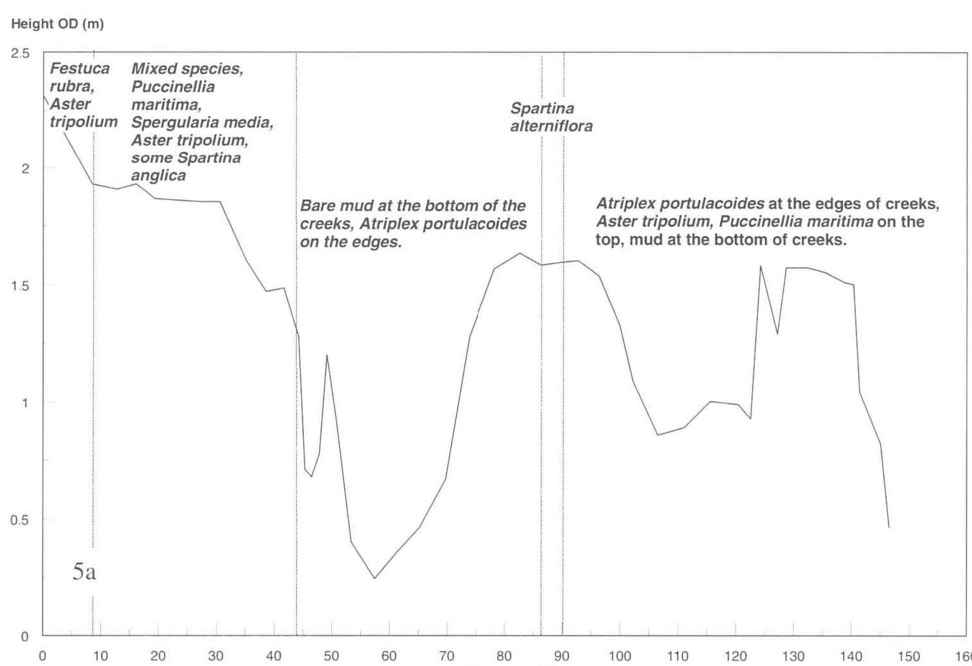
The three marsh profiles are quite similar and can be seen in Figs. 5a, 5b and 5c. The height at the top of the marsh was between 2–2·5 m OD. The raised parts of the marsh were all c. 1·5 m OD and the creeks c. 0·5 m OD. *Puccinellia maritima* tended to be found on higher elevations around 1·5 m OD or above and consequently was more abundant towards the back of the marsh. There appeared to be no particular pattern to the distribution of *S. alterniflora*. In Transect 1 *S. alterniflora* was found from 1·58–1·6 m OD. It occurs in Transect 2 from 1·1–1·59 m OD with *S. anglica* and at 1·67 m OD in Transect 3 with *S. anglica*. *Spartina anglica* was found from 1·2–1·87 m OD in Transect 1, from 1·2–1·59 m OD in Transect 2 and from 1·42–1·88 m OD in Transect 3.

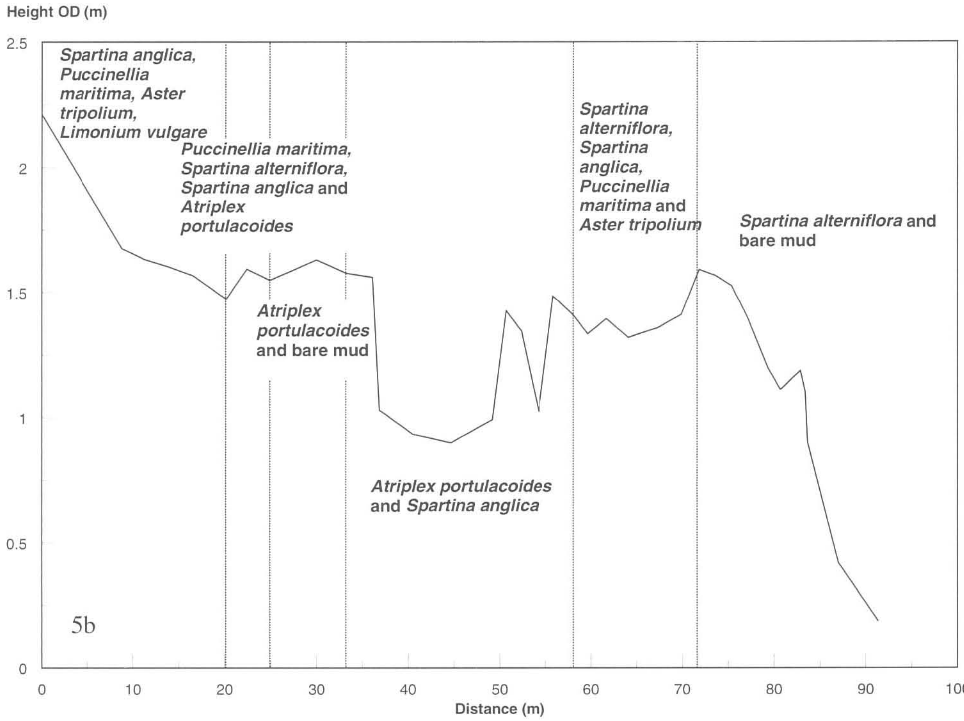
SURVEY OF PREVIOUS SITES

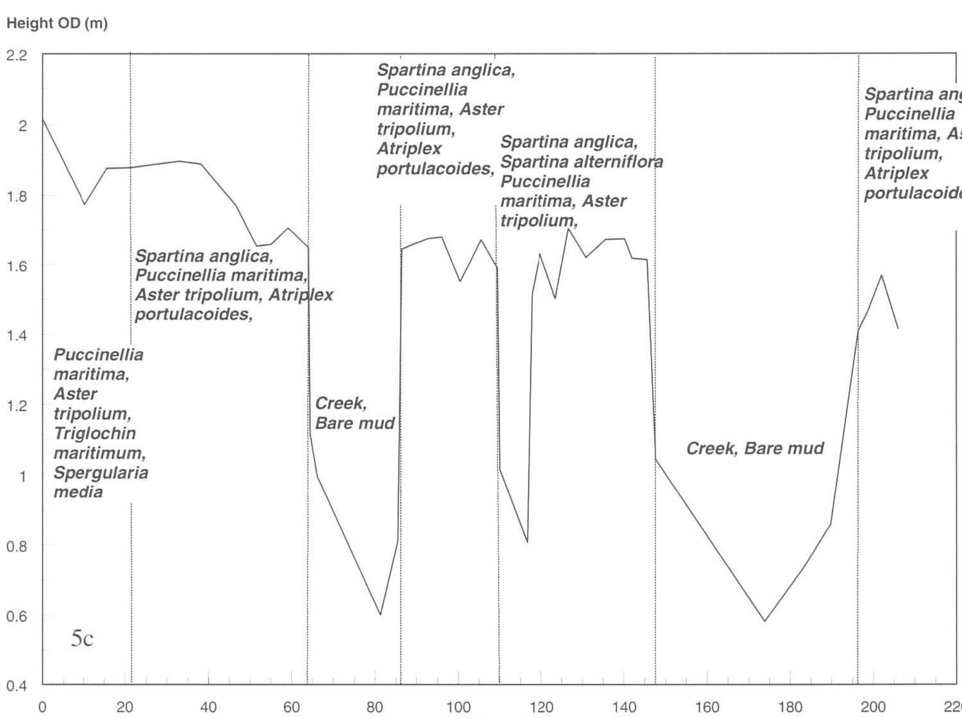
Many of the sites where *S. alterniflora* was recorded in the past (before 1910) have now been developed for docks and port facilities such as the river Itchen and the area between Hythe and Cracknore Hard. The river Test has also been developed, the eastern shore now consists of docks and port facilities whilst the Marchwood site on the western shore is quite isolated.

S. alterniflora used to be found along a stretch of Southampton Water east of Weston point. However, the shoreline here is now bare mud and shingle; the *S. alterniflora* habitat has completely disappeared, presumably due to erosion. There is a similar situation at the Hook (near to the College of Maritime Studies, on the shore near Newtown (SU4905) from where *S. alterniflora* was last recorded in 1907. There is no longer any salt marsh here and the substrate is composed of shingle and sand rather than mud. All that remains of the marsh is a small patch of *S. anglica*.

S. alterniflora was common in the Hamble at Burlesdon, Lincegrove, Hamble-le-Rice and Warsash. There has been less development of the river Hamble than the river Itchen and there are







FIGURES 5 a., b., & c. Topographic profiles of the transects which were established at Bury Marsh, Marchwood. The most abundant plant species have been added to the profile.

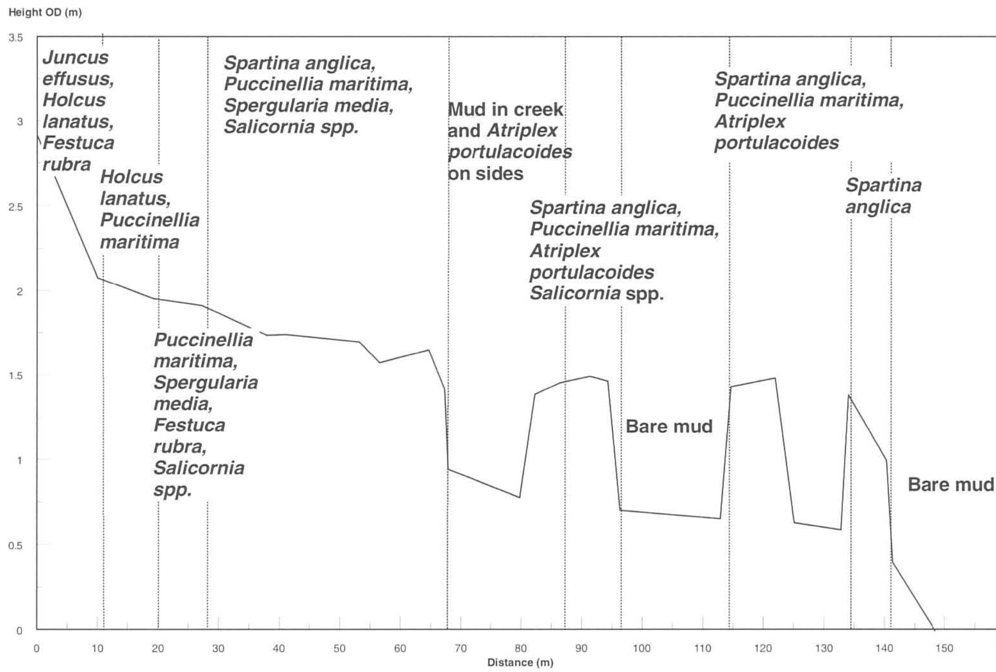


FIGURE 6. The topographic profile of the transect established at Hacketts marsh on the River Hamble.

still areas of mature marsh at Burlesdon (Lincegrove and Hacketts), that have been given protected status. *S. alterniflora* was last recorded from these marshes pre-1910. The reasons for decline of *S. alterniflora* here are unclear. Unlike the river Itchen it is not due to loss of habitat through development. We established a transect on Hacketts marsh to compare the topographic profile and vegetation with Bury Farm Marsh, Marchwood. This profile can be seen in Fig. 6. The top of the marsh is around 2 m OD in height. There is a flat area containing a lot of *Puccinellia maritima* which has been quite heavily grazed between 1·5 m OD and 2 m OD. The bottom of the creek is approximately 1·7 m OD. The other raised marsh areas are at a height of 1·5 m OD and contain small amounts of *Atriplex portulacoides*, *Salicornia* spp. and *Spartina anglica*. *S. anglica* is found throughout the marsh, growing between heights of 0·99–1·91m OD. At the front it grows on top of cliffs approximately 1 m high. It is not found on the low-lying bare mud at the front of the marsh and does not form as dense stands as it does at Marchwood. *Puccinellia maritima* is abundant particularly at the back of the marsh. Other marsh species include *Aster tripolium*, *Limonium vulgare*, *Atriplex portulacoides*, *Juncus maritimus* Lam., *Salicornia* spp. and *Triglochin maritimum*.

DISCUSSION

REASONS FOR THE DECLINE OF *SPARTINA ALTERNIFLORA*

As well as the direct impacts of industrial and marine developments such as loss of saltmarsh habitat there are indirect impacts such as changes in wave action and tidal currents, changes in sediment deposition and pollution which have implications for the whole of the estuary system, including the existing site at Marchwood. There has been much erosion of saltmarshes and many areas where *S. alterniflora* used to grow are now low-lying mud or shingle, the saltmarsh having completely disappeared.

It is not clear why *S. alterniflora* has persisted at Marchwood, while becoming extinct on saltmarshes in the Hamble. Marchant (1964) suggested that Marchwood is unique in its uneven topography; however, this was not based on topographical levelling and our study suggests that Hacketts Marsh is not dissimilar.

At Marchwood, the *S. alterniflora* population has declined significantly since 1964. This is probably due to an interaction of factors. *Spartina anglica* has played a role, as it has completely replaced *S. alterniflora* in areas where mixed swards once occurred. The degree of tidal inundation is considered to be a dominant factor influencing plants in the intertidal zone; it affects a number of factors, including degree of anoxia, salinity and build-up of chemicals. Determination of the level above Ordnance Datum at which a species occurs should give some idea of the ecological conditions that it prefers or can tolerate and suggest factors that limit its distribution. The topographic levelling showed little difference in height above Ordnance Datum between the upper and lower limits of the two. However, competition between the two species is not the only factor in the decline of *S. alterniflora* on uneroded marsh at Marchwood. Marchant (1964) noted that pure stands of *S. alterniflora* were showing signs of decline even though *S. anglica* was not present.

Pollution may have affected vegetation generally by weakening the plants. Marchant (1964) suggested that reclamation work downstream altered tidal movement and scour in the estuary which reduced the size of the marsh and deepened the channel. The regular dredging of the deep-water channel may be important. The soft mud at the surface of the marsh may have crept laterally into the deep channel and lowered the level of the overlying marsh. The dredgings are taken to the reclamation area so the supply of water-borne silt has been reduced, which causes the marsh accretion rate to be reduced. The lowering of the marsh increases waterlogging and tidal immersion of sites. In low-lying waterlogged sites the sediment that is deposited is also more easily removed by re-suspension than at sites of higher elevation where it may have a chance to dry out and become part of the marsh surface so the process is cyclical and self-enforcing (Reed & Cahoon 1992). Finally, there may be an age-related decline in vigour because there is no sexual reproduction of *S. alterniflora* in Britain. Clones of *S. anglica* decline in vigour with age (e.g. Thompson *et al.* 1991) and it is likely that a similar process occurs in *S. alterniflora*. Marchant (1967) noted that herbarium specimens of *S. alterniflora* collected in the 19th century are larger than plants growing at Marchwood in the 1960s.

CONCLUSIONS

The loss and decline of *Spartina alterniflora* from many of the sites in Southampton water appears to be due to changes in land use. This includes direct impacts from construction as well as indirect effects from changes in tidal action, channel topography and increased pollution. *Spartina anglica* may have out-competed S. *alterniflora* in other areas. At some of the sites such as Hacketts and Lincegrove marsh in the Hamble it is difficult to determine an obvious impact and loss may be due to a combination of factors. We consider the best strategy for conservation of *S. alterniflora* to be preservation of its habitat at Marchwood. Periodic monitoring of the site would determine whether erosion at the front of the marsh is continuing and whether *S. alterniflora* populations are being invaded by other species. If the dieback of *S. alterniflora* on the remaining sections of marsh since 1964 is due to the loss of sediment, it would perhaps be appropriate to consider whether the marsh can be protected. Future research should examine the physical processes taking place at this site and determine the rate of erosion, size of particles and types of sediment which are involved in marsh construction. Possible actions for protection may include deposition of dredging spoil which is already being removed from the deepwater channel nearby. The low-lying areas at the western end of the marsh might be most suitable for deposition. Control of *S. anglica* may also be needed.

ACKNOWLEDGMENTS

This work was commissioned and supported by Ian Pearson from English Nature. We would like to thank Duncan Hornby and Kathy Hodder for help and advice on GIS.

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(Accepted August 2000)