# UNIVERSITY OF SOUTHAMPTON

FACULTY OF ENGINEERING, SCIENCE AND MATHEMATICS

School of Civil Engineering and the Environment

# *Spartina anglica* population and environmental studies within the Solent salt marsh system

By

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## ABSTRACT

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# *SPARTINA ANGLICA* POPULATION AND ENVIRONMENTAL STUDIES WITHIN THE SOLENT SALT MARSH SYSTEM

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The thesis examines the possible causes of decline of *Spartina anglica* marshes along the south coast of Britain with emphasis on the Solent marshes.

The study shows that although there may be some genotypic differences between *S. anglica* gathered from sites in Britain. The disparities are not large enough to explain the significant differences in morphological vigour of *S. anglica* observed in the field. It concludes that the discrepancies observed in the field are the result of phenotypic differences resulting from environmental factors.

The work shows that in the *S. anglica* marshes of the south coast, anaerobic soil conditions prevail with impeded drainage being the most likely cause of the dwarf growth forms and lack of re-colonisation of pans and mudflats observed in the field.

The thesis concludes that the ultimate demise of the *S. anglica* marshes of the south coast of England is the result of frontal and creek erosion of the mature marsh and the failure of *S. anglica* to establish itself on the newly exposed sediments of the foreshore.

When *S. anglica* establishes itself in a flood /ebb neutral zone of an estuary, it changes the bathymetry to that of ebb dominant morphology. As a result eroded sediment is swept away with the outgoing tide. Furthermore, *S. anglica* is then unable to recolonise the exposed foreshore sediments because of its low redox potential resulting from poor permeability which is the consequence of the of historic overburden pressure of a once colonising marsh.

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## Declaration

I, Toru Tsuzaki declare that this thesis entitled *Spartina anglica* population and environmental studies within the Solent salt marsh system, is the result of my own original research. This thesis is structured to include three papers, submitted for international peer review publication. The papers are co-authored, which represents a significant input from Prof. Trevor Tanton during supervision, project development and publication preparation. The work is however, extensively the original work of Toru Tsuzaki

- this work was done wholly or mainly while in candidature for a research degree at this University;
- where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
- where I have consulted the published work of others, this is always clearly attributed;
- where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
- I have acknowledged all main sources of help; and
- where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;

Signed…………………………………………………………………….

Date:……………………………………………………………………….

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# Definitions / Glossary

| | |
|---|---|
| Carryover effect | An effect whereby a phenotypic or genetic characteristic persists over time. |
| Culm | A stem or stalk. The jointed and usually hollow stem of grasses. |
| Inflorescence | Collective term for flowering, arrangement of flowers or the flowering parts of a plant. |
| Freatic | Sediment zones below that of the water table. |
| Panicle | A raceme and any loose, diversely branching flower cluster. |
| Ramet | Individual plants within a population which is a clone from the original plant material. |
| Rhizome | A root like subterranean structure, commonly horizontal in position that usually produces roots below, and sends up stems to the surface. |
| Sediment budget | The finite quantity of mobile sediment within an estuary system. |
| Surface gradient | The slope of the marsh surface from the terrestrial to the marsh forefront. |
| Tidal hydraulics | The main tidal regime within a given estuary (influenced by the ebb/flood channels and current velocities of an estuary). |
| Tidal prism | The volume of water entering and leaving the estuary in a tidal cycle. This will be modified by increasing the intertidal area and could affect net accretion/erosion status of the estuary. |
| Tiller | A plant shoot that springs from the root or bottom of the original stalk. |
| Tillering | The production of new tillers formed from a single clone. |
| Viable seed | A fully formed seed pod filled with seed germ |
| Wrack mats | A dense vegetative mat composed of mainly dead halophyte stems and seaweed strands. |

# Chapter 1: Introduction

In the early 1800s, small areas of salt marsh were present in the western Solent, with *Spartina maritima* being the native species of *Spartina* at the time (Tubbs, 1999). *Spartina alterniflora* was discovered in 1836 at the mouth of the Itchen estuary. The hybridisation of this species with the native *S. maritima* formed the sterile hybrid *Spartina townsendii,* which was only able to reproduce vegetatively (Stapf, 1914; Gray & Raybould, 1997). The spread of the infertile hybrid was rapid, with areas around Poole Harbour to Pagham Harbour being rapidly colonised from 1870 to 1923, displacing much of the less vigorous parent species from its habitat. It was not until the discovery of the fertile variant known as *Spartina anglica* however, that rapid spread began to occur throughout the UK, and the world (Gray *et al.,* 1991; Raybould *et al.,* 1998). The differentiation between *S. townsendii* and *S.anglica* was finally resolved by Hubbard (1954) and later by Marchant (1964) who identified that *S. anglica* had double the number of chromosomes (Marchant) and was able to reproduce both vegetatively and through seed. The development of *S. anglica* had displaced the infertile hybrid and was responsible for salt marsh expansion throughout the years (Charman, 1991). The maximum extent of the Solent coast salt marshes were found to be in the early 1940 -1950's when it occupied an approximate area of 3326 ha (Doody, 1985). However, since that time the area of *S. anglica* on the south coast has progressively declined.

*Spartina* death was first noticed in the Solent area in the south coast of England, in 1920 by Oliver (1925) who wrote about the destruction of whole clumps of *Spartina* from Poole Harbour. Hubbard (1965) also compared aerial photographs from 1924 to 1952 and estimated that the area of *Spartina* in Poole Harbour had been reduced by 247 ha, or 27.5 % of the 1924 area and termed the phenomenon '*Spartina* die-back'. Between 1953 and 1965 Southampton University extensively investigated the die-back of *Spartina* from the Solent marshes (Goodman, 1957; Barker, 1964; Ivemy, 1966). Patchy degenerations appeared within the Lymington marshes which were previously healthy. This patchy distribution began to spread throughout the south coast from the 1930's to current times. By the end of the 1950's marsh degeneration has become very rapid and extensive (Goodman *et al.*, 1959). The degeneration of marsh has continued since Hubbard &Stebbing's (1967) estimate of 2481 ha, the area of marsh declining to 1057 ha by 1990 (Tubbs, *pers. comm.*).

Tubbs (1984) has also shown that in less than 25 years the area of *S. anglica* marsh within Langstone and Chichester Harbours has declined dramatically.

In recent history, the arrival (and disappearance) of *S. anglica* is possibly the single biggest event which changed the geomorphology, biodiversity and economic value of the salt marsh environment in many coastal locations (Gray *et al.*, 1995, 1997). The ability of *S. anglica* to colonise deeper water than most salt marsh plants, and its ability to spread through either seedling or by dispersal of plant fragments, made it the ideal candidate for colonising and stabilising mudflats and reclaiming land (Ranwell, 1964). However, the apparent failure for the species to maintain many of the marshes that it once created is a perplexing problem that has implications for both coastal ecology and coastal protection.

Over the years, a large number of research studies have been conducted on a wide range of factors, that are known to affect the growth of salt marsh vegetation and in particular *Spartina sp.* as shown in Chapter 2 and Appendix A. To date they have not shown any conclusive evidence that one or combinations of factors are the cause of the rapid decline observed on the south coast of England.

The main aim of this study is to identify, why after the spectacular success of *S.anglica* marsh development, degradation set in which has resulted in substantial marsh loss along the south coast of England.

The most widely researched aspect of *S. anglica* ecology is the process of die-back which is thought to be caused by the degeneration of clonal material and the instability which has been exhibited by *Spartina* species throughout the world (Thompson *et al.,* 1991a; 1991b; 1991c; Ayres & Strong, 2001). Alternatively, the development of toxic conditions under anaerobiosis, when *Spartina sp.* has occupied a particular environment for a period of time can ultimately lead to plant death (Goodman & Williams, 1961; Tubbs, 1984.) Like others after them, Goodman & Willliams (1961) realised that *S. anglica* lost vigour when observed in die-back sites. Similarly, extensive areas of die-back also occurred in *S. alterniflora* marshes of the south east United States in 2000-2002 where establishing its cause, proved to be as equally as elusive (Mendelssohn & McKee, 1988).

In order to ascertain whether the marsh degeneration is due to *Spartina* dying back through genetic or physiological processes, a series of pot experiments and reciprocal transplant experiments will be conducted to establish whether the plant material in itself shows signs of degenerative characteristics (Chapter 3). Furthermore, to test the environmental conditions for which *Spartina* currently occupy during a typical season in the UK, monitoring of edaphic factors has been carried out in two contrasting marshes to identify any differences in marsh characteristics which may result in the marshes change in succession status (Chapter 4). The results from each chapter will be discussed to ascertain how the different drivers for marsh development may be interlinked or independent from each other and how it may affect marsh succession (Chapter 5). A general discussion to the cause of marsh decline in the south coast of England is presented followed by recommended course of action and further research prospects (Chapter 6, 7 and 8 respectively).

# Chapter 2: Literature Review

There is an extensive literature review on the factors affecting the growth and development of *Spartina* marshes and in particular *S. anglica* marshes.  This literature review presents an overview to the most researched factors. A summary table is presented in Appendix A.

## Genetic variability within *Spartina* marshes

Evidence suggests that the evolutionary origin of *S. anglica* is that of classic allopolyploidy, the hybridisation of *S. maritima* and *S. alterniflora* in the Solent in the middle of the 19th century producing the sterile hybrid *S. townsendii*. Subsequent chromosome doubling restored fertility and produced the allopolyploid *S. anglica.*

Differences in vegetative stature, tiller densities, inflorescence size, have been frequently observed between successionally adjacent populations (Hill, 1984; Marks & Trsucott, 1985; Hill, 1986; Mullins & Marks, 1987) such that populations from ecologically similar populations are more alike than those from successionally adjacent populations (Thompson, 1991). Hill (1991) reported that the morphological distinctness between low and high marsh populations on the Dee Estuary was retained, when clonal material were grown under uniform conditions in cultivated trials. She also discovered that, in comparison with clones transplanted from a different marsh zone, clones transplanted back into their original marsh zone performed better. This suggested that there is genetically based variation among these populations. However, the lack of electrophoretically detectable protein variation in this species (Raybould, 1988), the high proportion of bivalent pairing at meiosis (Marchant, 1968), and the extensive vegetative spread of individual clones suggests that the phenotypic variation is due to the plasticity of a small number of genotypes. This thesis tests the hypothesis of whether the decline can be associated with either genetic and/or phenotypic variability. This will be explored further in Chapter 3.

## Pollen limitation, seed viability and seedling survival

S. *anglica* differed from the infertile relative *S. townsendii* through its ability to set seeds. This characteristic has been noted in many papers (Kneebone, 1972; Marchant, 1964; Gray *et al.,* 1991). It has been noted however that *S. anglica* seed set can be sporadic in its nature (Daehler & Strong, 1994). Raybould *et al.,* (1998) noted a relationship between the levels of seed set and the mean prevailing atmospheric temperature with it producing larger quantities of seed during the warmer years compared to colder years. Similar behaviour was noticed in marshes in North Carolina (USA), (Seneca, 1969) and in the Ribble Estuary (UK), (Marks & Truscott, 1985). The variability of seed set, pollen limitation and seedling survival are important factors in the ecology of *S. anglica* and worthy of investigation in its own right. Hill (1986) and Thompson *et al.,* (1991a) identified that the most likely mode of propagation is through vegetative methods and that therefore the scale of *Spartina* loss experienced in the Solent marsh system is unlikely to be the result of issues of seed set, and for this reason this line of investigation was not investigated further in this study as a major cause of marsh loss. The subject of plant fertility is of interest in its own right and a separate paper is presented in Appendix B.

## Vegetative expansion

*Spartina sp.* utilises a traditional grass-type colonisation strategy expanding from a single rhizome rose in a concentric pattern usually through underground rhizomatous growths. In this way, some rhizomes can separate from the main body of roots and form another rose from which to grow. These stand-alone colonial units of grass are known as stands, which are typically found on the foreshore of expanding marsh systems. Eventually, if conditions prevail, the stands will meet and form swards. According to Tubbs *et al.,* (1999) *Spartina* dominated the Solent marshes in the early part of the 19th century using this effective form of propagation. However as this study will demonstrate, the vegetative expansion once exhibited by *Spartina* is not as vigorous as in the past. One such theory is that of plant density, where the plant in essence is competing against itself for resources. Since resources are limited overcrowding leads to less vigorous plants (Bertness & Yeh, 1994, Castellanos *et al.*, 1994). Secondly, it has been suggested that a plant which exhibits clonal vigour if not limited by any factors can continue to survive indefinitely (Gray *et al.,* 1991). However, as the clone replicates minor variations may appear in its genetics or it becomes infected by a virus which may manifest itself phenotypically through time, leading to weaker growing plants. This topic will be discussed further in Chapter 3.

### Temperature

Differences between air and water temperature can be seen in the salt marsh environment. In summer, the flooding water may be cooler than the air, and in the winter a frozen marsh surface may be rapidly immersed in water several degrees warmer. Such rapid changes in temperature can be physiologically disruptive. Reproductive structures, for instance, are frequently susceptible to temperature injury (Langer, 1979). Differential temperature between root and shoot can also affect morphogenetic processes (Klepper, 1991) and seed germination is also known to be controlled by temperature variations (e.g. Mooring *et al.,* 1971; Marks & Truscott, 1985; Ungar, 1987).

Most salt marsh plants rely on the C3 pathway with optimum photosynthesis at a temperature range of 15 – 25 °C. *Spartina* however, belongs to plants with a C4 pathway (Long *et al.,* 1975) with an optimum range of 30 – 47 °C (Gray *et al.,* 1991; Packham & Willis, 1997). Photosynthetic activity is reduced at 10 °C and below and ceases at 7 – 9 °C (Long *et al.,* 1975; Mallott *et al.,* 1975; Dunn *et al.,* 1981; Gray *et al.,* 1991). Seed production and germination is also highly sensitive to temperature. This is important for the spread of *S. anglica* as at its northern limit seeds stay dormant below 4 °C and germination increases from 7 to 25 °C (Taylor & Burrows 1968; Hubbard 1970). Also, canopy development does not begin below 9 °C (Gray *et al.,* 1991). In the Solent air temperatures remain relatively stable averaging from 4 °C to 28 °C depending on the season. However, extremes of temperatures do occur and these are documented further in Chapter 4.

### Competition

The role of competition between different halophytes appears to be a balance of trade-offs, with abiotic and biotic factors setting the boundaries to the competitive nature of the species. *Spartina sp.* is tolerant to many abiotic factors such as submergence (Ranwell *et al.*, 1964; Morley, 1975), temperature (Seneca & Blum, 1984) and salinity (Gray & Scott, 1977). These tolerances have given advantages to the species such as *Spartina*; for colonising coastal habitats which are inaccessible to many less adaptable species (Levine *et al.,* 1998). Hudson (2001) has shown that *Spartina* is not competitive in habitats where other pressures such as grazing may exist, and where other species maybe more tolerant to grazing pressures (Grazing as a factor is outlined below). Given the mono-specific nature of the main stands throughout the Solent marsh system, with only small amounts of mixed marsh vegetation at the terrestrial intertidal zone of the upper marsh, suggests that inter species competition is not an issue on the Solent marshes. In addition, areas devoid of *Spartina* also appear to be devoid of all types of halophytes, therefore the effects of competition was not investigated further as it does not appear to be a major contributing factor to the decline of *Spartina* in the study area.

### Effects of grazing

The salt marsh plant community and physical nature of the plants is affected by grazing animals, particularly when marshes are grazed at high intensities. Two types of grazing may be present, perennial, usually by domestic animals (cattle, sheep or horses) (Ranwell, 1961) or seasonally by large number of animals such as migratory geese (Bazely & Jefferies, 1985; 1986; Olff *et al.,* 1997). In some areas both types of high intensity grazing take place. High level of grazing can have a long lasting effect on the physical and chemical nature of the marsh and on the salt marsh plant community. Reduction of canopy height by removal of biomass alters the light environment (Bakker *et al.,* 1993; Wilson & Jefferies, 1996). This can elevate soil temperatures with consequent effects on rates of evaporation and salinity. Removal of biomass also reduces seed production either by direct consumption or by reducing production by suppression of flowering. This can reduce population levels of some species, particularly if the grazing is selective (Srivastava & Jefferies, 1996; Olff *et al.,* 1997). Trampling damages mature plants and directly disrupts seedling establishment, as well as compaction of the soil surface which also hinders growth of new plants. Grazing can affect nutrient cycling on marshes grazed by large numbers of snow geese (*Anser caerulescens caerulescens*); nitrogen cycling is accelerated through rapid deposition in goose faeces (Bazely & Jefferies, 1985). This leads to significantly higher levels of primary production, although standing biomass is reduced by the grazing itself. At the same time plant species diversity declines (Bazely & Jefferies, 1985; 1986) probably through a combination of changes in the nutrient levels and the changes in seed production, seedling establishment and trampling damage. These effects may also be influential in maintaining existing patterns of zonation by stopping or at least slowing the process of succession (Crawley, 1983; Bazely & Jefferies, 1985).

Heavily grazed marshes are typically characterised by a lack of dominant structural diversity and reduced biodiversity as palatable or trampling-intolerant species are usually absent (Bazely & Jefferies, 1986). Typically, such marshes become dominated by stress-tolerant grasses as annual or perennial herbs decrease or are "grazed out". Intensive grazing over long periods, as in domestically grazed marshes, leads to development of relatively species-poor plant communities, which are typically dominated by salt-tolerant and grazing–tolerant grasses such as *Puccinellia maritima* and *Salicornia spp*. (Rowcliffe *et al.,* 1998). Most of the halophytes have a relatively low tolerance to grazing and trampling and some are positively selected by grazers due to their high nutrient content (Rowcliffe *et al.,* 1998). Where grazing is less intense the halophyte species can persist and thrive resulting in more diverse plant communities which are not dominated by a single species.

Many salt marshes in England and Wales have traditionally been grazed by large domestic animals (mainly cattle and sheep) and these sites (mainly on the west coast) show plant communities which are strikingly different from the largely ungrazed marshes of the south and east England (Gray, 1972; Gray & Scott, 1977). Many of these 'ungrazed' marshes are however grazed at low intensity by wild vertebrates. This includes migratory geese such as the Brent goose (*Branta bernicla*) along with resident goose species (Geylag, *Anser anser*); and also rabbits (*Oryctolagus cuniculus*), hares (*Lepus europaeus*) and roe deer (*Capreolus capreolus*). The mosaic patterns of zonation and the relatively diverse plant communities seen in these lightly grazed salt marshes may be a product of the small scale variations in physical and chemical conditions, plus biotic factors including low intensity grazing by wild vertebrates. Grazing of this nature by more than one species of wild vertebrate grazer has not been considered in past research. In the UK, intense grazing by single species (geese) has been investigated (Summers *et al.,* 1993). Elsewhere in the world the attention has usually focused on sites which are grazed intensively by wild animals. In particular, research has focused on the influence of migratory birds such as snow geese (Bazely & Jefferies 1985; 1986) or brent geese (Olff *et al.,* 1997).

Grazing animals can be considered disturbance factors and there may be parallels to Connell's much quoted and widely applied "intermediate disturbance theory" (Caswell, 1978; Connell, 1978). The applicability of this term to herbivory itself is a subject of some discussion (McGuinness, 1987; Bertness, 2001; Sousa, 2001). Grazers physically disturb plants by consuming them, trampling on them and by changing their chemical environment (Edwards & Gillman 1987; Bertness 2001). Grazing (or disturbance) on marshes at high intensities produce marshes that are relatively species poor (e.g. west Britain) (Gray & Scott, 1977) and those with intermediate grazing may be expected to be more species rich and more structurally diverse (Zedler *et al.,* 1999). Relatively few examples of this are documented: the emphasis of research has been on the impacts of intense grazing. Doody (1985) found that a Rockliffe marsh on the Solway was lightly grazed with a consequence of greater structural diversity than other heavily grazed marshes in the region. The *Spartina* marshes at Keyhaven and Lymington experience ruminant grazing towards the upper marsh area, notably by ponies and horses. Grazers rarely visit the islands that have formed out in the main coastal area, where the main decline in *Spartina* is observed. Therefore grazing pressures is not considered further in this thesis.

### Tidal inundation

*Spartina* has been known to colonise mudflats when it is covered by water for approximately 6 hr $d^{-1}$. This ability to colonise low lying areas of the marsh is partly due to the species possessing a large internal lacunae system (arenchyma) which allows the transport of air from the shoots to the roots (Arenovski & Howes, 1992; Naidoo & Naidoo, 1992). The tolerance of *S. anglica* to long periods of inundation has been widely researched. Ranwell *et al.,* (1964) observed *Spartina* submerged in some locations for a maximum 9 hr $d^{-1}$. It is expected that this may change due to rises in sea level and changes in climate which may accentuate the periods of inundation. However, the demise of *Spartina* marshes have been occurring in locations where *Spartina* is often not submerged for such extensive periods as suggested in the literature.The *Spartina* colonies in the Solent struggle to survive in locations where the tidal inundation is rapid and the retention of water in the sediment is high. The effects of such conditions are described in water-logging below and in Chapter 4.

### Water-logging and anoxic conditions

There has been a lot published on this subject but considerable uncertainty still remains.

The early work mainly focused on the lack of vigour by *S. anglica* on the south coast of England. The decline in the vigour of *S. anglica* was observed in the 1950's where Goodman & Williams, (1961) and Ranwell *et al.,* (1964), both noted the strong negative correlation between water-logged sediments, redox potential and plant vigour.

In the 1970s and early 1980s a number of authors pointed to water-logged conditions and poor drainage as the underlying cause for decreased production and die-back in *S. alterniflora* marshes. Mendelssohn & Seneca (1980) for instance, measured soil drainage in the field and observed a positive linear relationship between the degree of soil drainage and plant height, with differential soil drainage accounting for 70 % of the variation in plant height along the transects studied. They also observed significant differences in soil redox potential, which was correlated with differential drainage. In the tall height zone where soil drainage was greatest, redox potential indicated greater aeration, while in the short zone where low soil drainage persisted, redox potentials indicated that the soil was the most anoxic.

Initially it was thought that the different growth forms of *S. alterniflora* could be genetic (Chapman, 1960; Stalter & Baston, 1969). There is evidence that some subtle genetic differences occur among ecotypes that differ in height, colour and flowering periods. It is thought that these differences may have evolved among marshes in response to a latitudinal gradient (Anderson & Treshow, 1980). However, after a number of seedling growth tests (Mooring *et al.,* 1971) as well as field fertilisation, translocation experiments, and electrophoresis (e.g. Shea *et al.,* 1975; Valiela *et al.,* 1978), it is generally agreed that the different forms are environmentally induced.

A number of workers have conducted controlled greenhouse experiments to try and quantify the relationship between aeration and growth. For instance, Linthurst (1979) conducted a greenhouse experiment to investigate the correlation between aeration and growth of S. *alterniflora* and found that reducing conditions were highly correlated with aerial and root weight, as well as with plant height. They also showed that as aeration increased it resulted in a decrease in pH and soluble sulphides. He argued that the adverse effect of water-logging is the result of associated changes in soil aeration and pH. Similarly, Linthurst & Seneca (1980) showed in a greenhouse experiment that soil aeration alone had a positive effect on growth, with *Spartina* having 6.3 times more biomass under aerated conditions than anaerobic conditions. Linthurst & Seneca (1980) also showed that if pots of *S. alterniflora* were placed in the marsh to different depths the tallest sward had the best aeration and plant growth.

Pezeshki (1997) showed that there was a positive linear relationship between depth to water table on a salt marsh and plant height, with approximately 70 % of the variance across the marsh being accounted for by water table depth. The redox potential of the soils declined with increased levels of water-logging. They also showed in a field trial that growth and development was impaired under water logged conditions. When cores of *S. alterniflora* sward were cut from the tall, medium and short cores of marsh and placed in a replicated water logging trial in the glass house, the plants from the tall and medium height sward in the drained and partially drained treatments performed worse than the flooded treatment, while the dwarf sward showed no significant differences. Similarly, in the glass house experiment plant height, density, and aerial standing crop of tall *S. alterniflora* cores were significantly greater in the undrained soil treatment, than in the completely drained treatment. For medium-height *S. alterniflora* culm density and aerial standing crop were also significantly greater in the undrained treatment. In the water-logged plot, the water level was lowered to the level of the soil surface on a tidal cycle. If the water was allowed to remain stagnant on the surface to a depth of 0.05 m, the *Spartina* in the flooded swards performed better than those in aerobic soils. They were unable to explain these apparently contradictory results. It is clear that the experimental conditions must have created different soil conditions than were observed in the field in some subtle way. Lack of replication of drainage conditions indicates that the experimental design was suspect and their results must be treated with caution.

Mendelssohn & McKee (1988) transplanted streamside *S. alterniflora* swards into more water-logged and less productive inland marsh areas. They observed a rapid decrease in soil redox potential and increase in the concentrations of interstitial water sulphide and $NH_4$, and in root alcohol dehydrogenase activity. One year later, standing crops of transplanted swards were significantly reduced compared to streamside controls. Reciprocal transplantation from inland to streamside areas resulted in the amelioration of the detrimental conditions associated with the water-logged inland marsh and an increase in standing crop to levels equivalent to streamside controls. They observed that soil salinity and pH were not significant factors in causing reduced growth of *S. alterniflora.* They concluded that sulphide toxicity, in combination with extended periods of anaerobic metabolism in the roots, was a major factor associated with reduced growth of the plant and may be a cause of the extensive die-back observed in *S. alterniflora* marshes.

Wiegert *et al.,* (1983) excavated four parallel trenches in a *S. alterniflora* sward, one meter apart and six meters long, ending in a creek, and introduced plastic drainpipes with holes to drain the area, and therefore increase the interstitial exchange of water. They also set up two control plots, one across the creek directly opposite the experimental site, where they dug four trenches and filled them without drainage pipes. A second control area, next to the drained plot was designated as a undisturbed control. The results suggest that increased movement of water, lower concentration of sulphide, and greater standing crop exists in the drained area. King *et al.,* (1982) considers that the increase in productivity around the edge of a marsh are the results of increased drainage lowering soluble sulphides and iron in the soil. The relationship of water-logging and anoxic conditions with regards to *S. anglica* is little studied and further information is discussed in Chapter 4.

### Wave action and sediment erosion

It is widely believed that salt marshes are able to dissipate wave energy over the marsh surface, to the extent that this surface offers a buffering function and reduces the approaching wave height (Moller *et al.,* 1999). The surface of a young *Spartina* marsh accretes sediment causing the surface of the marsh to rise which changes both the morphology and tidal hydrology of the area (Gray *et al.,* 1991). In the case of a sheltered estuary where the sediment availability is finite, the marsh rises at the expense of the foreshore sediment at the front of the marsh. The result being the formation of deep vertical steps at the marsh / foreshore interface, this abrupt termination at the marsh face takes the brunt of the approaching wave and results in large areas of erosion. The increased wave action has been noted to correlate closely with rates of erosion. Ke & Collins (1993) and Johnson, (2000) also noted that wave attack is often the primary cause of salt marsh recession in the Solent marshes

### Photoperiod

The quality and duration of the light reaching the plant canopy is an important control on marsh development. Light is argued to be limited by the sediment laden tides, as well as by the sediment deposits left on leaves after the tides have ebbed. Hubbard & Partridge (1981) for instance suggested that the turbidity of tidal water could be a factor limiting plant growth and expansion of the salt marsh. Hubbard (1969) however, working with *S. townsendii* in laboratory conditions, could not establish a definite link between alternation in the light regime through tidal immersion and phonological changes. The actual effect of the silt layer on the canopy after tidal deposition on light capture / or gas exchange by leaves, has rarely been investigated or proved relevant. Fischer *et al.,* (2000) identified that wrack mats may cause localised disturbance to the *Spartina* marsh surfaces through impeding light and mechanical damage to stands, sometimes resulting in denuded areas forming. However, the sizes of the wracks are rarely equivalent to the area of the dieback seen in the marshes of the Solent. *Spartina* at some point in its development must have tolerated the turbidity of the water in order to reach the extent to which it currently occupies, therefore effects of inadequate photoperiod which may cause localised disturbance is not a major factor in the demise of large expanses of marshes seen in the Solent

### Salinity

A number of factors have been proposed to limit the growth of *S. alterniflora.* Interstitial salinity for instance, has been correlated with plant production, with several authors reporting an inverse relationship between *S. alterniflora* production and salinity (e.g. Adams, 1963; Mooring *et al.,* 1971; Haines & Dunn, 1976; Parrrondo *et al.,* 1978; Smart & Barko, 1980; Linthurst & Seneca, 1981).

However, the importance of salinity in this respect has been brought into question, since many marshes have been shown not to exhibit a salinity gradient between tall and short stands of *Spartina* (Broome *et al.,* 1975; Blum *et al.,* 1978; Buresh *et al.,* 1980; Howes *et al.,* 1981). Even when some differences in the salinity of interstitial water and plant dissolved nutrients have been observed between the sediment of the streamside and inland marsh locations, these have not been deemed sufficient to account for the difference in productivity of the various *S. alterniflora* height forms (Broome *et al.,* 1975; Mendelssohn Seneca 1980; Delaune *et al.,* 1983;). Moreover, Valiela *et al.,* (1982) have observed that plant production in short grass areas of moderate interstitial salinity is often not affected by irrigation with freshwater.

## Fungal infections

Investigations into identifying fungal pathogens which may have an impact on *S. anglica* have been conducted by a number of investigators. (Goodman, 1957; Barker, 1964; Ivemy, 1966; Gray *et al.,* 1990; Raybould *et al.,* 1998) and others have investigated the effect of the fungus on *S. alterniflora* (Bason *et al.,* 2007) but have so far proved inconclusive in identifying whether fungi are likely to directly attack healthy plants. Ivemy (1966) suggests that fungus mainly affect plants as a secondary infection and only likely to infect plants when they have been stressed or weakened from other causes. The only fungus which has been known to cause any impact on *S. anglica* populations is the ergot fungus *Clavicep purpurea*, which is known to attack the seeds. Raybould *et al.,* (1998) noticed that in Poole Harbour the infestation of *C. purpurea* on *Spartina* increased over time, and reached epidemic proportions by the end of their surveys (80 % infestations were common). Although ergot may have detrimental effects on the sexual reproductive capability of *S. anglica*, the plants were able to competently regenerate successfully through vegetative reproduction, and no lasting effects were noted on the plants themselves post infestation (Tsuzaki, unpublished).

## Nematodes

Nematode distribution can vary significantly, with high numbers of nematodes recorded in sites of high productivity. *S. alterniflora* are known to sometimes produce galls caused by the root nematode *Melanoidoyne*. (So far there is little evidence to suggest that the formation of these galls has a physiological effect on the plant (Plantard & Bardou-Valette, 2007).

It has also been noted that *Spartina* can influence the abundance of the benthic community. Chen *et al.,* (2007) investigated *S. alterniflora* stands and noted that it had generally lower nematode trophic diversity than the mixed community locations, suggesting that the expansion of *Spartina* led to a simplification of the benthic food web. The relative abundance of bacterial-feeding nematodes tended to increase in *S. alterniflora* marshes compared to *P. australis* marshes. The increased bacterial-feeding nematodes in *S. alterniflora* stands are likely to reflect the altered decomposition processes, rates and pathways, which may modify belowground nutrient cycling of the estuarine ecosystems. Site effects were generally detected in the comparison of sediment properties and nematodes. Sediment water content, electrical conductivity, bacterial biomass and litter biomass were identified as the most important factors in the shaping of the nematode communities, however direct effect of nematodes on *Spartina* colonies is not investigated as it is beyond the scope of the study,

**Virus infections**

The only known virus to be investigated in association with *Spartina* is the *Spartina* mottle virus which has shown to manifest itself within the leaves of its host. Jones (1980) investigated the effects of the virus on the general health of *Spartina* and concluded that it does not have any immediate detrimental effect on *Spartina sp*. Subsequent studies have not revealed anything further about its pathological characteristics (Gotz *et al.*, 2002). However, Raybould (1988) suggested that with the colonial nature of the plant, the accumulation of viruses could occur and over many years of regeneration may have an impact. This is still yet to be proven.

**Climate change**

Gray & Moog (2001) examined the response of *P. maritima* and *S. anglica* to increase in $CO_2$ and temperature in simulated conditions, similar to those scenarios of climate change. They found that *Spartina* fared well with both the increase in temperature and increases in greenhouse gases due to its C4 metabolism. They concluded that the niche habitat of *Spartina* is changing, and the limit of extent for *Spartina* is now moving further northward expanding and pushing its northern boundaries. Likewise, the southern extent of the habitat boundary may become a more hostile and competitive environment for *Spartina* to compete against other grass species such as *P. maritima.* The effects of climate change on a species distribution would warrant further research.

### Sedimentary processes

The presence of *S. anglica* on mudflats greatly enhance the rates of sediment deposition, and increases surface elevation through the reduction of current energy in the sward, thus producing low-energy depositional conditions (Stumpf, 1983; Elliott *et al.,* 1998). Temmerman *et al.,* (2007) also showed that the binding of sediment by plant roots does offer some resistance to erosion; they also indicate that the degree and nature of the influence of the vegetation must be determined for different site conditions, since differences between species in root distribution and tensile strength determine disparities in erodability. For this reason, *Spartina* has often been planted to facilitate these processes and potentially assist with shoreline stabilisation and land reclamation.

Fragoso (2001) conducted experiments investigating the effects of sediment gain or loss from those of inundation on the growth of *S. anglica*. Results show that plant growth was enhanced by increases in surface elevation; furthermore, results indicate that vertical change in surface elevation significantly affects plant growth independently of inundation.

The influence of sediment processes on life cycle of *S. anglica* marshes is discussed in detail in Chapter 4 and 5.

### Nutrient availability

Fertilization experiments have shown that nitrogen availability may also limit the growth of *S. alterniflora* (Sullivan & Daiber, 1974; Valiela & Teal, 1974; Gallagher 1975; Mendelssohn 1979a, 1979b; Buresh *et al.,* 1980). However, Nixon & Oviatt (1973) have indicated that nitrogen concentration can only account partly for differences in productivity. Prolonged treatment of short *S. alterniflora* stands with nitrogen fertiliser, for instance, failed to increase productivity to a level equal to the one observed in the banks of creek channels (Valiela *et al.,* 1978; Buresh *et al.,* 1980). Moreover, areas of short *S. alterniflora* have been found to have higher concentrations of interstitial $NH_4^+$ than adjacent tall stands throughout the growing season (Mendelssohn, 1979b; Howes *et al.,* 1986).

Howes *et al.,* (1986) studied the correlation between the aboveground biomass of *S. alterniflora*, the oxidation status of the sediment, the concentration of available ammonium and interstitial salinity. They found that values of sediment redox potential provided the best prediction of above ground biomass, a relationship that was observed to prevail between years and different marshes. The bio-availability of ammonium ions are related to the changes in sediment redox potential, for this reason the effects of sediment redox potential will be developed in Chapter 4.

### Mechanical stresses

The mechanical effect of tidal currents on plants varies according to location within the marsh, the age of the plant and the size and strength of the roots and rhizomes. Investigators have suggested that a major factor of seaward expansion of some species is their inability to withstand strong currents, as young plants with poorly developed root systems are more susceptible to uprooting. *Salicornia sp.* seedlings for instance, require a threshold period of two to three days free of tidal currents in order to be able to develop sufficient roots to withstand subsequent tides (Wiehe, 1935; Chapman, 1960). *Aster tripolium* are suggested to require a tide-free period of five days for the successful establishment (Chapman, 1941). The length of the required tide-free period is likely to depend also on factors such as sediment type, tidal range, current velocities and climatic conditions (Adam, 1990).

Another factor associated with tidal inundation is the potential of mechanical stress resulting from sediment deposition. Alizai & MacManus (1980), for instance, measured up to 2.6kg/m$^2$/tide of sediment stored at one time by *Phragmites communis* in the Tay estuary, Scotland. Likewise, French & Spencer (1993), working in a macro-tidal back-barrier marsh in North Norfolk, England, found a maximum of 13.8g/m$^2$/tide retained by *Atriplex sp.*, 2.94g/m$^2$/tide in an *Aster sp.* dominated marshes and 1.7g/m$^2$/tide in a general salt marsh community.

### Acid sulphate soils

Metals such as aluminium, iron and manganese are common and abundant in many soils, and normally not toxic in salt marshes due to chemical equilibrium maintained by pH conditions and buffered to near neutrality through reduced redox potential (Gambrell, 1994). Soils that are normally water saturated are under reduced conditions, meaning dissolved oxygen is depleted and the reduced forms of many metals are present.

When normally flooded and reduced soils are allowed to dry out, such as in rice cultivation, oxidised acidic conditions may develop and high concentrations of soluble metals may exist (Hanhart *et al.,* 1997). Under acidic conditions, plants may become stressed by a high availability of potentially toxic metals (Prasittikt & Gambrell, 1989). Coastal salt marsh soils are potential acid sulphate soils. When seawater floods reduced coastal marsh soils, sulphate are biochemically reduced to sulphide, which reacts with Fe (II). Forming Pyrite ($FeS_2$), which is stable under reduced conditions. Oxidation of soils through lowering of the water table causes pyrite to oxidise to sulphuric acid ($H_2SO_4$). The formation of acid decreases the pH and causes $Al^{3+}$, $Fe^{2+}$ and other metals to become mobile in the soil solution. One potential cause of the degeneration of marshes could be oxidation of soil metal sulphides resulting in increased acidity and metal toxicity (McKee *et al.,* 2004). Metal toxicity negatively affects growth of marsh vegetation. Schier & McQuattie (2000) investigating the effect of water stress on aluminium toxicity theorised that an increase in water stress due to drought would enhance Al toxicity. This phenomenon has been investigated in the US with particular attention drawn to the Louisiana marshes where large expanses of marshes have died due to drought conditions. The death of a large expanse of marsh particularly in regions not exposed to prominent physiologically demanding regions may be related to marsh degradation in the Solent salt marshes, this is investigated further in Chapter 4 and 5.

### Sulphur in the coastal environment

In coastal soils, the chemistry of sulphur is given particular importance (Howarth & Teal, 1979; Boto, 1984; Raven & Scrimgeour, 1997). Howarth & Teal (1979) showed that sulphate reduction in marsh surface accounts for consumption of carbon that is about equal to the net primary production, while respiration using other electron acceptors, such as oxygen and nitrate is much less important. The concentration of sulphate in seawater, normally 25mM, is 10 to 100 times the concentration commonly found in freshwater, making the volume-specific redox (and associated pH) effects much greater, as well as increasing the concentration of potentially toxic end products such as soluble sulphides (Raven & Scrimgeour, 1997).

Sulphide is produced in anaerobic environments when there is a supply of organic matter and sulphate ions ($SO_4^{2-}$). This ion is used by bacteria such as of the genus Desulphovibrio, as a terminal electron acceptor in respiration (Postgate, 1959; Ponnamperuma, 1972; Zehnder, 1988). These bacteria are important to the chemistry of coastal soils in particular, because they tolerate high concentrations of salts as well as sulphides. They become particularly active as redox values lower than -75 mV (Harter & McLean 1965) and function best in the pH range of 5.5 to 9.0 (Postgate, 1959; Connell & Patrick, 1968), which is endemic of water-logged salt marsh soils. Soluble sulphides are a product of anoxic respiration and are released into the soil and therefore under field conditions some sulphide remains in soluble form both as the acid sulphide ion and as hydrogen sulphide ($H_2S$), which although a gas, is highly soluble (Ingold & Havill, 1984).

A number of investigations have examined the toxic effects of dissolved sulphides on plants under water-logged conditions (e.g. Goodman & Williams, 1961; Armstrong & Boatman, 1967; Allam & Hollis, 1972; Ingold & Havill, 1984; Havill *et al.,* 1985) and some authors have correlated the distribution of some halophytes with the occurrence of soluble sulphides. Ingold & Havill (1984) and Havill *et al.,* (1985) for instance grew plants in controlled laboratory conditions, using defined media that excluded other reduced substances that in nature may affect plant growth, and added known amounts of sulphide. They concluded that although anaerobic sediments undoubtedly contain a wide variety of other reducing substances, sulphide concentration accounts for much of the inhibition observed in plant growth.

## Conclusion

From the vast amount of peer reviewed and grey literature available it appears that many factors affect the growth of *Spartina*. In many marshes the main reason for poor plant development is through degeneration of the plant material and / or water-logging conditions causing anaerobic conditions in the root zone. The majority of the research which lent support to the idea, that the regulation of *Spartina* growth is governed by the degree of interstitial anoxic conditions, comes from research which is predominantly from the US. Ultimately research on the development of *S. alterniflora* has become extensive while comparatively little empirical studies have been carried out on *S. anglica* since the 1990’s (Raybould, 1988; Thompson, 1991 and Gray *et al.,* 1991).

Given the large number of *S. alterniflora* studies, a degree of subjective validity could be granted to studies lacking appropriate replication due to the coincidences of their results with the observations reported by correlative studies. Many of the studies were laboratory based (Goodman, 1957; Koch & Mendelssohn, 1989; Koch *et al.,* 1990) and proved that variables can have deleterious effect under laboratory conditions. However, laboratory results from hydroponic experiments do not necessarily predict the response of plants in the field and even less about the performance of an entire ecosystem.

The evidence reported from hydroponic experiments, in-situ experiments and greenhouse experiment results in principle, should lead to the conclusion that creek bank plants ought to be taller and full of vigour than the more water-logged culms occupying the pan areas. This is however not the case in the Solent marshes where most of the marsh is uniformly unhealthy. It seems appropriate therefore to reconsider the possibilities that these factors or group of factors may be operating in some other capacity.

It is therefore argued that the effects of sediment conditions between an accreting marsh and eroding marsh would need to be further considered in order to satisfactorily explain *S. anglica* vigour in the field and subsequent marsh succession theory. In the past, the environment components were analysed independently of the studies involving plant morphotypes. By comparing both elements concurrently, would explain why some salt marshes that were rapidly expanding in the last century, may now be in terminal decline and why some salt marshes have appeared relatively stable. The work described below therefore sets out to try and establish the cause of marsh decline on the south coast of England.

The following investigations are proposed:

The morphological variation between *S. anglica* marshes would need to be disaggregated between genetic variation and variability due to phenotypic plasticity adjusting to environmental conditions. This will be carried out by performing greenhouse experiments and reciprocal transplant experiments (Chapter 3).

Concurrently, the physiochemical properties of the various marshes will be ascertained during the reciprocal transplant experiment. This is in order to obtain real-time changes in marsh edaphic conditions and to correlate this with the physiological responses displayed by the transplanted *S. anglica* (Chapter 4).

Thirdly, the results will be discussed to ascertain how the measured factors fared in comparison with other results and where the current theory stands (Chapter 5 and 6).

# Chapter 3: Factors affecting growth of *Spartina anglica* in Salt Marshes on the South Coast of England; Clonal deterioration or Environmental Change

## Introduction

*Spartina anglica* (Hubbard) is a fertile hybrid cord grass that developed from the infertile hybrid S*partina townsendii* (Groves) in the Solent on the south coast of England. This infertile hybrid was the result of a cross between *Spartina alterniflora* & *Spartina maritima*. The hybrid showed great vigour, colonising foreshore mudflats and rapidly spreading from the Solent along the south coast of England and around the British coast (Goodman *et al.*, 1959; Marchant, 1964; Gray *et al.*, 1991). In these early papers., *Spartina* (species unconfirmed) was recorded as being 0.30 - 1.30 m high with pioneering stands expanding radially at the rate of 2-3 m $yr^{-1}$ to form closed stands (Chater & Jones, 1957; Goodman, 1960; Hubbard, 1965). Natural vigour and help from introductions for coastal protection purposes resulted in *S. anglica* rapidly colonising British mudflats and throughout the rest of the world. In some areas it has become a noxious species smothering the mudflats essential for migratory birds and biodiversity (Frid *et al.*, 1999; Hammond, 2001). By the 1930's the Keyhaven and Lymington *Spartina* marshes on the Solent had extended to occupy in excess of 2500 ha of the former mudflats lying between mean low water and mean high water neaps (Tubbs, 1999). By the late 1950's the salt marshes of the south coast of England had formed into extensive raised stands, but it was also noted that the marshes were losing their vigour and areas of *S. anglica* in the inner marsh were dying and turning into mud pans, a phenomenon that Goodman & Williams (1961) termed '*Spartina* die-back'. As the marshes degenerated, what was left of the *Spartina* swards were morphologically inferior to those seen in the past, and the front of the marsh was experiencing extensive erosion. This phenomenon is still present and as a result the once extensive *Spartina* marshes have largely reverted back to mudflats with the *Spartina* marsh breaking into islands, separated by widening creeks and mudflats (Lawn, 2001; Williams, 2006). Die-back and the lack of vigour is widespread in the marshes below a line from Essex (Dengie, Blackwater estuary) through to the Bristol channel (Goodman *et al.*, 1959; Charman, 1991; Bray *et al.*, 2000). In general, north of this line the *Spartina* marshes look healthier and appear to be maintaining their original vigour, (Marchant, 1964; Hill, 1984; Charman, 1991). A similar phenomenon to "die-back" has also been observed in the marshes of *S. alterniflora* in Georgia (USA) and Louisiana (USA), which have experienced a rapid and extensive decline in recent years, with *Spartina* showing lack of vigour and vast tracts of rapidly dying marsh, a phenomenon that has been called "*Spartina* browning" (McKee *et al.*, 2004). The description of the latter phenomenon is not unlike that of the "die-back" observed in the UK, and its causative agent is proving equally elusive.

Since the 1930's the raised marshes have also been experiencing extensive frontal erosion and this phenomenon is still present today. In these marshes, *Spartina* is not observed re-colonising the newly eroded foreshore as it does in many of the more stable marshes such as the Ynyslas marshes on the Dovey. This lack of pioneering vigour on the exposed mudflats that *Spartina* once colonised indicates that either the environment has changed or the hybrid vigour that it once exhibited has been lost. As a result, the once extensive *Spartina* marshes in the south of England have largely reverted back to mudflats, with the *Spartina* marsh breaking into islands, separated by widening creeks (Lawn, 2001; Williams, 2006).

Many studies have been conducted to try to explain this lack of vigour in *Spartina* marshes. The potential effects of adverse soil sediment chemistry in the anaerobic sediments indicate that *Spartina* death and the formation of pans is likely to be related to toxicity problems associated with water-logged conditions and very low redox potential. The results were quite site specific and confined to where die-back is present and less conclusive in explaining the overall poor growth rate in the marsh (Goodman & Williams, 1961; Mendelssohn & McKee, 1988). It has also been noted by a number of authors that there is a relationship between the age of *S. anglica* marsh and subsequent loss of vigour, where successively older marshes were found to suffer from poor regeneration after natural winter die-back (Gray *et al.*, 1991; Thompson *et al.*, 1991a; 1991b; 1991c). Localised populations of plants are known to experience genetic drift (Gray, 1987) and this has been proposed as a possible explanation for the lack of vigour. Other researchers have looked for other explanations for the loss of vigour, for example Holmer *et al.,* (2002); and Pennings *et al.,* (2005) looked at possible effects of physiological factors. Potential fungal or viral causes were investigated by Jones (1980) and Raybould *et al.,* (1998) and nematodes by Mesel *et al.,* (2003), but none of the studies provide an adequate explanation for the lack of vigour. Hence, despite a large body of work we still cannot adequately explain the plants loss of vigour on the south coast of England.

This study was designed to establish if the lack of vigour of the *S. anglica* swards in the Solent is the result of a decline in the vigour of the clonal material or is it the result of changing factors in the environment since its first establishment.

## Materials and methods

The growth and vigour of *S. anglica* was studied at three sites (Figure 1). The 4,230 hectare North Wootton marsh in the Wash, on the east coast of England (UK grid reference TF 59905 256003) where the marsh appears to be expanding; The 600 hectare, Ynyslas marsh on the Dovey estuary on the west coast of Wales (SN 61786 94065) where erosion and regeneration appear to be in dynamic equilibrium; and the 740 hectare Keyhaven marshes in the west Solent on the south coast of England (SZ 30571 90897) where the marshes are in recession.

The North Wootton salt marshes are characterised by accreting foreshore mudflats (Pye, 1995) with unbroken salt marsh extending seaward for up to 1.2 km. The deep silts of the marsh are dissected by drainage channels that are up to 2 m deep. The foreshore is being colonised by *Salicornia europaea* which gives way landward to colonising clumps of *S. anglica,* and eventually to a closed sward where *S. anglica* predominates. *S. anglica*, *Aster tripolium* and *Puccinellia maritima* predominate in the upper marsh. The *S. anglica* looks vigorous and with the exception of topographic depressions it has a high proportion of tall tillers and flowering shoots. Plants at the front of the marsh generally appear shorter than the main body of the marsh, possibly due to the greater time of submergence. There is no evidence of extensive die-back or sward regression (Brown, *Pers. comm.*; Moller, *Pers. comm.*; Garbutt, *Pers. comm.*).

Figure 1: Site map of study areas A) Ynyslas, Ceredigion B) North Wootton, Norfolk, C) Keyhaven, Hampshire, UK. (Orientated north)

The Ynyslas grazed *Spartina* marsh extends along the southern bank of the Dovey estuary extending seaward some 500 m from the sea wall at the widest part. The sediments of the upper marsh are predominantly clay and rich in organic matter, but gets progressively coarser down the gradient until at the forefront of the marsh where it is mainly coarse sands. *S. anglica* and *Salicornia europaea* are the colonising species of the foreshore. The mature sward of the marsh is a mixed salt marsh with *S. anglica*, *P. maritima* and *Festuca rubra* dominating. The mudflats were rapidly colonised by *Spartina* during the 1950's (Chater & Jones, 1957; Goodman *et al.*, 1959) and the *Spartina* is well established with step formations in the marsh and active signs of colonisation of new deposition zones. *S. anglica* plants appear to grow taller in the middle rather than at the forefront of the marsh. *Spartina* die-back was not observed in our site survey, although small areas of shallow pond formation showed no sign of colonisation in the upper marshes.

The western Solent marshes (inclusive of Keyhaven / Lymington / Pennington and Sowley marshes) are rapidly eroding mature marshes, with no recolonisation of the mud at the exposed foreshore. They are protected from wave action by Hurst Spit and the Isle of Wight, with *cheniers* providing local protection along parts of the seaward edge, but despite this they have been in recession since the 1920's (Bradbury, 1995; Tubbs, 1999; Colenutt, 2002) with erosion taking place by both recession of the seaward edge and the widening of the drainage channels, to a point where the marsh is becoming a series of islands. The predominating species of the marsh is *S. anglica* with *Atriplex portulacoides* growing around the salt marsh fringe 'cliff edges'. The sediment is predominantly silty clay with significant amounts of organic matter. The *S. anglica* sward has extensive root systems and shows good tillering in the main body of the sward, although on visual inspection it does not appear as tall as of the other two sites. Die-back occurs in incipient pans and in some areas where it is exposed to strong wave action. The *Spartina* population appears to have lost its pioneering vigour as there has been negligible re-colonisation of the shallow bare mudflats. The sheltered foreshore environment consisted of the site facing the direction of the prevailing winds and conditions. Hawkers Lake (SZ 31100 91100) near Keyhaven was a ideal site as the fore front was relatively intact with bare mudflats, which are approximately 1 m from the main sward and easily accessible. For the sward environment, Hawkers Lake was utilised as it represents an area of mono-specific stands. The lake was also ideal as it required access by boat which restricted access for potential acts of vandalism and tampering from grazing. The plants were colour coded with short bamboo canes bearing coloured tags for easy distinction of each plant.

The pans sites were also identified on Hawkers Lake where areas in the centre of the island appered to be completely denuded of plant material. These areas tend to be concentric in shape and typically 0.15 and 0.2 m lower in elevation compared to the rest of the surrounding marsh. During the winter months the area appears to be inundated with water most of the time, while during the summer month's mosaic cracking was evident during periods of extended dryness. These sites in particular can be highly variable in environmental conditions.

Sowley Pond (SZ 37700 96000) behind a shingle spit is the only known area of the marsh which has experienced colonisation by *S. anglica* in recent years, which is thought to be through unplanned realignment (Nicholls, *Pers. comm.*). Fencing was installed to prevent grazers and the general public accessing the study sites. The site selection for the mudflat, sward and pan site was identified using similar logic aforementioned above for the Keyhaven sites.

### In-situ site measurements

From September through to February 2005 / 2006 each of the sites described were sampled to ascertain the mean morphological characters and conditions of the *Spartina* populations. Although the vegetation was not actively growing, the spikes and leaves of last season's growth were still intact. The sampling areas were checked to ensure that they were representative of the lower, middle and upper marsh zones. On each marsh a sampling area of 1 km$^2$ was divided into four quarters where 10 x 1 m$^2$ randomly selected quadrat were sampled within each quarter, providing forty sampling sites on each marsh. In each, quadrate measurements were made of plant height (from basal node to tip of longest flowering spike) of ten flowering tillers and ten non flowering tillers (from the basal node to tip of flag leaf), tiller density (per m$^2$), leaf length (Mean length of the top three leafs of the tallest tillers, measured from the ligules to the leaf tip), and above ground biomass (dry weight gm$^{-1}$. Chemical measurements were also made at each site of Redox potential (mV), pH, salinity (PSU) and permeability (Auger hole test) (Smedema, *et al.,* 2004)

### Transplant experiment

Comparative transplant trials were conducted on the Keyhaven / Lymington marshes for a period of twelve months, to assess the relative vigour of the North Wootton population with that of the indigenous Keyhaven population in the Keyhaven environment. Large clumps of *S. anglica* were collected from the Keyhaven and North Wootton upper marshes in early November, planted in clumps of 20 to 30 tillers in large containers filled with John Innes 3 compost and kept watered in an unheated greenhouse until transplanting in spring. Efforts were made to only collect *Spartina* which were fully flowering. The two populations were transplanted in March in a fully randomised block of 10 replicates at two locations referred to as Keyhaven and Sowley sites. At each site, blocks were planted in three experimental plots consisting of a) an open mudflat, b) existing *Spartina* marsh (cleared of vegetation) and c) within saltpans thus covering the 3 main soil environments of the marsh. The clumps of sward from North Wootton were split into transplanting material which consisted of about 0.05 – 0.07 m of rhizome material (0.2g ± 0.05 sampling error) with a terminal rhizome tiller and two lateral tillers. The culm heights varied from 0.07 – 0.10 m. Rhizomes from North Wootton and Keyhaven marsh were 0.006 (S.E. ± 0.0005) m and 0.005 (S.E. ± 0.0006) m respectively in diameter. The morphological characteristics of the plants at the site were monitored bi weekly at each of the plots. In addition, seed development and tiller replication was also recorded.

### Glasshouse pot experiment

To help identify the causes of observed morphological differences in *Spartina* at each of the three field surveys, a replicated pot experiment was conducted to identify the potential effects of sediment when environmental factors such as flooding and anaerobic conditions were removed. The three populations of *Spartina* from Keyhaven, Ynyslas and North Wootton were planted in the soils from the same three marshes in a 3 x 3 randomized block experiment with six replicates.

*Spartina* was collected in April 2004 from the pioneering edges of the marshes and divided into transplanting material, consisting of a ramet with a small amount of root and a rhizome of 0.05 to 0.10 m. The plantlets were transplanted into 0.15 m diameter, 0.20 m deep pots with sediment from one of the marshes, North Wootton (75% silt, 17% clay and <6% organic matter), Keyhaven (68% silt, 19% clay, 2% sand 11% organic matter), and Ynyslas (sands coarse 90% and 10% silt <1% organic matter). The plants were placed in an unheated greenhouse to promote early seasonal growth, placed in shallow trays and watered daily with tap water during the spring and summer. Liquid fertiliser (Miracle gro® 15:35:15 @ 3g $l^{-1}$), was added at the start of the second year then once a fortnight during the growing season to avoid nutrient limitations.

Survival, non-flowering plant height, tiller number, leaf area and number of flowering/seeding tillers were measured once every two weeks throughout the trial. Plants were identified as senescing when two thirds of the plant became yellow in appearance and the tillers had not grown in height from the previous measurements. The total above ground biomass was harvested at the end of each year, and the below ground biomass was harvested at the end of the experimental period and dried at 50 °C for 1 week before weighing (Handa & Jefferies, 2000). Regular inspection of the plants for pot bound roots were performed, none were evident until the end of the third season.

**Statistical procedures**

The number of replicates utilised for this study was following the Z table procedures. Previous experiments showed a similar figure of approximately 10 replicates for a transplant experiment to be in a chance of being statistically viable.

The examination of frequency distributions and probability plot of each character indicated no significant deviation from normal distribution; therefore, analysis was performed on untransformed data. Analysis of variance (ANOVA) was performed on the measured values for each characteristic using MINITAB (v.12), to examine the relative effects of populations, treatments and block effect, with blocks as a random variable. Scatter plots of residual values showed no trends, indicating homogeneity of the residual variance. Tukey's LSD tests were performed on main effects, and found to show significant variance. To quantify the relative levels of variability between and within treatments, the variance of the logarithm of the individual measures of each trait was calculated and the F ratio of between and within-environment variation determined. The first, second and third year interactions between sites and populations were tested for significant difference using Shapiro-Wilk's test (Taskinen *et al.*, 2005). All the experiments were originally based on a balanced design. There were difficulties obtaining replicates for certain experimental procedures. In these cases a general linear model was used in which equal importance was assigned to each treatment. Slight deviations from normality were tolerated as analysis of variance have been considered to be robust to $P<0.01$ deviations (Underwood, 1997)

## Results

The *Spartina* on the Keyhaven marsh showed significantly lower plant height and above ground biomass than the other two marshes, being less than half that of the Ynyslas and North Wootton marshes (ANOVA $F_{2,39}$ 3.55 $P<0.01$). The North Wootton population showed the strongest development (Table 1). The *Spartina* in the transplant experiment which were planted in April 2005 failed to establish, the cause of the failure was not identified. The trials were re-planted in 2006, and showed no significant difference in the initial rate of growth in the two populations in any of the plots (ANOVA $F_{2,39}$ 18.123 $P=0.675$). There were however significant differences during the growing season. The survival of transplants in the Keyhaven sward was greater than 98 %, but over winter the mean survival dropped to 75 %. Within the Sowley sward-soils, nearly all plants survived for four months before declining to a final 45 % at the end of the season (Figure 2).
During collection of material, there was signs of moribund areas of the Keyhaven marsh, some of the collected material exhibited signs of rhizome rot, characterised by blackening of the rhizome apex, while the rhizomes of the North Wootton population were white in colour, twice the diameter and exhibited extensive rhizome branching. The *Spartina* on the Keyhaven marsh appeared to have longer roots than that of the other marshes, extending some 0.5 m with little secondary rhizomes. The rooting behaviour of the Ynyslas population varied down the marsh. Plants in the sward area of the upper marsh had well developed lateral roots while those on the lower pioneering part of the marsh exhibited strong well developed deep roots. The North Wootton population lacked long rhizomatous roots but had extensive lateral root systems.

**Table 1: Mean plant height, third leaf length, tiller density and above ground biomass of *S. anglica* growing on the North Wootton, Ynyslas and Keyhaven marshes (± 1 standard error).**

| | Locations | | |
|---|---|---|---|
| Characteristics | North Wootton | Ynyslas | Keyhaven |
| Mean Plant Height (m) | 1.03 (± 0.58) | 0.89 (± 0.55) | 0.41 (± 0.61) |
| Mean Third Leaf Length (m) | 0.65 (± 0.04) | 0.55 (± 0.05) | 0.33 (± 0.05) |
| Density (Tiller/m$^2$) | 352 (± 28) | 338 (± 30) | 187 (± 19) |
| Above Ground Biomass (g/m$^2$) | 747 (± 55) | 689 (± 55) | 273 (± 59) |

Attempts to establish plants on the mudflats at Keyhaven failed, as did replanting attempts in July. The mudflats are known to be eroding (Lawn, 2001; Ke & Collins, 2002) and this may be contributing to the loss. However, the one surviving plant was very poorly developed, smothered in algae and had a blackened root system. Within the Sowley mudflats, the plants survived well until July. However, all the populations progressively died over the following four months (Figure 2). Within the Keyhaven pans the population steadily declined from planting, with 50 % of the population remaining by November, but after over-wintering only 20 % survived. In the Sowley pans the population survived well for the first three months, before declining to leave only 20 % surviving by the start of the following year's growing season. The North Wootton population produced significantly taller tillers and longer leaves in areas where the transplants survived.

In the sward and pan soils the surviving plants of the North Wootton population grew faster at the start of the season than the Keyhaven population, resulting in significant differences in height (ANOVA $F_{2,39}$ 3.22 $P<0.001$) in the mid season. In the pan soils this difference had disappeared by the end of the season. Differences in the length of the top three leaves of the transplants showed a similar response pattern as plant height, with leaves in the sward transplants being longer than those in the mudflat or pan environment (Figure 3). The rooting depths of the transplants of the North Wootton population were significantly longer than those of the Keyhaven population. The rooting depth of transplants in the sward were consistently longer than in both the pans and the mudflats, the latter population dying at the end of the season (Table 2).

The Keyhaven transplanted population effectively stopped tillering from July onwards, while the North Wootton population continued tillering. By the end of the season the North Wootton population had produced significantly (ANOVA $F_{2,39}$ 5.21 $P<0.001$) more tillers than the Keyhaven population, (Total of 17 and 11 tillers respectively).

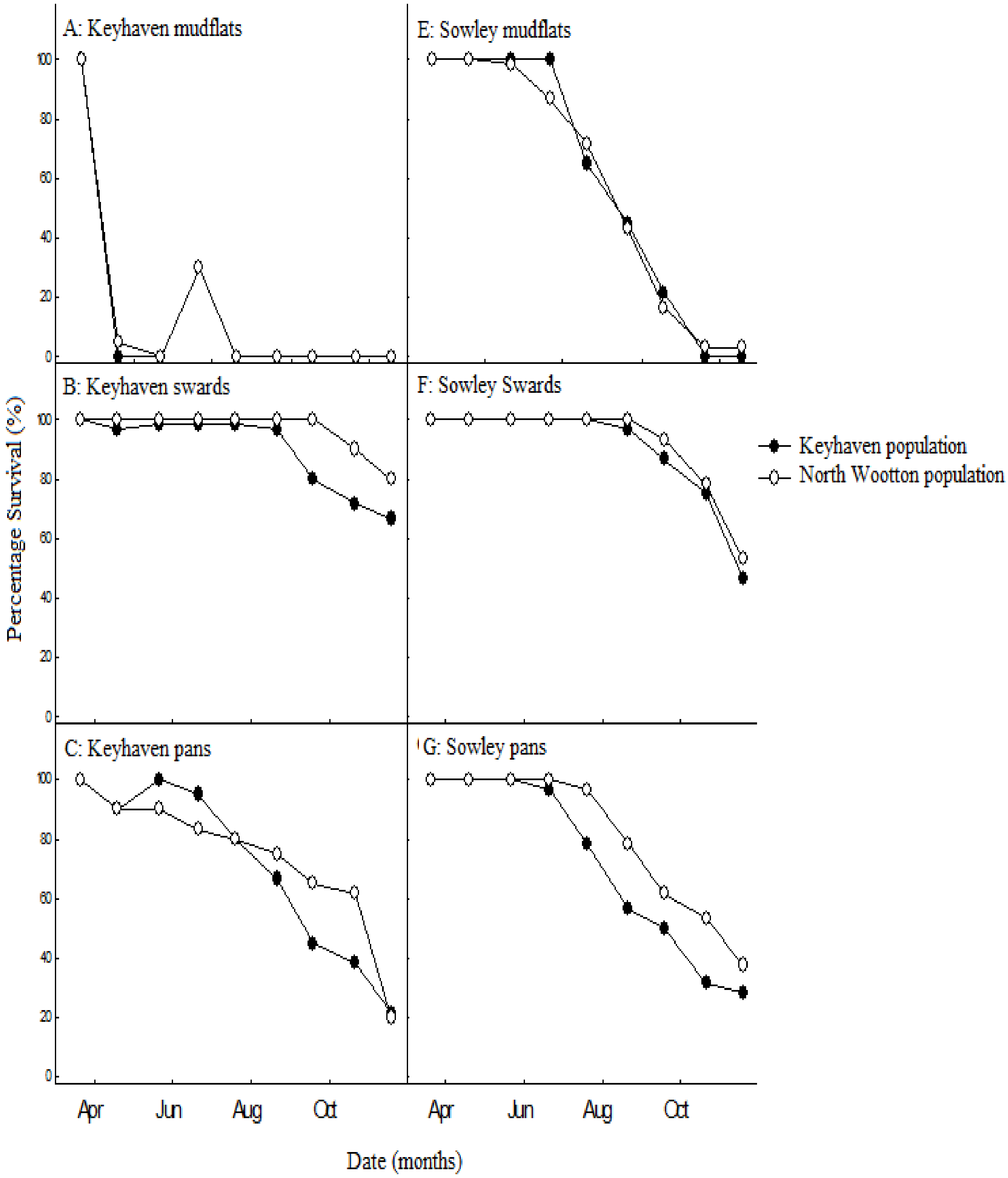


**Figure 2: Survival of Keyhaven and North Wootton populations of *Spartina* transplanted into three different habitats on the Keyhaven and Sowley marshes.**

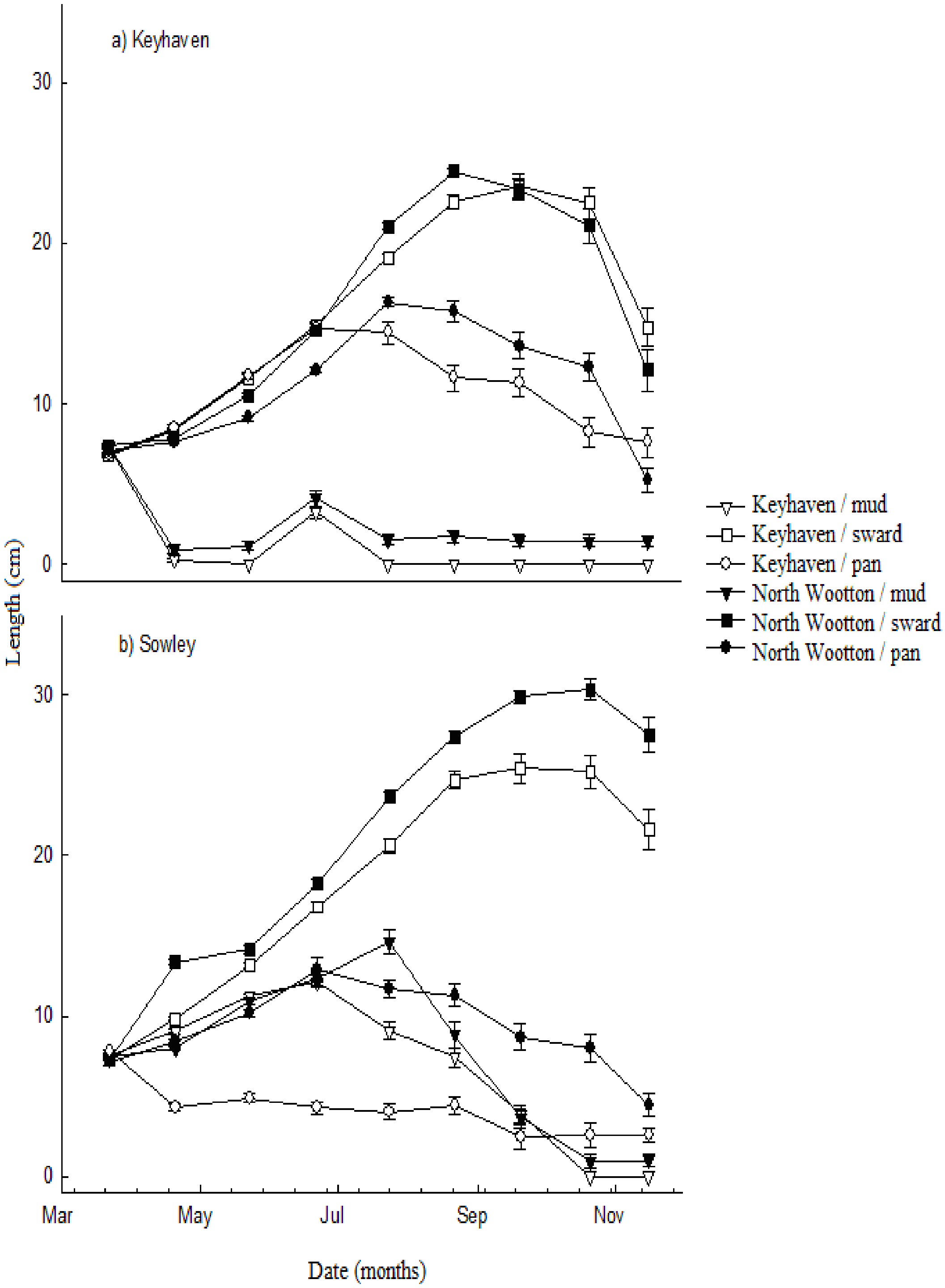


**Figure 3: Mean leaf length of the top three leaves for transplants of *Spartina* populations from the North Wootton and Keyhaven transplanted into the foreshore mud, swards and pan at a) Keyhaven b) Sowley.**

**Table 2: Mean rooting depth (cm) of *S. anglica* of North Wootton and Keyhaven transplants in six habitats on the Keyhaven marsh.**

| | Site | | | | | |
|---|---|---|---|---|---|---|
| | Keyhaven | | | Sowley | | |
| Population | Mudflat | Sward | Pan | Mudflat | Sward | Pan |
| North Wootton | 5.4 | 19.1 | 8.4 | 6.3 | 24.1 | 9.7 |
| Keyhaven | N/A | 13.9 | 2.5 | N/A | 18 | 4.3 |
| Mean (n=54) | S.E. population = ± 2.27 | | | S.E. site = ± 3.64 | | |

The transplants in the sward soils produced significantly more tillers than those planted in the mudflats and pans, (13, 0, 2 respectively). The transplants did not flower although flowering was evident in the surrounding marsh.

### Comparison of plant growth of three populations of *S. anglica* grown in differing sediments

In the glass house transplant experiment the Keyhaven population proved the most difficult to establish, and a few pots required two re-plantings before the trial became fully populated (Table 3), with 98 % of the plants failing to establish within the first month. The Ynyslas planting material also suffered heavy losses during the first month with 33 % needing replanting. A few further deaths were encountered over winter with the North Wootton plants experiencing 4 deaths in the Keyhaven sediments. In subsequent years the Ynyslas and North Wootton populations showed 95 % and 100 % survival respectively, while the Keyhaven population consistently lost approximately 10 % every year. This indicates that the Keyhaven population has a problem re-establishing in sediments which are not common to the plants natural habitat.

The Ynyslas population was significantly taller (ANOVA $F_{2,39}$ 3.22 $P<0.001$) than the Keyhaven and North Wootton population at the end of the first growing season, and significantly (ANOVA $F_{2,39}$ 4.11 $P<0.001$) taller than Keyhaven population at the end of the second and third growth season (Figure 4). This was observed to be the result of the Ynyslas population starting to grow up to a month earlier than the other two populations. There were no significant differences between the heights of the plants grown in the different sediments. At the end of the growing seasons the maximum differences in plant height was 17 % while in their natural environment in the marshes it was 150 %.

Over all three growing seasons the North Wootton and Ynyslas population in the pot experiments produced significantly consistent larger leaf area than the Keyhaven population (17 to 40 % larger respectively) (Figure 4) (ANOVA $F_{3,53}$ 8.31 $P<0.01$). Similar results were also observed for the numbers of tillers produced where despite the slow start in growth season 1, the Ynyslas population consistently produced the greater number of tillers (Table 5) It is important to note that at the end of the first growing season the Keyhaven population had a greater leaf area when grown in the Keyhaven sediments, and that by the end of the third growing season the Keyhaven and North Wootton populations had a significantly greater leaf area when grown in their respective sediments (Table 4).

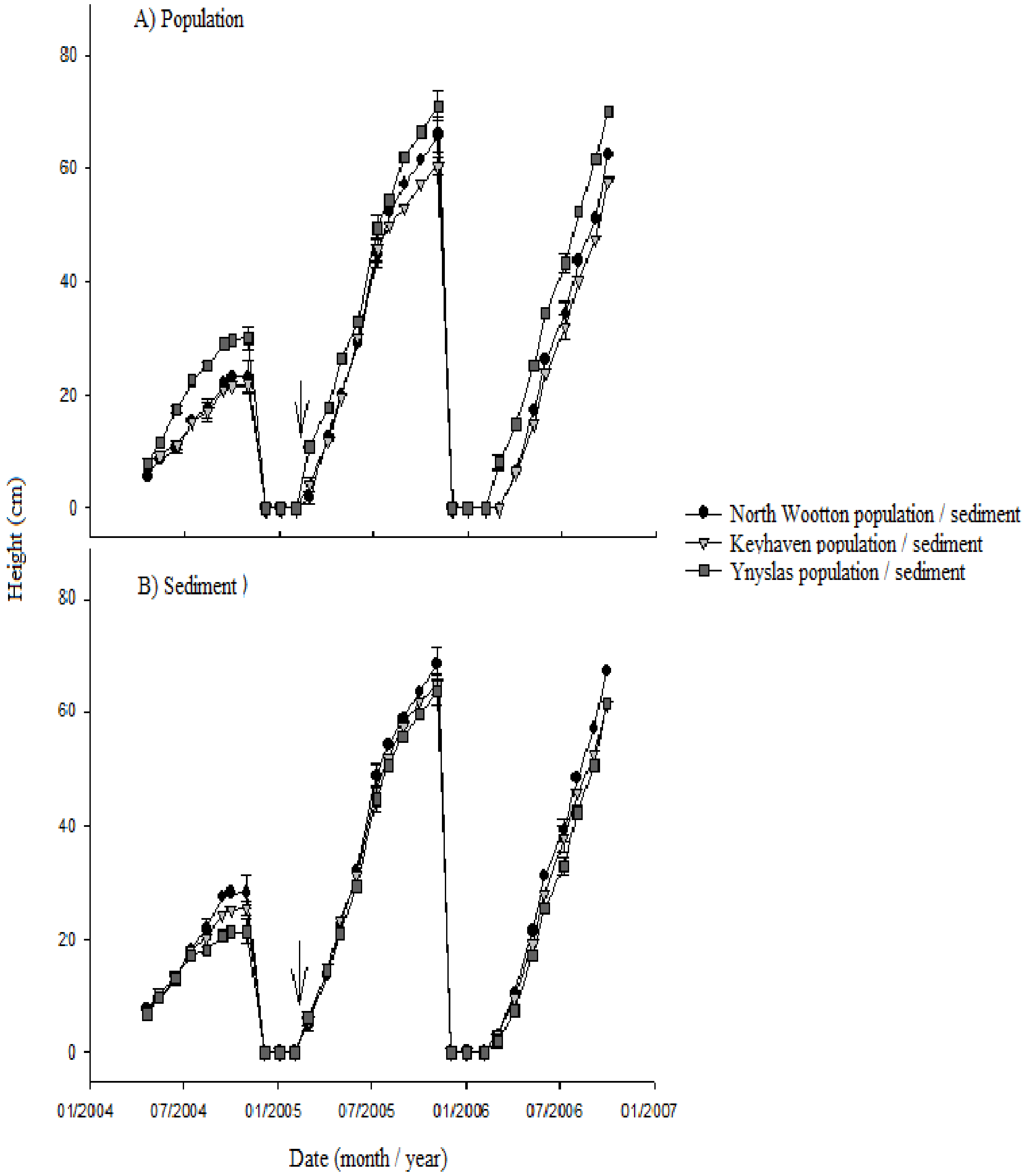


**Figure 4: (a) Mean plant height (mm) of the North Wootton, Keyhaven and Ynyslas populations of *S. anglica* grown in pots. (b) Seasonal changes in mean tallest plant height (mm) of plants grown in sediments from the North Wootton, Keyhaven and Ynyslas (fertilizer added to irrigation water from the date indicated by the arrow).**

**Table 3: Survival of *S. anglica* plantlets in the glass house experiment during the first month after transplantation (counted individuals).**

| | Soil | | | |
|---|---|---|---|---|
| Planting material | Keyhaven | North Wootton | Ynyslas | Total |
| Keyhaven | 3 | 8* | 6 | 17 |
| North Wootton | 0 | 1 | 0 | 1 |
| Ynyslas | 5 | 1 | 0 | 6 |
| Total | 8 | 10 | 6 | |

* Dead plants were replanted after the first month

**Table 4: Mean leaf area (cm$^2$) for the three growing seasons after transplanting (Bold indicates interactions, standard errors (s.e.) = ± 1, mean n = 54).**

| | End of first growth season | | | | End of second growth season | | | | End of third growth season | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Sediment type | | | | Sediment type | | | | Sediment type | | | |
| Population | Keyhaven | North Wootton | Ynyslas | Mean | Keyhaven | North Wootton | Ynyslas | Mean | Keyhaven | North Wootton | Ynyslas | Mean |
| Keyhaven | **33** | 36 | 12 | 27 | **339** | 233 | 259 | 277 | **324** | 249 | 244 | 274 |
| North Wootton | 38 | **57** | 14 | 36 | 318 | **330** | 321 | 324 | 321 | **332** | 326 | 326 |
| Ynyslas | 49 | 51 | 15 | 38 | 393 | 291 | 314 | 333 | 340 | 307 | **378** | 333 |
| Mean | 40 | 48 | 13 | | 350 | 285 | 299 | | 345 | 292 | 307 | |
| Leaf area | s.e. mean = ± 3.6 | | | | s.e. mean = ± 9.1 | | | | s.e. mean = ± 13.1, | | | |
| | s.e. interaction = ± 6.3 | | | | s.e.interaction = ± 15.5 | | | | s.e. interaction = ± 15.8 | | | |

**Table 5: Mean numbers of *Spartina* tillers (tillers per plant) for the three growing seasons after transplanting (Bold indicates interactions, standard errors (s.e.) = ± 1, mean n = 54).**

| | End of first growth season | | | | End of second growth season | | | | End of third growth season | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Sediment type | | | | Sediment type | | | | Sediment type | | | |
| Population | Keyhaven | North Wootton | Ynyslas | Mean | Keyhaven | North Wootton | Ynyslas | Mean | Keyhaven | North Wootton | Ynyslas | Mean |
| Keyhaven | 3 | 3 | 2 | 5 | 13 | 8 | 8 | 10 | **13** | 10 | 10 | 11 |
| North Wootton | 3 | 4 | 1 | 5 | 6 | **19** | 7 | 11 | 8 | **21** | 11 | 13 |
| Ynyslas | 1 | 2 | 1 | 2 | 13 | 17 | **13** | 14 | 11 | 19 | **19** | 18 |
| Mean | 4 | 5 | 3 | | 11 | 14 | 10 | | 11 | 16 | 13 | |
| Tiller N$^{o}$ | s.e. mean = ± 0.29 | | | | s.e. mean = ± 0.96 | | | | s.e. mean = ± 1.05 | | | |
| | s.e. interaction = ± 0.36 | | | | s.e.interaction = ± 1.53 | | | | s.e. interaction = ± 1.6 | | | |

By the end of the first year the North Wootton and Keyhaven populations produced twice as many tillers as the Ynyslas population. However, in subsequent years the Ynyslas populations produced significantly more tillers compared to the other populations (ANOVA $F_{3,53}$ 3.54 $P< 0.001$). A two fold increase in tiller production was observed after fertilizer was added. At the end of the experiment the Keyhaven population produced an average of 10 tillers per plant, significantly less than the North Wootton and Ynyslas population which produced 13 to 15 tillers respectively (Table 5). It is important to note that after fertilizer was added, both the Keyhaven and North Wootton populations produced significantly more tillers in the second year when grown in their native sediments

The Keyhaven population only produced two flowering spikes in the third growing season and none of the seeds were viable. The North Wootton population produced an average of one or two flowering tillers per plant over all three seasons, but seed viability was low with no seeds germinating at the end of the first year, and an average of two viable seeds per plant in the second and third years. The Ynyslas population was the most fertile, typically producing one or two flowering spikes per plant, and producing significantly more viable seeds (27 % ANOVA $F_{3,53}$ 4.22 $P<0.001$) than the other clonal material, with an average of 5, 12 and 3 viable seeds per plant being produced over the three seasons in the Keyhaven, North Wootton and Ynyslas sediments respectively.

All three populations produced a significantly greater weight of root/rhizome when grown in their own sediments, than when they were grown in sediments from the other two marshes (ANOVA $F_{3,53}$ 7.69 $P<0.01$), (Table 6). In the Ynyslas sediment, the Keyhaven population produced significantly less than the other two populations (ANOVA $F_{3,53}$ 4.11 $P<0.001$). There was also an observable difference in rhizome structure; the North Wootton population produced rhizomes before producing lateral buds which grew to become either rhizomes or stems, while the Keyhaven population did not produce many buds and was reluctant to form secondary rhizomes. This difference was most visible in the more free draining North Wootton and Ynyslas sediments.

Multivariate analysis of all measured variables in the pot experiment indicated that the Keyhaven and Ynyslas populations showed the widest divergence from each other (Shapiro-Wilk's $P<0.01$), and that there was no significant divergence between the North Wootton and Ynyslas populations. Keyhaven and North Wootton populations showed sufficient evidence to suggest they were distinct from each other (Shapiro-Wilk's $P<0.001$). These findings were consistent over all three years.

**Table 6: Mean root/rhizome biomass (dry weight g/plant) at end of third growing season.** ***(bold = significant interactions)*** **(n = 54) (s.e. – standard error).**

| | Sediment type | | | |
|---|---|---|---|---|
| Population | Keyhaven | North Wootton | Ynyslas | Mean |
| Keyhaven | **288** | 202 | **90** | 193 |
| North Wootton | 255 | **313** | 214 | 261 |
| Ynyslas | 249 | 273 | **365** | 295 |
| Mean | 264 | 263 | 223 | |

s.e. mean = ± 14.3, s.e. interaction = ± 25.8

## Discussion

Field observations clearly show that the *S. anglica* on the Keyhaven marsh was less vigorous (leaf area, plant height and leaf length) than those on the North Wootton or Ynyslas marshes, being less than half the size. The North Wootton population in the transplant experiment had significantly taller tillers and greater leaf area than the Keyhaven population. These differences were also significant in the replicated pot experiments supporting the hypothesis that the differences could be partly genotypic in nature. Others have also noted significant differences between different populations when grown under controlled conditions and suggested that the differences could be genetic in nature (Taylor, 1965; Hill, 1986; Thompson *et al.*, 1991c). However, under the controlled conditions of the pot experiment differences were only observed in the first year, indicating that the differences are likely the result of carry-over effect (i.e. the vigour of the transplanting material), a phenomena noted by (Hill, 1991). Other pot trials where clonal differences were claimed (Hill, 1991; Thompson *et al.*, 1991a; Thompson *et al.*, 1991c) were not run over sufficient time periods to show that the observed differences could have been a result of the carry-over theory (Mayr, 1963).

In the field transplant trials, the North Wootton population had significantly longer roots than the Keyhaven population. In the sward and pan soils the surviving plants of the North Wootton population grew faster at the start of the season than the Keyhaven population, resulting in significant differences in height by mid-season. In the pan soils however, this difference ceased to exist by the end of the season. Due to restrictions on the Natural England license for this experiment, which was only valid for one season, the experiment was stopped in autumn. Hence these differences could not be attributable to carry-over effects or genotypic differences.

In the pot experiments, considerable difficulty was experienced establishing the Keyhaven population compared with the North Wootton and Ynyslas populations, particularly when in their respective native sediments. Problems of poor establishment of transplants from older populations have been observed by other researchers, who found that transplants from mature old marshes do not fare well in transplant trials or pot experiments compared with planting material from new pioneering populations (Taylor, 1965; Hill, 1986; Gray *et al.*, 1991; Thompson *et al.*, 1991a). All three populations in the pot experiment were from the leading edge of the marsh, but the material from the North Wootton and Ynyslas were from pioneering clumps, whereas because of marsh erosion at the Keyhaven site the transplanting material was most likely from a mature marsh sward. Therefore the results confirm those of earlier experimenters. The cause of poor transplant establishment and development in the first year of material from mature swards is unlikely to be the result of a genetic component as suggested by Bradshaw (1965); Jain (1978); Gray (1985); as the vigour returns and the carry-over effect diminishes in the second and third year.

The above results would suggest that phenotypic plasticity and environmental factors explains most observable differences in tiller vigour between *S. anglica* populations on the different marshes. However, there is some evidence that some genotypic selection of *S. anglica* has taken place. Under controlled conditions the Keyhaven population produced no viable seeds, whereas the other two populations consistently produced viable seeds over three seasons. All three populations developed significantly greater root mass when grown in their own sediment, and the Keyhaven population grew significantly less than the other two populations when grown in the Ynyslas sediments (Table 6). All populations had greater leaf area when grown in their own sediments, which is consistent with Khan *et al.*, (1966) and Jain, (1978) who suggested that some phenotypic plasticity within the populations may be under genetic control. Further, multivariate analysis of all measured variables indicates that there is significant divergence between the Keyhaven and Ynyslas populations.

The lack of establishment in mudflat and pan regions of the Keyhaven marsh indicates that soil conditions are not suitable for colonisation by *Spartina* from either Keyhaven or the North Wootton. This may be the result of adverse effects related to anaerobic soil conditions, a phenomena studied by Goodman & Williams, (1961) and Mendelssohn & Kuhn*,* (2003). It was also noted that the rhizomes of the *Spartina* in the Keyhaven sward exhibited some browning, whereas in the other two marshes this was absent. When established in aerobic Keyhaven potted soils, this condition was not present in the newly developed rhizomes, indicating that it appears to be related to the aerobic conditions of the soil.

It can be concluded that lack of plant vigour and die-back of the *S. anglica* in the Keyhaven / Lymington marshes, compared with the Ynyslas and North Wootton marshes is a complex issue but is mainly the result of differences in the in-situ environmental conditions. Adverse growth conditions in the anaerobic soils, particularly those of the mudflats and pans is a major cause of the poor state of these marshes, but erosive conditions on the foreshore is another factor that could be seriously limiting establishment. Vegetative propagation is the main way that *Spartina* colonises bare mudflat (Marchant, 1964; Raybould, 1988) but a number of studies, including this one, have shown that transplant material from actively expanding stands is essential for good vegetative reproduction of *Spartina*. Such material is lacking on the mature Keyhaven / Lymington marshes and this further reduces the chance of recolonisation of the mudflats exposed by the eroding marsh. Lack of viable seeds also further aggravates the possibility of recolonisation. It is clear from these results that the introduction of plantings from healthier marshes would do little to overcome the loss of the south coast marshes.

The results clearly indicate that sediment conditions in the Keyhaven marsh and foreshore are no longer suitable for establishment and strong growth of *Spartina,* but this constraint is removed if the sediments are allowed to become aerobic.

# Chapter 4: Factors Causing Poor Plant Development and Colonization of *Spartina anglica* in Salt Marshes on the South Coast of England; The Root Environment

## Introduction

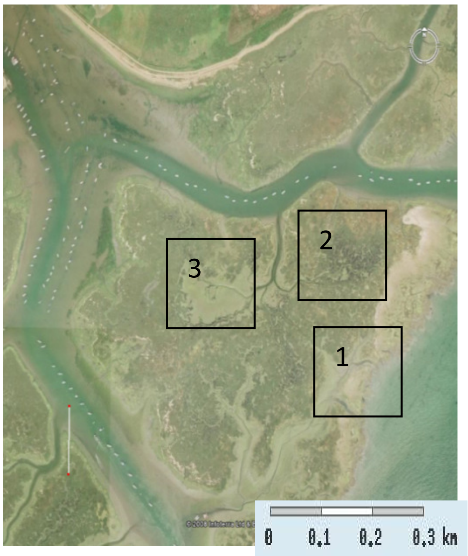
In Chapter 3 it was shown that *S. anglica* on the Keyhaven marshes had lost both the vigour and pioneering ability that it once possessed and which is still exhibited in *S. anglica* on the Ynyslas and North Wootton marshes. This is particularly prominent in the middle of the marsh were swards have died, a phenomenon that Goodman & Williams (1961) coined '*Spartina* die-back'. It was also shown in Chapter 3 that although there may be some clonal differences between the *S. anglica* from the Ynyslas, North Wootton and Keyhaven marshes, the differences were insufficient to explain the poor performance of the *Spartina* growing on the Keyhaven marshes compared with the vigour of the *Spartina* on Ynyslas and North Wootton marshes. A pot experiment also demonstrated that when clonal material from Ynyslas, North Wootton and Keyhaven were grown in pots containing disturbed sediments from the three marshes maintained in an aerobic state, the relative performance of the three clones were very similar and the small differences in performance did not reflect the large morphological differences observed in-situ. This indicates that the environmental factors in-situ are the most likely cause of the poor performance of *Spartina* on the Keyhaven marsh.

Goodman & Williams (1961) investigated *Spartina* 'die-back' in the Keyhaven/Lymington marshes and considered that the phenomenon appears to be linked to water-logged conditions and low redox potential. Die-back has also been observed throughout the world in other species of *Spartina*, the problem being particularly acute in the *Spartina alterniflora* marshes of Mississippi delta region and the southern United States, where it is also sometimes referred to as 'browning', (Delaune *et al.,* 1984; Mendelssohn & McKee 1988; Mendelssohn & Kuhn 2003). It exhibits very similar morphological characteristics to that of the *Spartina* die-back occurring in the UK. McKee *et al.*, (2004), however, attributed this problem to an extended drought period causing vast area of marsh to die while the remaining plants appeared stunted. Alber *et al.,* (2008) also concluded that the most probable cause of die-back was drought, although he also pointed out that there were a number of cases where the evidence pointed to different and often site specific causes, such as snail infestation, smothering with seaweed and changes to the marsh's hydrology. Fungal and bacterial infections have also been noted in weak and dying *Spartina* stands, but Barker (1964) and Ivemy (1966) showed that they were opportunistic after damage resulting from anaerobic conditions.

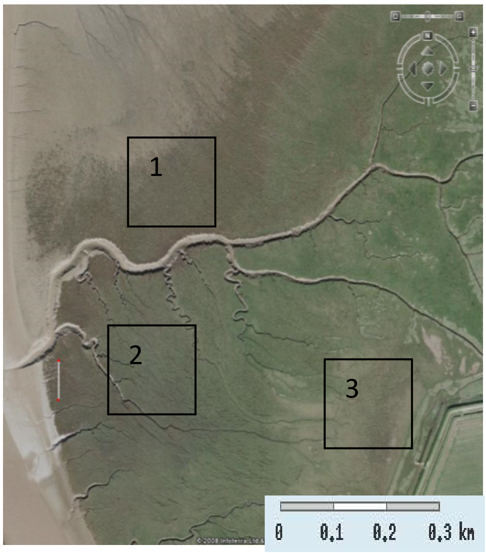
This study investigates the physical conditions of the soil in the sward, pans and foreshore of two marshes. Those of the Keyhaven marsh on the south coast of the UK, that have a long history of die-back and a sward that exhibits a dwarf stature; and a foreshore devoid of pioneering *Spartina* (Ke & Collins, 1993; 2002). In contrast with the North Wootton marsh on the east coast of the UK where the sward exhibits a tall stature, die-back areas are uncommon, and the foreshore dotted with colonising *Spartina* (see Chapter 3).

## Material and methods

The study and sampling locations on the North Wotton and Keyhaven marshes are shown in Figure 5.



Keyhaven



North Wootton

| Site Name | NGR (WGS84 Long – Lat UTC) |
|---|---|
| Keyhaven site 1 | SZ 314 909 (50.718003,-1.555585) |
| Keyhaven site 2 | SZ 314 911 (50.719022,-1.556207) |
| Keyhaven site 3 | SZ 311 910 (50.718213, -1.559640) |
| Wootton Site 1 | TF 592 265 (52.811478,0.363386) |
| Wootton Site 2 | TF 592 260 (52.808106, 0.363793) |
| Wootton Site 3 | TF 599 257 (52.806886,0.372334) |

**Figure 5: Location of the Keyhaven and North Wootton marsh sediment and sampling sites, 1) mudflat, 2) sward 3) pan areas (Main map courtesy of Google and Channel Coastal Observatory).**

The soil temperature and salinity were recorded using a soil temperature thermometer (Standard mercury soil thermometer) and conductivity probe (Jenway model 4070) placed in the wet soil. Redox potential was measured with a sealed platinum tipped electrode (Hanna HI 8014, Thermo Russell KCEPTR11), while pH was measured with a polymer gel filled combination pH electrode (Hanna HI 8014, Thermo Russell KCE11). Both electrodes were pressed into the soil surface at 5 and 20cm depths. The electrodes were left in-situ until the readings stabilised at ±5 mV or ±0.1 pH variation. Measurements were made at monthly intervals between March 2004 to November 2006, with 10 replicates within each of the mudflat, sward and pan locations (N = 10). Infiltration rate was measured using a standard double infiltrometer, and permeability measured using the Auger Hole method (Smedema *et al.,* 2004) with 5 replicates. The depth from surface to water table was measured at 10 locations in July 2007. Elevation data was obtained via a DGPS device (GARMIN Etrex Venture CX).

Diversity and abundance of burrowing macro-invertebrates were determined by digging a 0.15 $m^2$ soil column in July and counting the number of macro invertebrates. Fifteen samples were obtained from each of the mudflat, sward and pan locations. Sediment samples were collected at low tide from mudflat, sward and pan areas from both the Keyhaven and North Wootton marshes in February 2006. Two soil cores were obtained using a length of PVC plastic tube (0.12 m diameter by 1.2 m) inserted into the sediment. The samples were stored intact in the tubes and placed in plastic bags and frozen until analysed. The cores were separated into 0.05 m and 0.2 m sections, wet weighed and dried. The British standard (BS1377-1 1990) method was used to determine particle size distribution. The cohesive sediments (<63µm) were dispersed by use of sodium hexametaphosphate $(NaPO_3)_6$ and sodium triphosphate ($Na_5P_3O_{10}$). The material was dry sieved and the hydrometer method employed for the finer fraction (<63 µm). Organic content was determined by measuring weight loss of dried sediment after heating in a furnace at 550 °C for 4 hours.

### Statistical analysis

Data was analysed using Analysis of Variance (ANOVA), and comparisons made with the Tukey's post-hoc pair wise significance tests between treatments.

### Results

The difference in elevation between the main marsh and the mudflat at all marsh sites varied significantly (between 0.15 and 2.8 meters). There are abrupt eroded high undercut faces on the leading edge of the marshes in the western Solent, but this feature was much less common at Wootton where the foreshore is undergoing colonisation with there being a slow transition in height from the mudflats to the rear of the marsh.

Classifications of soils of the two marshes are given in Table 7 and a summary of particle size analysis with depth in Figure 6. The North Wootton marsh soils were lighter, containing significantly more sand and less clay than the Keyhaven marshes. In both marshes the proportion of sand increased with depth although the North Wootton soils had by far the highest sand content. Silt content tended to decline with depth.

**Table 7: Soil classification of the North Wootton and Keyhaven marshes.**

| | Foreshore | | Sward | | Pan | |
|---|---|---|---|---|---|---|
| Depth | Wootton | Keyhaven | Wootton | Keyhaven | Wootton | Keyhaven |
| 0-0.5 m | Sandy loam | Clay loam | Sandy clay loam | Clay loam | Clay loam | Silty clay loam |
| 0.5– 1m | Sand | Clay loam | Sandy loam | Clay loam | Sandy loam | Clay loam |

The particle size distribution of the sediments across the North Wootton marsh, were more varied than the Keyhaven sediments, which tended to be quite uniform. The pioneering forefront of the marsh at North Wootton had a very high sand content while the mature sward was an organic rich sandy clay loam.

It can be seen in Table 8 that the sward and pans of the Keyhaven marsh contained high levels of organic carbon, 22 and 20% respectfully, while those at North Wootton was lower, particularly in the sward where they fell to <1 %. In the mudflats organic carbon levels at Keyhaven were twice those of North Wootton. These differences were most likely to be due to the high water table observed in the Keyhaven marsh (Table 8), reducing the capacity for oxidation of the organic matter. The water tables in the North Wootton marsh were consistently lower than in the Keyhaven marsh, which are a testament to the higher conductivity (Table 10), and lower precipitation of the North Wootton marsh compared to the Lymington marsh, which were 700 and 1060 mm $y^{-1}$ respectively in 2006. Examination of the organic detritus in the pan soils at Keyhaven indicated that they were once colonised by *Spartina* which explains their high organic matter content

The Keyhaven marsh generally showed a low abundance of burrowing invertebrates (<5 individuals/$m^2$) in the sward and pans although *Hydrobia ulvae* was abundant near the surface. In contrast North Wootton showed an abundance of burrowing invertebrates with *Hediste diversicolor* and *Macoma balthica* being the most prevalent burrowing species identified. The abundance data is given in Table 9.

The soil permeability of the Keyhaven marsh was significantly lower (T-test $P<0.01$) than those of the North Wootton marsh (Table 10). This difference is a reflection of the soils being heavier than those of the North Wootton marsh. The differences in soil texture however, do not appear large enough to explain why the permeability of the Keyhaven sward at $2.94^{-5}$ $ms^{-1}$ are an order of magnitude lower than those of the North Wootton sward at $1.25E^{-04}$ $ms^{-1}$. The most likely explanation for the differences is the poor permeability of the abundant undisturbed organic matter in the Keyhaven sediments.

**Table 8: Soil physical characteristics Keyhaven and North Wootton marshes, (n = 20 unless marked *; standard error (s.e.) ± 1 in parenthesis).**

| | Mudflat | Sward | Pan | | Tukey's Contrast |
|---|---|---|---|---|---|
| **organic carbon (% dry weight)** | | | | | |
| **Keyhaven** | 12.4(± 0.57) | 22.3.± 1.82 | 19.55± 1.29 | P<0.001 | S = P < M |
| **Wootton** | 6.2± 0.31 | 0.8 ± 1.03 | 5.1 ± .49 | P<0.001 | S = P < M |
| **%Soil Water (Gravimetric)** | | | | | |
| **Mar 2006** | | | | | |
| **Keyhaven** | 59.2± 1.47 | 54.6± 1.29 | 64.9± 1.8 | P<0.01 | S = P = M |
| **Wootton** | 38.5± 1.47 | 24.6± 1.31 | 35.1± 1.4 | P<0.001 | S < P <M |
| ***June 2006*** | | | | | |
| **Keyhaven** | 45.8± 0.76 | 45.3± 0.73 | 55.0± 0.56 | P<0.001 | S < P < M |
| **Wootton** | 41.8± 0.62 | 12.6.± 0.53 | 16.1± 0.46 | P<0.001 | S < P < M |
| **Nov 2006** | | | | | |
| **Keyhaven** | 56.7± 0.68 | 50.1± 2.24 | 58.3 ± 0.82 | P<0.001 | M < P < S |
| **Wootton** | 36.2± 0.83 | 28.9± 1.76 | 28.3 ± 0.91 | P<0.01 | M <P = S |
| ***Mean Elevation (above OD) (m)** | | | | | |
| **Keyhaven** | 0.16 | 0.48 | 0.23 | P<0.001 | S < P < M |
| **Wootton** | 0.72 | 2.78 | 1.23 | P<0.001 | S < P < M |
| **Water Table (m from surface)** | | | | | |
| **Keyhaven** | 0.12 | 0.14 | 0.13 | | |
| **Wootton** | 0.44 | <1 | 0.28 | | |
| ***Salinity (psu). n=10** | | | | | |
| **Keyhaven** | 32.6± 0.6 | 32.9±0.4 | 33.1±0.22 | n.s | |
| **Wootton** | 32.7± 0.5 | 32.8±0.3 | 32.4 ± 1.1 | n.s. | |

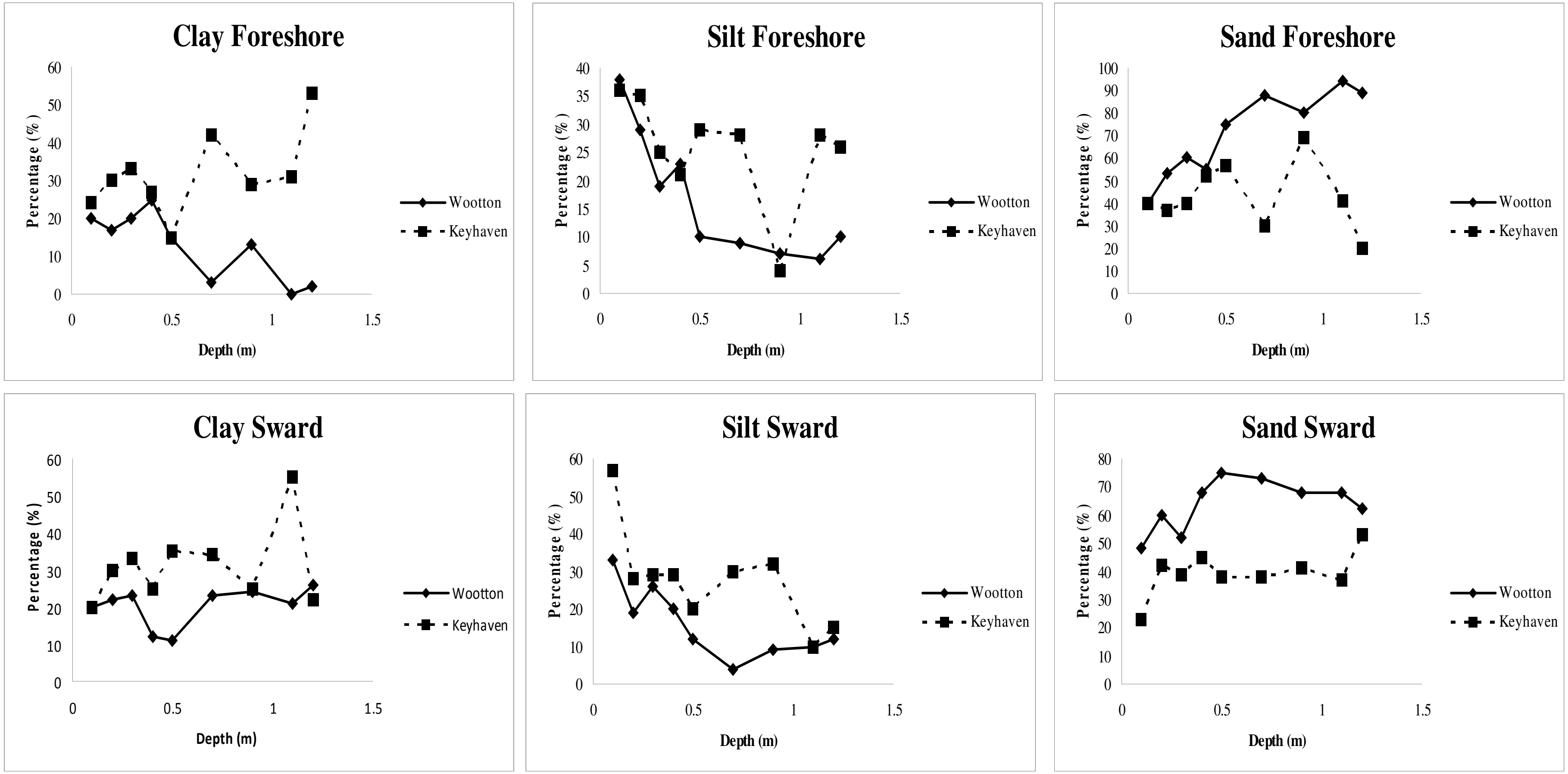


Figure 6: Mean particle size distribution with depth for the soils of the Keyhaven and North Wootton marshes.

**Table 9: Summarised abundance of burrowing invertebrates at Keyhaven and North Wootton marsh (n = 15 per location) (Standard error (s.e.) in parenthesis).**

| | Foreshore | | Sward | | Pan | |
|---|---|---|---|---|---|---|
| | Keyhaven | Wootton | Keyhaven | Wootton | Keyhaven | Wootton |
| Polychaete | <3 | 125 | 0 | 82 | 0 | 49 |
| | (s.e. N/S) | (s.e. ±52) | (s.e. N/S) | (s.e. 48) | (s.e. N/S) | (s.e. ±31) |
| Bivalves | <3 | 162 | 0 | 36 | <4 | 12 |
| | (s.e. N/S) | (s.e.  ±71) | (s.e. N/S) | (s.e. ±18 | (s.e. N/S) | (s.e. ±10) |

**Table 10: Permeability of the foreshore, sward and pans of the Keyhaven and North Wootton marshes, (n=5) (standard error in parenthesis).**

| Site | Foreshore | Sward | Pans |
|---|---|---|---|
| North Wootton | $8.847E^{-05}$ m/s<br>(± $2.967^{-05}$ m/s) | $1.2526E^{-04}$ m/s<br>(±$0.5961^{-04}$ m/s) | $3.564E^{-06}$ m/s<br>(±$1.2986E^{-06}$ m/s) |
| Keyhaven | <$1E^{-9}$ m/s<br>(± N/S) | $2.94132^{-5}$ m/s<br>(±$0.51965^{-04}$ m/s) | <$1E^{-9}$ m/s<br>(± N/S) |

## Seasonal changes in salinity, pH and redox potential

Salinity levels of both marshes were fairly uniform and close to that of sea water at an average of 32 to 33 PSU, although values as low as 27 PSU were observed, which is consistent with the brackish to saline environments.

There were only minor seasonal changes in soil pH at 0.05 and 0.20 m depth in the sward, pan and mudflat soils of the Keyhaven and North Wootton marshes; it remains between 7 and 8 throughout the year (Figure 7). The exception was the soil at 0.05 m depth in the pans at Keyhaven where the pH started to fall from its winter level of 7 to 7.5 in June, and falling to a mean of 5.3 (with extreme measurements of 4.4) being recorded in August, before rising again to just above 7 in late September when water logging conditions resumed. The depressions of Keyhaven pans generally contained surface water during the winter and spring months as these regions of marsh are highly impermeable, but in the summer months they dried with surface cracking being observed to depths of 0.08 to 0.12 m, and ferrous oxide was observed on the surface indicating aeration of the surface layer.

The redox potential of the North Wootton marshes remained consistently higher than the Keyhaven marshes (Figure 8). In the North Wootton marsh the redox potential at 0.05 m depth did not fall below -100 mV in the sward, pan and mudflat soils and rose above +100 mV in the summer months. At 0.15 m depth the redox potential of the North Wootton soils followed a similar pattern as the sward soils, but the soils of the pans and mudflats fell between -150 to -190 mV in the winter, before rising in summer with redox potential of the marsh and pans rising to +100 mV and the foreshore to about -40 mV.

The redox potential of the Keyhaven sward soils at 0.05 m depth exhibited a similar behaviour to that of the Wootton soils throughout the year, with only slightly lower redox potentials in winter of -100 mV compared with the – 50 to -80 mV in the North Wootton sward soils, (Figure 8). At 0.15 m depth the redox potential of the sward soils at Keyhaven fell from close to zero in August to -160 mV in winter. In contrast to the North Wootton foreshore, sediments at Keyhaven remained anaerobic all year with the mean redox potential falling to -260 mV in winter and rising to -50 mV in the summer. The redox potential of the pan soils at 0.05 m depth at Keyhaven fell to –200 in the winter but rose for a short period in summer to an average of +94 mV. The increase in the redox potential in the surface layers of the Keyhaven marsh was the result of surface drying and cracking and FeO deposits could be observed on the surface of the pans in July due to iron oxidation. The rapid decline in the redox potential of the Keyhaven marsh in autumn coincided with the start of the demise of transplanted plants described in Chapter 3.

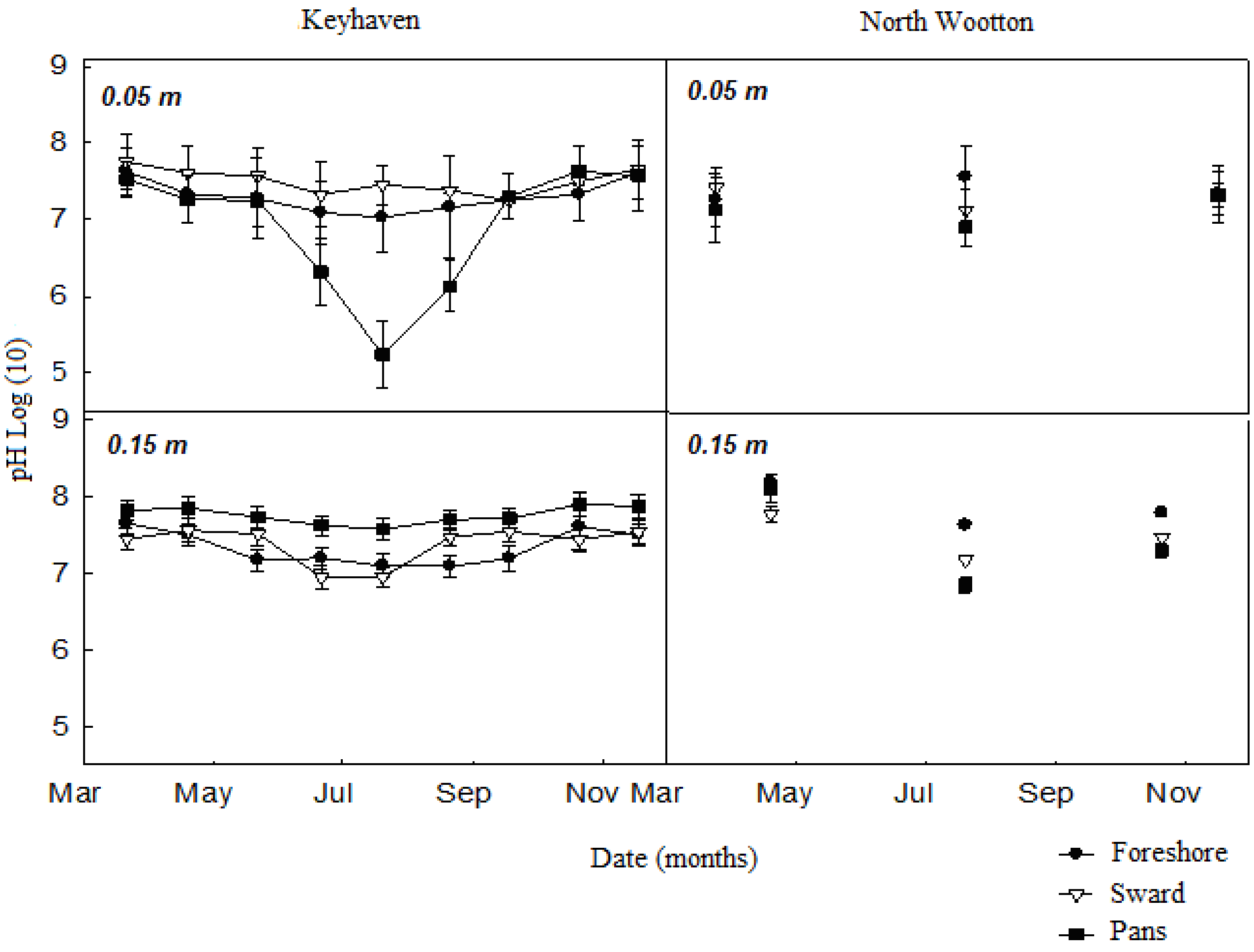


**Figure 7: Mean pH of Foreshore, sward and pans at 0.05 and 0.15 m in Keyhaven and North Wootton marshes) (n = 10) (bars indicate standard error (s.e.) ± 1).**

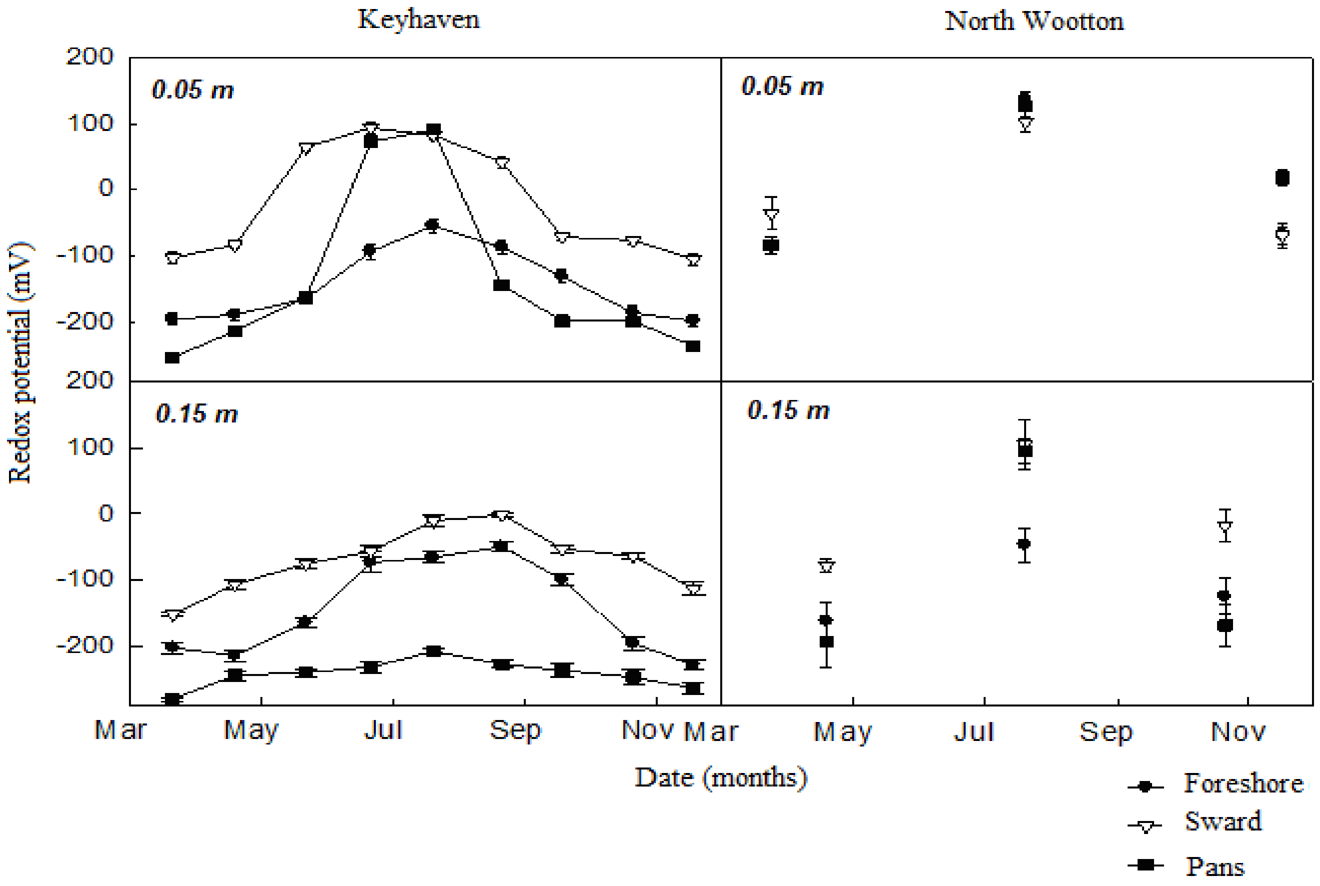


Figure 8: Redox potential of foreshore, sward and pan at 0.05 and 0.15 m at Keyhaven and North Wootton (n = 10).

## Discussion and conclusion

In areas with low redox potential the plants at Keyhaven showed signs of reduced growth, poor rootlet formations, shallow rooting depth and browning of some roots. The low redox potentials observed on the Keyhaven marshes when compared with those of the North Wootton marsh are the result of low hydraulic conductivities, which lead to water-logging conditions throughout the marsh. This is brought about by the heavier soils of Keyhaven marsh compared to that of North Wootton marsh.

A number of workers have demonstrated the link between low soil redox potential and the poor growth of *Spartina sp.* Goodman's (1957) investigations of the decline in vigour of *S. anglica* in the Solent showed that extended anaerobic conditions in these marshes result in the marsh dying. Since then several workers have also shown the correlation between poor *Spartina* growth and plant death as a result of aerobic soil conditions brought about by poor drainage (Mendelssohn *et al.,* 1981; Pezeshki & Delaune 1988; Pezeshki *et al.,* 1989, 1991). Mendelssohn & Seneca (1980) found that root elongation of *S. alterniflora* was reduced as soil Eh approached values below c. +350 mV and further decreases when soil Eh fell below +200 mV. He also observed that the net photosynthetic rate decreased as soil Eh declined, with the rate of photosynthesis declining to 40 % of the control with a soil redox potential of -180 mV. He concluded that low soil Eh has an adverse effect on plant functionality and that there is a need for periods of soil aeration to allow plants to resume normal functioning. The redox potential of the sediments at Keyhaven was also a long way below the -50 mV that Anastasiou & Brooks (2003) noted resulting in a sharp decline in plant health. Mendelssohn *et al.,* (1981) who observed *S. alterniflora* metabolic activity in field anoxic conditions, argued that the root tissues in *S. alterniflora* does not conduct sufficient oxygen to the roots for complete aerobic respiration in highly reduced substrates. They proposed that root oxygen deficiencies occurring in *S. alterniflora* may produce variations in its height and productivity.

Many authors have used the oxidation-reduction potential as an indicator of the reduction state in wetlands and salt marsh soils (Quispel, 1947; Gotoh & Yamashita, 1966; Armstrong, 1967; Bagander & Niemisto, 1978; Armstrong *et al.,* 1985; Pezeshki *et al.*, 1989; Argese *et al.,* 1992; Naidoo & Naidoo, 1992; Kostaka & Luther, 1995; Osgood & Zieman, 1998) and have also concluded that the distribution and production of plants in these environments are positively correlated with sediment redox values. Low redox potentials at Keyhaven are brought about by poor drainage which results from a combination of the soil having a high silt/clay content and high organic matter, that both reduces hydraulic conductivity to a level that ensures low redox potentials in anaerobic conditions. These conditions do not exist in the marshes where the sediments have good drainage properties such as North Wootton.

It can be concluded that the most likely cause of *Spartina* die-back in the south coast marshes of England, is due to very low redox potentials, particularly in the autumn and winter as first noted by Goodman (1960).

The water-logged conditions at Keyhaven have resulted in appreciable organic matter building up due to lack of oxidation in the anaerobic soils conditions. Organic matter content at Keyhaven is very high at up to 70 %. At this level the organic matter is likely to impede drainage as it takes on the properties of peat which typically only have hydraulic conductivities of $10^{-5}$ to $10^{-8}$ $ms^{-1}$ (Wong *et al.,* 2009), thus aggravating the problem of poor drainage further as the amount of organic matter accumulates. The high organic matter content is also expected to increase the oxygen demand of the soil which further reduces the redox potential of the water-logged soils.

A number of researchers in the United States consider that the sudden death of *S. alterniflora* on the south east coast marshes could be the result of a dry summer (McKee *et al.,* 2004; Smith, 2006; Alber, *et al.,* 2008). This may be the case as drying out of anaerobic sulphur rich saline marsh soils is known to result in a crash in pH to very low levels, due to the production of sulphuric acid and the formation of acid sulphate soils which kills all life (Dent, 1986). The only highly anaerobic soils in this study that showed signs of drying out and a drop in pH were surface layers at Keyhaven pans which fell on average to pH 5.2 ( lowest 4.4) but these showed a rapid rise to 7.5 when aerobic conditions were re-established in autumn. If the soils had dried out further the pH could well have crashed to toxic levels, since in the laboratory when the soils were artificially dried they crashed to 2.6 which would certainly have resulted in the death of *Spartina*. Acid sulphate marshes have the potential to become neutral as the sulphate ion is reduced back to sulphite, thus hiding the cause of the die-back. Although this could well be the cause of death of the Southern United States marshes it does not appear to be the cause of die-back on the south coast of England, where moisture content changed little throughout the year and low pH was only observed in pans that were devoid of vegetation.

If the soil conditions in a marsh are such that water-logged conditions exist for most if not all of the year, stunted growth and 'browning' can be expected to occur and that over time the build up of un-rotted organic matter is expected to lead to even lower redox potential and more problems with die-back as the marsh matures. Most drainage in fine particle soils is known to take place through the macropore structure of the soils (Tanton *et al., 1988*). The Fauna of the soil plays a major role in creating this structure through their network of burrows. Unfortunately, as the redox of the soil falls the population of invertebrates collapses as evidenced by the results in Chapter 3, with the very low populations in the anaerobic soils at Keyhaven and the high populations in the sediments at North Wootton. This loss of macropore drainage channels therefore leads to even lower hydraulic conductivity, water-logging and extremely low redox potential.

When *S. anglica* colonised the mudflats in the Solent it was fast growing and exhibited strong hybrid vigour until the late 1950's when the older swards began to lose vigour and large area of die-back appeared (Goodman, 1960). The question must then be asked why did *S. anglica* become established in the first place in these fine textured silts and how have conditions changed? Prior to the arrival of *S. anglica* in the Solent the salt mashes were fairly modest in extent compared with what they reached in the 1950's following the arrival of *S. anglica*. They did not extend into deep water and hence the depth of the sward soils was fairly shallow compared with the depths that are observed today. These marshes appeared to have been fairly stable (Ke & Collins, 2002). This would indicate that the marshes were not as anaerobic as they are today otherwise they would have been suffering from extensive die-back and this is not reported in the literature. This may have been because the marshes were not so expansive and this allowed adequate lateral drainage to prevent excessive anaerobic conditions developing. The possible explanation for this is that when *Spartina* first colonised the unconsolidated mud and extended the marsh into deeper water, the original foreshore must have had reasonable permeability to allow it to colonise. The organic matter levels could also have been fairly modest due to high invertebrate activity, thus reducing the potential for extremely low redox potential and providing ideal conditions for *Spartina* colonisation. Once established the marshes were reported to extend rapidly across the mudflats and rise rapidly, (up to $0.15 g/cm^2/year$), (Ke & Collins, 2002). It is known that marshes with a high rate of sediment accretion do not exhibit die-back or weak growth as presently observed in the Keyhaven marsh. Two possible explanations for this exist. Firstly, in a marsh with a supply of fine sediment as the sward rapidly rises there is new sediment for the roots to occupy and the density of dead roots does not have time to accumulate to a sufficient level to reduce hydraulic conductivity, but as the height of the marsh grows as a result of overburden pressure, the lower deposited sediments compact over time and the dead organic matter accumulates to a level that reduces permeability and increases oxygen demand, with the result that anaerobic conditions begin to prevail. Secondly, since the colonised unconsolidated sediments of the Keyhaven foreshore has high silt and clay content, as the marsh develops, the original foreshore sediment beneath the rising marsh is surcharged with an ever increasing depth. This overburden pressure brings about partial consolidation of the underlying foreshore sediments making the sediment less permeable. Clearly, if these changes reduce permeability to a critical level die-back will result. The low permeability of old foreshore sediments exposed by erosion described in this paper indicates that this process could easily be the explanation for the decline in vigour of the Keyhaven marshes.

It is interesting to note that in the once rapidly eroding marshes in the Solent, *Spartina* does not recolonise the exposed mudflats as the marsh recedes. This is as described in the reciprocal transplant trials in Chapter 3. This is perhaps not surprising given the low hydraulic conductivity and the accompanying low redox potential observed in this thesis. There are two possible causes of this, the first is as described above, when the foreshore sediments were overrun with colonising *S. anglica* marsh; the fine sediments were consolidated to a level that inhibits effective drainage when erosion of the marsh exposed them. The second is that the ebb currents have removed the unconsolidated top layers leaving deeper consolidated layers exposed.

There is also evidence in Langstone Harbour on the south coast of England that consolidation of sediments and anaerobic conditions is the cause of lack of vigour in the old marshes and re-colonisation of mudflats exposed by erosion is sparse. Where changes in channel morphology have lead to sediment deposition zones on the edge of the degraded marsh, *Spartina* is showing the original vigour it showed when the harbour was originally colonised.

In conclusion, the low redox potential resulting from water-logging is the cause of *Spartina* poor growth, die-back and pan formation in mature swards in the south of England. The balance between healthy mature marshes, such as the one observed at North Wootton, and the ailing marshes of the south coast is dictated by the balance between fine and coarse soil particles in the sediments. If they are such that anaerobic conditions prevail for much of the year the vigour of the *Spartina* sward can be expected to deteriorate. The vigour of *Spartina* stands varies across the marsh, while this may be due to small changes in the soil permeability, other localised factors are also likely to play an important role in fine tuning the outcome, such as tidal characteristics, submergence time, location in the marsh, exposure to waves, precipitation (Ranwell, 1963; Ranwell *et al.,* 1964; Pye, 1993; Moller *et al.,* 1999; Quaresma, 2003). Although pH did not appear to be a significant factor in die-back in the Solent marshes, the acidification of the surface soils during summer in the pan soils at Lymington provides support for the work in the USA that implicated drought as being the likely cause of the massive die-off that was experienced over vast tracts of *S. alterniflora* / *Typha alternilflora* marsh (Brown & Pezeshki, 2007).

# Chapter 5: Salt Marsh Development

Salt marshes develop and thrive in sheltered shallow coastal environments that either have a positive or neutral sediment balance. Although these environments are inherently unstable, most marshes tend to exist in dynamic equilibrium with the physical forces of nature that influence them over long periods of time. This equilibrium can however easily be destabilized by human activities and there are many examples where localised loss has occurred as a result of channel dredging and widening, river diversion, construction of coastal defence and land reclamation, (Ranwell, 1972; Adams, 1990; Reed, 1990; Pethick, 1993). In the past century land reclamation has been the main cause of loss with up to 80 % of European salt marshes being lost as a result (Mobberley, 1956; Ranwell, 1967; Drok, 1979; Bakker, *et al.,* 1993; Dugan 1993; Castillo *et al.,* 2002;). Nevertheless in the UK, north of a line between the Bristol Channel and the Wash there are still many examples of areas of salt marshes that appear to either be in dynamic equilibrium with their environment or expanding, such as can be seen in the marshes of North Wootton on the east coast and in the upper Solway Firth on the England / Scotland border on the west coast. These marshes like many marshes have existed for centuries (Adam, 1990; Boorman, 2003).

There are however, many locations on the south coast of England where in the past 50 years the areas of salt marsh that once appeared to be in dynamic equilibrium or expanding have been declining, but the cause of the decline is not obvious (Gray *et al.,* 1991; Johnson, 2000; Boorman, 2003). These areas of marsh are of high ecological value and play an important part in providing cost effective coastal protection in many locations. Their loss is therefore of considerable importance. This chapter sets out to establish why the *S. anglica* marshes in the south of England are declining while many marshes appear stable or in some cases expanding.

## Developmental history of the south coast of England salt marshes and their decline

The salt marshes in the natural harbours and estuaries of the south coast of England have existed for many centuries. The mixed sward was typically made up of *Armeria maritima*, *Plantago maritima*, *Puccinellia maritima*, *Aster tripolium*, *Atriplex* *portulacoides,* and *Spartina maritima.* In the early 1920's, however, a hybrid *Spartina* developed in the Solent on the south coast of England. This new species showed strong hybrid vigour becoming the predominant species in the sward of the existing marshes and colonising the foreshore to depths far beyond that which its parent species could survive -0.96 m O.D. (Hubbard & Stebbings, 1968; Adams & Bate, 1995) Its hybrid vigour allowed the area of marsh to rapidly expand as it spread throughout the Solent estuary and along the south coast of England, the spread being speeded by artificial introductions to stabilise mud flats, (Gray *et al.*, 1991). Introductions have since spread it throughout the world with the result that its success has resulted in it becoming a noxious weed having destroyed valued habitats in a number of locations (Daehler & Strong 1996; Petit, 2004; An *et al.,* 2007).

By the late 1950's, there were extensive *S. anglica* swards within the Solent on the south coast of England, with the total area of the Lymington / Keyhaven marsh alone being some 2500 ha extending several hundred meters seaward (Tubbs, 1999). Much of the front of the marsh was protected from wave action by *cheniers* which developed as the marsh rose, but where the *cheniers* were absent the waves eroded steps of up to 1.5 m high on its leading edges. Since the 1950s however, the area of marsh has been declining and at the current annual rate of erosion at the periphery of between 1.8 m and 5.4 m a year the final demise of the marsh is inevitable. The New Forest District Council estimates that the salt marshes will cease to exist by some date between 2030 and 2040 (Colenutt, *pers. comm.* 2009). This pattern of loss of *Spartina* marshes has occurred in all but a few of the marshes that once thrived along the South Coast of England, for example in Poole harbour, Tamar Estuary and Langstone harbours (Hubbard & Stebbings, 1968; Gray *et al.,* 1991; Tamar Estuary Conservative Forum, 2006).Many people have considered why the south coast marshes of England might be disappearing and many theories have been put forward as possible causes including, *Spartina* 'die-back', loss of sediment supply, increased storminess and / or wind increasing erosion, pest and / or disease attack, loss of genetic vigour, boat wash erosion, and sea level rise, (Goodman & Williams, 1961; Teal & Weiser, 1966; Hubbard & Stebbings, 1968; Manners, 1975; Parrondo *et al.,* 1978; Linthurst & Seneca, 1980; Marks & Mullins, 1984, Koch & Mendelssohn, 1989; Gray *et al.,*1990, Marks & Mullins, 1991; Raybould *et al.,* 1991a, 1991b; Thompson, 1991a, Thompson 1991b, Thompson 1991c; Pye, 1995; Moller *et al.,* 1996; Gray *et al.,* 1998; Johnson, 2000; Ayres & Strong, 2001; Ainouche *et al.,* 2003; Plantard & Bardou-Valette, 2007;). Although some of these causes can clearly explain some local areas of marsh loss, none can explain the widespread nature of the decline. Many authors have argued that the main cause of marsh loss on the south coast has been caused by the so called 'die-back' that occurs as a result of anoxic soil conditions, (Goodman, 1957; Goodman *et al.,* 1959; Lambert, 1964) However, despite extensive research with studies extending back as far as the late 1950's there has been no conclusive evidence that any one of them can adequately explain the demise of the south coast marshes nor why in general, apart from the effects of obvious anthropogenic activities, the area of the *S. anglica* marshes further north on the east and west coasts of Great Britain are not in general decline (Johnson, 2000).

In both *S. anglica* and *S. alterniflora* marshes four kinds of sward decline can be noted;

1) A general decline of vigour in the marsh with tall vigorous swards of *Spartina* declining over time to the dwarf form, characteristic of the Lymington/Keyhaven marshes (Goodman *et al.,* 1959) and in many *Spartina* marshes vigorous and dwarf forms can be observed in different areas of the marsh (Shea *et al.,* 1975);

2) Marshes, in which patches die, but not exclusively in the inner marsh, the dead marsh usually forms pans. A phenomenon readily observed in many marshes sited on fine sediments, (Tubbs, 1984). Goodman *et al.,* (1959) referred to this as 'die-back';

3) Widespread rapid death of the marsh that may appear over one season, a phenomenon that occurs extensively in *S. alterniflora* marshes on the south east coast of the USA (Mendelssohn and McKee, 1988). With this type of rapid dieback is thought to result from drought causing a temporary hostile soil environment and the sward has been observed to slowly recover over a number of years (Alber *et al.,* 2008).

4) Loss of the raised marsh as a result of frontal wave and creek erosion without re-colonisation of the exposed foreshore (Cooper *et al.,* 2001; Lawn, 2001).

Many authors assume they have a common cause and do not differentiate between the different symptoms, and look for one generic cause of *Spartina* marsh decline, or death.

Salt marshes only develop in intertidal areas that are sufficiently shallow and protected from wave action to allow marsh establishment. Protection may be provided by any one of a number of features. The gently sloping shallow foreshores that allow wave energy to be dissipated before it reaches the shallows, land masses limiting wind fetch, spits, bars and *cheniers* that intercept the waves and protect the shallows behind them from wave action. What is clear from visual inspection of the marshes on the south coast of England is that loss is mainly occurring as a result of erosion of the vertical step on the leading edges of the marsh. With erosion of the creeks, the channel profiles appear concave. This loss is clearly observed from aerial pictures, an example of which is shown below (Figure 9). Where the area of *Spartina* marsh is declining, the plants generally show poor vigour and there is little or no re-colonisation of an apparently suitable foreshore. The question that then arises is what has changed that has caused these marshes to change from expanding to declining? This chapter argues that there are three types of marshes, those which are expanding, those in dynamic equilibrium with their environment, and unstable salt marshes. Although marshes may change from one form to another if the nature of their environment changes.

**Figure 9: The dispparence of salt marshes in Lymington can be seen in two aerial photographs in 1946 and 2008 (Courtesey of Channel Coasal Obersavtory).**

## Expanding *Spartina* marshes

These types of marshes occur where a suitable *Spartina* species has been introduced into an un-colonised suitable habitat such as occurred in the Solent in the 1920s (Groves, 1927) and more recently in China (Li, 2009), or where existing *Spartina* marshes are on flood dominant shores with an external supply of sediment which provides an accreting foreshore, as can be observed in the North Wootton marshes in the Wash on the east coast of England (Pye, 1995). In this environment the front of the marsh does not have a steep frontal erosion step caused by wave erosion, and the foreshore is characterised by clumps of colonising *Spartina* stands which merge to form a closed sward in the upper foreshore. The marsh then steadily rises to a plateau level at the back of the marsh. The shallow foreshore and the colonising clumps of *Spartina* reduce wave energy and effectively protect the front of the rising mature marsh from coastal erosion, (Moller, *et al.,* 1996; 1999). These marshes can thrive in either coarse or fine sediments. The side creeks of these marshes tend to appear convex in profile. If further expansion is halted due to deep water or exposure to wave action beyond the protected area, the area of marsh is likely to come into dynamic equilibrium.

## *Spartina* marshes growing in dynamic equilibrium with their environment

These types of marshes develop in sheltered coastal habitats with flood dominant or balanced tidal prisms with only small changes in estuary / beach sediment balance, and where the sediments have sufficient permeability to prevent the development of highly anoxic reducing conditions. The Ynyslas marshes which are in the flood dominant south bank of the predominately ebb dominant Dovey estuary, (Brown & Davis, 2007; 2010) appears to exhibit this kind of behaviour, see Chapter 3. In these marshes, *Spartina* is able to colonise the foreshore seaward to a depth / flood duration which is characteristic of the species, which in the case of *S. anglica* in the Solent was -0.96 m (Hubbard & Stebbings, 1968). Over time the new swards increase in height as they trap sediment from the incoming tide until they come into equilibrium with the height of tide. The rate of rise depends on the amount of suspended sediment and the height of the marsh relative to mean high tide level (Ranwell *et al.,* 1964). *S. anglica* in particular has been shown to be able to colonise deeper water than other salt marsh species (Ranwell, 1972; Adams, 1990), and hence has been able to expand the area of many of these marshes. It is postulated that if the foreshore is not undergoing sediment deposition from outside sources, the level of the foreshore in front of a young developing marsh can fall as a result of mobilization by wave action, and sediment being transported up onto the marsh on the incoming tide. This is a phenomenon that has been observed in the Solent (Lawn, 2001). In the absence of a bar or *cheniers* to protect it wave action erodes the front face of the mature marsh, and as a result the seaward face retreats landward. In a flood dominant environment as the marsh retreats sediment tends to be re-deposited on the foreshore. As the level of the foreshore rises again it can be recolonised by *Spartina* and over time in the absence of a bar or *cheniers*, wave action erodes the front face of the mature marsh and as a result the seaward face retreats landward. As the marsh retreats sediment tends to be re-deposited on the foreshore. As the level of the foreshore rises again it can be recolonised by *Spartina* and the cycle begins again. The result is that over time the marsh exhibits distinct step and terrace geomorphology, the height of terrace rising towards the back of the marsh, a phenomenon that can be observed today in the Ynyslas marshes in the Dovey estuary.

The second type of location is to be found on foreshores and mudflats in sheltered locations with ebb dominant tides where the external supply of sediment is equal to the export of sediment. In these locations *Spartina* marshes can also be in dynamic equilibrium with their environment, as long as one of two criteria's are fulfilled, either the ebb tide velocity is insufficient to mobilize the sediment, or the site has sufficient external supply of sediment from marine and/or riverine source to balance the tendency of ebb dominant tides to export sediment. The barrier marsh at Blakely Point on the west coast of England is a good example. In these marshes the tidal prism is strongly ebb dominant but cliff erosion provides a reliable source of sediment to balance export, (Burningham & French, 2006). Because ebb dominant tides favour the export of fine sediments, "stable" marshes in these locations tend to consist of coarse sediments. If the supply of sediment becomes cut off as a result of coastal protection work and/or the supply of sediment reduced due to dredging work, then the area of marsh would be expected to decline.

## Unstable *Spartina* marshes

Instability in a marsh can clearly be brought about by changes in the physical environment. For example, a decline in sediment supply in an ebb dominant system as described above. Instability that can cause marsh erosion can also be brought about by changes to the bathymetry as a result of meandering or dredging of the main channel, which in turn can cause areas of estuary that were once flood dominant to become ebb dominant (Dronker, 1986). Changes in wave climate brought about by natural coastal processes or manmade structures are also known to affect marsh stability (Moller, *et al.,* 1999). We consider that there is also another form of instability that can be brought about by the colonisation of *Spartina* itself, the very act of which can initiate a self destruct mechanism. It is proposed that this process explains most of the loss of marshes on the south coast of England. This phenomenon is explored below.

The estuaries and harbours of the south coast are predominantly ebb dominant but because of hydrographical characteristics they contain shallow areas where the tidal prism can be neutral or flood dominant and where historically sediment accumulated to form tidal flats (Dyer, 1997). It is in these sheltered areas that salt marshes develop. The arrival of *S. anglica* on the south coast in the 1920's with its ability to grow in deeper water than existing salt marsh species allowed the existing salt marsh to extend seaward onto unconsolidated foreshore sediments deposited in geological time (Tubbs, 1999).

As already pointed out, unless there is an external supply of sediment the height of developing marsh rises at the expense of the sediment on the uncolonised foreshore. This results in an increase in the depth of water in front of the marsh, as was observed on the Keyhaven marshes in the Solent, (Ke & Collins, 1993; Lawn, 2001). This increase in water depth immediately in front of the marsh is expected to increase the amount of wave energy impacting on the front of the marsh, thus increasing the rate of frontal erosion.

As the developing marsh traps sediment and rises from the foreshore it changes the geometry of the environment with the mean height of the marsh rising from a sloping foreshore, that was below mean sea level, to a fairly flat marsh with a height well above mean high sea level.

A dendritic network of channels and creeks provide drainage for the waters of the outgoing tide.

If the front of these types on marsh are protected by stable *cheniers* they can remain as a marsh in dynamic equilibrium with their environment for some time, but if they are not protected from waves by some form of physical protection the marshes become susceptible to erosion by waves at low tide, (Quaresma, 2003). This change can however, have a dramatic effect on the sediment balance of the coastal environment as these changes impact on the local bathymetry which in turn affects the nature of the tidal prism. Dronkers (1986) showed that in irregular shaped basins (meandering and braided channel systems with tidal flats) the tidal current variation is influenced by the geometry and that two types of geometry can be distinguished. 1) Shallow channels with depth decreasing landward with tidal flats below mean sea level and 2) Deep channels throughout, tidal flats above mean sea level. In the first case he argues that the period of slack water before ebb will exceed the slack period before flood and that these conditions will favour the import of fine sediment. In the second case the inverse is true and sediment export is favoured. Hence, the development of *Spartina* marsh in flood dominant locations within predominantly ebb dominant estuaries without a large external supply of sediment, will favour a switch to ebb dominance and the export of sediment. The creeks that carry much of the tidal inundation water from the interior marsh over the foreshore on the outgoing tide deepen and widen under the ebb dominant condition,s with the sides of the channels going from a convex profile that is observed in accreting conditions to concave. These deep channels act as a drainage conduit for the receding tide, providing rapid pathways for the export of the sediment mobilized from the edge of the marsh.

After erosion of a mature marsh the sediment foreshore again becomes reinstated, but despite their being shallow water areas of foreshore Sp*artina* appears to be reluctant to recolonise it. Then the question arises, why *Spartina* is not recolonising these areas like those in marshes that are in dynamic equilibrium with their environment. It has been shown that there has been no significant decline in hybrid vigour and that if transplanted into disturbed sediments in pots it can establish and thrive, as described in Chapter 3. The only possible cause of lack of colonisation is that it must be the result of changes in its local environment that has taken place as a result of colonisation and erosion of the *Spartina.*

In temperate regions *S. anglica* can develop and thrive in sheltered shallow marine environments in a wide range of soil types in water depths up to -0.96 m O.D. (Chapter 3; Hubbard & Stebbings 1968; Adams & Bate, 1995). It is however reluctant to colonise poorly drained fine grained organic rich sediments and plant establishment can be very difficult. If established, plant development is poor and the plants short lived (Chapter 3; Groenendijk, 1986; Hill, 1986). These sediments have long periods of water-logged conditions in winter that create extremely low redox potentials in the surface soils, (Chapter 4; Ranwell *et. al.,* 1964; Linthurst, 1979; Linthurst and Seneca, 1981; Argese *et al.,* 1992; Otte *et al.,* 1993; Leendertse *et al.,* 1996; Boorman *et al.,* 2001. Although *S. anglica* is tolerant of mildly reducing soil conditions it is highly sensitive to moderate to severe reducing condition, (Chapter 4; Delaune *et. al.,* 1984; Koch *et al.,* 1990; Van der Welle *et al.,* 2007) with the exception of sands, nearly all marine sediments rich in organic matter are anaerobic at depth. For instance Spencer, (2002) showed that above 0.10 m depth the silty sediments of the Medway estuary in the UK tended to be oxic or only mildly reducing, but at lower depths redox potential could be as low as -350 mV. Evidence presented in Chapter 4 indicates that extreme low redox conditions tend not to occur in the shallow surface layers unless sediments have high clay/fine silt content and/either contain water-logged organic matter or become consolidated to an extent that effective drainage is prevented. The work also showed that extreme anoxic conditions rarely occur in summer at shallow depth in unconsolidated sandy or free draining silty sediments, such as can be found on Ynyslas sediments in or the North Wotton marshes, since they tend to be sufficiently free draining that when the tide goes out air enters the shallow surface layers. Aeration is also encouraged by tunnelling macro invertebrates such as polychaete worms (*Nereis sp.)* and bivalves (*Macoma sp.)* which thrive in these soils (Gribsholt & Kristensen, 2002). Unfortunately, anaerobic conditions do occur in summer in the surface layers of the heavier consolidated fine heavy textured soils such as those observed in the Keyhaven mudflats and pans that have very low permeability, and shown in Chapter 4. *S. anglica* cannot survive.

The question then arises is how could *S. anglica* have colonised the mudflats of the south coast of England in the 1920's and 30's that it is now reluctant to recolonise the mudflats in the same locations. The most likely explanation is that it is due to changes in the soils properties. The density of marine estuarine clay/silt sediments is known to vary widely depending upon a number of factors such as the sand fraction, duration of consolidation, organic matter, and microorganisms, slope, duration above water levels and previous history, but as is normal in soils the density generally increases with depth for any given soil type, (Torman, 1999; Bale *et al.*, 2007; Amos *et al.*, 2010). Old mature sediments that have been compacted by overburden pressure tend to be the densest whilst recently laid down sediments have the lowest density (Torman, 1999). Recently laid down sediments can have a density of < 1.2 while old compacted sediments can have densities above 1.7 and it is recognised that in some cases dense surface sediments may result from changes in channel geometry exposing sediments once compacted by overburden pressure, (Bale *et al.*, 2007). As the density of a given sediment increases the permeability decreases, for example Torman, (1999) showed that the permeability of recently settled mud from the river Scheldt decreased by an order of magnitude, from about $1 \times 10^{-5}$ to $4 \times 10^{-6}$, when the density increased from 1.1 to 1.25 $\text{tm}^3$. Clearly the permeability of any given sediment may be affected by many factors as well as bulk density and in particular soil class, organic matter and biological activity but for any given sediment permeability is expected to decrease as the soil becomes compacted.

It is therefore proposed that the lack of recolonisation of exposed mudflats resulting from marsh erosion in the ebb dominant estuaries of the south coast of England is the result of the eroded sediments not resettling on the foreshore, and that the exposed mudflats are denser than when they were first colonised and that this was brought about by compaction of the underlying sediments from the overburden pressure of the raised salt marsh. As a result of these increased densities permeability has declined dramatically and the redox potentials fallen below the level that will allow *Spartina* to re-establish.

## Discussion and conclusion

Although the types of marsh described above are all distinguishable in the field it is clear that there is a progressive transition between all types of marsh and all intermediate stages can be found in natural systems depending on the sediment soil class, the nature of the tidal prism, local bathymetry and tidal range.

By their very nature, all coastal environments are in a state of flux and their morphology changes over time. Although some of these changes occur in geological time, others can be quite abrupt, such as changes brought about by exceptional storms or human activities which may cut off the supply of sediment to the whole marshes. Within an estuary, although the tidal prism may in general be described as neutral or predominately ebb or flood dominant, there are normally considerable variation in the intensity and direction of tidal dominance depending on the presence of flood and ebb channels. Natural and anthropogenic changes in the coastal environment can also bring about change in the nature of the tidal prism which can bring about a change from one type of marsh to another, for instance from stable or expanding to one which is either in dynamic equilibrium or declining. Nevertheless these types of changes tend to be local in nature and do not explain the widespread losses that have and are occurring in the *Spartina* marshes of the south of England.

# Chapter 6: General Discussion

It is clear from the literature that many factors affect the growth and development of *Spartina* and any one of them can cause decline in the wellbeing of the sward in localised areas. However, from the review of the literature it is clear that some environmental variables appear to be less important than others in affecting the wellbeing of the *Spartina sp.* swards, for example smothering by algal or debris mats, pollution, change in hydrodynamics of the local environment, and overgrazing all tend to be localised phenomena (Chapman, 1960; Ranwell, 1961). Other factors, however, have a much more devastating effect, like the sudden death of vast areas of *S. alterniflora* observed over the south eastern states of America following a dry summer (Mendelssohn & McKee, 1988).

Many workers have suspected that clonal genetic deterioration could be the cause of decline in plant vigour on the south coast of Britain and other locations around the World, but the work described in Chapter 3 and the work of others (Thompson *et al.,* 1991 a.b & c), indicate that although clonal differences in *S. anglica* and *S. alterniflora* may be present, the differences are not large enough to explain the large disparities in morphological forms, tall, medium and short, that are observed in different marshes or even in the same marsh.

It is therefore concluded in Chapter 3 that the differences in vigour observed in the field are most likely the result of phenotypic differences resulting from environmental factors and are not of genotypic origin.

The work described in Chapter 4 and the literature (Mendelssohn *et al.,* 1980, 1981; Delaune *et al.,* 1984; Pezeshki, 1989; Prasittikt & Gambrell, 1989; Anastasiou & Brooks, 2003) clearly shows that the observed differences between morphological growth forms of *S. anglica* in the marshes of Britain are positively correlated with soil redox potential, with dwarf growth forms appearing in marsh soils that experience long periods of water-logging and consequently develop highly reducing conditions. The removal of the anaerobic soil conditions in a glass house experiment, Chapter 3 resulted in the recovery in the vigour of stunted *Spartina* collected from the Keyhaven marsh, with growth being similar to that of clonal material collected from vigorous *Spartina* stands on the Ynyslas and North Wootton marshes. At extremely low redox potential the *Spartina* plants die and new plants cannot colonise those sediments. The work of others also strongly supports these conclusions, (Delaune *et al.,* 1984; Gambrell *et al.,* 1991; Anastasiou & Brooks, 2003). Although reducing conditions in the soil appear to explain the lack of vigor in the *Spartina* swards of the Keyhaven marshes it does not explain their widespread decline which is clearly resulting from erosion of the marsh edges.

Many authors do not differentiate between the different symptoms, and look for one generic cause of *Spartina* marsh decline or death after assuming they have a common cause. Some of the underlying causes of decline may be linked while others may be independent. The decline in the vigour and wellbeing of *Spartina sp.* has been widely reported with four kinds of decline being recognisable:-

1) A general decline of vigour in the marsh with tall vigorous swards of *Spartina* declining over time to the dwarf form characteristic of the Lymington/Keyhaven marshes (Goodman *et al.,* 1959; Mendellssohn & McKee 1988). The work described in Chapter 4 points to low soil redox potentials resulting from water-logging being the cause of many cases lack of vigour and poor growth..

2) Widespread rapid death of the marsh that may appear over a season, that occurs extensively in *S. alterniflora* marshes on the south east coast of the USA and which was initially termed 'browning'. The general consensus of researchers is that this type of death is most likely the result of adverse short term changes in soil chemistry brought on by drought (McKee *et al.,* 2004; Smith, 2006; Fine & Thomassie, 2007). Salinity associated with drought conditions was considered to be a possible cause of loss since salinity can have an adverse effect on *Spartina* growth and development, but field evidence is lacking (Brown & Pezeshki, 2007). Another serious phenomenon is the readily reversible short term extreme acidification of the sulphate rich soils on exposure to air as discussed in Chapter 4. To date however the underlying cause remains unclear.

3) Marshes, usually located on heavy sediments, with patches of dying marsh. This is usually but not exclusively evident on the inner marsh in which over time the dead areas of marsh form pans. This phenomenon is readily observed in many marshes sited on fine sediments such as the marshes on the south coast of England. Goodman *et al.,* (1959)

referred to this as ‘die-back’. The work in Chapter 4 also links this with low soil redox potentials which inhibit growth and possibly vegetative spread, but which are not low enough to prove fatal.

4) Loss of the raised marsh as a result of frontal wave and creek erosion without recolonisation of the exposed foreshore (Lawn, 2001; Fragaso, 2001)

It is also suggested that the ‘browning’ should be reserved for the rapid death of *Spartina* such as occurred in the southern states of America, (McKee *et al.,* 2004; Smith, 2006; Fine & Thomassie, 2007) and those deaths resulting from low redox potential that have been noted in both Britain and America should be called by the name given to it by Goodman *et al.,* (1959) “*Spartina* die-back”.

The major decline in the area of marshes at Lymington/ Keyhaven is the result of frontal and creek erosion, although it is clear that *Spartina* die-back accounts for the development of pans and some localised areas of degeneration (Chapter 4). Then why is erosion happening at some marshes but not at others. Lawn, (2001) showed that since the period of *Spartina* colonisation, expansion and decline of the Lymington/ Keyhaven marshes there has been no change in wave height, wind velocity, wind direction and frequency of storms, therefore these factors are unlikely to be linked with marsh erosion driven decline. The Portsmouth tidal gauge data shows that sea level rise in the Solent is approximately 1.8 mm per year and that it has been at that level through the period of *Spartina* colonisation, expansion and decline, so sea level rise is not thought to be linked to the decline in area of the Lymington/ Keyhaven marshes.

The argument was made in Chapter 5 that the main cause of loss of the Lymington/ Keyhaven marshes is frontal and creek erosion of the mature marsh and that the failure of *Spartina* to re-establish itself on the newly exposed sediments of the foreshore. The demise of the *S. anglica* marshes of the south coast of England is most likely the result of its own success that set in motion an inevitable self-destructive process. The basis for this argument is that in ebb dominant estuaries, such as most of the south coast estuaries of England, *S. anglica* establishes itself on the areas of foreshore that because of local bathymetry are either flood dominant or flood/ ebb neutral. Under such conditions incoming tide is faster than the outgoing tide and hence the sediment balance is positive (Dronkers, 1986; Pethick, 1993).

When these mudflats become colonised by *Spartina,* the surface of the marsh rises and changes the bathymetry in the immediate area of the marsh to one that is expected to have extensive shallow flats at high tide and deep gullies and creaks. Such profiles are known to be ebb dominant with high velocity on the outgoing tides (Dronkers, 1986) which favours export of sediment. Hence, as the edges of the marsh are eroded by wave action the sediment is exported with the receding tide. Chapter 5 argues that the only way this net export can be prevented is if there is an external supply of sediment. It further argues that *Spartina* is then unable to recolonise the exposed foreshore sediments because of is low redox potential resulting from poor permeability, which is the consequence of the historic overburden pressure of the eroded marsh.

The decline of the *Spartina* marshes of the south coast of England is of considerable concern both from an environmental perspective, with most of the marshes being local or national designated and many of them being designated as internationally important under the RAMSAR wetlands convention. The UK therefore has an international obligation to maintain them. They are also very important in providing soft coastal sea defences that alleviate the need for very expensive coastal defence works. There is therefore considerable pressure to try to halt their decline and if possible reinstate some of the eroded marsh. However the cause of decline raises particular difficulties for both retaining the existing areas of marsh and for reinstatement of lost marsh as both would require that the profile of the localised foreshore be altered to one that is considered to be flood dominant, i.e. shallow channels with depth decreasing landward with tidal/marsh flats below sea level.

## Chapter 7: Recommendations

The management options for a particular marsh depends on both whether they are eroding, stable, or expanding and the nature of the environmental factors that are affecting the wellbeing of the marsh

This work was initiated to try and establish the cause of decline of the *S. anglica* marshes on the south coast of England with the hope of then developing a methodology to reverse their decline. Unfortunately, the work argues that the most likely cause of decline of the marsh area is a change in the tide dynamics, from a flood dominant tidal regime to an ebb dominant regime, which was brought about by the very establishment of *S. anglica* on a flood dominant foreshore which inadvertently changed the bathymetry of the foreshore. As the foreshore soils of the Keyhaven/ Lymington marshes consist of thixotropic cohesive marine sediments it makes engineering interventions very difficult, as these sediments are inherently of very low strength (Amos, *et. al.* 2010). If the area of marsh is to be increased the marsh environment would need to be changed, from one which favours deep channels and extensive tidal flats above mean sea level, to one with shallow drainage channels decreasing in depth landward with tidal flats below mean sea level as the latter favours flood dominance.

It is therefore suggested that in eroding *Spartina* marshes that have developed profiles that favour the net export of sediment, the engineering solution has to be either lower the marsh level to below mean sea level to reinstate flood dominance or to change the hydrodynamic nature of the area to make it a net importer of sediment.

Some recent marsh engineering example are presented in Appendix C. Using experiences from the past examples, lowering the profile of a marsh to below mean sea level is not technically feasible without destroying the salt marsh itself. This just leaves the option of making an eroding marsh a net importer of sediment. There are two ways in which this might be achieved, 1) increasing the regular external supply of sediment to a level that exceeds the rate of erosive losses and/or 2) decrease the level of erosion. In practice the solution could be a combination of both. In most circumstances providing a regular increase in the supply of sediment is not practical and one of dumping of sediment, such as that tried in Pool Harbour, (Pool Harbour Commission, 2008 is unlikely to be effective in the long term as the hydrodynamic regime becomes out of sync and the system will work to regain the status quo. Therefore the only potential viable option would be an off shore structure such as a breakwater that would both reduce wave high, and the rate of erosion and to change the tidal patterns in the local vicinity to encourage localised flood dominance and increased sedimentation. Numerical models could help identify the optimum geometry of such offshore structures to create sheltered lagoons and investigate their ability to favourably modify the tidal prism in the vicinity of a marsh to one which is flood dominant. Unfortunately such solutions are likely to prove costly to implement and to some extent be unproven technology. In the end it must be a political and socio economic decision on whether such expensive solutions can be justified, as opposed to the alternative of letting nature take its course and then build hard engineered coastal defences in locations where it is deemed to be economically viable. Although socio economic justifications are not the remit of the thesis an example of such processes are described in Appendix D.

## Chapter 8: Further Work

Over the past 50 years there has been a considerable body of work published on *Spartina sp*. which makes it almost unique, as it is not a crop or even an iconic species. The arrival and spread of the new species *S. anglica* generated research interest through its ability to colonise new exposed mudflats, providing coastal protection and sediment stabilisation at low cost (Brampton, 1992). *Spartina* marshes are important for wildlife both because of the foreshore habitat that they can destroy and the marsh habitat that they can create. When the *Spartina* marshes started to disappear the benefits that they had created in many locations began to be lost, and this prompted the second surge in research. Of particular concern in many locations is the loss of coastal protection when the marshes are disappearing, and the cost involved in providing hard engineering solutions to once again protect the coastline and the important wildlife habitats that these areas provide.

Since erosion is the major cause of salt marsh loss, a better understanding is needed of the process that takes place in the foreshores fluid dynamic environment. This is where colonisation by *Spartina* can change the sediment erosion and deposition process, during which the life cycle of marsh from creation to its ultimate loss can be observed. Such an understanding is essential if engineers are to create an environment to sustainably support salt marshes.

Another important aspect of *Spartina* loss is the compacted anaerobic fine sediments of the degraded foreshores that are exposed when *Spartina* marshes are lost as a result of erosion. Research is needed to establish if the conditions that once existed in the downgraded foreshore sediments, can be recreated to an extent that *Spartina* can once again recolonise it. Such research would need to increase sediment permeability, while at the same time preventing erosion of the disturbed sediment.

# Appendix A: Example of factors controlling the growth of halophytes in salt marshes (Adapted from Fragoso, 2001)

| Type | Factor | Reference | Chapter reference |
|---|---|---|---|
| Biological / Ecological | Seedling vigour and survival | (Kneebone, 1972, Seneca, 1969) | Appendix B |
| | Genetic variation | (Ainouche *et al.,* 2001; Ayres & Strong, 2001) | Chapter 3 |
| | Vegetative Expansion | (Adam, 1990; Hill, 1986) | Chapter 3 |
| | Pollen limitation | (Bertness & Shumway, 1992) | Appendix B |
| | Seed production | (Daehler & Strong, 1994, Marks & Truscott, 1985, Mullins & Marks, 1987) | Appendix B |
| | Seed unavailability | (Groenendijk, 1986, Marks & Truscott, 1985, Mooring *et al.*, 1971) | Appendix B |
| | Parent Plant Density | (Bertness & Yeh, 1994, Castellanos *et al.*, 1994) | Chapter 3 |
| | Clonal Age | (Thompson *et al.*, 1991a, Thompson *et al.*, 1991b, Thompson *et al.*, 1991c) | Chapter 3 |
| | Nutrient Availability | (Ewing *et al.*, 1994, Wilsey *et al.*, 1992) | N/A |
| | Temperature | (Seneca & Blum, 1984; Long *et al.,* 1975; Mallott *et al.,* 1975; Dunn *et al.,* 1981) | Chapter 4 |
| | Competition | (Hudson, 2001,; Beeftink, 1985; Bertness, 1991) | N/A |
| | Grazing | (Ranwell, 1961) | N/A |
| Hydrological / Sedimentary | Tidal Inundation | (Howes *et al.*, 1981, Ranwell, 1964, Reed & Cahoon, 1992) | Chapter 4 |
| | Water-logging | (Goodman & Williams, 1961, Mendelssohn & McKee, 1981, Mendelssohn & McKee, 1988; Fragoso, 2001) | Chapter 4 |
| | Interstitial Water Movement | (Wiegert *et al.*, 1983; Gardner, 2005; Harvey *et al.,* 1987; King *et al.,* 1982) | Chapter 4 |
| Hydrological / Sedimentary (cont.) | Wave Action | (Morley, 1973; Moller *et al.,* 1999) | Chapter 4/5 |

| | | | |
|---|---|---|---|
| | Sediment Erosion | (Lee & Partridge, 1983; French & Spencer, 1993; Hutchinson *et al.,* 1995) | Chapter 4/5 |
| | Soil compaction | (Metcalfe *et al.*, 1986) | Chapter 5 |
| | Inadequate seed dispersal | (Huiskes *et al.*, 1995) | Appendix B |
| | Inadequate Photoperiod | (Hubbard, 1969; Hubbard & Partridge, 1981) | N/A |
| | Local Salinity Levels | (Adam, 1990, Deleeuw *et al.*, 1991, Nestler, 1977, Ungar, 1962, Waisel, 1972; Parrondo *et al.*, 1978) | N/A |
| Climate Change | Climate Change | (Gray & Moog, 2001) | N/A |
| Pollution | Heavy Metals | (Mrozek, 1980, Mrozek & Funicelli, 1982; Foy *et al.,* 1978 Fizgerald *et al.,* 2003; Gambrell, 1994; Gambrell *et al.,* 1991) | N/A |
| Pathogens | Herbicides | (Truscott, 1984, Hammond, 2001) | N/A |
| | Ergot | (Raybould *et al.,* 1998 Eleuterius, 1970; Eleuterius & Meyers, 1974; Boyle, 1976) | Appendix B |
| | Virus | (Jones, 1980; Gotz *et al.,* 2002) | N/A |
| | Nematodes | Plantard & Bardou-Valette, 2007; Chen *et al.,* 2007) | N/A |

# Appendix B: Fecundity and the Breeding System in *Spartina anglica* Marshes in the Solent

## Introduction

*Spartina anglica* is a rhizomatous perennial grass that has occupied much of the intertidal mudflats of the UK and around the world. The infertile hybrid *Spartina x townsendii* shared similar morphological characteristics to *S. anglica* however, lacked the critical seed production. Although localized colonisation was rapid and well documented (Oliver, 1925; Goodman, 1960; Ranwell, 1967) much of the colonisation was through rhizomatous propagation. In recent times, *S. anglica* is considered as the most common *Spartina* species in the UK where *S. townsendii* has disappeared from much of its historical range (Gray *et al.,* 1991).

The recruitment of *S. anglica* through seed formation can be highly affected by zonal differences (Marks & Mullins, 1991), seed diseases (Gray *et al.*, 1990), self incompatibility (SI) (Raybould *et al.*, 1998) and salinity (Taylor & Burrows, 1968). The clonal nature of *Spartina* presents problems for the demographics at the genet (colony) level, as they are often long lived and individual plants are difficult to identify in the field. Clonal plants exhibit significant levels of population structure and demographic differences and the introduction and death of individual genets can severely affect the genetic composition of a population. Noble *et al.,* (1979) suggests that perennial recruitment of new genets to the population is relatively rare, and the dynamics of the population is dominated more by the birth and death of clonal modules than that of the whole genets. Therefore the presence of individual tillers and seed production provide a vital role in maintaining genetic diversity, whether or not they attain functional independence.

Limited investigations have been conducted on the interactions between seed production and environmental conditions for *S. anglica*. Work by Hubbard & Stebbings (1967), Marks & Truscott (1985) and Mullins & Mark (1987) proved that *S. anglica* showed variation in seed set from one marsh zone to another however, little is still known about the processes of recruitment and the influence of low seed set on the population dynamics of the plant community (Shumway & Bertness, 1992). Early studies may have underestimated viable seed production by the mixed communities of the infertile *S. townsendii* and fertile *S. anglica*. Taylor and Burrows (1968) demonstrated variability in seed set between years at the same site and between sites in a single year. Goodman (1957) also noticed variability in seed set of 92% and 18% on Lymington marshes in successive years. It is difficult to draw general conclusions in the literature, as the sampling frequencies were not designed to allow estimations of such variation. However, systematic sampling like that of Marks & Truscott (1985) or Marks & Mullins (1987) has demonstrated consistent differences in seed set between the pioneer and mature *Spartina* zones. The presence of two different types of marshes presents an opportunity to study the intraspecific differences and identify limitations of the genetic variation within *S. anglica*. The Keyhaven marshes (The Solent, Hampshire) show characteristics of an degenerating marsh with a receding forefront (Bradbury, 1995, Lawn, 2001) it is expected that very little recruitment through either vegetative or seedling recruitment exist. As a contrast, marshes located at the Ynyslas (Dyfi Estuary, Ceredigion) and North Wootton, (The Wash, Norfolk,) show expansion and definite signs of recruitment in the main marsh and the pioneering edge.

For this study the potential seed bank, the conditions of seed and pollen, germination rates and plant morphology of both marshes are investigated in order to ascertain the differences in the seed production capacity and fecundity of two environmentally distinct salt marshes. Given the evidence from the literature review, I hypothesise that 1) *S. anglica* grown within common garden conditions would exhibit similar flowering and seed set characteristics irrespective of marsh type. 2) Due to the eroding salt marsh in the south coast however, the establishment of *S. anglica* will be depressed by the lack of colonisation through seed 3) there is an inherent pressure from edaphic factors not to mention biological factors, which may have created selection pressures on the populations.

## Materials and methods

Twenty samples of *S. anglica* panicles were collected in first two weeks in September 2004, 2005 and 2006 (Table 11). The collection times were decided on personal observations in the field and various evidence of flowering times (Marks and Truscott, 1985; Groenendijk, 1986; Fang *et al.,* 2004). The collection of these samples ranged from western (Ynyslas, Ceredigion, Wales), southern (Keyhaven, Hampshire, England) and eastern (North Wootton, Norfolk, England) marshes of the UK. Samples were taken at randomised locations of the entire marsh, carefully noting the locality in relation to tidal inundation and the vegetative appearance and site description (pioneer, sward and mature marsh). *Spartina* colonies with similar morphological traits were collected within a 1 $m^2$ quadrate area. The seed producing panicles were collected within this area, and classified as a sample. Care was taken in handling the panicles as many were already infected with *Clavicep purpurea* and other secondary infections such as *Fusarium sp*. These were recorded and destroyed while unaffected panicles were stored in bags at approximately 5°c until ready for use within the laboratory.

**Table 11: Geographical locations of each of the samples taken from the marshes around the UK in 2004, 2005 and 2006.**

| Locations | Sample size ($N^o$) | GB National Grid |
|---|---|---|
| Keyhaven, Hampshire, UK | Mature (20) | SZ305909 |
| | Sward (20) | SZ308906 |
| | Pioneer (20) | SZ313904 |
| north Wootton, Norfolk UK | Mature (20) | TF604259 |
| | Sward (20) | TF605265 |
| | Pioneer (20) | TF602269 |
| Ynyslas, Ceredigion, UK | Mature (20) | SN623936 |
| | Sward (20) | SN622940 |
| | Pioneer (20) | SN622942 |

### Sediment seed bank

In April 2005, 10 soil cores (depth of 0.10 m, diameter of 0.10 m, Volume 0.314 $m^3$) were taken along 3 transects in Keyhaven, Ynyslas and North Wootton marshes. Each transect consisted of vegetation zones 1 (Pioneer), 2 (sward) and 3 (mixed mature). This sampling was repeated in July 2005 (after peak germination), September 2005 (before peak seed fall) and January 2006 (after peak seed fall).

Each core was spread over a 0.35 m (l) x 0.20 m (w) x 0.07 m (d) propagator tray filled with a mixture of the core material and John Innes seed compost. The experiment was set up in laboratory conditions and growth was carried out in a greenhouse. The greenhouse was unheated with ambient daylight and temperature ranging from 5 °C – 12 °C. The trays were kept moist with rain water collected in a container when needed. Seedlings were recorded and removed as soon as they were identifiable. Samples were stirred once a month to expose seeds buried within the sediments. Germination was observed over 10 months for the April and July samples. The September samples were overwintered by placing outside the greenhouse covered until February and compared with the January sample collected in 2006.

### Drift litter seed bank

Marine detritus was categorized into two types. Large deposits of fragments of rhizomes and culms of *Spartina sp.* (static litter) usually found at the base of sea walls and large static objects, and large algal mats (drift litter). Three locations of the static litter were sampled while algal mats along a transect (Figure 10) following elevation were sampled from zones 1, 2 and 3 in September 2004, January 2005, September 2005 and January 2006. 20 samples were collected from each location and spread on John Innes compost, seedling were identified and removed over a period of 6 months.

a) b) c)

**Figure 10: Pan view of transect used for the drift seed collection for a) Keyhaven and b) Ynyslas, c) North Wootton. Each survey consisted of 300 m from the forefront to as far back to the sea defence as possible.**

### Flowering and seed set (common garden experiment)

To help identify morphological differences in seed set of *Spartina* at Keyhaven, Ynyslas and North Wootton, a replicated pot experiment was conducted. Three populations of *Spartina* from Keyhaven, Ynyslas and north Wootton were planted in the soils in 2004 and monitored throughout 2005 and 2006 from the same three marshes in a 3 x 3 randomised block experiment with six replicates.

*Spartina* was collected in April 2004 from the pioneering edges of the marshes and divided into transplanting material consisting of a ramet with a small amount of root and a rhizome of 5 to 10cm. The plantlets were transplanted into 15 cm diameter 20cm deep pots with sediment from one of the marshes, Keyhaven (68% Silt, 19% clay, 2% sand 11% organic matter), and Ynyslas (sands coarse 90% and 10% silt <1% organic matter). The plants were placed in an unheated greenhouse to promote early seasonal growth, placed in shallow trays and watered with tap water daily during the spring and summer. Liquid fertiliser (Miracle gro® 15:35:15 @ 3g litre$^{-1}$), was added at the start of the second year then once a fortnight during the growing season to avoid nutrient limitations. When flowering tillers became visible, the height, number of panicles were measured fortnightly throughout the flowering period. Regular inspection of the plants for pot bound roots were performed, none were evident until the end of the third season.

## Germination method

Germination times were measured and numbers of viable seeds were counted from each marsh (Keyhaven, Ynyslas and North Wootton). Panicle collections were made at the forefront, sward and pans, these were checked for any infection, threshed and taken back to the Southampton University laboratory. The seeds were then weighed (g) and measured for length and width (mm) before being placed into a plastic container. A fertile batch of seeds from Holland (North Wadden Sea) was used as a control (Koutstaal, B. pers. comm.) The containers were each filled with saline solution (35ppm NaCl) at 5°c for 2 weeks (Fang *et al.*, 2004). Tests were conducted on six replicates of 100 randomly selected seeds in the spring of 2005, 2006 and 2007. After 2 weeks in cold storage, the seeds were transferred to a series of propagators each filled with light sand and seed compost (John Innes 2) 50:50 mix, under normal daylight conditions with an ambient temperature of 21°c – 25°c. The seeds were kept in this condition for up to 80 days. After germination the seedlings were allowed to grow until 5cm tall in the germination chamber. The surviving seedlings were transplanted into individual pots to grow on in the botanical garden greenhouse.

*Spartina* seeds were taken to include all spikelets whether or not they contained a caryopsis. Filled seed refers to spikelets containing a caryopsis. There is some difficulty in precisely separating the processes of germination, emergence and establishment. Seeds which germinate do not necessarily emerge – hence the latter term is preferable when considering the appearance of seedlings. Establishment is assumed to have occurred when the seedling has formed its first true leaf. This is a pragmatic division, based on the assumption that the seedlings are capable of pursuing an existence independent of their seed reserves.

A comparison was also made of the viability of seeds obtained through the greenhouse grown variants and the collection made from their native habitats.

## Pollen analysis

A collection of *S. anglica* panicles were made across the western Solent from Keyhaven, Lymington, Tanners Lane, Beaulieu and Calshot Spit during Oct – Nov 2006 (Figure 11).

The collections were made along a series of transects from high to low marsh carefully noting heights of main panicle and national grid reference. The panicles were stripped of their spikes and stored cold (5 °C) in sealed Petri dish for a day before analysis.

**Figure 11: Locations of pollen collection from locations across the western Solent. A) Keyhaven, B) Lymington, C) Tanners lane, D) Beaulieu E) Calshot Spit.**

Pollen viability was tested using the fluorocein diacetate (FDA) method of Heslop –Harrison *et al.,* (1984) and Raybould (1989). Anthers were collected after they have been exerted from the spikelet, but before anthesis, and the pollen tapped out in the FDA stain. The stain consisted of 0.5M sucrose and $10^{-3}$M $Ca(NO_3)_2$ saturated with FDA. This was made up fresh, just before use, by adding a 0.2% solution of FDA in acetone drop by drop to 2ml of the sucrose and $Ca(NO_3)_2$ solutions until the solute appears permanently cloudy.

The pollen was left in the stain for approximately 5 minutes and was then examined under U.V. fluorescent microscopy. In the pollen grains, esterase activity breaks down the FDA to form fluorescein, which fluoresces under U.V. light. The fluorescein only accumulates in grains that have intact plasma membranes, so that only viable grains fluoresce. For reference, viable pollen samples were taken from the stock Ynyslas plants which produced viable seeds

### Statistical analysis

All measured characteristics analyzed with both one way and two way analysis of variance (ANOVA) and a post-hoc multiple comparison were carried out using Tukey's LSD, Dunn's and Holm-Sidak Method. The data failed normality and equal variance to the <0.0001 level. However, Underwood (1997) states that analysis of variance is a stringent enough test that if it failed normality or equal variance raising the value of significance is still a valid test (from 0.0001 (1%) to 0.001 (10%)).

## Results

### Plant characteristics

At Keyhaven there is no evidence of a pioneering sward. Therefore seed production is limited to the main marsh islands.

Seed production was significantly different between the marshes. The overall percentage of viable seeds was overall quite low (<50%). The number of viable seeds produced in Keyhaven is significantly lower (ANOVA $F_{19,149}$ 87.456 $P<0.001$) overall than either North Wootton or Ynyslas population regardless of zone. There is also a significant difference in plant characteristics seed tiller height between the population (ANOVA $F_{28,298}$ 146.150 $P<0.01$) .Apart from this inherent difference between populations. There is clearly evidence that suggests that *S. anglica* produces two distinct peaks of flowering tiller heights, this seems to be correlated with the relative position of *Spartina* in the marsh.  There were no significant differences between the populations in the sward zones. The significant differences were associated with the pioneer and mature zones which displayed significant differences in height. All of the Ynyslas and Keyhaven sites are inundated twice (diurnal) by the tide and show a substantial number of shorter flowering tillers at the forefront of the marsh. Towards the sward area of the marsh the average height of the flowering tillers increases substantially although within the Keyhaven marsh the differences between the pioneer and sward zone was indistinguishable. The majority of the Keyhaven and Ynyslas populations show a healthy increase in tiller height at the sward – mature zone. The North Wootton population has the first peak at a similar height (0.50 m) this was particularly in the areas of the forefront where pioneering colonies were starting to form.  This is followed by another peak in tiller height at (0.90 m). These plants seemed to be established in areas of dipped pans and in colonial swards about 2 m in diameter – all in the mature zones. The *Spartina* swards located in these zones were substantially taller and denser than those found in the lower zones of the marsh.

The variation within sites was low in areas such as north Wootton and Ynyslas. Apart from the pans which form amongst the swards of some of these marshes showed uniform development of tiller height.

The Keyhaven marshes showed significant variation to tiller height and spike which is shown in Figure 12.

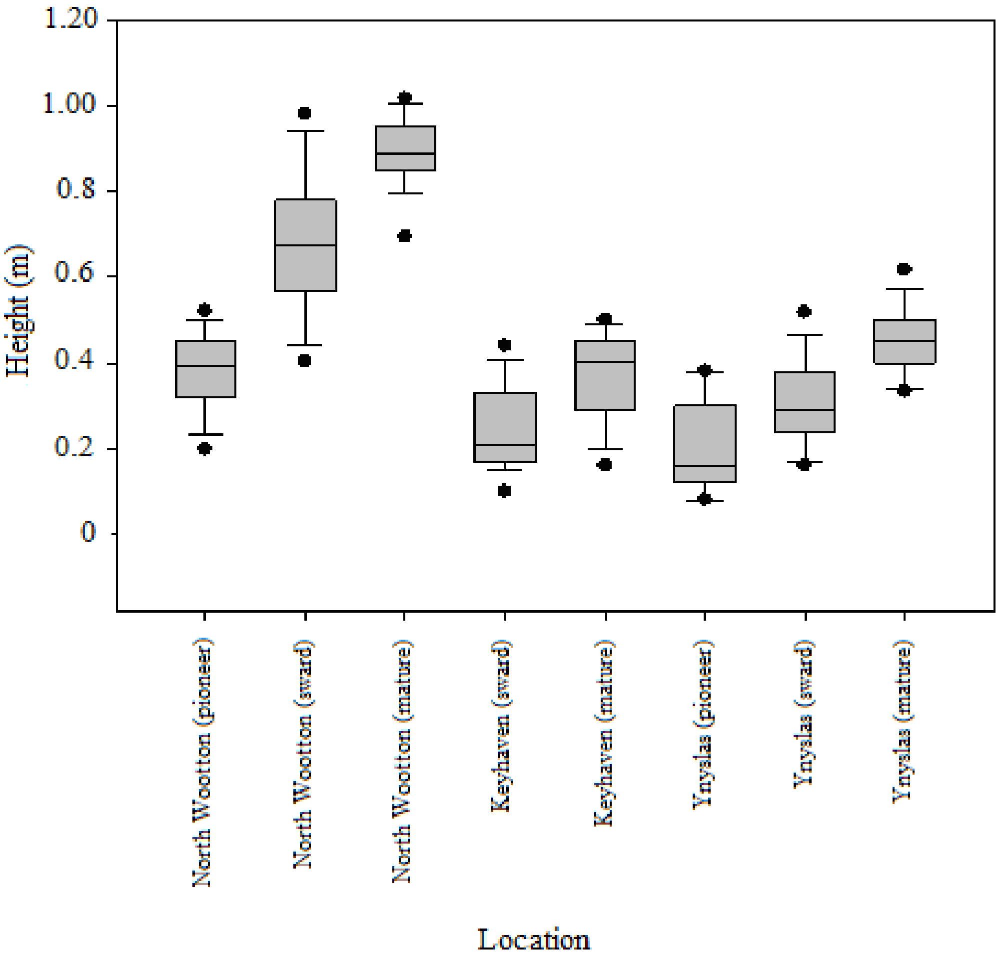


**Figure 12: Box-plot representing variation in flowering tiller height for all zones at Keyhaven, North Wootton and Ynyslas marsh in 2005.**

The pans forms an interesting conundrum as in the North Wootton the plants within these depressions show much more vigorous growth and stature compared to those from Keyhaven where dieback is apparent. The subsequent lowering of the sediments along with the retention of water within the pools may be ideal for *S. anglica* however the conditions can then easily become unsuitable with the consistent water-logging and bad drainage found in the southern salt marshes but need to be confirmed

### Variation in yearly seed formation within populations

During the three year period of this study, significant variation within seasonal seed production was not evident. The seeds produced in the localities were quite uniform through each flowering cycle and not significantly different between the seasonal developments of the seeds. This experiment only involved one collection during the year, it did not take into consideration the later development of inflorescence in certain populations and species as documented in (Anderson & Treshow, 1980; Marks & Truscott, 1985; Bertness, *et al.*, 1987)

### Physical seed characteristics

The upper and lower marshes produced significantly less seeds per panicle than those taken in the middle of the marshes (i.e. centre of the islands) (

Table 12). The shorter flowering tillers on the pioneering marsh evidently produced the least amount of seeds (Keyhaven mean = 3 - 6 seeds). The North Wootton and Ynyslas marshes represented a more uniform distribution of seed growth and showed no significant differences between localities. Although many tillers at the North Wootton and Ynyslas were shorter at the forefront many appeared to be damaged by wave action or current scour. Those physiologically shorter still produced a full complement of seeds per panicle (Ynyslas and North Wootton mean seeds = 13 seeds).

The Seed characteristics of *S anglica* for each marsh were significantly different between the different marshes. Ynyslas tended to have the weightier seeds (but not necessarily in dimensions (ANOVA $F_{19,149} = 111.18$ $P<0.001$) the same at the interaction between population and interaction for Length (mm) and Width (mm) (ANOVA $F_{19,149}$ 102.28 $P<0.001$) but not for seed weight

**Seed Germination Test**

Germination was extremely low for the all but two of the populations, ranging from 0 to 5% for Keyhaven, north Wootton and between 45 to 75%

**Table 12: Characteristics of *S anglica* seeds collected from the Keyhaven, North Wootton and Ynyslas in the UK.**

Oct/Nov 2004

| Population / Zone | Average seed weight (g) | Average seed height (mm) | Average Seed width (mm) | Percentage per $m^2$ of infestation from *C purpurea* (%) | Number of (filled) viable seeds (%) |
|---|---|---|---|---|---|
| | | | Of 100 randomly collected seeds | | |
| Keyhaven / Mature | 0.0031g ± 0.0001 | 16.92 ± 0.2 | 1.7 ± 0.03 | 8% | 2% |
| Keyhaven / Sward | 0.0026g ± 0.0002 | 16.62 ± 0.1 | 2.3 ± 0.03 | 10% | 3% |
| Keyhaven /Pioneer | 0.0030g ± 0.0001 | 14.37 ± 0.2 | 2.2 ± 0.03 | 12% | 0% |
| north Wootton / Mature | 0.0048g ± 0.0006 | 18.43 ± 0.2 | 2 ± 0.02 | 35% | 21% |
| north Wootton / Sward | 0.0050g ± 0.0004 | 17.74 ± 0.2 | 2.2 ± 0.2 | 32% | 26% |
| north Wootton / Pioneer | 0.0043g ± 0.0008 | 17.82 ± 0.2 | 2 ± 0.02 | 19% | 24% |
| Ynyslas / Mature | 0.0048g ± 0.0009 | 18.62 ± 0.2 | 2 ± 0.02 | 27% | 45% |
| Ynyslas / Sward | 0.0051g ± 0.0008 | 17.93 ± 0.2 | 2.2 ± 0.2 | 28% | 47% |
| Ynyslas / Pioneer | 0.0044g ± 0.0012 | 18.01 ± 0.2 | 2 ± 0.02 | 17% | 36% |

Oct/Nov 2005

| Population / Zone | Average seed weight (g) | Average seed height (mm) | Average Seed Width (mm) | Percentage per $m^2$ of infestation from *C purpurea* (%) | Number of (filled) Viable seeds |
|---|---|---|---|---|---|
| | | | Of 150 randomly collected seeds | | |
| Keyhaven / Mature | 0.0040g ± 0.0002 | 17.0 ± 0.20 | 2.1 ± 0.02 | 4% | 2% |
| Keyhaven / Sward | 0.0053g ± 0.0002 | 16.8 ± 0.14 | 2.2 ± 0.03 | 8% | 6% |
| Keyhaven / Pioneer | 0.0030g ± 0.0003 | 14.7 ± 0.18 | 2.2 ± 0.03 | 10% | 7% |
| north Wootton / Mature | 0.0043g ± 0.0004 | 18.6 ± 0.17 | 2.3 ± 0.03 | 32% | 24% |
| north Wootton / Sward | 0.0065g ± 0.0003 | 17.8 ± 0.21 | 2.4 ± 0.03 | 23% | 32% |
| north Wootton / Pioneer | 0.0053g ± 0.0005 | 18.1 ± 0.18 | 2.4 ± 0.04 | 17% | 33% |
| Ynyslas / Mature | 0.0068g ± 0.0003 | 17.0 ± 0.16 | 2.4 ± 0.03 | 29% | 42% |
| Ynyslas / Sward | 0.0086g ± 0.0014 | 17.8 ± 0.16 | 2.7 ± 0.02 | 23% | 46% |
| Ynyslas / Pioneer | 0.0059g ± 0.0010 | 16.8 ± 0.16 | 2.4 ± 0.03 | 19% | 43% |

Oct/Nov 2006

| Population / Zone | Average seed weight (g) | Average seed height (mm) | Average Seed Width (mm) | Percentage per $m^2$ of infestation from *C purpurea* (%) | Number of (filled) Viable seeds |
|---|---|---|---|---|---|
| | | | Of 150 randomly collected seeds | | |
| Keyhaven / Mature | 0.0039g ± 0.0002 | 16.5 ±0.209 | 2.2 ± 0.02 | 8% | 2% |
| Keyhaven / Sward | 0.0048g ± 0.0002 | 14.9 ± 0.16 | 2.3 ± 0.03 | 10% | 5% |
| Keyhaven / Pioneer | 0.0030g ± 0.0001 | 15.1 ± 0.20 | 2.1 ± 0.03 | 15% | 10% |
| north Wootton / Mature | 0.0045g ± 0.0002 | 17.1 ± 0.23 | 2.2 ± 0.02 | 24% | 14% |
| north Wootton / Sward | 0.0059g ± 0.0002 | 18.3 ± 0.19 | 2.3 ± 0.03 | 23% | 19% |
| north Wootton / Pioneer | 0.0059g ± 0.0002 | 17.9 ± 0.18 | 2.2 ± 0.03 | 11% | 24% |
| Ynyslas / Mature | 0.0063g ± 0.0005 | 18.0 ± 0.17 | 2.4 ± 0.02 | 32% | 37% |
| Ynyslas / Sward | 0.0107g ± 0.0016 | 19.1 ± 0.19 | 2.7 ± 0.02 | 28% | 36% |
| Ynyslas / Pioneer | 0.0062g ± 0.0001 | 16.9 ± 0.16 | 2.5 ± 0.03 | 16% | 35% |

**Table 13: Mean seed germination characteristics for the population x location (combined all years).**

| | | | | ANOVA | |
|---|---|---|---|---|---|
| Characteristics | Mean | Min | Max | P-value | MSE |
| *Germination time(days)* | | | | | |
| Keyhaven x Mature | 65 | 63 | 67 | <0.001 | ± 0 |
| Keyhaven x Sward | 64 | 59 | 68 | <0.001 | ± 0.8 |
| Keyhaven x Pioneer | 0 | 0 | 0 | <0.001 | ± 0 |
| north Wootton x Mature | 39 | 31 | 53 | <0.001 | ± 1.5 |
| north Wootton x Sward | 52 | 40 | 62 | <0.001 | ± 2.2 |
| north Wootton x Pioneer | 57 | 46 | 63 | <0.001 | ± 2 |
| Ynyslas x Mudflat | 32 | 15 | 46 | <0.001 | ± 1.7 |
| Ynyslas x Sward | 38 | 17 | 54 | <0.001 | ± 2.5 |
| Ynyslas x Pioneer | 33 | 20 | 54 | <0.001 | ± 1.8 |
| *Germination (%)* | | | | | |
| Keyhaven x Mature | 2 | 2 | 2 | N/S | 0 |
| Keyhaven x Sward | 1 | 1 | 1 | N/S | 0 |
| Keyhaven x Pioneer | 0 | 0 | 0 | N/S | 0 |

| | | | | | |
|---|---|---|---|---|---|
| north Wootton x Mature | 10 | 8 | 13 | 0.4 | ± 6.9 |
| north Wootton x Sward | 32 | 12 | 43 | 0.56 | ± 23.3 |
| north Wootton x Pioneer | 5 | 9 | 3 | 0.234 | ± 5.95 |
| Ynyslas x Mature | 56 | 13 | 68 | <0.001 | ± 32.18 |
| Ynyslas x Sward | 26 | 10 | 46 | <0.001 | ± 12.96 |
| Ynyslas x Pioneer | 13 | 3 | 26 | <0.001 | ± 8 |
| *Seedling survival (%)* | | | | | |
| Keyhaven x Mudflat | 0 | N/A | N/A | N/A | 0 |
| Keyhaven x Sward | 0 | N/A | N/A | N/A | 0 |
| Keyhaven x Pioneer | 1 | 0.3 | 1 | N/A | ±0.61 |
| north Wootton x Mudflat | 5 | 1 | 8 | N/A | ±2.63 |
| north Wootton x Sward | 12 | 3 | 16 | <0.5 | ±4.36 |
| north Wootton x Pioneer | 16 | 5 | 33 | <0.245 | ±6.53 |
| Ynyslas x Mudflat | 28 | 18 | 32 | 0.1 | ±14.63 |
| Ynyslas x Sward | 25 | 12 | 18 | 0.001 | ±13.2 |
| Ynyslas x Pioneer | 6 | 2 | 19 | 0.001 | ±3.69 |

There was a wide variability in the germination rates of the seeds. Germination success is defined as when a shoot or root tip is first noticed emergent from the seed. There was variation between germination in seeds from different marshes and in particular with the Keyhaven variety which only produced two seedlings throughout the entire trial. The Ynyslas population was the most successful and started germinating from 15 days after the treatment.

Comparison of germination from material from 2004 against the recent 2005 experiment showed that after storage, the Keyhaven variety still produced very little seeds, although the Ynyslas population produced a better crop than the subsequent years (Table 14).

**Table 14: Table of seed germination after storage since 2004, all growth data are germination (%) of the 2004 season (analysis conducted from 150 randomly selected seeds).**

| Year | Ynyslas | Keyhaven | north Wootton | Holland (control) |
|---|---|---|---|---|
| 2004 | 42% | 0/% | 39% | 57% |
| 2005 | 64% | 2% | 55% | 89% |
| 2006 | 76% | 0% | 62% | 78% |

## Sediment seed bank

The emergence of seed from soil cores was very low in this area and only a comparatively few species had any sediment seed bank of any appreciable size. *Spartina* seedlings were not evident compared to its abundance in the macrophyte community. *Spartina* seeds were found in zone 2 and 3 but were lacking in zone 1.

The seed bank was dominated mainly by *Atriplex* and *Suaeda* species. Seasonally, *Salicornia* and *Aster* were also present. (Table 15) There was a natural trend for an increase in diversity of species towards zone 3 of the marsh this may coincide with tidal levels. Although the pioneer region can be discounted as there were no seeds, the sward and mature zones showed a seasonal difference between the growth and the production of a variety of species. The *Spartina* seeds found within both zones showed little viability and showed no natural germination. There was little evidence to support the existence of a viable seed bank for *Spartina*. *Suaeda* were well represented within the July collection, possibly due to the annual nature of these species, although *Artiplex* were also common throughout the September and January collection

**Table 15: Species composition of seed collected from racks A = Keyhaven, B= Ynyslas, C= North Wootton (P – Pioneer, S – Sward, M – Mature).**

A) Keyhaven

| Species | 2004 (Sept) | 2005 (Jan) | 2005 (Sept) | 2006 (Jan) |
|---|---|---|---|---|
| *Spartina spp.* | P – NA | P – 1 | P – 25 | P – 14 |
| | S – 12 | S – 18 | S – 14 | S – 137 |
| | M – 38 | M – 86 | M – 21 | M – 247 |
| *Juncus spp* | P – 0 | P – 0 | P – 0 | P – 0 |
| | S – 0 | S – 0 | S – 0 | S – 0 |
| | M – 12 | M -1 | M - 8 | M – 11 |
| *Artiplex portulacoides* | P – 0 | P – 12 | P – 79 | P – 18 |
| | S – 123 | S – 85 | S – 128 | S – 331 |
| | M – 228 | M - 152 | M – 198 | M – 672 |
| Other | P – 562 (*SaPicornia*) | P – 175 | P – 78 | P – 87 |
| | S – 122 | S – 189 | S – 786 | S – 72 |
| | M - 173 | M - 263 | M -871 | M – 68 |

B) Ynyslas

| Species | 2004 (Sept) | 2005 (Jan) | 2005 (Sept) | 2006 (Jan) |
|---|---|---|---|---|
| *Spartina spp.* | P – 56 | P – 145 | P – 36 | P – 128 |
| | S – 189 | S – 345 | S – 263 | S – 411 |
| | M – 395 | M – 1168 | M – 376 | M - 1322 |
| *Juncus spp* | P – NA | P – NA | P –NA | P – NA |
| | S – NA | S – NA | S – NA | S – NA |
| | M - 4 | M - 2 | M - 13 | M - 45 |
| *Aster tripolium* | P - 12 | P - 4 | P - 12 | P - 8 |
| | S - 87 | S - 11 | S - 169 | S - 86 |
| | M - 168 | M - 213 | M - 866 | M - 786 |
| Other | P – 368 | P – 124 | P – 323 | P – 325 |
| | S – 335 | S – 482 | S – 332 | S – 258 |
| | M - 186 | M - 362 | M - 121 | M - 147 |

C) North Wootton

| Species | 2004 (Sept) | 2005 (Jan) | 2005 (Sept) | 2006 (Jan) |
|---|---|---|---|---|
| *Spartina* | P – 192 | P – 245 | P – 326 | P – 148 |
| | S – 239 | S – 525 | S – 1263 | S – 711 |
| | M – 635 | M – 3228 | M – 1376 | M - 1522 |
| *Salicornia europaea* | P – 9124 | P – 2082 | P – 8972 | P – 1752 |
| | S – 898 | S – 971 | S – 896 | S – 586 |
| | M - 87 | M - 368 | M - 686 | M - 9786 |
| *Aster tripolium* | P – 118 | P – 134 | P – 122 | P – 352 |
| | S – 165 | S – 1121 | S – 1139 | S – 266 |
| | M – 962 | M – 975 | M – 547 | M – 2186 |
| Other | P – 12 | P -8612 | P – 41 | P – 797 |
| | S – 762 | S – 862 | S – 86 | S – 786 |
| | M – 982 | M - 868 | M - 972 | M - 897 |

Comparing the September seed collection to the January seed collection showed similar results in species emergence (Table 15), although the number of species present is significantly different. This would imply that winter storage maybe the trigger to the germination of seeds for these species, the survival of the seeds throughout the winter period, maybe heavily dependent on the prevailing environmental conditions.

The variation between the detritus racks between zones per collection were significantly different (ANOVA $F_{19,99}$ 62.65 $P<0.001$) for both Ynyslas and North Wootton, exhibiting almost five times as many seeds in the mature zone as there is in the pioneer zone particularly in the January collections. This highlights the importance of the mature or sward zone as an active area of recruitment for new genets. Keyhaven results show a low abundance of *Spartina* seeds for all zones in comparison to *Spartina* seeds found in Ynyslas or North Wootton (MANOVA $F_{48,198}$ 123.21 $P<0.001$).

Comparing the cores with the racks, there were no seeds in the pioneer zones whilst the sward and mature zones showed a diverse numbers of seeds from mainly *Artiplex sp.* and *Salicornia sp.* These seem to germinate readily in the petri dish environment.

**Drift litter seed bank**

*Aster sp.* was the main species in this area, although *Salicornia sp.* and *Spartina* seeds were also found amongst the group. A large portion of the litter consisted of *Spartina* culms and fragments of spikes. Occassionally, *Suaeda sp., Atriplex sp.* and *Plantago sp.* species were found as they emerged but were not significant enough to be classed as a seed bank. *Spartina* seeds although present were found not to germinate when planted in the experimental conditions or when forced to germinate in a petri dish. The difference in species composition was apparent with the collection times (April, September and February). Although from April to September saw a regular abundance of all seed types. In the February survey, the drift litter were large samples, presumably from the winter storms although the numbers of seeds found within them were lower than that found during the peak seed production period.

### Seed infestation by Ergot (*Clavicep purpurea*)

Seeds collected from the Keyhaven area showed evidence of high infections of Ergot fungus between 50 to 70 %. The Keyhaven population exhibited over 85 % infected seeds (total seed count) in comparison to Ynyslas, and North Wootton which showed dramatically lower cases of the infection 17 - 27 % and 20 - 30 % (total seed count) respectively.

There is also a trend (with exception to Keyhaven) which suggests that marsh zones also play an important role in the distribution of ergot infected seeds. The upper marsh localities produced the greater case of infected seeds in comparison to the middle or lower marsh.

### Pollen viability

The pollen of each of the site transects were analyzed using the FDA method. There was limited pollen fertility within the southern *Spartina* populations, the productivity of pollen production from *S. anglica* in the south coast is very low ranging from 0 to 26% (Table 16) with a mean of 1%, based on counts of 500 grains from each transect location. The majority of the plants have shown complete plant sterility. There were also cases within the analysis where florets had six anthers rather than the usual three. This suggests that the southern marsh as a whole may be undergoing aneuploidy.

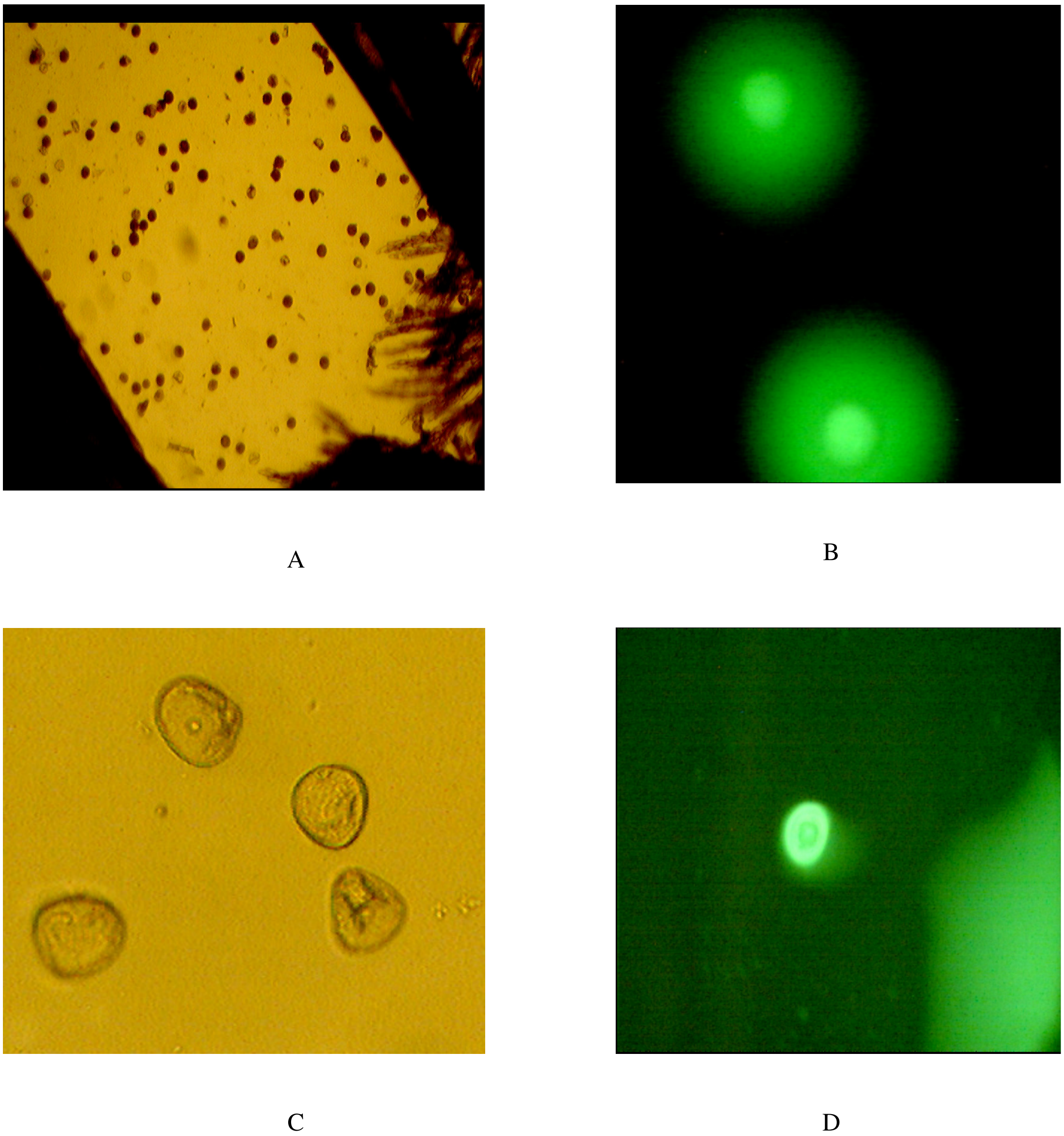
The pollen was distinctly misshapen and lacked complete fluorescence which is characteristic of *S. townsendii*.

These results show that the *S. anglica* pollen were not viable at the time just prior to anthesis. This may suggest that some of the *S. anglica* plants in the south coast may in fact be *S. townsendii*.

**Table 16: Pollen fertility in *Spartina* from the Solent (n = 500).**

| Site | Date of collection | NGR* | Grains showing |
|---|---|---|---|
| Ynyslas stock<br>*S. anglica* | 5/07/2006 | | 93% |
| Keyhaven 1 | 10/07/2006 | SU 312 910 | 1% |
| Keyhaven 2 (Mid) | 10/07/2006 | SU 311 910 | 2% |
| Keyhaven 3 | 10/07/2006 | SU 316 909 | 2% |
| Lymington 1 | 10/07/2006 | SU 342 949 | 1% |
| Lymington 2 | 10/07/2006 | SU 343 947 | 1% |
| Lymington 3 | 10/07/2006 | SU 342 945 | 1% |
| Tanner Lane | 10/07/2006 | SU 364 950 | 1% |
| Tanner Lane (Mid) | N/A | | |
| Tanner Lane | N/A | | |
| Beaulieu (Upper) | 14/07/2006 | SU 435 985 | 2% |
| Beaulieu (Mid) | 14/07/2006 | SU 436 984 | 1% |
| Beaulieu (Lower) | 14/07/2006 | SU 436 982 | 3% |
| Calshot (Upper) | 14/07/2006 | SU 482 021 | 18% |
| Calshot (Mid) | 14/07/2006 | SU 482 022 | 26% |
| Calshot (Lower) | 14/07/2006 | SU 484 024 | 4% |

*NGR = National Grid Reference



A

B

C

D

**Figure 13: Comparison between reaction of the pollen from *S. anglica* from Ynyslas (A and B) and *S. anglica* seeds from the western Solent (C and D (Photograph A was taken at x 50 magnification. All other photographs were taken at x 250 magnification).**

## Discussion

One objective of this study was to determine to what extent populations of *.S anglica* may have undergone differentiation in response to local level environmental differences. Although the growth trials in the greenhouse provided little evidence of such differences as did the reciprocal experiments there were certain traits such as seed production, flowering tiller height and culm height which proved to be quite significant depending on habitat.

Dethier & Hacker (2005) suggested that exhibiting high fecundity, shorter generation times, habitat generality, and high adult and propagule mobility were characteristics which made a species an effective biological invader. The invasive *Spartina* hybrid must have exhibited similar traits to develop into its niche. This study suggests that *S. anglica* has significant variation between the population to produce different quantities and quality of seeds. The flowering times found in the greenhouse were quite similar to the times found in the wild. The removal of the limiting environmental factors (water-logging, salinity and nutrient deficiency) and the uniformity of the conditions evidently introduced vigour back into *S. anglica* from Keyhaven although seed production remained poor even throughout the three years.

For the seed characteristics several explanations are presented as to the reason for the differences

Evidence suggests that flowering height is affected by locality and conversely affects the amount of seeds produced. *Spartina* from Keyhaven has a similar range of seed production throughout the different zones.

## Genetic recombination

*S. anglica* is an allopolyploid with the chromosomes from the parental species of *S. maritima* and *S. alterniflora*. The chromosome doubling of the infertile hybrid *S. townsendii* resulted in the fertile *S. anglica*. The evidence collected from this study indicate a sudden drop in production of viable seeds coupled with the resemblance to *S. townsendii* morphology there is speculative evidence at least to suggest that *S. anglica* in the Keyhaven region may have reverted to *S. townsendii* morphology. Marchant (1968a, , 1968b) and Raybould (1988) noticed that *S. anglica* populations have included the odd specimen of *S. alterniflora* or *S.*

*townsendii* within clones, this could suggest that some sort of genetic aneuploidy occurring and the original *S. anglica* hybrid vigour is becoming less prominent Other hybrid species have also undergone changes such as these. Recently Town *et al*., (2006) used *Brassica* and *Aradopsis* polyploids as example species to identify gene deletion mechanism as a model for speciation. Ellison *et al.,* (2006) investigated the phylogenetics of clover (*Trifolium*) and found 19 instances of aneuploidy just in one genus. This needs further investigation which will be covered in a future publication.

### Flowering phenology

Many of the *Spartina* species have highly variable seasonal flowering periods (Mobberley, 1956, Fang *et al*., 2004). *Spartina anglica* which resembled morphological traits in the field with respect to seed production resembled the same in the pot experiments.

We found floral characteristics to be not as plastic but sustained throughout the three years of growth. Hill (1991) reported that floral characters frequently show greater levels of variation than vegetative traits. Raybould (1989) used the petri dish method of Lundqvist (1961) to study cross-pollination of *Spartina* from geographically widely separated populations. In all cases, pollen tube growth was halted rapidly and tubes had the typical appearance of “weak” (Shivanna *et al*., 1982) self incompatibility (SI) reaction. They also found that between heavy seed set and hot summers there may be a breakdown of the SI system and flowering may commence. In our surveys the lack of viable pollen would rule out the chances of fertilisation regardless of the SI reaction. The continual existence of the Keyhaven populations even with low capabilities of seed production may be a selected trait according to the theory of R and K selection (Macarthur and Wilson, 1967). If a species selecting for competitive ability invest more in vegetative growth – the reproductive effort therefore declines with successional maturity. This fact would coincide with populations of the Solent indicating that the spread of the *S. anglica* population may have occurred from a central nucleic population such as Keyhaven where the reproductive efforts are minimal.

### *Clavicep purpurea*

Ergot fungus, *Clavicep purpurea* have been intensely investigated, (Gray *et al*., 1990, Gray *et al*., 1998) and can be seen to be a major threat to seed recruitment in *S. anglica*. Being a parasite of the grass gynoecia when a floret becomes infected it becomes a scleoria, and eventually the whole seed is then lost to the parasite. Infection rates have been extensively monitored over time and in Mississippi 96% of inflorescence were infected in 1968 with an estimated 68% reduction in seed set (Eleuterius, 1970). The sampling effort was increased to cover the Gulf of the East coast states except New York, Connecticut and Maine found ergot in most marshes with rates of infection ranging from 10 to 100% (Eleuterius and Meyers, 1974). In Poole Harbour an 85% infection rate was sustained for over 10 years (Gray *et al.*, 1998). *Clavicep purpurea* interrupts seed set and production severely enough to produce selective pressure in *S. anglica* reproduction. Within the Keyhaven population there were approximately low infection rates. In contrast to North Wootton and Ynyslas this was between 17 to 30 %.

As a consequence to the infestation of *C. purpurea,* even before *S. anglica* has a chance to release the seeds into the population there is already a decrease in possible seed recruitment. Keyhaven for example is such a small area with limited areas of vegetation it would be easy for an epidemic such as *C. purpurea* to cause a selection pressure in the local population.

There is also another theory that suggests that other marshes have such vast areas of *Spartina* that the sheer production of seeds, outweighs the development of *C. purpurea* infection or at least minimises the effects. Evidence from the results suggests that tidal inundation affects the development of the infection. The population in North Wootton and Ynyslas showed minimal infection of *C. purpurea* in the pioneering zones of the marsh. This may be correlated with the fact that *S. anglica* produced little viable seeds in the pioneering zones.

### Seed set and lack of genetic vigour

The pollen grains examined within this study have shown that they are not functional. Raybould (1989) conducted similar experiments with *S. anglica* which suggests that they may be exhibiting a self incompatibility complex (SIC). *S. anglica* as a species runs an increased risk of an incompatibility reaction due to their dodecaploid configuration and the availability of multiple loci to form the SIC alleles. Furthermore, the hybridization event which formed *S. anglica* may have caused the species to produce specific numbers of the loci which makes incompatibility unavoidable. The only way a compatible cross could form is by extensive recombination, using pollen and stigma that have no alleles in common. However, it has already been established that recombination is unlikely due to preferential pairing, so it is unlikely that this situation would ever occur in *S. anglica*. However, *S. anglica* produces seeds, therefore there must be a period when self incompatibility breaks down. This could be an increase in environmental effects such as temperature or a period of stress which undermines the SIC reaction. During the greenhouse experiment (Chapter 3) there was a substantial increase in seed formation within the Ynyslas plants. While not truly non-sterile it appears that high temperatures can temporary disable the SIC reaction. Ascher and Peloguin (1966) and Chen & Gibson (1973) found that self incompatibility could be reversed when their infertile plants were grown in temperatures above 30 °C. It is plausible that environmental factors could operate within the field that create a periodic breakdown of self incompatibility, and therefore the sporadic nature of *S. anglica* fertility.

## Conclusion

The experimental results suggest that *S. anglica* in the Keyhaven marsh produce low quantities of viable seeds. In addition to this, the environmental conditions at Keyhaven (Chapter 4) suggest that what little viable seeds produced would struggle to survive in the sediments. However, *S anglica* have been found in varieties of different sediment types (Dethier & Hacker, 2005) and varying environmental conditions. In effect the genets of *S anglica* clearly show they have a broad ecological tolerance which makes them much more able to colonise extreme environments such as the marsh forefront.

Even with an extreme tolerance there are still survival limitations to this species and some evidence of this may have already been exhibited with the Keyhaven population. Long & Mason (1983) developed a hypothetical sequence of salt marsh development which shows the stages of the three populations that was used for this investigation. The Ynyslas salt marsh resembles that of a low pioneering salt marsh with many incipient pans and low creeks. Particularly in the pioneering zone the salt marsh has a convex profile and during high tide the marsh is completely submerged. The North Wootton and Keyhaven are of the higher, mature salt marsh with the more extensive creeks and drainage channels. In marshes such as these mature marsh platforms form, with each successive segment lower than the previous. During the high tide only the mature zones of the marsh are still visible. The critical difference is the recolonisation of the marsh at the pioneering zone. In the North Wootton this occurs with prolific progress. However the mudflats immediately adjacent to these marsh island areas at Keyhaven are eroding at a phenomenal rate and the release of these sediments have reduced the areas the *Spartina* has available to colonise. The only possible areas of colonisation would be areas already colonised by *S. anglica* where the shelter of the stand would allow adequate protection for germination and growth.

This recession of the marsh entails that as the population is getting smaller there is a chance that the seeds would be self pollinating and there is strong evidence to suggest that frequent self pollination can cause lower seed set and in-viability (Daehler and Strong, 1994; 1996).

There was considerable variability in the number of seeds of cores and litter found on the marsh. This is probably due to the natural depressions and tidal levels which occur in the marsh surface and shows a gradient in density with distance from foreshore to sea wall. Depletion of the seed bank occurs through seed germination, death, predation and export of the sites. The periods in which the seedling has to survive is not long, Groenendijk (1986) found that all remaining ungerminated *Spartina* seed had deteriorated four months after introduction. Hill *et al*. (1986) found that dormant viable seeds increased significantly with site elevation. Loss of viability may be due for example, to fungal attack, desiccation, water-logging or anaerobic conditions. Wildfowl and passerines have been observed to feed on *Spartina* seed (Ranwell, 1967) and may significantly deplete the seed stock, the impact of the passerines being confined mainly to the upper marsh.

The Solent system has a double high tide and an increasing sea level due to climate change and isostatic adjustment (Gardiner *et al.*, 2007). It may be possible that the conventional concept of the substrate seed bank is not appropriate in this salt marsh environment where the tide may remove a large proportion of the seed, which is then either expelled through the estuary or left to concentrate in drift line, where conditions are not suitable for settlement. This study has demonstrated the presence of *Spartina* seed in drift line litter. Samples were taken at various times throughout the year (April, September and February) and the seed composition changes over time. Curtis (1937) and Goodman (1957) both report germination of *Spartina* seeds on the drift line. Desiccation will presumably cause a loss of exposed seed in drift line litter; although a large proportion of seed would be expected to survive in large accumulations of litter. In this case the large accumulations did not necessarily produce a greater survival of seedlings, as the drift litter naturally move with the tides and storm events and therefore are often exported out the estuary.

Some indication of the proportion of seeds that are exported from the salt marsh can be gained from the work of Jackson (1984), who estimated from litter traps that approximately 15 - 20 % of the above ground annual net primary production of *Spartina* was exported from a salt marsh site on the River Stour, and that approximately 30 % of that was recovered on the drift line. Dead flowering culms and seed constitute a large proportion of this material. The proportion of seed exported from the salt marsh is expected to be related to the frequency of flooding. For sites where the frequency of flooding is relatively low, a high proportion of seeds are incorporated into the sediment. Within the Solent region the relative flat nature of the sediments involved a constant flooding of the marshes and therefore material is carried away with the ebb tide. This is evidenced by the lack of newly emerging seedlings from any of the islands in Keyhaven.

The potential for long distance dispersal of *Spartina* seed, into or out of the Solent, is unknown; Studies of the systems hydrodynamics have confirmed that the maximum ebb current is approximately 1.1 and 1.5 times greater than the flood (Ke & Collins, 1993), therefore material is more likely to be exported from the site. The lack of import suggests that there will be little exchange of seed between coastal habitats. However, if seed are dispersed mainly in the surface waters there may be a different pattern of movement.

The absence of a persistent *Spartina* seed bank means that the amount of seed available for future recruitment is extremely low. It is fortunate that *Spartina* as a species are not dependent on a seed bank to maintain the population from year to year (Watkinson *et al.*, 1979). The other bank of dormant buds - or rhizomes – may also contribute to the colonisation of new sites by the establishment of fragments. This suggests that life history strategies of the *Spartina* populations at Keyhaven may have reverted back to a form, similar to the infertile hybrid *S. townsendii.* However, the pattern of *Spartina* spread from the past must have been achieved by favourable environmental conditions allowing both fragment and seed colonisation. We therefore conclude that the environmental conditions not only impact the plants directly but create an evolutionary pressure which has limited variation and colonisation rates. It is evident from this study that the current state of colonisation for *Spartina* within the Solent to be negligible.

# Appendix C: Coastal Engineering Options

The demise of *Spartina* salt marsh and the change in the morphology of the coastal environment has socio-economic and coastal engineering implications. In this section, the socio economic implications are described and a critique to the current theories for coastal protection reviewed.

Some of the key options to salt marsh management are reviewed below.

## Coastal engineering options

Salt marshes can be broadly divided into three types of management techniques

- Techniques aimed at managing the erosion and accretion of marsh sediments: include but not limited too: Intertidal recharge, breakwaters, vegetation planting, and source control.
- Techniques aimed at building new salt marsh environments include: Managed realignment, regulated tidal exchange system.
- Techniques aimed at holding the current boundaries between coastal and terrestrial environments include: Hard engineered options and erosion management techniques

Each of the techniques will be presented below along with appropriate case studies where relevant.

## Vegetation planting

Vegetation planting can be used in a variety of situations as an exclusive technique or more commonly, in combination with other restoration or habitat creation methods. Through deliberate planting, particularly using *Spartina* species, erosive tidal flows can be dissipated by the plant stems, with the resultant effects of a decrease in current velocity, increased sediment deposition and an increase in the level of the mudflats and marshes.

Salt marsh vegetation can only be established successfully, if the physical and biological conditions are satisfactory. Natural colonisation should, therefore be considered as the preferred option for salt marsh vegetation establishment rather than artificial transplantation as per Chapter 3.

Salt marsh vegetation will establish in areas of suitable elevation with sufficient protection from high energy tides and waves. However, there are a number of considerations that need to be taken into account before vegetation planting is deemed suitable. Of particularly importance are the following:

- Is there history of salt marsh growth in the area? – is there any underlying concerns which would make this option unsuitable?

- Is the coastline in an erosive state? In which case, landward re-alignment maybe a more suitable option?

- Is the mudflat at a suitable slope, elevation, drainage, salinity, hydrology and substrate? Existing marshes will help determine these factors

Wave action and influence of tidal range are the most important components in determining the type of plants that should be used. Exposed shorelines with high wave energy, which are not afforded additional protection from wave breaks, may experience plant wash out or low survival rates for species/individuals unable to tolerate wave stress. The elevation of the planted surface and the relationship with tidal range which will influence potential survival rates should be used to determine the species selected. This requires careful consideration, as inappropriate times and durations of submergence will cause plant mortality. The combination of elevation and shore morphology with a particular set of wave conditions can also greatly influence the stress placed on plants. Similarly, the salinity of the water and the substrate is important in determining species survival rates, since some species are better able to tolerate saline conditions than others.

The ability of *Spartina sp.* to survive under a wide range of conditions and to propagate by rhizome has led to its widespread use in the UK for coastal reclaim. *Spartina* has the ability to colonise in different locations and in different parts of the intertidal in relation to the tidal frame, however as this thesis has indicated some places have died back and become moribund.

## Constraints

The species used for transplanting should represent the natural species assemblages for the area, in order to avoid the introduction of exotic species and problems with species competition; thereby maintaining the biodiversity of the site. Ideally, transplants should be taken from sources close to the intended planting sites, since minor genetic differences may alter a plants ability to withstand particular environmental conditions.

Under UK and EU legislation, the consent of the relevant countryside agency (e.g. Natural England, Countryside Council for Wales and Scottish Natural Heritage) is required for the introduction of any species into designated sites. It is, therefore, advised that the relevant agency is consulted at an early stage.

The establishment of salt marsh on mudflats can reduce the area available for feeding birds and where mudflats is a designated feature, this could be considered to represent a significant impact.

Examples where vegetation planting has been carried out:

- Planting and Sowing Experiments, Tollesbury Marsh, Essex
- *S. anglica* planting in Bosham, Chichester Harbour, West Sussex;
- *S. anglica* planting at Wytch Farm Gathering Station, Dorset;
- Experimental realignment Site at Abbotts Hall, Essex;
- Salt marsh restoration programme for pollution control and *S. anglica* transplanting, Southampton Water; and
- *S. anglica* planting Humber Estuary, Yorkshire

Further references can be obtained from Burd, (1989) and Brooke *et al.,* (2000).

## Sedimentation fencing

Sedimentation fences were originally pioneered in Holland and Germany and was first applied in the UK in the late eighties/early nineties. It was originally applied in areas where ongoing intertidal erosion was a problem, particularly in southeast England. Following several experimental studies, the sedimentation field technique is believed only to be successful if the local sedimentary process trended towards accretion. In areas where the trend is towards erosion the fences have proved ineffective. Consequently the use of sedimentation fencing in recent years has declined and it is now used only in combination with a number of other techniques on a small scale, rather than as an exclusive, stand alone technique.

The fences are designed to slow the passage of water thereby facilitating the deposition of suspended sediments. Essentially there are two types of techniques; brushwood groynes and sedimentation fields, polders.

### Brushwood groynes

Brushwood groynes generally consist of two parallel rows of wooden stakes, spaced approximately 300 mm apart at 600 mm intervals, driven deep into the mud. Different orientations of the fences have been tested but in general, the best orientation is perpendicular to the foreshore. A variety of materials can be used as infill between the stakes, including willow brushwood, geotextile cladding and straw. Overall however, brushwood has been found to be durable. The groynes minimise wave action, slow currents and promote sedimentation. To some extent the erosive effects of wave and tide-generated shear stress are also diminished, thus allowing the fine-grained fraction of the sediment to settle out (Colneutt, 2001). As a result, the sedimentation of suspended matter is enhanced, both behind the groynes and in front of the salt marsh edge.

### Sedimentation polders

Sedimentation polders enclose a width of mature upper marsh together with a similar width of mudflat seawards of the marsh, by construction of a perimeter fence. Ditches are dug in a regular pattern across the polder to collect deposited sediment which is cleared and piled on the banks between the ditches. The fields can be up to 400 m square, although many of the experimental sites constructed in the UK have been smaller, varying between simple groynes 30 - 50 m apart and larger, more complex fields 100 -150 m square. Gaps in the fencing along the seaward line of each enclosure allow the tide to flow into a single series of channels within the area. These are maintained to control the flow and sediment deposition. The main ditches are dug perpendicular to the coast while other trenches (or grips) are dug parallel to it. The main ditches, direct the waters of the flooding tide onto the upper areas of the marsh and allows the carriage of sediment towards the shore, this is instead of depositing the sediment offshore (Colenutt, 2001). This approach also involves re-excavating the ditches and grips and placing this sediment in the intervening space thus, overtime, the general level is raised (as the ditches fill and create a new surface) until the process is no longer required. The pattern of gripping can be seen clearly in some eroding salt marshes and, in the erosion phase, can provide preferential erosion lines.

### Constraints

Ongoing maintenance is essential as the fences tend to loose the infill material which is swept away by the tide and deposited on adjacent areas of salt marsh, potentially causing vegetation mortality if not removed immediately. As the infill and damaged stakes are lost, the fences become less effective and erosion of the accreted material occurs. The grips must also be constantly excavated to maintain the effectiveness and prevent the sediment from being washed out of the ditches.

The construction of the fences can have a major impact on the environment through trampling and disturbance during construction and maintenance, the infill material can be washed out of the fences and deposited on the marsh, with potentially significant deleterious effects on the vegetation and in extreme cases navigation. The structures themselves can have a local impact by increased scour immediately adjacent to the fences. There is also a visual intrusion into the estuarine landscape at low tide and, potentially, a hazard to boat traffic at high tide. Rapid accretion of sediment can cause swamping of benthic intertidal invertebrates and, thus may reduce the overall resource available to birds, at least in the short term. Rapidly deposited sediment can also be unstable and erode away again on higher tides.

Pre-scheme monitoring should try to assess the accretion/erosion status of the mudflat/salt marsh system. This can be achieved by analysing historic O.S. maps and/or aerial photographs. For a more detailed assessment, topographic surveys could be carried out to assess changes in elevation. Note that the technique is believed only to be successful if the local sedimentary trend is towards accretion.

Several sedimentation fences experiments were trialled in the late 80's and early 90's at various locations in the UK, particularly in Essex (Holder & Burd, 1990); although monitoring of these sites suggested that their effectiveness was limited. Examples include Cudmore Grove and various sites along the Dengie Peninsula and Strood Channel, Essex

The following references provide further information to this technique: Wagret, (1968); Beeftink, (1977); Holder & Burd, (1990); Colenutt, (2001).

## Sediment recharge

### Intertidal recharge

Intertidal recharge aims to mitigate deficits in estuarine sediment by restoring the functioning of mudflats and salt marshes through the introduction of sediment onto or adjacent to intertidal areas. In most cases this is considered to be a sacrificial sediment supply but can be an important response to critical conditions. It can provide a sustainable solution in some circumstances and provide additional time to investigate the sustainable options in others. Most schemes utilise sediment derived from the navigational dredging of ports and harbours and, in doing so, provide a "beneficial" use for this material but other sediment sources have also been considered.

Coarse material derived from capital dredging is more typically suited to protective recharge schemes than finer material (which may be sued to raise salt marsh levels or provide material landward of the coarse sediment). The behaviour of sand and shingle once deposited is more predictable than fine sediment. In contrast, the finer cohesive material derived from maintenance dredging is less likely to remain at the disposal site unless protected by a barrier or placed in quiescent conditions. The former may be achieved by sand and shingle placed as recharge material or through other constructed bunds. Placing material in quiescent conditions is often practically difficult in terms of the access/costs for appropriate vessels/plant/machinery to handle the material. There is also a much greater potential for indirect ecological effects (e.g. through sediment re-suspension) which may be a particular issue for shellfish or where sediment loads may smother adjacent salt marsh. The beneficial placement of maintenance dredged material within the UK, to date, has been relatively small-scale.

Dredged material can be used in several different ways. These are: 1) recharge of reclaimed land to raise its elevation prior to managed realignment; 2) Direct recharge of existing salt marsh to raise elevations for plant colonisation; 3) Sub-tidal placement of sediment or ‘water column recharge’ to reduce the tendency for erosion of adjacent intertidal margins and; 4) Foreshore placement to increase the dissipation of wave energy, reduce erosion and/or trickle feed sediment back into the wider estuarine system.

Of all these applications, water column recharge and foreshore placement are the most widely used, with the latter receiving the most attention.

### Water column recharge

Rather than relying on tidal currents to lift the material from the sea bed, water column recharge involves introducing dilute material directly into suspension. The key issues with this approach is that the sediment must be introduced gradually in order that it does not drop immediately to the sea bed; and also to increase the sediment concentration over a wide area by modest amounts.

There are different methods possible of sediment release; that is, pumping it back down the dredging pipe or by ‘rainbowing’ it into the air over the water. If the sediment is added too quickly, the density between the added sediment-water mixture and the ambient water will be too large, causing the sediment to descend quickly to the sea bed in a dense plume. As much dilution must be achieved by introducing water as the sediment is released and by releasing the sediment from a moving dredger.

The tidal currents in the estuary have a limited capacity to carry sediment, as energy must be extracted from the turbulence in the flow to act against the force of gravity causing the sediment to settle towards the bed. This is another reason for requiring adequate dilution. Fine muddy sediment settles relatively slowly, and will take some time to settle to the bed. In addition to this fine sediment is likely to be transported a reasonable distance before deposition occurs.

**Foreshore placement: direct placement of dredged material (pumping)**

The most rapid way to recharge a foreshore is by pumping material ashore. Two approaches can be used.

Spraying from a dredger (rainbow discharging) moored close inshore, to cover the whole foreshore. This method is used most effectively along coastlines with low tidal ranges and low wave energy. The requirement for a vessel with a shallow draught, limits the amount of material that can be discharged. Consequently, this method is often restricted to small recharge schemes; and

Pumping via a pipeline which runs up the beach from a dredger moored off the coast, potentially over the dredge site. Large volumes of sediment can be pumped onto the foreshore over relatively short time periods, thus making this technique more suitable for large recharge schemes. On a much smaller scale, the direct placement of marina dredged material via pipeline discharge over relatively short distances may be a potentially cost-effective option, involving no re-handling costs storage of material or transportation to site by vessel. However, pumping distances and the potential disruption to navigation may restrict this option. Also, to sustainably replenish the entire intertidal and salt marsh profile, pipelines would need to permanently laid within the salt marsh system or repeatedly mobilised and removed.

In many cases, depending on the nature of the material some form of retaining structure (bund), either permanent or temporary, may be required to prevent the sediments from moving away from the site in which they were placed. This can be of particular concern when dealing with fine grained material which is delivered in a relatively fluid form on sloping ground, as the material may be lost due to gravitational forces. In important habitats (such as European designated sites), permanent structures are unlikely to be favoured.

**Foreshore placement: indirect placement of dredged material ("trickle charging")**

Trickle charging is a process which involves the slow recharging of foreshore by placing sediment either at a single point, or at a series of points, on a beach, mudflat or in the subtidal, and allowing either longshore or onshore currents (depending on location of sediment placement) to move and distribute sediment across the foreshore. Determining where to place the material will require a detailed understanding of longshore and onshore currents in the affected area. The advantage of this approach is that the resulting foreshore profile forms naturally and so should become an integral part of the mudflat/salt marsh system. The major disadvantage is that the recharge process is slow when compared to direct pumping.

Although the use of fine sediment for intertidal recharge is more suited to the natural system, without management, it could cause smothering of shellfisheries in adjacent areas and may cause a navigation hazard to small craft in inshore waters. Conversely the placement of sands and gravels on muddy foreshores can reduce the area available to feeding birds (and potentially introducing 'foreign' material into the system, or one that has not been apparent for sometime). There is also potential risk of material being lost from the recharge site and the redistribution of sediments could cause an increase in suspended sediments.

Bowmlam & Whomersley (2003) present the results of a sampling program investigating invertebrate (macrofauna) recovery rates following a beneficial use scheme involving the placement of fine-grained dredged material on a salt marsh of Westwick Marina in the Crouch Estuary. Results indicated a rapid colonisation of a fauna, typical of the surrounding salt marsh, with evidence to suggest that post-juvenile immigration was a predominant recovery mechanism at the recharge stations.

Potential benefits effects include:

- Increased wave attenuation and coastal protection;
- Increases protection for marsh edge;
- Facilitation of future marsh development;
- Increased habitat for conservation interests;
- Increased wildlife potential for estuaries; and
- Useful employment of dredged arisings.

It is important that the processes operating in the coastal or estuarine environment are sufficiently well understood to allow an appropriate sediment recharge technique to be selected and an assessment made of the overall suitability of the scheme. The minimum data requirements prior to carrying out intertidal recharge are, therefore

Historical analysis of maps and aerial photographs to determine the rate of salt marsh retreat and changes in the high and low water marks;

Topographic contour mapping of the foreshore (mudflat and salt marsh), corrected to Ordnance Datum, to give an actual elevation that may be related to tidal inundation;

- Measurements of the wave environment and tidal regime;
- Analysis of existing sediment properties and grading curves;
- Analysis of sediment properties and grading curves of the recharge sediment
- Modelling of wave climate, currents and sediment transport regime;
- Analysis of marine invertebrate communities; and
- Analysis of any existing pollutants in the foreshore and the recharge material.

**Constraints**

The main constraints associated with sediment recharge, in particular from dredged sources, include:

The use of finer sediment derived from maintenance dredging may be limited. Cohesive mud requires time to consolidate and dewater before becoming stable enough to support engineering structures or mature plant and animal communities. The timescale required for such processes might be outside the timescale for habitat creation or restoration schemes;

Finding suitable sources of dredge material may not be easy. Disposal sites may be restricted by coastal development, the location of intake and outfall pipes, navigation channels, land ownership and the proximity of fisheries, in addition to the presence of sensitive animal and plant communities.

Disposal of dredged material on land generally takes longer to plan, find resources, obtain permits and undertake, than disposal at sea. Although beneficial uses have to be sought as part of the application process for a Food Environment Protection Act (FEPA) license to dispose of dredged arisings offshore and; disposal on land can provide further difficulties as many regulatory incentives for reducing the amount of material to be disposed of at sea, can provide an incentive to encourage beneficial use schemes associated with development (or maintenance) in ports and harbours.

Significant changes may be expected in the short term following recharge. Therefore, monitoring should be intensive in the early stages, reducing in frequency over time, with provision made for changes in scheme based on the results of monitoring.

This approach has been implemented at various locations in the southeast of England, including: Hamford Water, the Blackwater Estuary, Colne Estuary and the Orwell Estuary.

For more information please see the following references, Hesp & Dixon, (1997); ABP, (1998); Posford Duvivier, (1998); Posford Duvivier, (2000); Colenutt, (2001); Bowlam & Whomersley, (2003) and Thomas, (2004).

### Breakwaters

As for sedimentation fencing, the use of breakwaters as an exclusive technique to prevent salt marsh erosion has declined in recent years. Difficulties in obtaining planning permission and the move towards soft engineering options have led to the decline of this technique. It is now typically used only in combination with a number of other techniques on a small scale, rather than as an exclusive stand alone technique.

Offshore and nearshore breakwaters can encourage the development of a stable salt marsh/mudflat profile through a reduction in wave energy. Several types of breakwater have been used for general shoreline protection, which largely take the form of submerged rocky reefs offshore, using a shore-parallel line of individual islands. An alternative, cheaper option to rock breakwaters is geotextile tubes. They are long tubes made from strong geotextiles, which are filled in-situ form breakwaters, groynes or levees. They can be used in water up to a metre deep and do not present the same difficulties in equipment access that rock or concrete structures face, with costs approximately a third cheaper.

In some cases a breakwater may be combined with brushwood fences, which connect the breakwater to the shore to act as a large-scale polder. The use of this technique in high energy wave climates, however, means that fences, if used, can be subject to severe damage. Breakwaters may also be combined with foreshore recharge and vegetation planting to enhance their overall effect.

They are usually positioned at or near low water to encompass as much of the intertidal profile as possible and provide protection for most of the tidal cycle. This has the advantage of allowing the circulation of sediment between the marsh and mudflat and the intertidal profile to respond to short term changes in wave energy. Where breakwaters are used without shore connecting structures, there is also less disruption of longshore sediment transport processes.

A breakwater, once installed, requires less maintenance than brushwood fences and polders, although repeated assessment should be made of their stability or requirement for re-orientation.

Given the potential influence on coastal processes, the biological resource (which could be beneficial in certain circumstances) and the landscape, schemes such as the placement of submerged breakwaters at Horsey Island require significant scientific justification in order to achieve consent. With the introduction of legislation such as the Conservation Habitats Regulations 1994 it is likely that it would be more difficult to obtain consent for such an approach today.

In general terms, hard engineering may not provide cost-effective and environmental acceptable solutions to prevent salt marsh erosion. Such techniques often conflict with ‘natural’ processes and can require expensive repairs and regular maintenance in order to provide an adequate level of coast and flood protection from the effects associated with climate change.

The impacts of offshore wave breaks are similar to sedimentation fences, including visual intrusion, smothering of invertebrate communicate if accretion rates are high, scour around the structure and potential hazard to navigation. Approaches such as the sinking of barges, in particular can have an impact on the foreshore, as the fill material may be excavated from the landward side of each barge removing this material from the mudflat.

It is important to determine the most suitable distance offshore, orientation and spacing of breakwater structures by modelling prior to installation. It may also be necessary to reorientate breakwater structures as offshore conditions change, although this can be expensive. The minimum data requirements to assess site suitability are, therefore:

- Historical analysis of maps and aerial photographs to determine the rate of salt marsh retreat and changes in the high and low water marks;
- Topographic contour mapping of the foreshore (mudflat and salt marsh), corrected to Ordnance Datum, to give an elevation that may be related to tidal inundation;
- Measurement of the wave environment and tidal regime; and
- Modelling of the wave climate, tidal currents and sediment transport to determine orientation and spacing, requirement for shore-connecting groynes or suitability of foreshore recharge. Post scheme monitoring should be similar to that recommended for brushwood fences and polders as the aim of enhanced accretion on the foreshore is the same.

In addition, however, the wave climate within and around the breakwater should be measured at intervals to check the design functions and ensure that it is still functioning as required.

Breakwaters have been placed offshore at various locations in Essex, including Horsey Island and on the Dengie Peninsula. For more information regarding specific schemes at Dengie, reference is made to Holder & Burd (1990) and Simm *et al.,* 1996.

Any management system should aim to control unfavourable influences, so that events such as trampling, pollution and/or eutrophication can be prevented or at the very least minimised.

## Source control

The control of pollutant inputs to a salt marsh system at source can only be achieved through local co-operation with adjacent land owners, particularly service providers (such as water treatment companies) and farmers.

Maintaining close relationships with local landowners should remedy most of these problems. If, however, the problem continues then the relevant regulatory authority may need to be informed.

## Management of a pollution event

Works to restore a salt marsh after an oil spill can be important, because cleaning vegetation and sediments is very difficult. The main generic options are:

- Mechanical recovery offshore from the marsh;
- Dispersal (using oil spill dispersants) offshore; and
- Booming of salt marsh shorelines and inlets. Of these options, if salt marshes do become oiled, the best approach is often to allow natural recovery. However, intervention may be needed if:
- Free oil is present which may be spread with tidal action.
- Oil on the marsh surface threatens birds or other wildlife.
- The recovery time of vegetation is predicted to take several years. If intervention is required, the main clean-up techniques include:
- Physical containment and recovery - booming and skimming of oil on the water in creeks and pumping bulk oil from the marsh surface, depressions and channels;
- Low pressure water flushing – however, results are variable, and the method must be used before oil penetrates the sediment;
- Sorbents - the rapid deployment of sorbents can reduce penetration into sediments;

- In-situ burning of oiled vegetation - while burning can increase damage, in winter, much of the vegetation is dead and the ground is likely to be wet enough to protect underground systems from heat damage; and
- Vegetation cutting – this may be justified if there is a threat to birds or other wildlife. This will have a lesser effect on subsequent yield if it is undertaken in autumn and winter.

### Improvement of drainage

The management of drainage inputs to the site to control freshwater input can only normally be undertaken with the co-operation of adjacent landowners. As for source control, the key to resolving this issue is the identification of the problem and then getting agreement to any remedial action that is necessary. This may involve the control of water inputs via a sluice or improving drainage to facilitate the flushing of water though the marsh. It may include altering existing or historic drainage patterns (potentially associated with land claim/reclamation) within the salt marsh itself.

Again, defining the objectives of the improvement action will be central to determining the action that ought to be undertaken. In some instances, for example, changes to salinity can increase diversity. However, large scale inputs of freshwater will most often lead to the loss of salt marsh vegetation.

### Ship wash

This can be simply resolved, normally in conjunction with the body responsible for navigation, through an imposed (and enforced) restriction on the speed of vessels, to a speed that reduces the wash caused. It may also be necessary to consider changing the direction of approach of vessels, to alter wave direction, in the vicinity of an eroding salt marsh.

### Management of access

Continued public access to a particular salt marsh area might sustain localised trampling and possible disturbances of nesting birds (in the summer) or wintering wildfowl. Even small numbers of pedestrians (particularly walking dogs) can disturb roosting and nesting birds (Boorman, 2003). The identification of areas sensitive to trampling or disturbance should be undertaken to assess whether access is having a damaging effect. Where necessary, the provision of public information on potential adverse effects and limited or re-routed access may be acceptable (Boorman, 2003). This can be achieved through the use of information boards that encourage appropriate use. The existence of public rights of way around much of the UK's coast, however, can represent a constraint to limiting or diverting access.

### Hard engineering techniques

As discussed earlier, there has been a move away from hard engineering techniques which aim to halt erosion and/or promote accretion to softer techniques which aim to work with natural processes. Although these techniques are receiving less attention, they could be used in the future on a smaller scale based on the site specific circumstances (and potentially in combination with sediment recharge or vegetation planting). In the past, such techniques have included:

### Rock barriers

Rock barriers work in a similar way to sedimentation fences, in that they combat erosion by reducing wave energy and tidal currents, and produce calm water in their lee which enhances sedimentation. They can have a significant ecological, hydrodynamic and landscape implications.

### Rock armouring/revetments

Rock armouring or revetments have been used to halt lateral erosion at the leading edge of the salt marsh and in creeks. They protect the cliff edge from mass failure by providing protection from wave action and tidal currents, but will limit the ability of the marsh to evolve or respond to changing forces, such as sea level rise. Historically, this form of protection has been undertaken on the Humber, Severn Estuary and in the Wash.

The use of ‘soft’ revetments has also been employed where rolls of coconut matting (coirs) have been placed along the eroding salt marsh cliff face. This largely experimental technique was implemented on Lymington marshes with limited success.

### Managed realignment

Managed realignment is a so-called ‘soft engineering’ coastal management technique that has received considerable attention in recent years. Rather than working against nature (e.g. by fighting erosion) the approach adopts a method which allows the landward migration or creation of intertidal habitats (including salt marsh) by the removal or breaching of an existing sea defence. Under the terms of the EU Habitats Directive (92/43/EEC) and the Rio Convention it is seen as a suitable method for the creation of compensatory habitat following the loss of intertidal through, for example, land claim, dredging, coastal squeeze or coastal defence works. Nevertheless, the potential influence of realignment sites on the wider estuarine system can be significant.

Therefore, extensive baseline survey is required to model or predict these effects, and to determine whether they are acceptable, before such a scheme should be progressed. Managed realignment is not a technique for the management of salt marsh. However, it is an important option in the range of options available to coastal/estuarine managers for both coastal defence and the maintenance of intertidal habitats. For that reason, it is also covered here.

Managed realignment broadly involves constructing a new flood defence line inland of the original, promoting the creation of salt marsh (or a combination of mudflat and marsh) on the land between the old and new lines and finally removing the front sea wall either partially or wholly. In the past, the land between the defences will have been reclaimed (from the intertidal) and through shrinkage during drying out and possibly continued accretion seaward of the defence, may be at a lower elevation than the habitat in front of the sea wall. Infilling may therefore be necessary to help generate the required conditions for the new habitat. Such schemes can involve the use of dredged material, pumped onto the site in order to build up the level of the sediment to an appropriate height for marsh development. Equally surcharging a site with sediment may not be necessary, depending on the prevailing local conditions. This ideally results in the development of a new area of salt marsh habitat, which acts as a protective buffer to the new sea wall and the higher ground behind.

The use of tiered defences involves creating a new sea defence line inland of the original and allowing only a degree of overtopping of the front defence. The rear defence will be at a higher level than the front line and protected by the front line and intervening land. The irregular overtopping of the front defence should allow halophytic vegetation to colonise and the creation of a new area with an enhanced ecological value.

Controlled abandonment (as distinct from managed realignment) is more suitable in locations where there is a natural rise to higher ground and no new defence line is necessary. Again, active management is likely to be required to create new areas of salt marsh behind the present sea wall. In this instance, once marsh becomes established, maintenance of the coastal defence would be discontinued and, with eventual failure of the defence, full tidal inundation of the newly created salt marsh would occur. Both forms of managed retreat produce a wider intertidal profile that is better able to respond to coastal processes and to reduce the effect of coastal squeeze.

These approaches differ from do-nothing, in that some form of active management is carried out to create either a new salt marsh habitat or a new sea defence line, or a combination of both. In addition, all schemes should be monitored regularly to assess the changes in the new marsh and to determine whether any additional work is required. This is more likely to result in a viable salt marsh than simply allowing the wall to disintegrate and flood the land behind, and should therefore be more successful in terms of both sea defence and habitat creation.

Techniques for creating and regenerating salt marsh are well documented. In particular, comprehensive guidance on managed realignment techniques is provided in the CIRIA guide ‘Coastal and estuarine managed realignment - design issues’ (Leggett *et al.,* 2004). This report is divided into three sections, intended to provide easy access for different users. Part 1 explains the objectives of managed realignment; Part 2 discusses whether realignment is appropriate for a particular site and how it may be achieved; and Part 3 provides technical guidance on design and implementation. The review identifies examples of best practice and lessons learnt relating to scheme design and associated impacts, discussing four case studies in detail. The reader is, therefore, directed to this document for a more in depth discussion of managed realignment and the conditions required to successfully implement a scheme. The rest of this section provides a summary of the main points that need to be considered when management realignment is an option.

There are many issues that need to be addressed when selecting a suitable realignment site. In addressing some of these considerations baseline data will need to be collected to predict/model the effects that the realignment scheme will have both in the realignment site itself and on the wider estuary. Such baseline data should include:

- Topographic surveys of the realignment site and adjacent marshes;
- Bathymetric surveys of the estuary;
- Current and suspended sediment monitoring; and
- Biological monitoring.

The DEFRA/Environment Agency (2002) review of managed realignment as a flood and coastal defence management option identified a number of potential constraints affecting opportunities for realignment. The relative importance of these factors will vary between schemes but, in general, consist of the following:

- Consents and legislation;
- Environmental issues;
- Funding and financial compensation; and
- Opposition from the community.

Each of theses constraints are discussed in more detail in the CIRIA managed realignment guide (Leggett *et al.,* 2004).

Potential effects

- Risk of increased erosion in other areas of the estuary due to an increase in the tidal prism, which causes faster tidal currents.

- Short term loss of grazing in the interval between the die-off of terrestrial plants (due to saltwater irrigation), on what was rough grazing pasture, and colonisation by salt marsh.
- Loss of ecologically valuable terrestrial habitat.
- Creation of salt marsh and mudflat habitat that may have been lost to other mechanisms (such as coastal squeeze).
- Providing the opportunity for the coast line to respond ‘naturally’ to changes in estuary processes.
- Increased coastal habitat for nature conservation purposes.

### Monitoring

Monitoring will have an important role, at both the implementation and post-project stages, in the assessment of the impacts of the project and to determine if the design is operating as intended. Normally implementation monitoring will involve observing and recording any particular features, such as archaeological finds, that become exposed during construction or any impacts on neighbouring industries such as shellfisheries. Post-project monitoring, and an associated action plan, may be set as a condition of a consent or license for the works (and will often be covered in an Environmental Impact Assessment).

The results of post project monitoring might lead to a re-design (or some other form of intervention or even compensation) where an unacceptable outcome is shown to occur.

Intervention should only occur, however, where the degree of change is unacceptable (compared to pre-defined criteria) and/or where an unacceptable change has been shown to exist for a sufficiently long period of time; it is important to recognise that sites will evolve over time and so the need (or otherwise) to react to initial change should be carefully evaluated. Monitoring of projects can also feed into other projects by providing an understanding of scheme design and performance.

The principal monitoring techniques which apply to manage realignment include:

- Topographical survey;

- Monitoring intertidal accretion rates;
- Monitoring intertidal erosion;
- Flow monitoring;
- Monitoring scour and counter wall erosion; and
- Ecological monitoring.
- For a more detailed discussion on monitoring for realignment sites the reader is referred to DEFRA (2002; 2010) and CIRIA (Leggett *et al.,* 2004).

The first managed realignment scheme in the UK was implemented in 1991 at Northey Island, Essex and was followed by schemes at Orplands and Tollesbury, also in Essex. Several schemes have been carried out since, largely in the south east region, and most recently at Abbots Hall Farm (Essex) and Frieston (Lincolnshire). The reader is referred to the CIRIA guide (Leggett *et al.,* 2004) for a listing of managed realignment sites established in the UK to date.

Further information is available in the following references. Atkinson, *et al.,* 2001; Hazeldon & Boorman, 2001; Crooks, *et al.,* 2002; 2004; DEFRA, 2002; Garbutt, *et al.,* 2003 and Leggett, *et al.,* 2004.

**Regulated tidal exchange systems**

Regulated tidal exchange is a form of salt marsh creation that allows the controlled inundation of previously defended land with saline water, using a combination of pipes and sluices. It differs from realignment schemes in that the sea wall remains intact. It is a potentially valuable tool in two particular scenarios: where coastal defences are likely to remain in place for the foreseeable future; and as the first phase of a longer term realignment strategy. A small number of projects have been developed in the UK but there are examples of larger projects overseas in the Netherlands, Germany and the United States.

Like managed realignment, this is not strictly a technique for the management of salt marsh. It is an option that should be considered as part of a broader strategy for managing marsh habitat (i.e. coastal management).

Regulated Tidal Exchange (RTE) Systems enable an area behind a sea defence to be gradually converted to salt marsh and/or mudflats. The process uses pipes, sluices or tide gates to allow regulated tidal flushing by seawater to create saline or brackish conditions behind the defence. This is a slow process that allows the land and local species to adjust their soil chemistry to the more saline conditions required by salt marsh and siltation to proceed gradually.

There are several techniques used to control the flow of sea water and not all techniques are suitable at all sites; some are more suitable for creating mudflats than salt marsh.

Techniques include:

- An open culvert, with no tidal flap through the sea wall. Tidal water will flow in and out on every tide as long as the invert level is around the mean low water mark. A variation on this method is to have a drop board on the landward side to prevent water flowing out of the culvert, creating a permanently flooded area.
- Culverts with manually operated flaps that let water through into an impoundment at high tide over several high tides, until desired water level is reached.
- Self regulating tide gates (SRTs) have one moving part and an adjustable float system, allowing the SRT to stay open and float on flooding and ebbing tides until the specified desired water level has been reached, at which point the SRT will close and stay closed. When the tide recedes on the outside of the site, the SRT automatically reopens, allowing the impounded water to flow out.
- Electronically operated tide gates. Flow is regulated by a vertical lift, rectangular tide gate on the seaward side that opens and closes electronically at desired water levels, which are monitored by pressure sensors. The gate is normally open for a short period on each rising and falling tide.

There are several essential requirements of potential sites for RTE:

- An existing sea defence such as a seawall into which a pipe, sluice or tide gate could be integrated;
- An area that can be flooded without flooding adjacent farmland (may require a bund to be constructed behind the primary defence);
- A nearby source of sea water to permit saltwater flushing. Sea water should ideally have enough suspended sediment to enable accretion at a higher rate than sea level rise;
- The site must be no less than 0.1 m lower than sea level at the highest part of the tidal cycle;
- The site must have a tidal range of at least 3 m;
- Impermeable underlying geology, not prone to erosion (i.e. not peat or chalk); and
- Gradients of at least 1 – 6 %, this will determine the ratio of salt marsh to mudflat.

When developing a RTE scheme it is essential to ensure adequate water exchange and a sufficiently high rate of accretion to keep pace with predicted sea level rise. Broadly speaking, sites with less than 450 - 500 inundations a year will tend to develop into salt marsh, while those with 450 - 600 will tend towards mudflat.

RTE can be useful in large managed realignment schemes where it is impractical to allow all areas that may potentially flood to be inundated at once. It therefore provides the opportunity for a phased approach to managed realignment. Large sites may be compartmentalised and only small areas introduced to tidal inundation at any one time, to potentially minimise impacts. RTE may also be useful prior to breaching a managed realignment site. By exposing land behind the defence line to carefully controlled inundations, the land may be encouraged to 'warp up' to a higher level (through sedimentation) in preparation for breaching or the removal of a defence.

However, RTE is a particularly useful technique where defences are likely to stay in place for some time. Furthermore, a new defence may not need to be constructed, potentially representing a cheaper option than managed realignment. RTE may also be appropriate at a number of sites in eastern England, where managed realignment may have negative impacts on wider estuary systems associated with increased tidal volume.

RTE has many benefits in common with both foreshore recharge and managed realignment, with the added benefit of a higher degree of control over hydrological processes. This means that a site could be set up to encourage a specific type of salt marsh or mudflat to develop and any undesirable impacts associated with increasing tidal volume following a managed realignment could be controlled.

### Constraints

The relatively small hydraulic capacity of spillways, culverts and pipes compared with defence removal or breach creation (realignment) usually tends to restrict their use to smaller sites of only a few hectares in size.

In addition, the existing defence line has to be maintained for as long as the tidal exchange system is to function, so potential defence cost savings associated with breach or bank retreat would not be realised or may be deferred.

The potential effects associated with RTE are similar to those associated with managed realignment

### Monitoring

Monitoring objectives will be similar to those for realignment schemes. In particular, baseline monitoring of ground levels, vegetation, invertebrates, current bird usage, water levels, salinity, changes in vegetation and invertebrates should be undertaken.

Regulated tidal exchange was first tried at Horsey Island, Essex and has subsequently been trialled in Chichester Harbour, and at Goosemoor Devon.

For further information please refer to Sharpe *et al.,* (2002) and Leggett, *et al.,* (2004)

### Increasing toughness

In an attempt to combat erosion, enhancing the bed roughness has also been attempted using artificial seaweed. This consists of polypropylene fronds attached at one end to a geotextile mat which is anchored to the seabed. However, this has been largely unsuccessful due to the difficulties of attaching the mats to the unstable bed under breaking wave conditions.

Other techniques to increase surface roughness have included seeding mudflats with mussel sprats.

### Invertebrate exclusion mats

Recent research by Hughes & Paramour (2004) has demonstrated that salt marsh accretion and colonisation of pioneering species can be promoted by removing invertebrates using mulch mats. In particular, they discuss the effects of the polychaete worm, *Nereis diversicolor*, in terms of sediment instability (through burrowing) and herbivory (feeding on *Salicornia spp.* seeds). They also suggest that the decline in recent years of *Zostera sp*. may also contribute to salt marsh erosion and suggest that sea grass beds could be transplanted to dissipate wave energy.

### Financial implications of management

All options for salt marsh management will have financial implications and these will be different depending on the technique adopted. Remedial techniques (i.e. silt recharge), for example, may be cheaper than hard engineering schemes, but are likely to require regular maintenance in order to be effective. All proposals must be economically sound when the total scheme life is considered and this should include the long term financial investment required to establish the salt marsh to the point where it is self-sustaining.

As stated above, the applicability of the technique to each situation must always be considered. In particular, the prevailing physical processes, as well as the key characteristics of the ecosystem, should be understood before a scheme is selected. It is possible that the cheapest scheme, implemented in inappropriate circumstances, could eventually prove to be more costly, either through the requirement for long term maintenance or as a result of impacts experienced elsewhere.

In many cases a remedial scheme may need to be combined with some form of hard engineering, with increasing costs, particularly if the erosive processes are far advanced and an existing defence has become unstable. However, conversely, if a scheme includes hard engineering it may be possible to reduce the capital and maintenance costs of the engineered defence. It is also important to consider the ecological benefits that may arise when selecting the most suitable management option. In all cases, there will be minimum baseline data collection and monitoring requirements.

Monitoring is essential to ensure the success of each scheme and provide supplementary information for future schemes. Long term data collection and monitoring, therefore, should be costed for as part of every salt marsh management scheme. It should also be recognised that this latter aspect of the work has the potential to contribute major financial savings in the long term.

## Appendix D: Socio-Economic Model

Salt marshes offer a wide range of different functions and services that are of value to people and therefore have an economic value. This can be measured in several ways. The easiest of which to understand is the concept of values having an economic worth that can be expressed in monetary terms. However, values can also be expressed in non-monetary terms, although such values are often more difficult to define.

Stuip *et al.,* (2002) identified that a number of different values can be defined according to the way that humans interact and benefit from salt marshes.

Use values are realised through human interactions such as direct use values; relating to the products and benefits that can be derived from the use of a salt marsh, such as food, materials and recreational use. Indirect use values; arising from the benefits provided to existing activities or resources through their occurrence can be thought of as services, for example flood control. Potential future use; arises where there is uncertainty over the future demand for a product or service and/or its availability in a salt marsh in the future. The potential future use value reflects the need to estimate, for example the benefit of conservation of the salt marsh.

Non-use values relate to the essential nature of the wetland and the worth that is placed on it by particular groups for example, non-use values include biodiversity or heritage.

Table 17 summaries the main types of salt marsh value and the categories that they fall into. Notionally, consideration of all the value types will give an indication of the Total Economic Value of a salt marsh.

The concept of economic worth and the definition of the functions of the salt marsh form the basis of economic appraisal. However, not all of the functions proposed for use in economic appraisal can be directly measured in monetary terms. Therefore, it may be necessary to identify ways in which impacts can be expressed as money values or to consider descriptive methods of valuation. There are a range of economic techniques available for placing money value on impacts where a direct (e.g. market valued based) value is not available.

**Table 17: Total economic value for wetlands**

| **Use Values** | | |
|---|---|---|
| **Direct Use Values** | **Indirect Use Values** | **(Potential) Future Use Values** |
| Salt marsh products | Flood Control | Potential future uses (as per direct and indirect uses) |
| Recreation and Tourism | Groundwater Recharge | Future Value of Information |
| Transport | Shoreline Stabilisation and Storm Protection | |
| Agriculture | Water Quality Improvement | |
| Peat / Energy | (Micro) Climate Change Mitigation | |

Summarised from Babier *et al.,* 1996

More generically, project appraisal (PA) can be used at a variety of different levels for the assessment of management options, from identifying where impacts may occur through to their monetary valuation. The aim of any project appraisal is to provide a decision maker with clear information on the choices that have to be made. This does not necessarily make the choices any easier. The amount of detail required for a project depends upon the type of decision that has to be made. In many cases, it will be sufficient to describe potential (or realised) impacts to salt marsh habitats, for example, in qualitative terms or to report impacts and proposed mitigation measures in their natural unit of measurement (e.g. number of hectares of a particular habitat type created or restored). In other cases, particularly where it is necessary to justify expenditure or to obtain funding, it may be necessary to report benefits in monetary terms. For example, the inclusion of managed realignment as part of the flood defence strategy will require full project appraisal where appropriate, including monetary valuation.

There are many forms of project appraisal techniques, assessing the economic as well as other potential values of salt marsh can be assessed using techniques such as Appraisal Summary Tables.

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