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Patterns in time and space on Solent saltmarshes: a combined palaeoecological and experimental approach

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Errata

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p.*i*, line 34: omit 'that'

p.5, line 10: *europaea*; also p.13, line 6 and 14; p.18, line 3; p.79, line 2; p.83, line 11; p. 109, second paragraph; p.112, line 8; p.123, last line; p.168, line 31; and p.169, line 4

p.23, line 18: Chenopodiaceae; also p.67, line 26

p.35, line 27: replace 'pollen' with 'spores'

p.44, line 31: replace 'then' with 'than'

p.59, line 6: add bracket after 1994

p.66, line 23: *Spartina* in italics

p.75, line 21: 'effected' should read 'affected'

p.82, line 25: add bracket after 'area'

p.122, line 17: 'manipulation' should read 'manipulations'

p.123, line 5: omit 'at'

p.131, line 18: replace 'sheers' with 'shears'

p.157, line 8: omit 'or'

p.158, line 12: omit first 'which'

p.161, line 26: replace 'montaine' with 'montane'

p166, line 5: 'effecting' should read' affecting'

p167, line 6: 'Myximatosis' should read 'Myxomatosis'

UNIVERSITY OF SOUTHAMPTON

ABSRACT

FACULTY OF SCIENCE

CENTRE FOR ENVIRONMENTAL SCIENCES

Doctor of Philosophy

PATTERNS IN TIME AND SPACE ON SOLENT SALTMARSHES: A COMBINED PALAEOECOLOGICAL AND EXPERIMENTAL APPROACH

By Malcolm David Hudson

The effects of three biotic factors (a new species, grazing, and plant-plant interactions) were considered on the spatial patterns and temporal changes observed on coastal saltmarshes. Palaeoecological methods and manipulative field experiments were conducted at several locations in the Solent region. The Solent has a rich resource of saltmarsh habitats, which are of high scientific value and are of national conservation importance.

Palaeoecological investigations were carried out on three sites (Beaulieu, Hythe and Marchwood) to investigate the long term effects of the appearance of the hybrid grass Spartina anglica C.E. Hubbard (common cord grass). Historical records were researched to complement the data obtained from the analysis of sediment cores, to characterise the saltmarsh environments before the appearance of the new species. The evidence suggests that before S. anglica appeared in the region (in the second half of the nineteenth century), mudflat and pioneer marsh were much more significant features of the Solent coast than they are at present.

Manipulative experiments were carried out at two locations on the Beaulieu Estuary. The effects of excluding large wild grazing animals (principally geese, rabbits and deer) on the plant communities were investigated by constructing experimental exclosures. These were monitored for three years, after which above ground biomass was harvested from randomly selected parts. Excluding grazing animals produced rapid structural changes in the plant canopy. Palatable species, which had previously been suppressed by grazing (e.g. Plantago maritima L.), proliferated rapidly. Some low-growing species, which had previously been conspicuous in the community (e.g. Armeria maritima (Mill.)), declined significantly, possibly due to shading by the increased growth of other species.

The importance of competition and facilitation in setting the positions of two plant species within the zonation of a saltmarsh was investigated by transplanting them to different vertical zones. When the lower marsh grass S. anglica was transplanted to the upper marsh it was outcompeted by more competitive plant species. When the surrounding above ground vegetation was removed, it grew successfully. The upper marsh rush Juncus gerardii Loisel was transplanted to the lower marsh. This species could not tolerate the harsher physical conditions at a lower level, but that the presence of neighbouring plant growth increased its success.

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CHAPTER 1

INTRODUCTION

Saltmarshes can be defined as areas of alluvial or peat deposits colonised by grasses, herbs and small shrubby terrestrial vascular plants, which are almost permanently wet and are frequently inundated with saline waters (adapted from Long and Mason 1983). They are found throughout the extra-tropical regions of the world in low energy environments with a supply of fine sediment (Carter 1988). In the tropics they are replaced by mangrove swamps. Saltmarshes typically occupy the interface between the land and the sea, and their biota have characteristics of both marine and terrestrial flora and fauna. This reflects the saltmarsh environment itself, which has both terrestrial and marine features, but is usually regarded as a highly modified terrestrial system. Saltmarshes have been described as "cohesive phytogeomorphological units" (Ranwell 1964) and their study must consider both the physical and biological processes involved.

Saltmarshes have increasingly come under threat in this century, mostly directly or indirectly through the activities of human beings. Coastal marshes are widely recognised as one of the landscape types most threatened by sea level rise (National Research Council (United States) 1987, United Nations Environment Programme 1990, Allen 2000). Mankind has traditionally settled around estuaries and coastal marshes and this has placed them under a variety of pressures. We have used coastal waters, estuaries and intertidal marshes for waste disposal to the extent that pollution is now an important factor in most coastal ecosystems (review Viles and Spencer 1995). At the same time, marshes have been reclaimed for agriculture, industry or housing; or "squeezed" by the combination of coastal defence construction and sea level rise (Doody 1992, WWF 2000). Furthermore, humans have been instrumental in the development and spread of new species, in particular the hybrid cord grass *Spartina anglica*, which has had a major impact on the ecology and physiography of most of the saltmarshes in northern Europe and elsewhere (review Doody 1982).

These problems, and others, cannot be addressed in isolation, as saltmarsh systems are generated and maintained by a combination of physical and biological factors acting in concert. In this thesis, I examine some aspects of these different areas of concern. In particular it focuses on how the factors affecting saltmarshes can act on different temporal and spatial scales. The role of disturbance and its effects on biodiversity are also considered. The following review examines the saltmarsh environment by initially considering the physical elements that underpin and largely shape marsh systems on the macro scale. It then examines the biological processes which, at least in part, account for the finer grain patterns which are observed in the plant communities of saltmarshes. Finally, the role of *S. anglica* in saltmarsh ecosystems is reviewed. At the end of this chapter, the rationale and specific aims of the thesis are given, which are then examined in three experimental chapters.

Geomorphology of saltmarshes

The physical environment of saltmarshes is dynamic, with depositional and erosional forces acting against each other to produce an accreting or eroding system. The balance of these forces is influenced by the ecology of the system: growth of microalgae stabilises a mudflat system; establishment of vegetation encourages further retention of sediment brought onto the marsh by flood tides; progressive sedimentation leads to further intertidal hydrological changes (review Allen 2000).

Vertical saltmarsh accretion depends on three factors
(i) the availability of suitable sediment
(ii) the energy of the tidal environment for resuspension or transport of sediment
(iii) the ability of plants to retain sediment

At any point in space and time there will be a relationship between the elevation and the sedimentation. As the marsh surface accretes vertically, the frequency of tidal inundation falls, and with it the delivery of sediment reduces. Rates of vertical accretion are typically 0-10 mm annually, but can be as much as 10 cm in a single year (Ranwell 1964a). Pethick (1981) has suggested that the age of the marsh accounts for much of this variation, but a number of other factors (e.g. tidal regime, sediment availability, difficulty of accurate measurement) are also involved (Steers 1977, Letztch and Frey 1980). Accretion rates also vary seasonally and at the same time vary spatially, i.e. across an individual marsh. Ranwell (1964a) found that in the Bristol Channel accretion in the summer was replaced by erosion in the winter. Similar trends have been found elsewhere (e.g. Letztch and Frey 1980).

Saltmarshes can also grow or retreat horizontally. Seaward extension of marshes takes place through colonisation of mudflats, initially by microalgae, and then with pioneer vegetation in conditions where wave energy is sufficiently low (Coles 1979). In theory, seaward growth could continue as long as there is sediment available until the tidal or wave energy becomes too high for plants to survive

(Adam 1990). In practice sediment availability often restricts the rate and extent of further growth as the size of the marsh increases (Jeffrey 1984). Human intervention often results in changes in the extent of saltmarsh systems by altering hydrological processes and sediment budgets. Gray (1972) documented the growth of saltmarshes in Morecambe Bay after the construction of railway viaducts stabilised the river channels, although more recently the eastern side of the Bay has eroded extensively (Adam 1990). Construction of sea walls behind a marsh can accelerate erosion by altering tidal patterns as well as preventing the landward migration of saltmarsh communities, where surface topography allows (Doody 1992). It is also possible that the movements of estuarine channels may display some long term periodicity (Haynes and Dobson 1969), and that the frequency of major storms and changes in weather patterns are also important influences in determining marsh morphology over longer time scales (Tooley 1992).

The factors affecting the morphology of saltmarshes can be regarded as operating over various temporal scales. Changes in sea level, and variations in rates of change, might fluctuate over decades or centuries (Thomas and Varekamp 1991, Tooley 1992). Shorter term cycles in tidal amplitude may superimpose changes over longer term trends (Gornitz *et al* 1982), and as mentioned earlier, within year seasonal variation in accretion and erosion also takes place (Ranwell 1964a). Superimposed on all of these are low frequency events such as storm surges (the frequency of which also varies over time) (Pye 1995) and natural and anthropogenic changes in both hydrology (Beeftink 1977) and ecology (Corre 1977). The position of creeks and river channels is also dynamic with changes observed over timescales of 10-100 years, although major changes may be the consequence of storm events rather than due to continuously active processes (Garafolo 1980).

Zonation, succession and pattern of saltmarsh plant communities

Zonation

Vascular plants can only colonise saltmarsh environments when stable low energy conditions prevail (the terrestrial plant species included in this thesis are listed in Appendix 1). Drying of mudflat surfaces and mucus produced by diatoms and other microalgae facilitates colonisation by promoting sedimentation and stabilising surfaces (Coles 1979). Mudflats often support eelgrasses (*Zostera* spp.) but these do not encourage sediment accretion in the same way as other saltmarsh plants. In suitable conditions, pioneer species that are tolerant of frequent inundation such as glassworts (e.g. *Salicornia europea*), annual sea-blite (*Sueda maritima*) and cordgrass (*Spartina anglica*) will colonise mudflat areas seaward of existing vegetation. Vegetation plays a dual role in the physical process of saltmarsh development, by both stabilising accreted material and trapping additional sediment (Randerson 1979). In England and Wales the lower marsh is (at or above Mean High Water Neap, MHWN) often dominated by sea purslane (*Atriplex portulacoides*) and common saltmarsh grass (*Puccinellia maritima*) (referred to as *Pu. maritima* in this thesis); sometimes with a sizeable amount of sea aster (*Aster tripolium*). As the marsh accretes vertically, typically further above Mean High Water (MHW), conditions become more suitable for the establishment of other species which are less tolerant of the physical disruption by waves and tides, or of long periods of inundation, such as sea lavender (*Limonium vulgare*), thrift (*Armeria maritima*), sea plantain (*Plantago maritima*, referred to as *P. maritima* in this thesis) greater sea spurrey (*Spergularia media*) and sea arrow grass (*Triglochin maritima*). The upper marsh (above Mean High Water Spring, MHWS) is characterised by the grass red fescue (*Festuca rubra*), which is also widespread in terrestrial ecosystems; rushes such as saltmarsh rush (or black rush) (*Juncus gerardii*); and sea rush (*Juncus maritima*); and there is often zone dominated by the highly competitive sea couch grass (*Agropyron pungens*) before truly terrestrial plant communities dominated by non-halophytes take over.

The preceding paragraph is very much a generalisation. While zones of vegetation are observed which are composed of specific assemblages (and there have been attempts to classify them, for example Adam (1980) or more recently Rodwell (2000)), often saltmarsh systems do not display such clear cut spatial characteristics, or contain a finer scale variability within the major zones. The reasons for this are considered below.

In the UK three main groups of saltmarsh plant communities have been identified using cluster analysis of community data (Adam 1978). In the south east of England "type A" marshes are widespread. These are relatively low in diversity, with *S. anglica* or *A. tripolium* present as pioneers, *A. portulacoides* common in the mid-marsh and *A. pungens* dominant in the upper marsh. "Type B" marshes are frequently shaped by domestic grazers, with *Pu. maritima* dominant in the pioneer and lower marsh zones , sometimes with some *S. anglica*; and with *F. rubra* and *J. gerardii* dominant in the mid and upper marsh zones. Type B marshes are common in Wales and north west England, where grazing of marshes by cattle and sheep has been a traditional element of local agriculture. Type C marshes, which are common in the west of Scotland are often species rich and include some non-halophyte plants and fen-like communities.

Succession

Classifications such as those developed by Adam (1978) or Rodwell (1999) do not always sit easily on the marsh systems themselves. Coastal marshes are viewed as good examples of classical primary succession from uncolonised tidal flat to a climax vegetation (e.g. oak woodlands), and this implies a series of directional changes in the flora and its physical environment (Randerson 1979). However, while zones of vegetation are often observed which resemble small parts of the classical halosere, it is widely accepted that this represents something of an oversimplification. Indeed, such clear zones of plant community types that are observed may not have developed entirely through successional processes (Long and Mason 1983, Gray 1992). The classical view assumes a steady rate of accretion in excess of the prevailing trends of sea level rise, but in much of northern Europe, particularly southern Britain, this is not the case (Tooley 1992). Redfield (1972) modelled the changes in New England marshes to include an ongoing rise in sea level, but integral to the model is the assumption of parallel zones of vegetation perpendicular to the shore. What is frequently observed is a complex mosaic of assemblages resulting from a whole variety of natural and anthropogenic factors operating on different spatial and temporal scales which creates a pattern of varying microhabitats across the marsh ecosystem. These factors include changes in soil type and particle size (Scholten and Rozema 1990); submergence times (Hubbard 1969, Huiskes 1990); salinity (Davy and Smith 1985); variable sea level rise (Gornitz *et al* 1982, Gough and Grace 1998); storm surges (Ranwell 1964a, Dolan and Davis 1992, Pethick 1992, Pye 1995); rainfall (Long and Mason 1983), grazing (e.g. Gray 1972, Bazeley and Jefferies 1985, Olff *et al* 1997); pollution (Baker 1979, Baker *et al* 1984); nutrients (Levine *et al* 1998, Van Wijnen and Bakker 1999); eutrophication (Ranwell 1981); competition (Gray 1992, Bertness 1991); interactions between flora and fauna (sometimes on more than one trophic level) (Tscharntke 1992); and disturbance events, for example by debris (Bertness and Ellison 1987, Cassells 1997 unpublished), by animals (Bazely and Jefferies 1986) or extreme weather events (Beeftink *et al* 1978); or of course, by humans in the form of coastal management (Beeftink 1977, Allen 2000). While there has been research into the effects of these factors their level of importance remains poorly understood and probably varies both spatially and temporally. Furthermore the variability of each factor is likely to operate on different scales from the other factors, so making an evaluation of their relative importance will always be difficult.

Redfield's (1992) successional model of saltmarsh development also assumes a migration landward of halophyte communities as the marsh accretes vertically. However, this process is often disrupted by human influences such as the construction of sea walls and land reclamation, which can also disrupt lower marsh areas by altering the physical processes of wave energy and sediment transport (WWF 1999). This may be contributing to the erosion currently taking place in southern England, as most of these saltmarshes are bounded by sea walls, in an environment of rising sea levels; and often with sediment removed from the system through dredging, or the construction of sea defences (Harmsworth and Long 1986 Associated British Ports 2000). Meanwhile where landward migration proceeds unimpeded the actual processes of change from terrestrial to saltmarsh have been little examined. Such an investigation of the history of such change, and of the ecological relations of the halophyte and terrestrial flora might produce some useful information about the rates of coastal environmental change and the processes that drive those changes.

Randerson (1979) devised a quantitative model based on data from the Wash in eastern England, that incorporated most of the above factors and helped to explain schematically how many of the variables contribute to the development of the vegetation patterns which are usually observed; and which Redfield's (1992) model did not address. However, the model only applies to marshes which are accreting, and is therefore not really applicable to most of the southern half of England (Gray, A. J. 1997, Pers. Comm.). The model was based on data from a series of points that are assumed to represent in space the sequence of events occurring through time at a single point. It therefore has a temporal component, but no spatial component, although the temporal component is itself derived from spatial observations. One major limitation of the model is that new biological material, that has influences on the spatial component of saltmarsh physical dynamics may disrupt the time sequences which are assumed (Randerson 1979). In view of the importance of *S. anglica* (see below) this seems to be a serious flaw.

Several studies in North America (see below) have suggested that the traditional concepts of succession are not really applicable in saltmarsh environment. These concepts were developed in environments which, physically at least, are stable over long time periods such as grasslands (Tansley and Adamson 1925) or successional field clearances (Bazzaz 1979). In coastal environments, particularly those that are usually low energy but subject to occasional high energy disturbance events, abiotic fluctuations can impose dramatic and unpredictable changes in conditions on the plant communities. This may render the ongoing autecological processes to be of relatively minor importance, which can, *in extremis*, effectively restart succession. Palaeoecological studies based on stratigraphy, pollen analysis and macrofossils have shown evidence of relatively frequent and abrupt changes in local environments without any predictable pattern (Meyerson 1972). At Guildford, Connecticut, this has resulted in whole plant communities being replaced, with evidence suggesting that the main factor is changes in sea level (Sears 1963). Clark and Patterson (1985) used evidence from pollen, Foraminifera, macrofossils, rhizomes and lithology from a saltmarsh on Long Island, New York to demonstrate that disturbances due to storms, barrier dynamics, cultural manipulation, sediment and sea level change seem to have more influence on the plant communities than biotic factors. However, although the methods of prediction of changes in sea level and weather patterns are becoming increasingly sophisticated, and are treated with widening respect (Hulme 2000), the prediction of the impacts of such changes on saltmarshes remains highly problematic (Huiskes 1990). This is partly because of the inherent complexity of the saltmarsh ecosystem (Reed 1995).

Gray (1992) has attempted to quantify the ecological niches of individual plants and found that physical factors can mostly explain the distribution of a species on a marsh. The vertical range of *S. anglica* was compared along 107 line transects in 19 different sites in southern and western Britain. Many variables were measured, but just four of these, all of which were physical, could be used to construct a reliable model to predict the upper and lower limits of *S. anglica*, i.e. :

$UL \quad = 4.74 + 0.483\ SR + 0.068\ F - 0.199\ L$

(upper limit)

($r^2 = 90.2, \ s = 0.50$)

$LL \quad = -0.805 + 0.366\ SR + 0.053\ F + 0.135\ Log_eA$

(lower limit)

($r^2 = 93.7, s = 0.35$)

(where SR is spring tidal range (m), F is fetch in the direction of the transect (km), Log_eA is the log_e of the estuary area (km^2) and L is latitude (in degrees north expressed as a decimal)).

The implication for this model for the relative importance of physical factors versus biotic factors is clear, at least in setting upper and lower limits of a species' range. This reinforces the belief that an individual species' range is largely governed by its ability to tolerate tidal submergence (or factors related to submergence). As elevation increases it is widely held that competition with other species increases (Gray 1980 and 1985). This may explain the slightly poorer fit of the upper limit model for *S. anglica* above, while at the lower limit *S. anglica* is operating almost in the absence of biological competitors. Indeed *"competition governs the location of upslope boundaries, whereas each species' downslope boundary occurs at a level on the marsh set by its physiological tolerance for submersion in salt water"* (Pielou and Routledge 1976). This principle has long been accepted for harsh environmental gradients, following the generalities developed in rocky intertidal environments by Connell (1961, 1972). Recently evidence has emerged that upper limits on rocky shores can be set by biological as well as physical factors, especially in the more benign conditions lower down the shore (e.g. Hawkins and Hartnoll 1985, see Raffaelli and Hawkins 1996, for review pp76-79). Furthermore, the work of Bertness on saltmarsh communities (see below) has shown that biotic factors are rather more complicated than this suggests. The factors governing where a species actually grows are very complex and explain the patchiness and smaller scale variability described above. Eleuterius and Eleuterius (1979) suggested that while tidal phenomena were important, other environmental factors *"especially edaphic factors and possibly biotic interactions"* were also considered to contribute significantly. Zedler *et al* 1999 found that microtopographical variations and waterlogging were probably responsible for the fine scale spatial patterns observed and suggested that the traditional classifications of "high", "middle" and "lower" marsh be replaced with a system that included elevation and landscape position.

Biotic Factors

The role of biotic factors and interactions has been examined by Bertness and co-workers in a number of trials on the East Coast of America. Bertness (1991) showed, using removal and transplant experiments, that plant distributions in the upper marsh were strongly dictated by interspecific competition. Bertness (1992) transplanted *Spartina alterniflora* from the low marsh to the upper marsh and found that when the transplants were kept free of neighbouring plants they were able to grow well. However, where grasses or rushes were present around the transplants, *S. alterniflora* was rapidly eliminated. Bertness suggested that the root morphologies and the timing of growth of the upper marsh plants give them crucial competitive advantages, but the below ground runners of *S. alterniflora* help it to colonise open areas in the lower marsh. Emergence times were also identified as important: the north American upper marsh competitive dominant *J. gerardii* excludes other upper marsh species due to its early growing season, which allows it to shade out its competitors (Bertness 1991).

Competition between neighbouring plants is not the only major biotic factor in operation. Bertness and Hacker (1994) showed that facilitative associations between different plant species can buffer neighbours from potentially limiting physical stresses and, in effect, extend their seaward distribution. Bertness and Leonard (1997) suggested that such positive interactions in intertidal communities are of greater importance than previously recognised, particularly in physically stressful environments. Brewer *et al* (1997) showed that positive interactions with other plants facilitates survival in the face of the abiotic stresses of the lower marsh. Harley and Bertness (1996) have shown that morphological changes in crowded saltmarsh plants allow them to withstand greater physical stresses. However, in the upper marsh, crowding by competitors acts against seedling establishment (Brewer *et al* 1997, Callaway and Pennings 2000). It seems that interactions between neighbouring plants are largely competitive (i.e. negative) at upper elevations, but that interactions become increasingly more positive down the marsh (Bertness and Hacker 1994). Chapter 4 of this thesis investigates some of these ideas in the context of marshes in the Solent region.

Disturbance

Disturbance has long been established as an important factor in establishing ecological pattern (Dayton 1971). Disturbance can generate gaps or patches which can act as refuges for less competitive "fugitive" species to persist. In the context of northern European saltmarshes, intermittent or chronic disturbance can be caused by the activity of grazing animals, by extreme weather, or by debris being deposited on the marsh surface by the tide (Bertness 1992, Pennings and Bertness 2001).

Saltmarshes are important ecosystems for large grazing animals. This can be domestic grazing by sheep or cattle, which on many sites in western Britain has been ongoing for centuries (Ranwell 1961, Gray 1972); or grazing by wild animals such as mammals (Ford and Grace 1998) or migratory birds (Bazely and Jefferies 1985, Olff *et al* 1997 Zacheis *et al* 2001). Domestic grazing tends to produce marsh systems of low biodiversity with largely uniform patterning, made up of mainly of grazing-tolerant grasses such as *Pu. maritima.* (Jensen 1985). Grazing events by wild animals tend to be more acute, both spatially and temporally. Wild boar (*Sus scrofa*) and nutria (also known as coypu) (*Myocastor coypus* Molina) can create 'eat-outs', where all above-ground biomass is removed and the whole integrity of the marsh can be threatened (Ford and Grace 1998). Migratory birds such as snow geese (*Anser caerulescens caerulescens*) can consume as much as 80% of above ground biomass. In these situations increased nutrient cycling through faeces stimulates high levels of productivity compared with ungrazed sites (Cargill and Jefferies 1984), which probably allows the vegetation to recover and maintain its integrity. Intensive grazing episodes can open gaps in the vegetation cover. Smith and Odum (1981)) found that *Scirpus robustus* colonised gaps in grazed areas of *Spartina alterniflora* marsh which are stable when not grazed. Where very large numbers of animals are present, grubbed up areas can become enlarged to form water-filled pans that can remain for long periods (Jefferies *et al* 1979).

Low frequency extreme weather events can have effects on saltmarsh plant communities. Bertness (1992) described how at high latitudes coastal marshes can be covered in ice or frost, and plants can be uprooted if pieces of ice sheet are moved by winter storms. This can open spaces for pioneer or annual species to colonise zones dominated by perennials: intense frosts in the Netherlands in the winter of 1962-3 allowed *A. tripolium and Sueda vera* to increase in a zone dominated by the shrubby perennial *A. portulacoides* (Beeftink *et al* 1978). Recovery from severe frost damage can take up to 15 years, with a gradual progression through successional stages from pioneer communities (e.g. *Salicornia* spp. and *S. vera*) to more stable lower marsh groupings (e.g. *A. tripolium* and *Pu. maritima*) (Beeftink 1977).

Debris also has a role in perturbing plant communities (Bertness and Ellison (1987). In New England saltmarshes *Distichlis spichata* and *S. europea* are associated with zones around the drift line which are regularly disturbed by "wrack" (dead plant debris) and are not found elsewhere. *D. spichata* is more tolerant of short term burial (i.e. 2-4 weeks) in that it suffers lower mortality rate than other marsh species. Burial by wrack for longer periods (i.e. 6 months) kills all underlying vegetation and leaves discrete bare patches around the drift line in the high marsh. *D. spichata* can colonise these rapidly with vegetative runners, and *S. europea* recruits to these patches with seed. Throughout the rest of the marsh other species dominate, and over time disturbed patches are overgrown by them. However these two persist through an ability to utilise patches and (in the case of *D. spichata*) a superior tolerance to disturbance events of this kind (Bertness and Ellison (1987). The survival of *S. europea* on these marshes is inherently linked to the wrack debris that generates the patches in which it persists. It is unable to colonise the pioneer zone at the bottom of the marsh because the substrate is too soft for seedlings to take root. The seeds of *S. europea* have a hairy coat which binds it to the wrack debris, so they are in place as the patches are formed (Ellison 1987). Study of green algal debris in a eutrophic estuarine marsh in southern England produced similar results (Cassells 1997, Unpublished). The main seed source on this site was probably the pioneer zone, but *S. europea* was present in patches generated by tidal deposition of algal mats at the drift line in the upper marsh. Areas of the marsh that were not affected by algal debris did not have patches of *S. europea* in the upper marsh.

The issue of disturbance is clearly a complex matter in itself. Chronic, intensive disturbance (e.g. by domestic grazers) changes the nature and structure of whole plant communities. Shorter term or less widespread events such as ice damage or burial with debris produce patches and or time periods in which less competitive but faster growing species can seize an opportunity. These effects have been observed in many ecological systems, for example in rocky shores (Paine and Levin 1981) or intertidal boulders (Sousa 1979).

Spartina anglica

Note on terminology:

S.anglica was not distinguished from *S. townsendii* until many years after its appearance. The Groves brothers named the newly-identified hybrid *S. townsendii* (initially with one *i*) (Groves and Groves 1880, 1882) and this name was applied to both the sterile F1 hybrid and the fertile amphidiploid until 1968. From then on the fertile amphidiploid has been known as *Spartina anglica*, and the sterile F1 (which is still present at some locations) as *Spartina townsendii* (Hubbard 1968, Gray *et al* 1991*)*. In the following sections the hybrid is referred to as *S. townsendii* unless the literature was referring specifically to the fertile hybrid, in which case *S. anglica* is used.

Over the last hundred years many saltmarshes and their plant communities have been perturbed by the evolution of *S. anglica*, or common cord grass (review Gray *et al* 1990). *S. anglica* is believed to have originated following the chromosome doubling of the sterile hybrid *Spartina townsendii* . This new species arose from the hybridisation of the native *Spartina maritima* and the north American *Spartina alterniflora*, which is believed to have arrived in the ballast tanks of ships docking in Southampton (Lambert 1964, Marchant 1967). The molecular evidence for this assumed parentage was described by Ferris *et al* 1997. The hybrid was first recognised in 1878 in Southampton Water and the amphidiploid may have arisen around 1890. The development of the fertile form was followed by a rapid spread along the south coast, by both natural spread and planting to aid land reclamation (review Doody 1982). The new species was able to colonise what was essentially a vacant niche: mudflats unoccupied by perennial plants, and it was able to outcompete the eelgrass *Zostera* once it became established. *S. anglica* also proved to be very effective at accreting sediment, and as a result saltmarsh habitats extended seawards wherever *S. anglica* had taken hold (Doody 1982). Often, the *Spartina* marshes then follow a restricted successional path: in Langstone Harbour, Hampshire, the marshes remain dominated by the colonising *S. anglica* swards which have not been succeeded by mixed saltmarsh even after several decades (Haynes and Coulson 1982): Adam (1990) described this as *"a picture of singular monotony"*. This is not always the case however, and a number of species (e.g. *Phragmites australis, Scirpus maritimus, F. rubra* and *Agropyron pungens*) have been observed to colonise mature *Spartina* marshes in Poole Harbour , Dorset, UK; where substantial vertical accretion had taken place (Hubbard and Stebbings 1968); and *Spartina* marsh on the Wash (UK) succeeded to *Atriplex/Puccinellia* marsh over a period of 25 years (Doody 1982). It seems likely that local conditions determine the successional path (if any), rather than *Spartina* marshes being destined to remain monospecific as long as they persist.

Die back of *S. anglica*

The processes of ecological (and consequent physical) change after the newly expanded *Spartina* marshes had developed. Initially *S. anglica* rapidly expanded, but then the rate of growth either slowed, or, particularly in the south of England, extensive "die back" of *S. anglica* swards took place, often within a few decades of the initial expansion. For example, at Holes Bay, Poole Harbour, die back started in the late 1920s; and, by 1981, 40% of the marshland formerly present in 1924 had been lost (Gray and Pearson 1984). Both the growth of the *Spartina* marsh and its subsequent recession had profound knock-on effects for the surrounding coastal systems. Large amounts of the sediment entrapped (e.g. 1.8m depth on former mudflats) were rapidly released into tidal waters, for example causing substantial shoaling of the navigation channels in Poole Harbour (Hubbard and Stebbings 1968, Gray *et al* 1990).

The cause of die back is widely held to be the creation of anaerobic conditions and a reducing environment due to the rapid rates of sedimentation, and resultant impeded drainage, associated with *S. anglica* swards (Goodman and Williams 1961). There is also a possible feedback which accelerates the process, as the build up of dead organic material in die back areas leads to further retention of water in surface layers (Gray *et al* 1991). Nearly 40 years on from the original research carried out at Southampton University, a proximal causative agent has still not been conclusively identified although the conditions associated with die back are clear (Gray 1991).

S. anglica and its parent *S. alterniflora* have particular adaptations to avoid anaerobiosis which may in part explain their ability to flourish in the harsh conditions of the lower marsh. They develop a fine mat of roots which grow in the more aerated surface layers and a system of "anchor" roots which penetrate to much deeper levels. These deeper roots remain viable in spite of the toxic, anaerobic environment which surrounds them, due to the presence of a series of air-filled cavities (aerenchyma) which are connected to the upper parts of the plant (Armstrong 1967, Baker 1979). These special adaptations may account for the success of *S. anglica* in low marsh environments which are often submerged. Plants without such adaptations may succumb to oxygen starvation itself, increased carbon dioxide levels, the phytotoxic products of anaerobic bacteria (e.g. sulphides and organic compounds), (Goodman and Williams 1961) or increased availability of heavy metals in the reducing conditions prevailing (Jefferies 1977). However, it seems that in spite of these adaptations *S. anglica* remains destined to be a victim of its own effectiveness in accumulating sediment.

Other factors may have a role in the die back process, but it has been impossible to prove this conclusively. There has been little evidence that the hybrid species is becoming unviable (Marks and Mullins 1990). *S. anglica* does not set much seed in the UK in most years, probably because it is self incompatible and has a very narrow genetic base (i.e. most pollen is probably recognised as "self") (Raybould 1989, Gray *et al* 1991). Occasionally large numbers of viable seed are produced, possible due to higher temperatures and humidity leading to breakdown of the self-incompatibility system (Gray *et al* 1991). It is believed however, to have largely propagated itself vegetatively, with occasional periods of more rapid spread marking brief phases of higher seed production and seedling establishment (Hubbard 1969, Gray *et al* 1991). The result of this process has been extensive stands with very little genetic variability (Raybould *et al* 1991); and this may account for the very high incidence of ergot fungus *Claviceps purpurea* (Gray *et al* 1991). This reduces the fitness of infected plants by severely reducing seed production, which is low in any case due to poor chromosome coupling in the hybrid. It may also weaken the plant such that they are less able to survive in toxic substrates, but this has not been proved (Gray *et al* 1991). Whatever its effects, ergot has not been shown to have a primary role in the die back process. Pollution, for example from chronic oil spillages may also have a role in die back on some sites (Baker 1984), but again it has not been possible to prove this conclusively, and the anaerobiosis hypothesis remains the most credible cause of die back .

Another possible reason for die back may be found in the association of the American parent species *S. alterniflora* with the ribbed mussel *Geukensia demissa.* These two species seem to share a facultative mutualism in which the mussels have access to a suitable habitat in which growth rates increase and mortality is lower, and the plant benefits through nutrient availability and enhanced sediment stabilisation (Bertness 1984). As a new species, no such mutualisms exist for *S. anglica* (there is no equivalent to *G. demissa* in Europe) although it shares many of the characteristics of its parent. It is possible that die back of *S. alterniflora* is prevented by the presence of the ribbed mussels in their burrows, which extends into the region which is anoxic in *S. anglica* stands. However, no effects by *G. demissa* on redox levels were detected by Bertness (1984), so it is not clear whether lack of such a mutualism can be seen as a cause of die back.

However, in spite of the special adaptations of *S. anglica*, which may account to a large extent for the competitive advantage it enjoys in lower marshes, die back has become widespread, particularly in southern and Eastern Britain where sea levels are rising (Charman 1990). The lack of such a level of adaptation of other saltmarsh species to anaerobic conditions may account for the frequently observed failure of other species to colonise *Spartina* die back areas.

When it occurs at the marsh edge, die back can be followed by erosion of the sediments, which are no longer stabilised by vegetation. This is not inevitable however: *Salicornia europea* was found on die back areas at Dengie, Essex (Doody 1985). When it happens within the marsh in areas where drainage has become impeded (for example by raised areas or "levees" at the edge of the marsh), pans or pools of standing water can form. These are described as separate types of die back in the literature (e.g. Manners 1975) but may in fact be the same process taking on slightly different manifestations due to its location. The actual sediment type may be important too: the fine-grained sediments of southern England lead to poor drainage and hence predispose the *Spartina* swards to die back (Ranwell *et al* 1964, Adam 1990). However Chater (1973) observed prolonged retention of water behind levees on the Dovey Estuary marshes in Wales, but found no sign of die back, so the chemical properties of the sediment, perhaps in promoting reducing conditions are probably of importance as well (Gray *et al* 1991).

Synthesis

This literature review has considered some of the factors that generate the zonation and patterns in saltmarsh ecosystems. While physical factors are widely regarded to be the main driving forces in producing and maintaining a marsh system, biotic factors play an important role in the broader framework. The role of interspecific relationships between plants has been shown by Bertness and his co-workers to be important. This work validates some widely held ecological theories in the context of saltmarsh communities, particularly on the relative importance of competition at different levels of environmental stress (e.g. Connell 1961, 1972; Hawkins and Hartnoll 1985). It also identified facilitation between plant species to be of greater importance than previously thought in areas of higher environmental stress (Bertness and Hacker 1994). The appearance of *S. anglica* in southern Britain gives opportunities to test some of these ideas further: it is a highly competitive species which has not been present for long enough to have evolved specialisms which could give it further advantages. It is dominant within a restricted zone of a marsh system but not usually present out of that zone. Its competitive relations with other dominants from higher marsh zones are not known, and these can be investigated using a manipulative approach developed from the experiments carried out in North America on other species (Bertness 1991).

S. anglica has had profound and well-documented effects on coastal ecosystems over the last 100 years (review Gray *et al* 1991). The effects it has had on plant communities over that time is less clear. It is generally held to have occupied a vacant niche, but in the field it can be seen to be growing in a community with several other species (e.g. *S. europea, A. tripolium, L. vulgare*), the abundance of which may be different compared with the pre *S. anglica* community. A palaeoecological investigation of this over several sites could prove valuable in establishing the spatial and temporal changes that may have taken place in the plant communities since the new species appeared.

The appearance of *S. anglica* can be looked upon as a perturbation or disturbance, which has had important consequences for biodiversity. Grazing is another disturbance factor that impacts on biodiversity. Intense grazing can reduce species richness of saltmarshes or even destroy the whole ecosystem, but grazing animals can also open gaps for fugitive species to colonise. Less intense disturbance can increase diversity by suppressing competitive dominants: this is well recognised in many ecosystem types (e.g. Connell 1978, review Sousa 2001), but has not been evaluated in the context of saltmarshes that are lightly grazed by wild vertebrates.

This thesis examines some of the themes introduced above using field data and experimental manipulations, using selected saltmarshes in the Solent region. Specific biotic factors are investigated with a general aim of identifying their role in establishing spatial and/or temporal patterns in the plant communities. Chapter 2 investigates the effects of the appearance of *S. anglica* by integrating a range of palaeoecological methods (on sediment cores) and an examination of a range of historical data; particularly focussing on the *pre-Spartina* environment. Chapter 3 investigates the role of wild animals grazing on saltmarshes in maintaining biodiversity. Chapter 4 looks at the role of plant-plant interactions in setting the zonation patterns observed on saltmarshes.

Three general null hypotheses will be investigated:

- *S. anglica* has had no effect on the composition of plant communities since it appeared in southern England
- Low level grazing has no effect on saltmarsh plant biodiversity
- Competition and facilitation do not have a significant role in generating and maintaining the zonation of *S. anglica* marshes

CHAPTER 2

PHYSICAL AND ECOLOGICAL CHANGES IN SALTMARSHES IN SOUTHERN ENGLAND BEFORE AND AFTER THE ADVENT OF *SPARTINA ANGLICA*

Introduction

Coastal environments have become a fertile area for palaeoecological research in recent decades (e.g. Long *et al* 2000, Allen (review) 2000). Many researchers have focussed on the use of palaeoecology as an end in itself, to describe changes in past plant communities and their environments (e.g. Meyerson 1972, Tooley 1985). Alternatively it is used as a tool for characterising rates of relative sea level rise, over various time scales (e.g. Thomas & Varekamp 1991, Tooley 1992, Long & Shennan 1994, Cundy and Croudace 1996). In this chapter I have combined some established techniques with newer methods to examine the consequences of the appearance, and rapid spread, of the hybrid grass *Spartina anglica* in coastal marshes in the Solent region, focussing on the ecological and physical changes which have taken place in this area over the last 200-300 years.

Spatial stability of saltmarshes

Saltmarshes are complex ecosystems; their structural and functional integrity are dependent upon the interaction of a range of physical and biotic factors (Figure 2.1). The tidal regime and environmental changes, such as relative sea level rise or storminess, are dominant in controlling vertical accretion rates (Allen 2000). However accretion is also dependent on sediment supply and the characteristics of the sediment itself (French 1993). The plant community also has a fundamental role: halophytic plants trap sediment and stabilise it within the marsh substrate (Randerson 1979). These plants themselves are subject to a range of forcing factors such as environmental stress, disturbance, competition and grazing (see review in Chapter 1) and have differing characteristics, which can influence rates of sedimentation and stability. *S. anglica* itself is recognised as being highly efficient at trapping sediment relative to other saltmarsh plants (Ranwell 1964a, Chung 1990, Allen 2000). Minor factors such as decomposition and autocompaction also affect the overall physical structure of the marsh (French 1993).

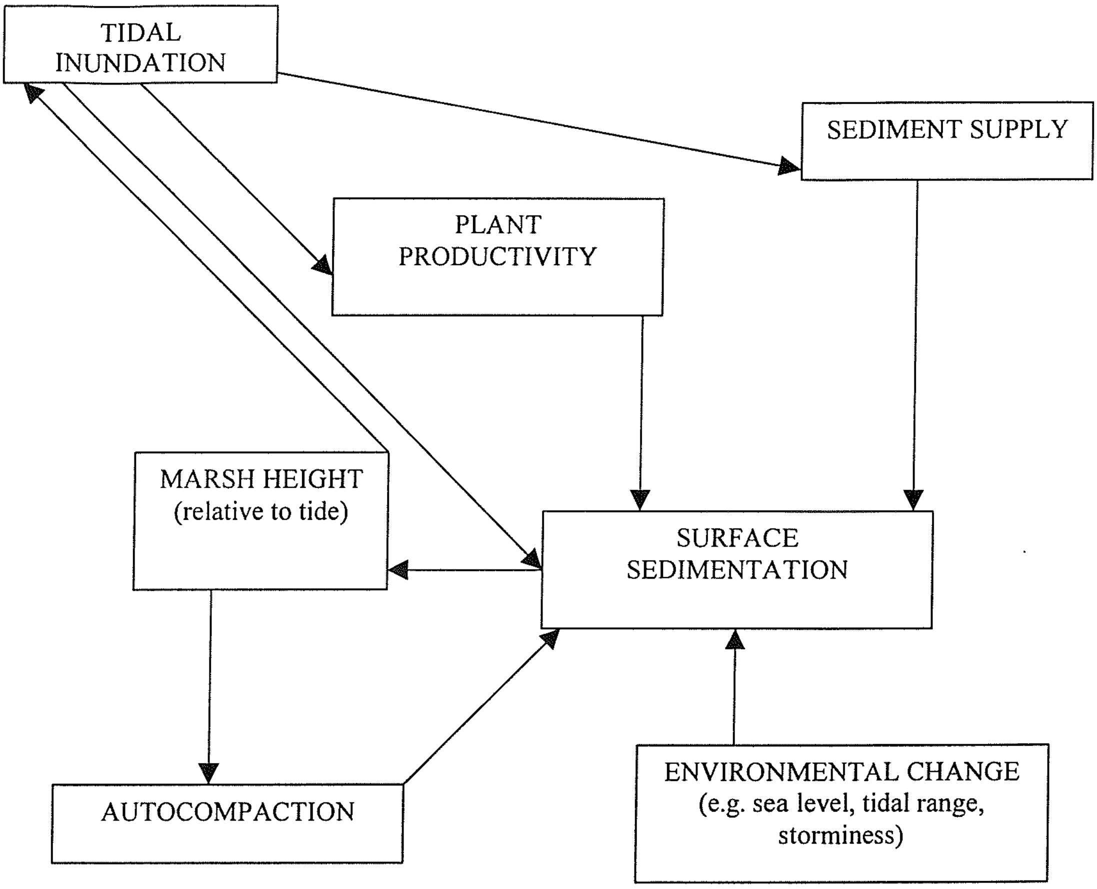


Figure 2.1 Factors interacting in a salt marsh system (adapted from Allen 2000)

Use of palaeoecological methods to characterise coastal environmental change

Use of geochemical information and biological material preserved in sediments are established palaeoecological methods. They can be use for dating stratigraphy, for estimation of accretion rates (Long *et al* 1999) and for the reconstruction of past communities (Tooley 1985, Lowe and Walker 1997). A few studies have taken something of a multi-proxy approach. For example, Clark and Patterson (1985) used pollen and macrofossils (plant material, plus limited use of Foraminifera) to trace marsh development on the north shore of Long Island, New York. Orson *et al* (1998) combined geochemical methods with long-term field observations and tide-gauge records to describe changes in accretion rates over up to 50 years. The methods that I combined in my study (principally palynology, geochemistry and macrofossils) are reviewed below and described in the Methods section.

Pollen has been routinely used in the reconstruction of past plant communities for many years (e.g. Godwin 1940), and has occasionally been used in a coastal context (Meyerson 1972, Tooley 1985). Some studies have used palynology to characterise late-Holocene coastal environmental change (e.g. Clark and Patterson 1985, Long *et al* 1999). There are problems with using coastal sediments: physical or biological reworking is much more likely than in, for example, an intact raised bog or a deep lake, particularly if the sediments are taken from the lower tidal levels. In addition, reworked sediment (e.g. from an eroding marsh cliff or an unstabilised mudflat) could be redeposited elsewhere on the marsh in the same tidal event that caused the erosion. Furthermore, pollen can be transported, by rivers and tides, from elsewhere, and it is possible that differences in buoyancy will distort the representation at the site under investigation (Hopkins 1950).

Coastal sediments, specifically from saltmarshes, can however be used for community reconstruction, but there are some major shortcomings. Many of the common saltmarsh plants are insect-pollinated (e.g. *L. vulgare* and *A. maritima*) and do not produce much pollen. In addition the pollen of several of the common groups are either taxonomically difficult (e.g. Chenopodaceae) or very hard to distinguish from their terrestrial counterparts (e.g. Poaceae). Furthermore, these difficult groups produce large quantities of pollen to facilitate airborne pollination. However, as long as data gathered from coastal sediments are treated with some caution, (and ideally using a multi-proxy approach to confirm findings), pollen preserved in intertidal sediments can be a useful tool as a stratigraphic indicator (Waller *et al* 1999). The rise of *S. anglica*-type pollen has been used by Long *et al* (1999) as part of a study of accretion rates and sea-level rise in Poole Harbour but they recognise the taxonomic difficulties it presents and used this in combination with other stratigraphic indicators, particularly the Anthropogenic Pine Rise (APR) (Barber 1981).

Pinus pollen is easily recognised and does not present any of the taxonomic difficulties of *S. anglica.* The Anthropogenic Pine Rise (APR) is an important, and more reliable, stratigraphic biomarker horizon than *S. anglica*, which dates from c.1800 AD. This can be identified from sediments in the Hampshire Basin and Dorset (Long *et al* 1999). This gives a reference point in the stratigraphy which reflects historically documented spread of coniferous plantations in Hampshire and Dorset (Barber 1981, Long *et al* 1999). However, although it is usually easy to locate the APR in pollen extracted from sediments, the exact stratigraphic date of the *Pinus* rise (APR) is uncertain. There is good documentary evidence of planting in the New Forest at 1800AD (Barber 1981), but over the wider area of Hampshire and Dorset, coniferous plantations were planted earlier than this date. Haskins (1978) suggests 1700 AD for the nearby Poole basin, and Waton (1983) suggests 1750 AD. *Pinus* pollen is known to be particularly well-dispersed, and can move very long distances in air (Tyldesley 1973) and water (Hopkins 1950), so for this reason all three potential APR dates might be used during interpretation (Long *et al* 1999).

Geochemical approaches such as Lead-210 (^{210}Pb) dating have been used for identifying anthropogenic and natural radionuclides as dating aids in coastal sediments, for example, in England, Poland and the Netherlands (Callaway *et al* 1998); on the estuary of the Connecticut River (Varekamp 1991); in New England (1986); and in the Solent region (Cundy and Croudace 1996). Lead-210 (^{210}Pb) arises as a daughter nuclide from part of the natural Uranium-series decay chain, with a half-life of 22.3 years. It is unstable in the atmosphere and is washed out to accumulate in aquatic sediments, where it decays to stable ^{206}Pb over about 150 years. There is also a small element of ^{210}Pb derived from U-series decay in the sediments themselves ("supported" ^{210}Pb) and this must be determined and subtracted from the atmospherically generated ("unsupported" or "excess") ^{210}Pb. By calculating the ratio of net atmospherically-derived ^{210}Pb to ^{206}Pb it is possible to estimate the time elapsed since it was deposited and thus the rate of sediment accumulation (Olsson 1986, Appleby & Oldfield 1992). Compared with more closed systems such as lakes, the sources of unsupported ^{210}Pb are quite complex in coastal environments. However, as long as accretion rates are sufficiently high (e.g. >0.03 cm per year), and bioturbation is low, saltmarshes are thought to be an appropriate environment in which to use this method (Appleby & Oldfield 1992).

Lead-210 (^{210}Pb) radioisotope dating using alpha-spectrometric measurement can be used to calculate accretion rates in saltmarshes, using the "simple model" dating method (Robbins 1978, Appleby & Oldfield 1992). This gives accurate accretion rates up to a period of c. 100-130 years before present, and allows reliable estimation of an age-depth profile. This is a useful range to have reliable dating as it coincides with the estimated dates for the first appearance of *S. anglica* in the Solent region (Gray *et al* 1991). Other anthropogenic radionuclides such as Caesium-135 from atomic testing are often used to confirm the age depth profile derived from the ^{210}Pb geochemical information (Cundy and Croudace 1996). These were not used here, partly because of the additional expense, but also as the stratigraphic relationships between the APR and the ^{210}Pb profile, (plus further stratigraphic markers such as the rise of *Spartina* itself in the pollen profiles) were considered to be sufficient to validate the information derived.

Reconstructing communities using macrofossils in coastal environments

Use of macrofossils for community reconstruction carries some of the same limitations as use of palynology, i.e. they can be reworked and redistributed. A macrofossil approach has not been widely used in community reconstruction from coastal sediments. Tooley (1985) used macrofossils to interpret early Holocene changes between marine and freshwater peat beds at Downholland Moss in south west Lancashire. This approach was quite successful, but poor preservation of macrofossils, of which seeds are the most reliable and easily identifiable, was a problem in some samples. Clark and Patterson (1985) used macrofossils along with a range of other biological material to reconstruct marsh development and they identified general assemblage zones in the stratigraphy, but these were also based on small numbers of identifiable seeds. They did identify rhizomes within the stratigraphy, but as the roots of several of the species growing in UK marshes can extend below the total depth of sediment sampled (over 1 metre in some cases), this did not seem to be a useful approach for this study, and macrofossil sorting was limited to aerial portions of plants only.

Methodological investigations

Palaeoecological studies have tended to rely on single cores (e.g. Meyerson 1972), or on transects composed of single cores at each position (Hubbard and Stebbings 1968, Long *et al* 1999). This is accepted practice in this field, although other areas of ecology place much more emphasis on the use of replicate samples and use of statistical methods to validate the findings, particularly where the medium being sampled is variable spatially or temporally (e.g. Underwood 1997). Single core approaches to palaeoecology have been tested in terrestrial environments (Turner *et al* 1989) but there has been little attempt to validate single core methodologies in intertidal palaeoecological studies.

Spartina in the Solent region

Spartina anglica was first described by the Groves brothers at Hythe, on Southampton Water (Groves & Groves 1880), initially naming it *Spartina townsendii.* These events are further considered later in this chapter. In this part of my thesis, I focus on the changes that the new hybrid brought about to the physical structure of the marsh systems and the nature of the plant communities themselves. It is well accepted that *S. anglica* rapidly colonised other marsh sites in the Solent region, producing major changes as it did so (Goodman *et al* 1959). It has become widespread over the whole of Great Britain, covering an area in excess of 10,000ha (Charman 1990). It is also accepted that *S. anglica* extended marsh systems seaward by occupying a vacant niche, or at least squeezing the true pioneer community seawards by colonising unvegetated mudflats (Gray *et al* 1991). The more recent processes of die back are well-documented (see Chapter 1), but we do not have a true picture of the effects of *S. anglica* on the marsh systems because the nature of the pre-*Spartina* community was not described at the time in any useful detail. Before the latter part of the 19th century there were very few reliable botanical or ecological records kept, and no "scientific" study of plant communities of a kind undertaken in the last fifty years. However, because the hybrid *Spartina* first appeared in the Solent region, and attracted a lot of attention from local botanists and latter-day coastal managers, a range of good and reliable records at libraries and archives in the region still remains. Furthermore, the University of Southampton carried out much of the early work in explaining *"the Spartina Story"* (e.g. Lambert 1964, Ranwell 1964a and b, Hubbard 1965, Marchant 1967, Hubbard and Stebbings 1968) and much of the archival material related to this is still accessible.

Aims

There is quite a range of historical information relating to *Spartina*, some of which has already been reviewed (e.g. Gray *et al* 1991, Tubbs 1999), but this could be integrated with reliable historical maps and data taken from material preserved in present-day marshes. I decided to use these resources along with the palaeoecological approaches considered above, which are themselves quite well-developed and reliable, to look back at the pre-*Spartina* environment.

The overall aim of this chapter was to characterise the spatial stability, distribution patterns and community structure of saltmarshes in southern England over a 200-300 year period from before the advent of *S. anglica* up to the present day. Historical records and maps have been searched for reliable evidence of the changes that have taken place. Palaeoecological techniques were used and new methods were developed to seek information that would complement the historical material. Sediment cores were collected from a series of saltmarshes in Hampshire. Analyses have included sediment description, macro- and microfossil techniques as well as the use of radiometric dating to establish an absolute and relative chronology for sedimentation. This was then used as a tool to interpret ecological data gained from macrofossils and pollen, which could then be related back to the documentary records. Two general hypotheses have been tested:

1. *Saltmarsh stability before* S. anglica *was greater than since.*

2. *Community structure and zonation patterns have been disrupted since the establishment of* S. anglica.

Methods

Study area and site selection

The three sites studied (Gins Marsh Beaulieu, Hythe and Marchwood) are located in the Solent region of Hampshire, Southern England (Figure 2.2). The geophysical background and evolution of the Hampshire Basin and the Solent coast are described fully in Hodson and West (1972), West (1980) and Velegrakis *et al* (2001). It is useful to have three sites to compare from the same geological unit (the Hampshire Basin) as they are likely to have some broad similarities in substrate type which can itself affect marsh dynamics (Allen 2000). These sites were chosen principally because they have a long and reasonably well documented ecological history: Hythe was the site from which the Groves brothers first took their samples identified as *S. anglica* (Groves and Groves 1879) and the other two sites have good recorded post-*Spartina* histories. They are also sites with relatively clear ecological zonation, which makes selection of coring positions more straightforward and aids in their interpretation, although the plant communities at each site are not identical.

Beaulieu: Gins Marsh

The Beaulieu River is one of the major rivers draining the New Forest. The estuary is a narrow, meandering channel and is tidal up to the mill dam in the town of Beaulieu, 10.4 km from the sea. The tidal range is 3.1m (neaps) to 4.3m (springs). The Beaulieu estuary is part of the north Solent National Nature Reserve (grid reference SU489024 to SZ390960) but is protected from the English Channel by the shingle spit at Needs Ore Point. As a result it is a low energy environment with extensive saltmarshes on both banks extending from the coast up to the medieval weir in the town of Beaulieu. Gins Marsh is located on the western bank of the Beaulieu estuary on land owned by the Beaulieu Estate (Figure 2.3). The marsh shows a clear zonation from a terrestrial oak wood, through a high marsh *Agropyron pungens* community NVC SM24, with a narrow *Festuca rubra Juncetum gerardii* fringe NVC SM16; an upper marsh *Puccinellietum maritimae, Limonium vulgare-Armeria maritima* sub community NVC SM13 where grazing by wild animals is an important ecological factor (see Chapter 3), a middle marsh *Halimione portulacoides* community NVC SM13, which grades into a lower *Spartina anglica* NVC SM6 with a narrow pioneer fringe of *Salicornietum europaeae* NVC SM 8 (community classifications from Rodwell 2000). The edge of the marsh is currently not eroding although there is extensive erosion of more recently formed marsh a few hundred metres to the south. Landward expansion has probably taken place over the last few centuries, as evidenced by the stunted and dying oaks fringing the marsh, which are characteristic of much of the Beaulieu estuary marshes (Tomalin 2000b). This reflects the long-term rise in relative sea-level in the region, which over the late Holocene has been estimated as 1-1.5 mm per year (Long and Tooley 1995), but over the last hundred years has accelerated to around 5 mm per year (Woodworth 1987, Cundy and Croudace 1999)

Southampton Water: Hythe and Bury Farm, Marchwood

Hythe and Bury Farm, Marchwood, are both situated on the Western Shore of Southampton. The intertidal zone of Southampton Water covers approximately 1,350 ha and about 190 ha of this is saltmarsh (Associated British Ports 2000), of which the two largest areas are the study sites. It has a fairly low tidal range, compared with many parts of the UK (2m at neaps to 4m at springs), and a characteristic double high tide (giving two hours' coverage.) which has proved useful for the development of large scale shipping in the area.

Hythe marshes (grid reference SU431074 to SU458056) is situated on the western shore of Southampton Water (Figure 2.4), and are of some historical importance (see above) and has several nature conservation designations. It is the largest continuous piece of saltmarsh on Southampton Water, extending almost without interruption 7km to Calshot Spit at the southern end of Southampton Water. The marsh at Hythe is mostly *Spartina anglica* NVC SM6 with a narrow area of *Puccinellietum maritimae* middle marsh community NVC SM13 at the upper end. The zonation is arrested by a small road, beyond which are hedges and pasture. The edge of the marsh is severely cliffed and eroding rapidly. Near the marsh edge there are extensive cheniers (deposits of shell material and gravel) which may be a factor in the erosive processes currently taking place. Other factors may also be contributing to the erosion at Hythe, including increases in storminess and easterly winds, changes in hydrodynamics and sedimentation (possibly due to shipping activities), water quality, grazing or die back of *S. anglica.* (Associated British Ports 2000)

Bury Farm Marsh, Marchwood (part of the Eling and Bury marshes, grid reference SU368135 to SU387115) is also located on the western shore of the Southampton Water (strictly, at the end of the Lower Test) and has a similar tidal regime to Hythe, and the same range of protective designations. The marsh grades from a narrow *Phragmites* reedbed community (behind which is a steep, wooded bank), through a species-rich mixed middle marsh *Puccinellietum maritimae* middle marsh community NVC SM13 into a *Spartina anglica* NVC SM6 lower marsh community with extensive creek systems fringed with a pioneer *Salicornietum europaeae* NVC SM 8. There are some areas of cliffing or erosion, but it seems that the marsh system is close to equilibrium. There is, however, relatively little intertidal mudflat at Bury Farm due to the long term dredging of a 'swinging ground' (a turning area for large ships) for the Western Docks on the opposite bank (Associated British Ports 2000).

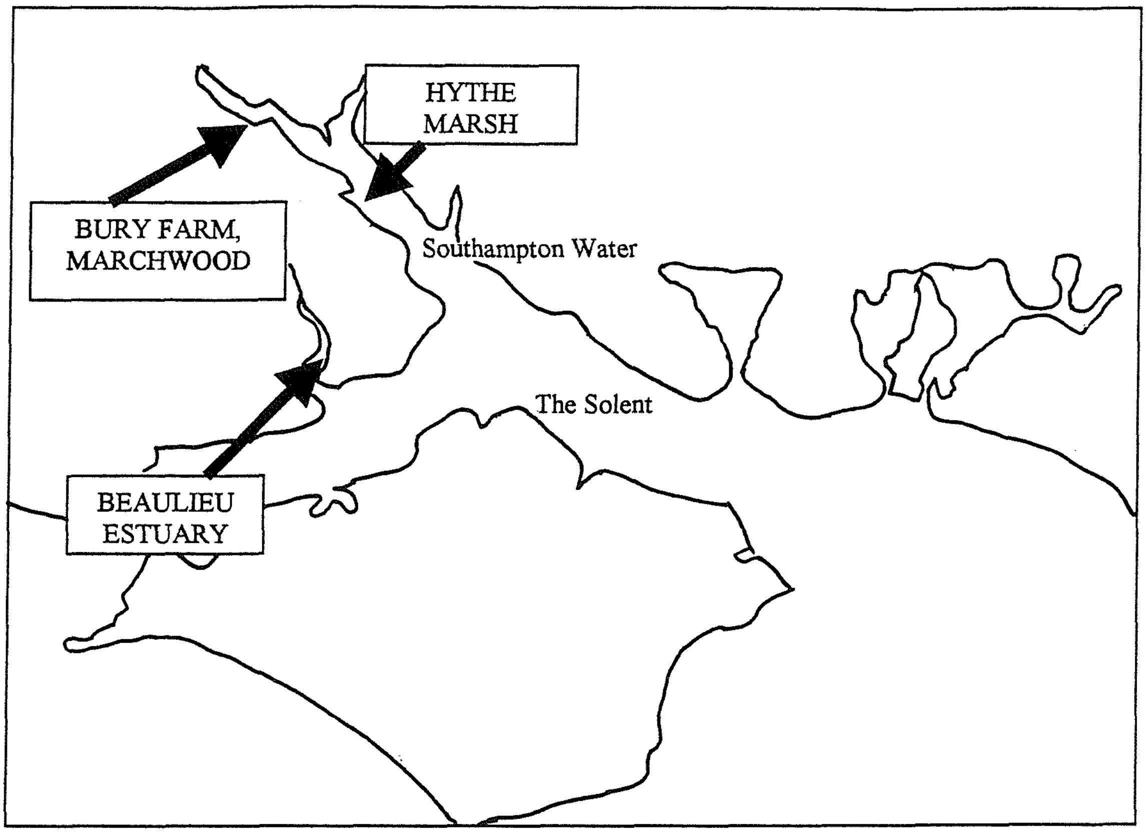


Figure 2.2 The Solent Area, showing site locations (not to scale)
(Crown Copyright www.multimap.com, accessed 26/04/2001)

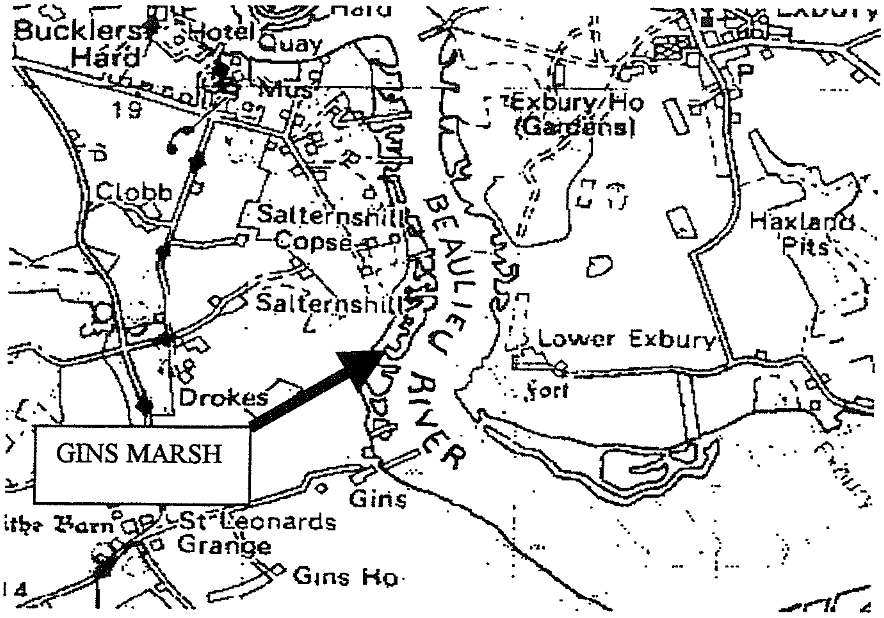
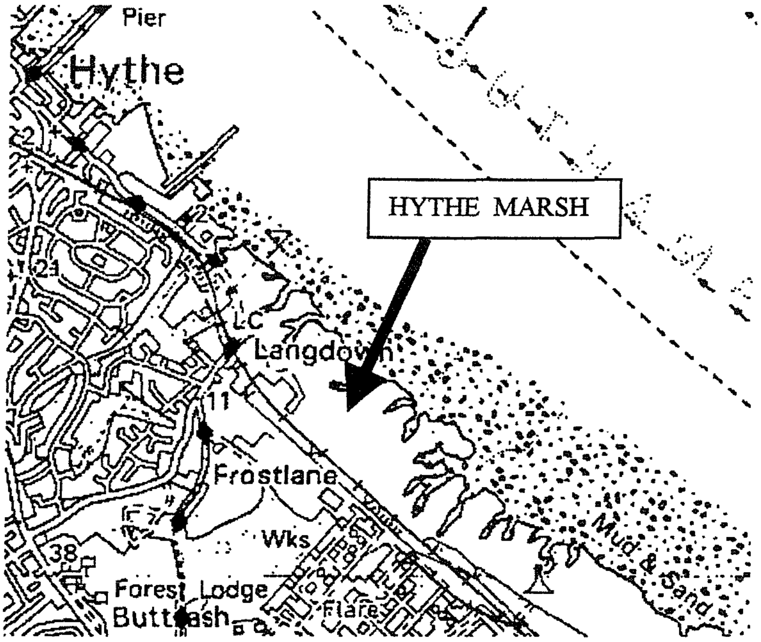
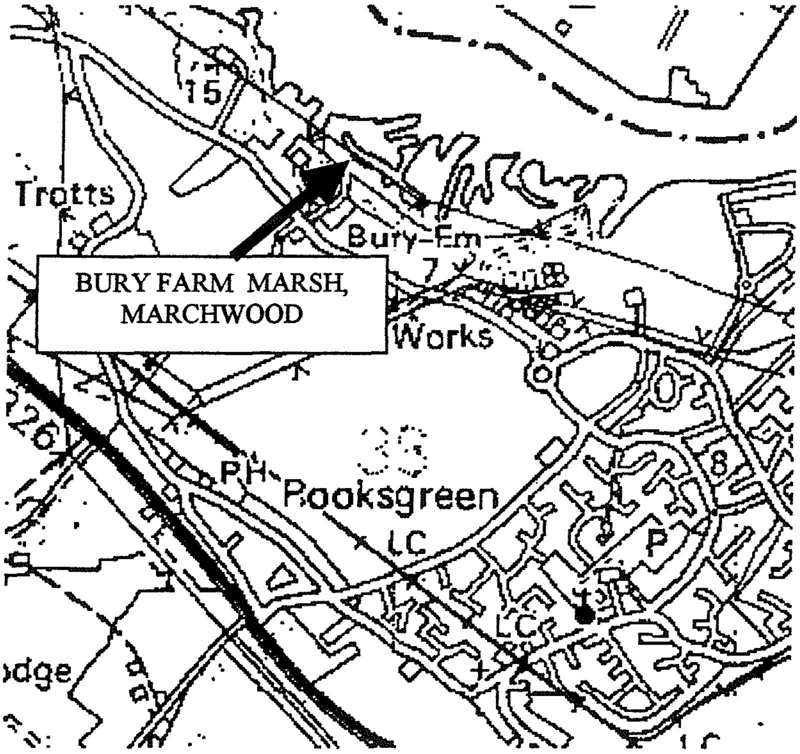


Figure 2.3 Lower Beaulieu Estuary, showing sampling site at Gins Marsh, (not to scale). (Crown Copyright www.multimap.com, accessed 26/04/2001)



(i) Sampling site at Hythe Marsh,



(ii) Sampling site at Bury Farm, Marsh , Marchwood.

Figure 2.4 Sampling site locations in Southampton Water, (not to scale). (Crown Copyright www.multimap.com, accessed 26/04/2001)

Historical Studies

Historical records (including scientific papers, biological flora, maps, and government papers: listed in full in Appendix 2.1) were searched for references to the appearance of *Spartina anglica*; but also for related species (*S. maritima, S. alterniflora* and *S. townsendii*); and for more general information about the physical and biological character of the study sites over the last 200 to 300 years. Collections of aerial photographs (e.g. from the Cartographic Unit, Department of Geography, University of Southampton) were also reviewed but these were mostly from recent periods and did not include sufficient accurate detail of marsh and mudflat limits below the tides.

The following archives and reference sources were used:

Cartographic Unit, Department of Geography, University of Southampton
Centre For Environmental Sciences Library and Reference Collection, University of Southampton
City of Southampton Central Library
Geodata Unit *Spartina* Archive Collection, University of Southampton
Hartley Library, University of Southampton: Cope Collection and Parliamentary Papers Collection
Wessex Medical Library (Biological Sciences section)
www.oldmaps.co.uk

Historical maps were examined, and data on coastal morphology has been collated using specialist software (*Surfer for Windows*, Golden Software). Accurate mapping in England started around 1870 with the first Ordnance Survey "County Series" at a scale large enough to see site-specific detail (1:10560). Maps since that date show the extent of vegetated marsh and mean low water which is a good indicator of the lower limit of intertidal mudflat. Several maps of the sites under investigation are available from much earlier dates, the survey methods used were unreliable and they can give little more than a qualitative summary of the character of the land (Professor M.J. Clark, Pers. Comm.2000). To quantify the physical changes in the geomorphology since 1870, transects were drawn on the maps and changes in transect length across saltmarsh, and across mudflat and saltmarsh combined, were measured. The transects used for core sampling in the field were taken, plus six additional transects at each site broadly perpendicular to the shore, and with suitable reference points visible on all of the maps (Appendix 2.2). The mean change in marsh; and in combined marsh and mudflat; were calculated to assess evaluate the changes taking place at each site.

Field sampling

Eighteen cores of saltmarsh sediment were taken in all, using a modified "Russian" pattern corer, between 28/4/1997 and 6/9/2000, from Beaulieu, Hythe and Marchwood. Sampling was focussed in the low and middle marshes where the likelihood of a continuous accreting record was highest and where the effects of any die back in *Spartina* would be minimised (Gray *et al* 1990). The upper marsh was not sampled, partly because of difficulty coring in very consolidated sediments, but also because the accretion rates at the uppermost level would have been too low to derive any accurate data with the methods used. At each site three replicate cores were taken from the lower marsh within an area of 1 m^2. A further three replicate cores were taken, higher up a transect starting at the shore, from the upper part of the middle marsh community (notation used subsequently: Beaulieu lower marsh cores GM1, GM2, GM3; Beaulieu upper marsh cores GM4, GM5, GM6; Hythe lower marsh cores H1, H2, H3 Hythe lower marsh cores H4, H5, H6; Bury Farm Marchwood lower marsh cores B1, B2, B3; Bury Farm Marchwood lower marsh cores B4, B5, B6).

Laboratory analysis

Stratigraphy was described, focussing on the nature of the sediment and the amount and type of organic material, including subfossil shell material. Radiographs of the cores were taken to identify laminations and potential discontinuities; and as a means for correlation between replicates.

The Anthropogenic Pine Rise (APR) was identified using pollen analytical techniques. Sub-fossil pollen was extracted from a 2 cm^3 sample using standard techniques (Moore *et al* 1991), including a long cold digestion in concentrated hydrofluoric acid (24-48 hours) to dissolve the large amounts of siliceous material (see Appendix 2.3 for full method). The APR was identified by counting *Pinus* pollen and a foreign reference pollen introduced at preparation (*Lycopodium*). A minimum of 100 grains were counted where possible. Initially samples were taken at regular intervals throughout each core, then closer sampling was carried out to accurately locate the increase in *Pinus* pollen. This gave a reference point in the stratigraphy, which reflects historically documented spread of coniferous plantations in Hampshire and Dorset at either 200 BP (before present), 250 BP or 300 BP (Long *et al* 1999, see above). *Spartina* pollen counts were also carried out on selected cores but because of the taxonomic difficulties (see above) and the time taken it was not felt to be worthwhile to carry out a full analysis of the palynology.

Using the APR as a reference point in the stratigraphy for 200-300 BP, lead-210 (^{210}Pb) radioisotope dating was carried out using alpha-spectrometric measurement of the grand-daughter radionuclide ^{209}Po. This approach was used to calculate vertical accretion rates up to c.100-130 years BP (and thus approximate stratigraphic dating as far as the dates of hybrid *Spartina* colonisation) using the "simple model" dating method (Robbins, 1978, Appleby & Oldfield 1992) (see above). The laboratory method used involved double acid leaching of 3g sediment from each determination level with ^{209}Po as an isotopic tracer, and autodeposition of the Po isotopes in the leachate onto silver discs. Discs were counted for a minimum of 4×10^5 seconds and detection limits were 0.1Bq/Kg. (method from Cundy *et al* 1997, based on Flynn 1968). Unsupported ^{210}Pb was estimated by subtracting the value of the constant (i.e. "supported") ^{210}Pb activity from the lower sections of the cores, as described above.

Plant macrofossils were extracted by dissolving sections of the core material using gentle stirring in warm water and disaggregated by adding a few drops of dilute (10%) hydrogen peroxide. After leaving several hours or overnight, the material was sieved to fractions of 1mm, 500μ and 250μ. The 1mm fraction contained the root mat and larger aerial portions such as stems, leaves and large seeds. The 500μ fraction contained finer, partly broken down plant material but also most of the seeds in the sample. The 250μ sample contained fine plant material and some Foraminifera and other small invertebrates. Fractions were wet sorted using a low power binocular microscope, and identifiable fragments of plant material extracted and identified using reference material taken in the field, plus standard reference guides (Ross-Craig 1948, Fitter *et al* 1985). While samples were being sorted they were preserved using 30-40% ethanol and kept refrigerated at 5°C.

The stratigraphic data was displayed using *Tilia 1.18* (Grimm 1992). Further analysis of changes in the palaeocommunities was carried our using PRIMER v5 (Clarke and Gorley 2001). Communities were compared using Bray-Curtis Similarity. Differences in communities within the stratigraphy can be displayed on dendrograms. Where the data are suitable, more information can be gathered by applying Multidimensional Scaling (MDS) to them: this allows the data to be displayed in multi-dimensional space, giving a clearer view of patterns of community change (Clarke and Warwick 1994).

Results

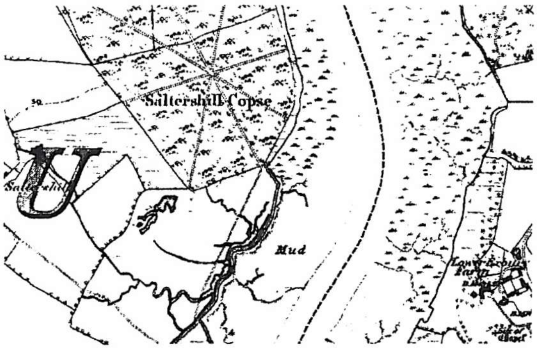
This section is in two parts. The first part comprises a presentation and analysis of historical maps of the sites, followed by a review of a range of literature and historical records that relate to the environments which the experimental work attempts to characterise. The second part presents the results of the work on sediment cores taken from the three experimental sites (Gins Marsh, Beaulieu; Hythe and Bury Farm, Marchwood).

Maps and Historical Information

Maps

Figure 2.5 shows data from a series of historical maps, starting from 1870 (Ordnance Survey 1:10,560) up to 1973 (O.S. 1:10,000) have been integrated using GIS (*Surfer for Windows*: Golden Software Inc.). Figure 2.6 shows changes in extent of saltmarsh, plus combined mudflat and saltmarsh based on the maps presented.

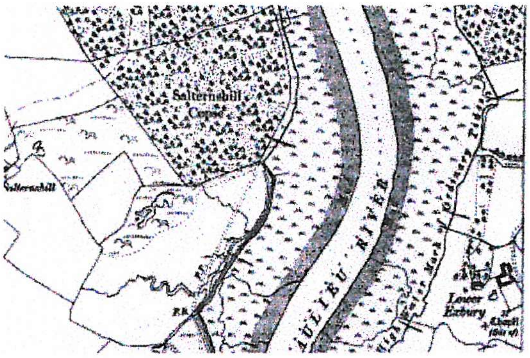
At Beaulieu (Figures 2.5 (i) & 2.6 (i)), the mean marsh transect length increased from 1870-1909, but the rate of increase has since reduced. At the same time the combined mudflat/saltmarsh transect length increased from 1870-1909, but has since decreased slightly. At Hythe (Figures 2.5 (ii) & 2.6 (iii)), the marsh transect length also increased from 1870-1909, which would coincide with the accepted dates for colonisation (Goodman *et al* 1959), but has since declined. This is consistent with the present eroding marsh cliff observed in the field. Mudflat and saltmarsh combined has gradually declined over the whole period, except from 1962-1973 when the mudflat area appears to have increased, which may in part by due to sediment released from marsh erosion. At Bury Farm, Marchwood (Figures 2.5 (iii) & 2.6 (iii)),the marsh and combined mudflat/marsh transect lengths decreased from 1870-1998 but have since been almost stable. However, inspection of the maps (Figure 2.5) shows that although the area of continuous mudflat at this site been largely stable, the offshore mudbanks (which were not included in the transects) have almost disappeared since 1898, and a vegetated area ("The Grassbank") has changed to mud and decreased in size. The mudflat changes are likely to be linked to increased shipping activity, and dredging, in the locality.



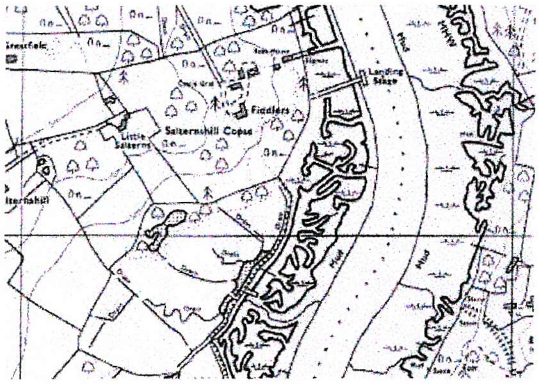
Gins Marsh, Beaulieu, 1870

Figure 2.5 (i). Map Information from Gins Marsh, Beaulieu,1870-1973.

Data From Ordnance Survey Maps:
1870 County Series, original scale 1:10560.
(Image from http:www.old-maps.co.uk/ Landmark Information Group)
1909 Hampshire Sheet original scale 1:10560
1973 Sheet SZ49NW, original scale 1: 10,000

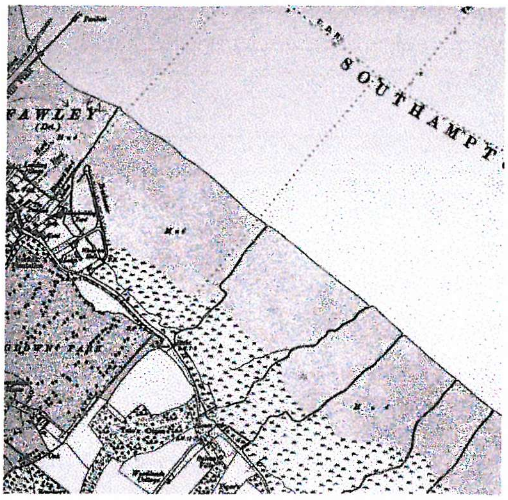


Gins Marsh, Beaulieu, 1909

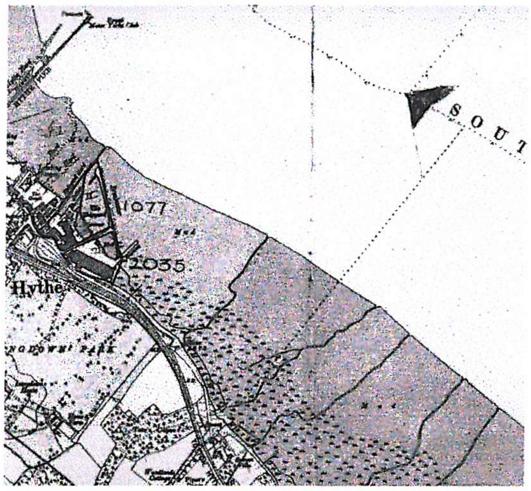


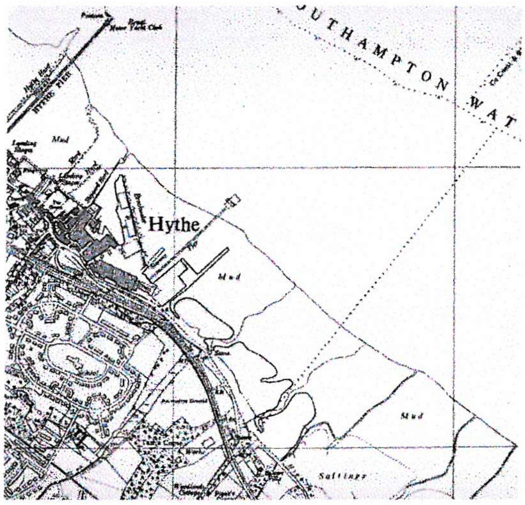
Gins Marsh, Beaulieu, 1973

Hythe Marsh 1870



Hythe Marsh 1909





Hythe Marsh 1931(above), and
Hythe Marsh 1973 (below)

Hythe Marsh 1962

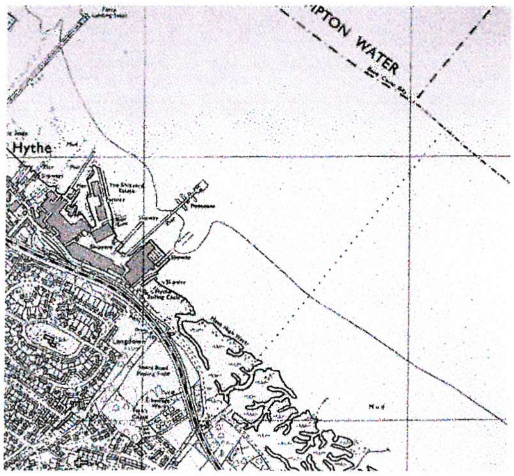
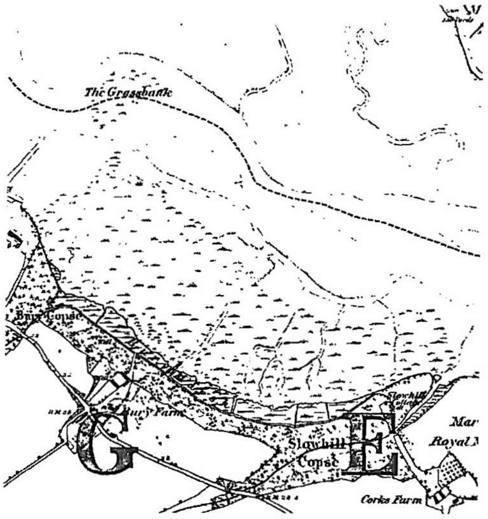
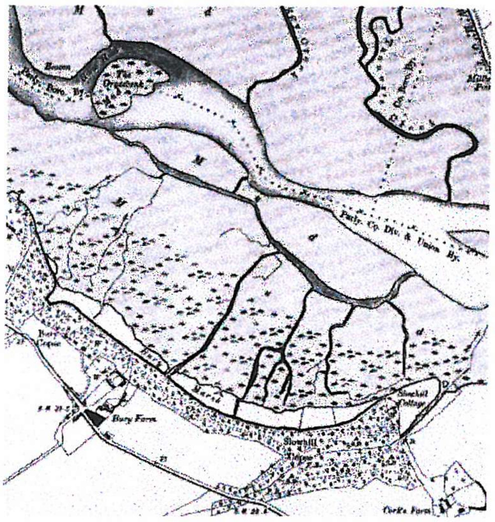


Figure 2.5(ii). Map Information from Hythe, Southampton Water, 1870-1973.

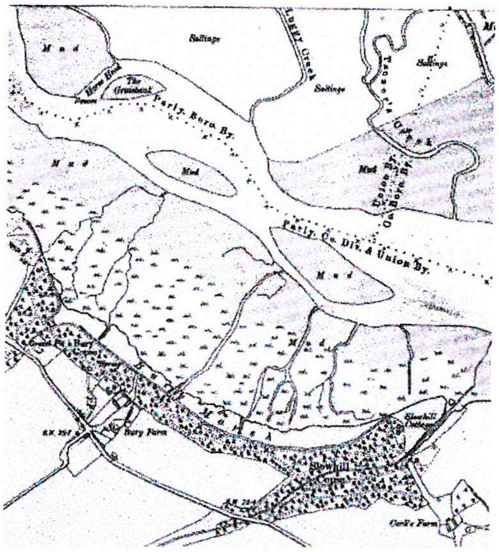
Data From Ordnance Survey Maps:
1870 County Series, original scale 1:10560.
1909 Hampshire Sheet original scale 1:10560
1931 Hampshire Sheet original scale 1:10560
1962 Hampshire Sheet original scale 1:10560
1973 Original scale 1: 10,000



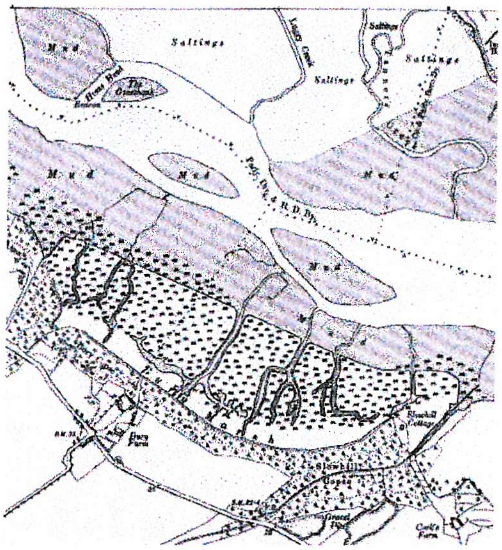
Marchwood 1870



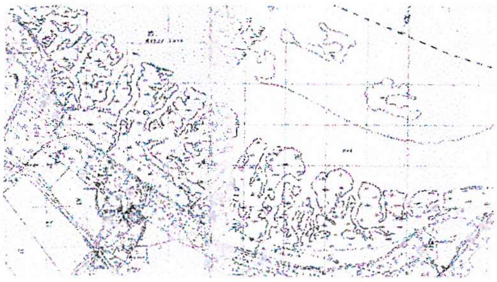
Marchwood 1898



Marchwood 1910



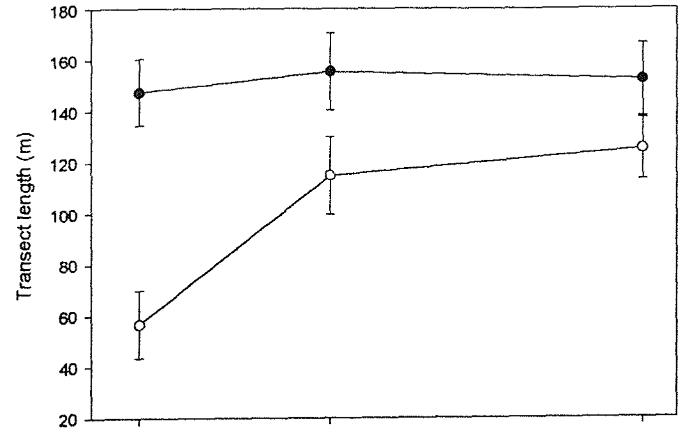
Marchwood 1931



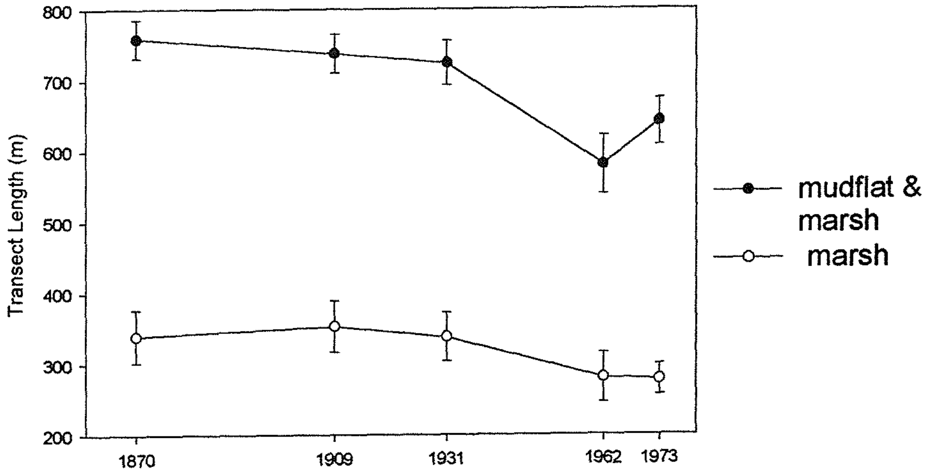
Marchwood 1965

Figure 2.5 (iii). Map Information from Marchwood, Southampton Water, 1870-1965.

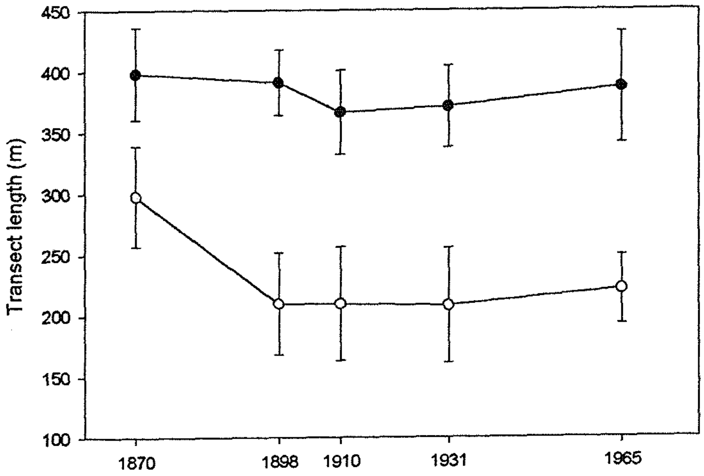
Data From Ordnance Survey Maps:
1870 County Series, original scale 1:10560.
(Image from http://www.old-maps.co.uk/)
(Landmark Information Group)
1898 Hampshire Sheet LXV SW,
original scale 1:10560
1910 Hampshire Sheet LXV SW,
original scale 1:10560
1931 Hampshire Sheet LXV SW,
original scale 1:10560
1965 Sheets SU3811 & SU3711,
original scale 1: 25,000



(i) Gins Marsh, Beaulieu



(ii) Hythe



(iii) Bury Farm Marchwood

Figure 2.6. Extent of Mudflat and Saltmarsh at: (i) Gins Marsh, Beaulieu, 1870-1973.; (ii) Hythe (1870-1973); and Bury Farm, Marchwood (1870-1975). Data from transects on historical maps, see Appendix 2.2.

Historical Information

Disturbance and Pollution

All three sites appear to have a continuous undisturbed history over the last 2-300 years. There was extensive shipbuilding in the area around Bucklers Hard, Beaulieu, from Tudor times, but there are no records of use of Gins Marsh as a hard or shipyard. Beaulieu was used as a harbour for landing craft and navy ships in World War 2, and this probably led to some lead pollution from diesel engine exhausts which has been identified in the stratigraphy from a nearby site (I.W.Croudace, 1998 Pers. Comm.). The two sites on Southampton Water have been subject to more pollution inputs due to their closer proximity to the industrial activity in Southampton and the surrounds. Notably there is the large Esso oil refinery at Fawley (adjacent to Hythe), which has been operational since 1921 and has been developed and enlarged significantly since the 1950s (Croudace and Cundy 1995). There have been some major spillages (Spellerberg 1991, pp.170-173), although the oil content of wastewaters has fallen in recent years from 30ppm to 3ppm (Dicks and Levell 1989). The refinery has also produced increased sediment levels of heavy metals, particularly copper. Other heavy metals such as lead and zinc are also present in high concentrations in intertidal sediments from this part of the Solent, probably from a range of sources (Croudace and Cundy 1995).

Spartina anglica

Appearance of *Spartina townsendii*, and what went before.

The key dates from the search of literature sources are listed in Table 2.1. There is a wide range of documented evidence surrounding the appearance, spread and die back of *S. anglica*: The spread around the Hampshire basin was reviewed in detail by Goodman *et al* (1959). Gray *et al* reviewed the history and spread in some detail in 1991, and this was further reviewed, in the context of the Solent area, by Tubbs (1999). The Groves brothers first identified a new hybrid in 1880, based on observations in 1877, and named it *Spartina townsendii* (Groves and Groves 1880). However 1870 is now usually taken as the earliest date for discovery of the hybrid based on a samples in the Warner Herbarium, University of Southampton (Sutherland and Eastwood 1916, Gray *et al* 1991). Sutherland and Eastwood (1916) did, however suggest that the description of *Spartina alterniflora* specimens from near Southampton in Sowerby (1861, cited in Sutherland and Eastwood 1916) was very close to the description of *S. townsendii* by Groves and Groves (1880). What followed is well-documented (see below), but what went before remains somewhat in dispute (Gray *et al* 1991). Tubbs (1999) described the actual date of appearance of the new form as *"conjectural"*. Sowerby's specimens at the very least confirmed that either the New World alien *S. alterniflora* or one of its early hybrid progeny was present, at the latest, by 1861. Meanwhile, Townsend (1883) in his *Flora of Hampshire* reported that *S. alterniflora* had been abundant at Hythe and several other sites on the western shore of Southampton water in 1850, and was first reliably reported as early as August 8th 1836 by Dr William Bromfield, one of the leading botanists of the early nineteenth century. Even this date is inconclusive as Dr Bromfield was told by a labourer that he had known of the plant at Southampton *"for upwards of 20 years"* (Townsend 1883, Tubbs 1999). Furthermore, sterile hybrids between *S. maritima* and *S. alterniflora* were collected in 1815, and the specimens are still in existence in the Herbarium of the Natural History Museum (Brewis *et al* 1996). As for site-specific detail relevant to this study; Lord Montagu of Beaulieu's evidence to the Royal Commission on Coastal Erosion from 1907 stated that an unconsolidated marsh system community was much more extensive in the Beaulieu and Lymington marshes in the nineteenth century. This suggests that a spread of *S. alterniflora* or *S. townsendii* was at most not widespread until the dates given below. His evidence also provides extensive information of the proliferation of "Rice Grass" in Southampton Water in the nineteenth century, although there is no site-specific detail other than that mentioned previously.

J. Groves, who had witnessed the transition from the pre-*Spartina* to post-*Spartina* environment, made some important comments in 1927 about the nearby Lymington marshes. *" Perhaps not many of those present can remember the entrance of Lymington River fifty years ago. I have a vivid recollection of how one used to go out onto the river at low tide between horrible-looking and malodorous banks of bare, half-liquid mud. Thanks to our Spartina the state of things is now quite different, and it would be difficult to find a more beautiful sight then of the Spartina-area in the same spot on an autumn evening with the setting sun shining on the golden stems and leaves"* (Groves 1927). Lord Montagu of

Beaulieu (1907) had also made similar comments about his early memories of the Beaulieu/Lymington marshes.

The key dates from the search of literature sources are listed in Table 2.1. Summarising the written evidence relating to the pre-*Spartina* environment in the Solent region it is clear that: unconsolidated mudflat/pioneer marsh was more widespread; the alien *S. alterniflora* was present in the early part of the nineteenth century, and certainly widespread from 1850-1870; the exact date of the appearance of the hybrid *S. townsendii* is uncertain (but was probably as early as 1860), and early hybridisation could have even occurred by 1815.

Table 2.1 Key dates in the early *Spartina* story
(Based on original literature and the reviews of Gray *et al* 1991, and Tubbs 1999)

Date	Event	Source
1815	Sterile hybrid *Spartina* collected (*S. maritima* x *S. alterniflora*)	Brewis *et al* (1996), samples still kept in the Natural History Museum Herbarium
1816 (or earlier)	Reported earliest sighting of *S. alterniflora*	Townsend (1883), based on anecdotal evidenc given to Dr William Bromfield in 1836
1836	Earliest reliable record of *S. alterniflora* at the lower Itchen	Townsend (1883), based on specimens taken by Dr William Bromfield in 1836
1850	*S. alterniflora* widespread in Southampton Water	Townsend (1883)
1861	Possible description of *S. townsendii*, mistaken for *S. alterniflora*	Sowerby (1861), cited by Sutherland & Eastwood (1916)
1870	First specimens of *S. townsendii*	Sutherland & Eastwood (1916)
1875 and earlie	Extensive mudflats still present at Lymington and Beaulieu	Montagu of Beaulieu (1907), Groves (1925)
1877	*S. townsendii* identified as a new species (specimens from Hythe)	Groves & Groves (1880, 1882)
1883	*S. townsendii* still only present at Hythe	Stapf (1908)
1887	*S. townsendii* recorded at Southampton	Stapf (1913)
c.1890	Appearance of fertile *S. anglica.* hybrid *Spartina* much more widespread	Stapf (1913), Marchant (1967)
1892	*S. anglica* first collected at Lymington	Goodman *et al* (1958)
1898	*S. anglica* planted at Beaulieu	Mills (1931), cited in Goodman *et al* (1958)
1907	*S.townsendii/S. anglica* widespread	Rayner (1909)
1920s onwards	Local onset of 'die back'	Manners (1975)

Spread of *S. anglica / S. townsendii*

The spread of the new *Spartina* species was studied in detail by botanists at the University of Southampton in the 1950s and 1960s (e.g. Goodman *et al* 1959, Lambert 1964, Hubbard 1965, Hubbard and Stebbings 1968, Marchant 1967). My literature search focussed principally on information relevant to the study sites. Goodman *et al*'s (1959) detailed review of the spread of what was then known generally as *S. townsendii* recorded 1898 as the first date of occurrence at Beaulieu, although they suggested that this may have been planted to aid natural spread which was already ongoing. It had already reached Lymington by 1892 (Goodman *et al* 1959), so it seems quite likely that it was already present in the Beaulieu Estuary by the end of the 1880s. Meanwhile in Southampton Water the new species did not spread rapidly at first- Stapf (1908) relates how it had failed to reach Cracknore Hard (3km north of Hythe, and adjacent to the Bury Farm marsh) by 1883. However Stapf (1914) describes how it had spread to Southampton by 1887: Marchant (1967) suggests that the late 1880s were when the fertile amphidiploid first arose. However, much of the material preserved in herbaria from 1892 to 1910, when the main spread took place, is believed to have been sterile *S .townsendii* (Goodman *et al* 1969, Gray *et al* 1991).

Certainly by 1907 *Spartina* marshes were part of the landscape in the Solent region. Rayner (1909) gave a meticulous account of the estuaries of the Solent based on a tour carried out in autumn 1907. He described how the "*giant* Spartina *held sway......... half way to Beaulieu village........it has annexed every foot of the salt mud it covers. It stretches right and left from the river mouth*". From this it is reasonable to infer that Gins Marsh, Beaulieu would have been one of the *Spartina* marshes he was describing. He also suggested that by 1907 *S. maritima* was almost extinct locally (one clump was found at Gilbury Hard, Beaulieu), and that at all sites in the region *S. alterniflora* was rapidly being displaced by the new hybrid. Hythe (the "*locus classicus* for *townsendii*") had no *S. alterniflora* by 1907, and Marchwood was a mixed *S. townsendii* and *S. alterniflora* marsh.

Palaeoecological investigations

General stratigraphy

The gross stratigraphy and information from radiographic analysis of the cores are shown in Table 2.2. Each of the lower marsh cores shows a gradual change in composition from predominately organic to mostly clay and silt. This is likely to be an indication of a change from a saltmarsh to mudflat palaeoenvironments. This was confirmed by the change in radiographic appearance at lower levels to more opaque (due to a higher mineral content), and the presence of fossil remains of mudflat invertebrates, particularly the typical mudflat bivalve *Scrobicularia plana,* in the lower parts of some lower marsh cores. This species is usually not found living in vegetated saltmarsh sediments (Campbell 1976). The middle marsh cores did not penetrate deep enough to extend into these palaeoenvironments, if present.

Table 2.2. Stratigraphic description of cores.

Site & Date Sampled	Core	Depth (m)	Description
Beaulieu, lower marsh 17/12/1996	GM1	1.80	0-1.05 m large amounts of organic material , mostly roots, increasingly humified below 0.75m 1.05-1.50m little organic material, (possible *Zostera* spp.) many *Hydrobia ulvae* shells 1.50-1.80 fine silt and clays, occasional *Scrobicularia plana* shells, woody fragments at 1.75m
Beaulieu, lower marsh 5/9/1997	GM2	0.8	0-0.8m large amounts of organic material , mostly roots, increasingly humified below 0.7m . No clear change to a more inorganic sediment
Beaulieu, lower marsh 5/9/1997	GM3	0.8	0-0.8m large amounts of organic material , mostly roots, increasingly humified below 0.7m. No clear change to a more inorganic sediment
Beaulieu, mid-marsh 23/3/1999	GM4	0.44	Dense, very compacted root mat, poorly humified
Beaulieu, mid-marsh 23/3/1999	GM5	0.44	Dense, very compacted root mat, poorly humified
Beaulieu, mid-marsh 23/3/1999	GM6	0.42	Dense, very compacted root mat, poorly humified
Hythe, lower marsh 24/02/2000	H1	1.30	0-0.98m mostly organic material, predominately roots, including woody root material (*A.. portulacoides*) 0.98-1.30m fine grey silt and clay, little lamination, *Scrobicularia plana* shell material present
Hythe, lower marsh 24/02/2000	H2	1.30	0-0.98m mostly organic material, predominately roots, including woody root material (*A.. portulacoides*) 0.98-1.30m fine grey silt and clay, little lamination, *Scrobicularia plana* shell material present
Hythe, lower marsh 24/02/2000	H3	1.30	0-0.98m mostly organic material, predominately roots, including woody root material (*A.. portulacoides*) 0.98-1.30m fine grey silt and clay, little lamination, *Scrobicularia plana* shell material present
Hythe, mid-marsh 9/11/00	H4	0.95	0-0.90m organic material, increasingly humified with depth 0.90-0.95m clay and silts with gravels at base
Hythe, mid-marsh 9/11/00	H5	0.95	0-0.90m organic material, increasingly humified with depth 0.90-0.95m clay and silts with gravels at base
Hythe, mid-marsh 9/11/00	H6	0.95	0-0.90m organic material, increasingly humified with depth 0.90-0.95m clay and silts with gravels at base
Marchwood, lower marsh 9/11/00	B1	1.05	0.90m organic material, increasingly humified below 0.80m 0.90-1.00m clay and silt, some grassy plant remains (possibly *Zostera* spp.) 1.00-1.05m dense blue-grey clay
Marchwood, lower marsh 9/11/00	B2	1.05	0.90m organic material, increasingly humified below 0.80m 0.90-1.00m clay and silt, some grassy plant remains (possibly *Zostera* spp.) 1.00-1.05m dense blue-grey clay
Marchwood, lower marsh 9/11/00	B3	1.05	0.90m organic material, increasingly humified below 0.80m 0.90-1.00m clay and silt, some grassy plant remains (possibly *Zostera* spp.) 1.00-1.05m dense blue-grey clay
Marchwood, mid-marsh 9/11/2000	B4	0.30	Dense and highly compacted plant material, mostly roots Angular flints and gravels at 0.2m and 25-30m
Marchwood, mid-marsh 9/11/2000	B5	0.30	Dense and highly compacted plant material, mostly roots
Marchwood, mid-marsh 9/11/2000	B6	0.30	Dense and highly compacted plant material, mostly roots

Geochemical analysis, pollen analysis and accretion rates

Geochemical analysis

Raw data and age depth profiles for all cores analysed (GM1, GM2, GM3, GM4, H2, H4, B2, and B4) are included in Appendix 2.4. Sediment accretion rates based on these data are shown in Table 2.3. All three cores from the lower marsh at Beaulieu were analysed (GM1, GM2, GM3). These results show a general consistency between replicates, although GM1 shows a slightly higher rate. This may be due to disruption of surface layers (three data points from 0-11cm appear to be anomalous: this might be due to disturbance or contamination: see Appendix 2.4). Cores from the two lower marsh sites on the Solent (Hythe H2 and Bury Farm Marchwood B2) show very similar accretion rates, as do the upper marsh cores from the same sites (H4 and B4). The high confidence intervals for the mean accretion rate from core B4 (mid marsh, Marchwood) may be attributed to some disturbance in the upper layers: the determinations at 0.5 cm and 3.5 cm appear to be anomalous (Appendix 2.4). Despite this, there is good consistency between this core and the mid marsh core from nearby Hythe (H4), and as expected the middle marsh at Marchwood (B4) is accreting slower than the lower marsh (B2).

Table 2.3 Sediment accretion rates from ^{210}Pb analysis at Beaulieu, Hythe and Marchwood.

Core	**Accretion rate mm a^{-1}**	**95% confidence interval**
GM1	4.2	3.6-5.0
GM2	3.3	2.7-4.2
GM3	3.2	2.7-3.8
GM4	1.5	1.0-2.9
H2	3.4	2.9-4.1
H4	1.3	0.8-2.9
B2	3.3	2.6-4.7
B4	1.8	1.0-8.8

Pollen analysis

Pollen analysis was carried out to estimate the stratigraphic level of the anthropogenic *Pinus* rise. Each of the cores showed a clear rise in *Pinus* pollen, which was found to be highly consistent in the replicate cores from each level. Figures for the pollen counts are included in Appendix 2.5, and the estimated stratigraphic levels for each core are summarised in Table 2.4. Total pollen counts were carried out on cores H2 and H3 principally to locate the *Spartina* rise, if possible. Because of the difficulties identifying *Spartina* pollen these must be interpreted with some caution, but the relationship between the *Spartina* rise with the APR and ^{210}Pb stratigraphy appears to be consistent with expectations. The position in both of these cores from Hythe lower marsh of the *Spartina* rise (0.65m), relative to the APR (0.85m) does confirm the general stratigraphic relationship of these two horizons. The *Spartina* rise was also identified in core H4, at 0.35m, which again broadly aligns with the stratigraphic APR (0.5 m). A *Pinus* rise was not located in cores B4, B5 & B6 (Bury Farm, Marchwood, middle marsh). The sediments here were too compacted to sample deeper than 0.28 m.

Table 2.4. Rates of accretion and stratigraphic depths from the three experimental sites.
(Due to uncertainty over the exact timing or the APR (Anthropogenic *Pinus* Rise), accretion rates are calculated from three possible dates see text for details and sources).

Site	**Core**	**Stratigraphic APR Depth (m)**	**Overall accretion rate (mm/yr) from *Pinus* data**			**Accretion rates pre-1900 (mm/yr) (using different APR dates)**			**Depth (m) from stratigraphic APR to 1900**	**Accretion rates 1900 to present (mm/yr) from ^{210}Pb data**	**Depth (m) (1900) from ^{210}Pb data**	**Recorded hybrid *Spartina* date**
			APR 1700	**APR 1750**	**APR 1800**	**APR 1700-1900**	**APR 1750-1900**	**APR 1800-1900**				
Beaulieu, lower marsh	GM1	0.36	1.2	1.44	1.8	*	*	*	0.36-0.43	4.2	0.43	1898
	GM2	0.36	1.2	1.44	1.8	0.15	0.2	0.3	0.36-0.33	3.3	0.33	1898
	GM3	0.36	1.2	1.44	1.8	0.15	0.2	0.3	0.36-0.33	3.3	0.33	1898
Beaulieu, Middle marsh	GM4	0.22	0.73	0.88	1.1	0.35	0.47	0.7	0.22-0.15	1.5	0.15	1898
	GM5	0.22	0.73	0.88	1.1	0.35	0.47	0.7	0.22-0.15	1.5	#	1898
	GM6	0.2	1.0	1.25	1.0	0.25	0.33	0.5	0.2-0.15	1.5	#	1898
Hythe, lower marsh	H1	0.85	2.83	3.4	4.25	2.55	3.4	5.1	0.85-0.34	3.4	0.34	1870
	H2	0.85	2.83	3.4	4.25	2.55	3.4	5.1	0.85-0.34	3.4	#	1870
	H3	0.8	2.67	3.2	4.0	2.3	3.1	4.6	0.8-0.34	3.4	#	1870
Hythe, Middle marsh	H4	0.5	1.67	2.0	2.5	1.85	2.5	3.7	0.5-0.13	1.3	0.13	1870
	H5	0.5	1.67	2.0	2.5	1.85	2.5	3.7	0.5-0.13	1.3	#	1870
	H6	0.5	1.67	2.0	2.5	1.85	2.5	3.7	0.5-0.13	1.3	#	1870
Marchwood, low marsh	B1	0.8	2.67	3.2	4	2.35	3.13	4.7	0.8-0.33	3.3	0.33	1880-1890
	B2	0.85	2.83	3.4	4.25	2.6	3.5	5.2	0.85-3.3	3.3	#	1880-1890
	B3	0.8	2.67	3.2	4	2.35	3.13	4.7	0.8-0.33	3.3	#	1880-1890
Marchwood, Middle marsh	B4	>0.28	>0.93	>1.12	>1.4	>0.5	>0.67	>1.0	>0.28-0.18	1.8	0.18	1880-1890
	B5	>0.28	>0.93	>1.12	>1.4	>0.5	>0.67	>1.0	>0.28-0.18	1.8	#	1880-1890
	B6	>0.28	>0.93	>1.12	>1.4	>0.5	>0.67	>1.0	>0.28-0.18	1.8	#	1880-1890

Notes:

* pre-1900 accretion rates cannot be calculated for GM1 as the APR level and the Pb-210 100 year level are out of order in the stratigraphy. The Pb-210 data may be erroneous.

Pb-210 analysis was carried out on cores GM1, GM2, GM3, GM4, H2, H4, B2 & B4.

Replicate data is used to make the calculations for pre-1900 accretion rates for cores GM5, GM6, H1, H3, H5, H6, B1, B3 B5 & B6.

Alternative APR dates from Haskins (1978), Waton (1983) and Barber (1981)

Recorded *Spartina* dates based on Goodman et al 1959. These dates are critically examined in the later sections of this chapter.

The inferred accretion rates for each site and marsh level based on combined palynological and geochemical data are shown in Table 2.4. The lower marsh at Beaulieu shows an accretion rate of 1.2-1.8 mm a^{-1} over the 200-300 year timescale, but has been accreting at 3.3 mm a^{-1} since 1900, i.e. post *Spartina* (based on cores GM2 & GM3). However, the marsh was accreting at very low rates (0.15-0.3 mm a^{-1}) in the pre-*Spartina* period. These relative changes are consistent with other studies (e.g. Long *et al* 1999). The middle marsh shows the same pattern, although, as would be expected from a more mature part of the marsh systems, accretion rates are lower (Allen 1990). The results from the other two sites are less clear: the lower marshes at Hythe and Marchwood do not appear to have accreted any more rapidly since 1900, although if the earlier date for the APR is taken rates have increased.

Macrofossil Stratigraphy

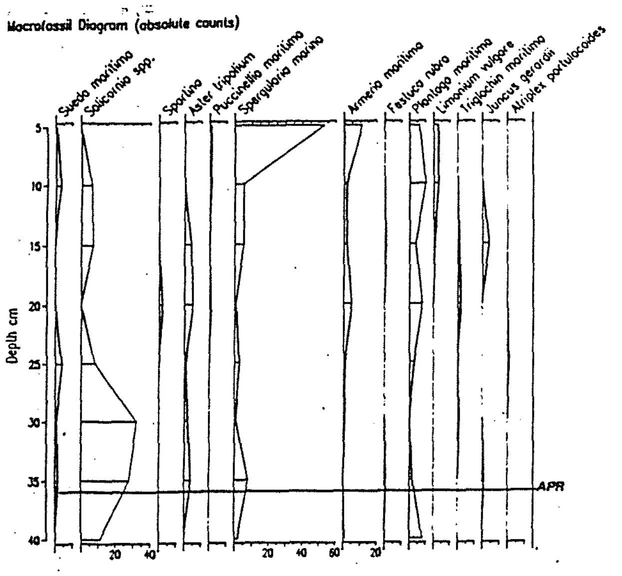
Macrofossil diagrams for all eighteen cores are shown in Figures 2.7-2.12. Species are arranged on the horizontal axis in the approximate order that they are found in the zonation of a typical marsh, starting on the left with pioneer species (after Gray 1992). The estimated stratigraphic level of 100 years BP (before present, i.e.1900), based on ^{210}Pb dating; an estimated level for the appearance of *Spartina*, based on the dates of first records and the ^{210}Pb accretion rates; and the stratigraphic APR are marked on each figure for reference (stratigraphic levels from Table 2.4).

Very little identifiable *Spartina* material was located in the sediments, although where some was found the stratigraphic level was above the estimated depth for the first appearance of the new species (in cores GM2 (Figure 2.7 (ii)) GM 4 (Figure 2.8 (i)), H1 (Figure 2.9 (i)), H3 (Figure 2.9 (iii)), H6 (Figure 2.10 (iii)), B4 (Figure 2.12 (i)), & B5 (Figure 2.12 (iii)), so the chronology is consistent. Generally the cores showed a consistent trend of an increasingly diverse sub-fossil assemblage towards the surface layers, with increased numbers of *P. maritima*, *Spergularia marina, A. maritima* and *L. vulgare* present in the upper layers of most of the cores. Fewer species, and for the most part smaller numbers of those species, were identified in the deeper parts: this may be an artefact of progressive degradation of the preserved material with increasing age (see Discussion).

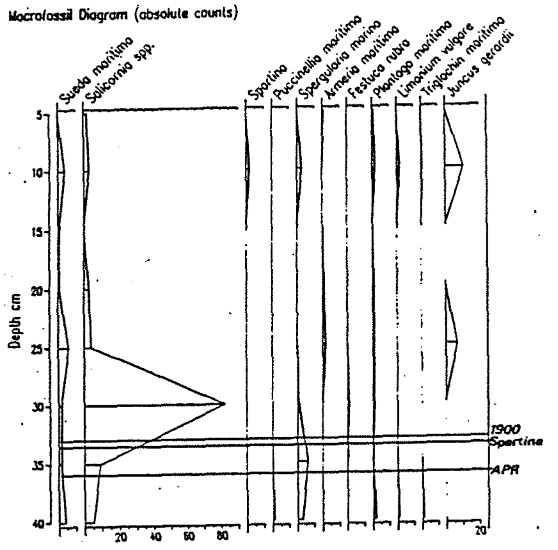
The lower marsh cores for Gins Marsh, Beaulieu (GM1, GM2, GM3) (Figure 2.7) showed a "bulge" of pioneer species (*Salicornia* spp. and, to a lesser degree *Sueda maritima*) in the lower levels (below 0.25 m). The bulge extended from above the estimated dates for the appearance of *Spartina* into the deepest parts of the cores. There was a rise in the number of *S. marina* seeds in the surface layers of core GM1, but this was not identified in the other two lower marsh cores from Gins Marsh. The middle marsh cores from the same site (GM4, GM5, GM6) also showed a distinctive bulge of pioneer species, at 0.2-0.3 m, but this was at a lower stratigraphic level relative to the estimated appearance of *Spartina* at the site than in the lower marsh cores; and the bulge is composed more of *S. maritima*, with a much less conspicuous *Salicornia* bulge (Figure 2.8). There were also a large number of *S. marina* seeds in the surface layers of these three cores.

Generally fewer seeds were identified in the lower marsh cores from Hythe (H1, H2, H3) and Bury Farm, Marchwood (B1, B2, B3), than at the lower marsh at Beaulieu (Figures 2.9 and 2.11). Given that the numbers are small, a pioneer bulge was also identifiable in the lower levels (0.5-0.85 m at Hythe, 0.45-0.85 m at Bury Farm), with *Salicornia* the principal component. This upper part of this bulge coincided with the estimated date of appearance of *Spartina* at these sites, based on documentary evidence and geochemistry, (0.44 m at Hythe, =1870; 0.40 m at Marchwood, =1880), although there was again a rise in *S. marina* numbers in the surface layers of some cores (H1, B1 & B3).

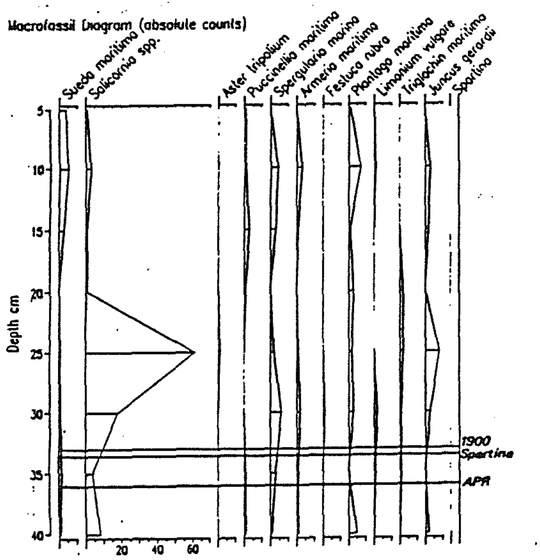
The data from the middle marsh cores from Hythe were less consistent. H5 showed a conspicuous *S. maritima* peak at 0.25m, and a large rise in the same species at the surface, but this was not found at the replicates (H4 and H6) (Figure 2.10). All three of these cores exhibited a similar *Salicornia* bulge to that found at Beaulieu in the lower marsh, although in this case the increased *Salicornia* lay below the stratigraphic level of the *Spartina* rise. Middle marsh cores from Bury Farm, Marchwood (B4, B5, B6) (Figure 2.12) showed a similar *Salicornia* rise, extending from above the suggested *Spartina* level (0.215 m) to the bottom of the core but also more consistently higher levels of *S. maritima* in the same parts of the stratigraphy. Core B6 had a conspicuous peak in *S. marina* near the surface (0.1 m) which was also apparent (with less seeds) in B4, but this was not apparent in B5.



(i) Core GM1

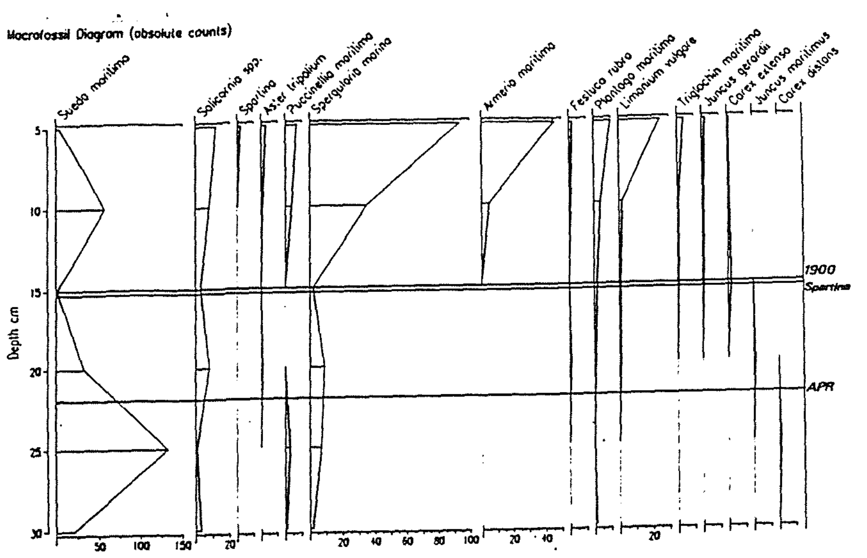


(ii) Core GM2

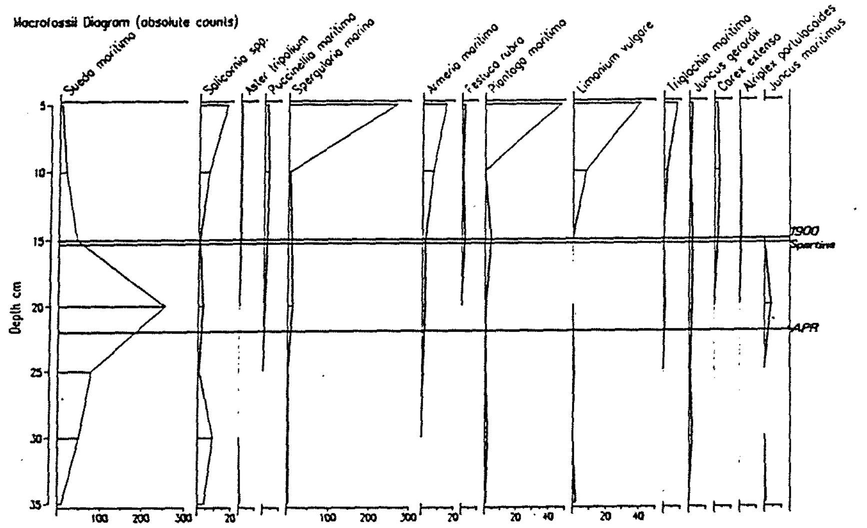


(iii) Core GM3

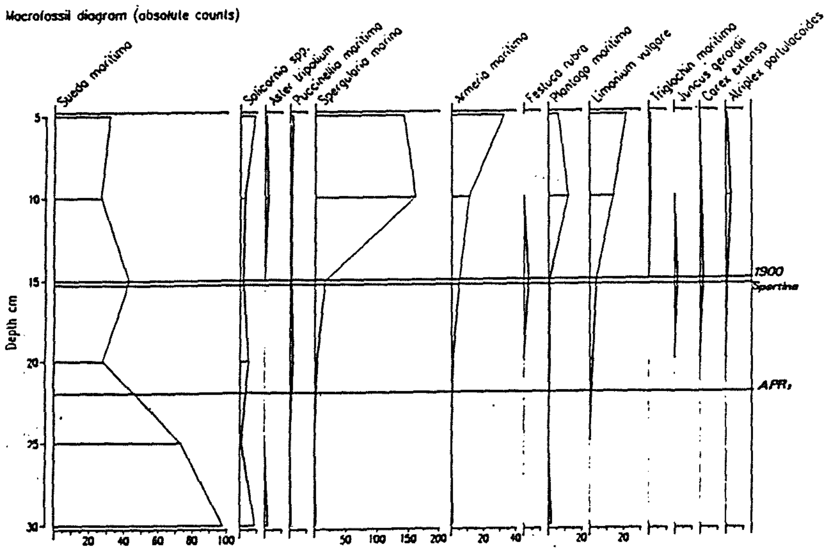
Figure 2.7. Macrofossil stratigraphy of replicate lower marsh cores from Gins Marsh, Beaulieu. (i)core GM1 (taken 17/12/1996), (ii) core GM2 (5/9/1997) & (iii) core GM3 (5/9/1997). Levels represent AD1900 (based on 210-Pb geochemistry, stratigraphic level of *Spartina* appearance, (based on documented date of appearance, after Goodman *et al* 1958) and Anthropogenic *Pinus* Rise based on pollen analysis of the same cores.



(i) Core GM4

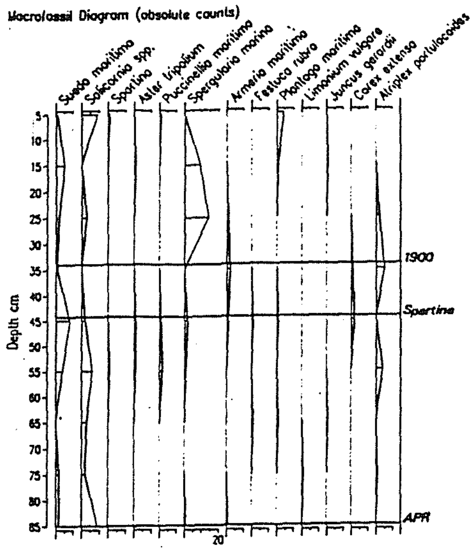


(ii) Core GM5

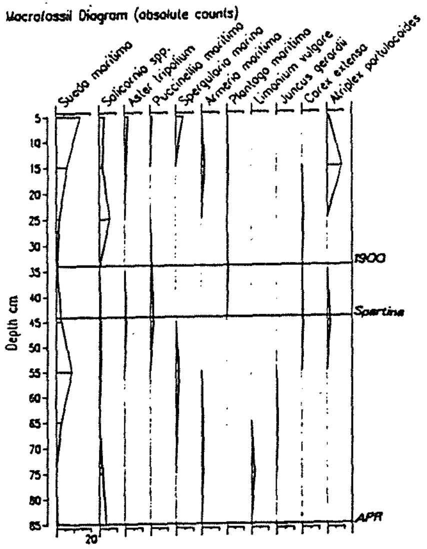


(iii) Core GM6

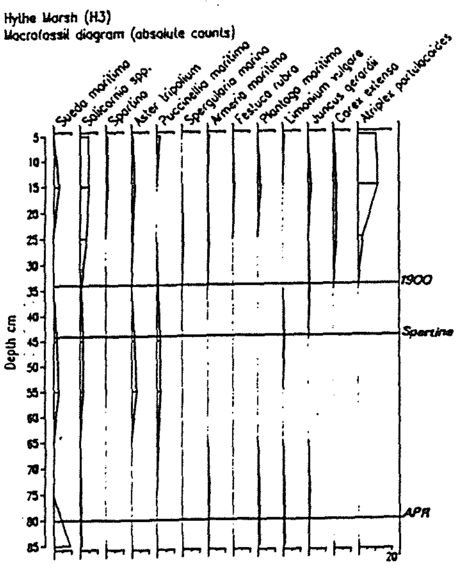
Figure 2.8 Macrofossil stratigraphy of replicate middle marsh cores from Gins Marsh, Beaulieu. (i) core GM4 (taken 23/3/1999), (ii) core GM5 (23/3/1999) & (iii) core GM6 (23/3/1999). Levels represent AD1900 (based on 210-Pb geochemistry, stratigraphic level of *Spartina* appearance, (based on documented date of appearance, after Goodman *et al* 1958) and Anthropogenic *Pinus* Rise, based on pollen analysis of the same cores.



(i) Core H1

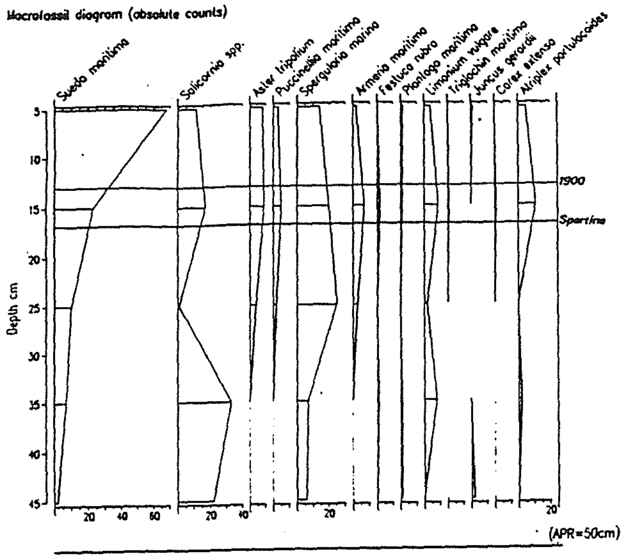


(ii) Core H2

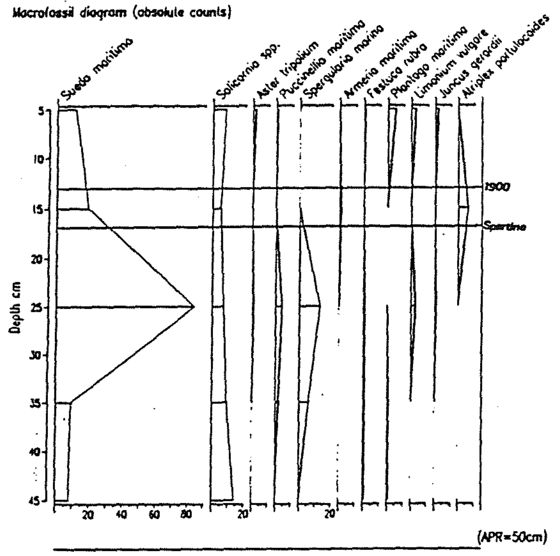


(iii) Core H3

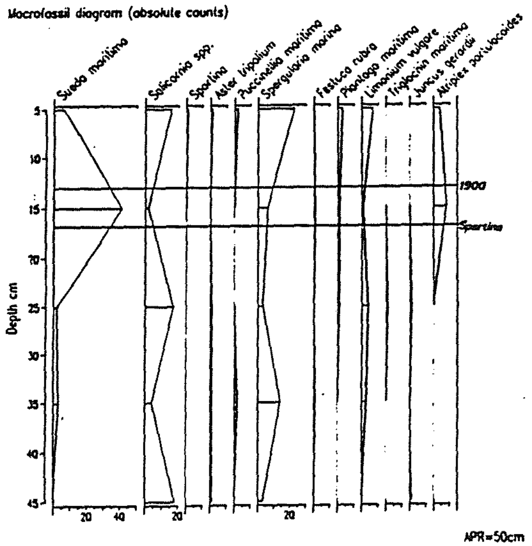
Figure 2.9 Macrofossil stratigraphy of replicate lower marsh cores from Hythe. (i) core H1 (taken 24/2/2000), (ii) core H2 (24/2/2000) & (iii) core H3 (24/2/2000). Levels represent AD1900 (based on 210-Pb geochemistry, stratigraphic level of *Spartina* appearance, (based on documented date of appearance, after Goodman *et al* 1958) and Anthropogenic *Pinus* Rise, based on pollen analysis of the same cores.



(i) Core H4

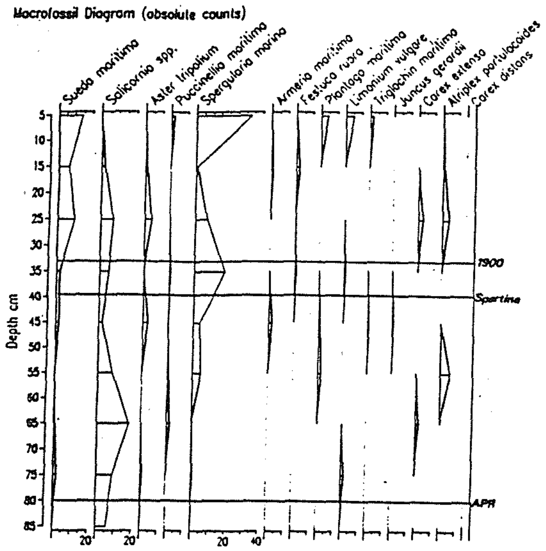


(ii) Core H5

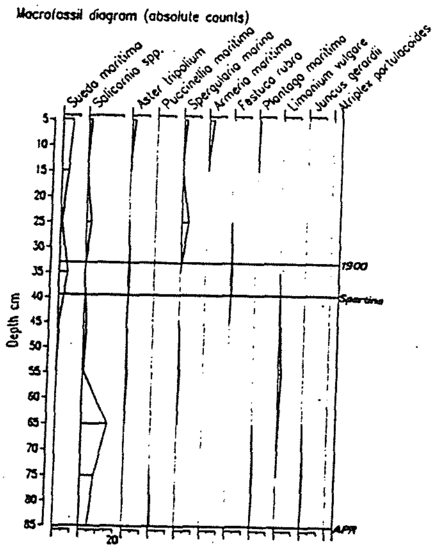


(iii) Core H6

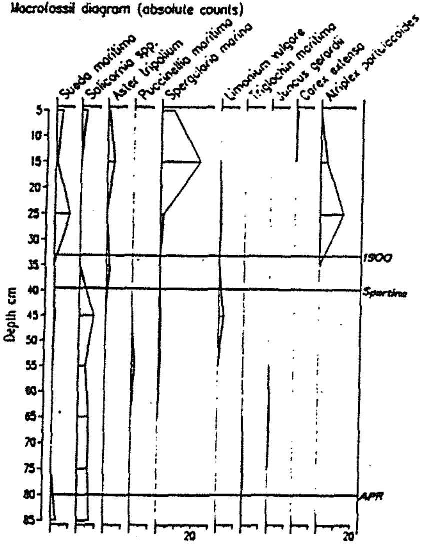
Figure 2.10 Macrofossil stratigraphy of replicate middle marsh cores from Hythe. (i) core H4 (taken 9/11/2000), (ii) core H5 (9/11/2000) & (iii) core H6 (9/11/2000). Levels represent AD1900 (based on 210-Pb geochemistry, stratigraphic level of *Spartina* appearance, (based on documented date of appearance, after Goodman *et al* 1958) and Anthropogenic *Pinus* Rise, based on pollen analysis of the same cores.



(i) Core B1

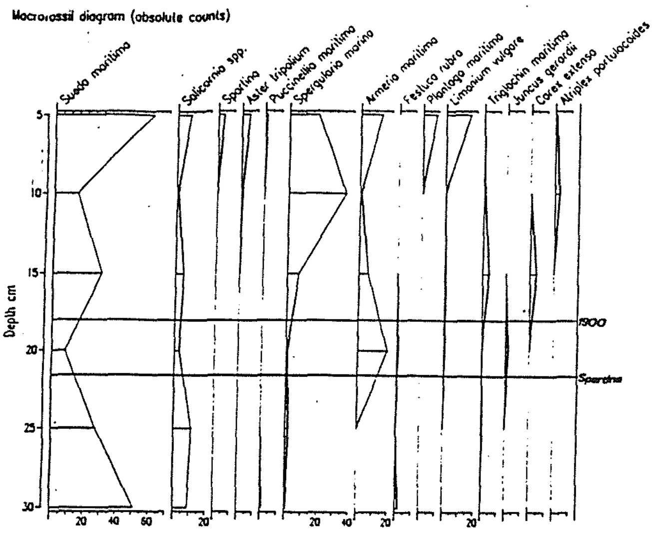


(ii) Core B2



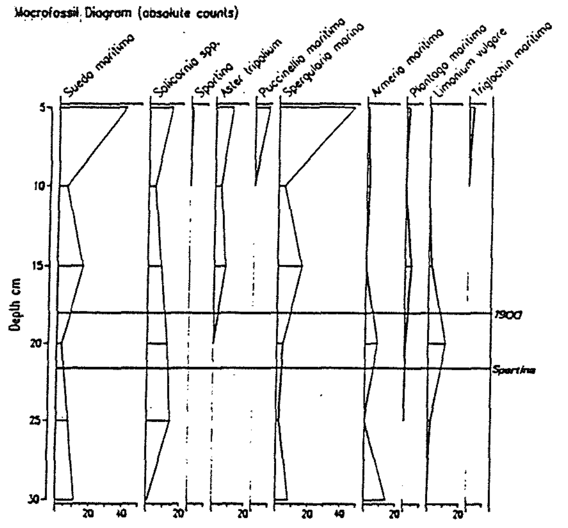
(iii) Core B3

Figure 2.11 Macrofossil stratigraphy of replicate lower marsh cores from Bury Farm, Marchwood. (i) core B1 (taken (9/11/2000), (ii) core B2 (9/11/2000) & (iii) core GM3 (9/11/2000). Levels represent AD1900 (based on 210-Pb geochemistry, stratigraphic level of *Spartina* appearance, (based on documented date of appearance, after Goodman *et al* 1958) and Anthropgenic *Pinus* Rise, based on pollen analysis of the same cores.



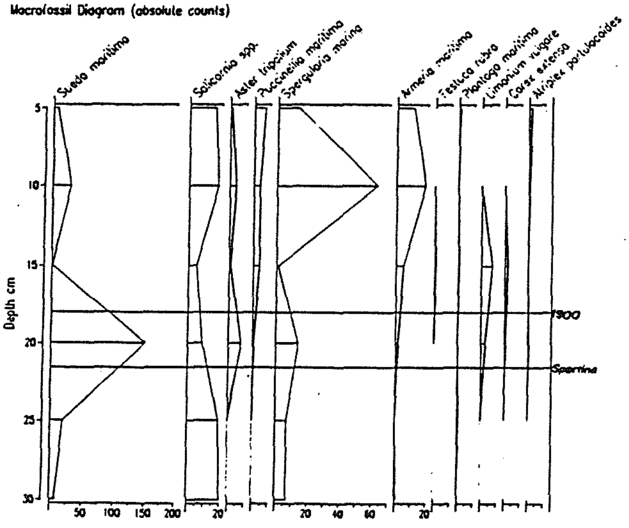
The APR was not identified in this core

(i) Core B4



The APR was not identified in this core

(ii) Core B5



(iii) Core B6

The APR was not identified in this core

Figure 2.12. Macrofossil stratigraphy of replicate middle marsh cores from Bury Farm, Marchwood. (i) core B4 (taken 9/11/2000), (ii) core B5 (9/11/2000 & (iii) core B6 (9/11/2000). Levels represent AD1900 (based on 210-Pb geochemistry, stratigraphic level of *Spartina* appearance (based on documented date of appearance, after Goodman *et al* 1958).

MDS analysis of community change

Figures 2.13-2.14 show analysis of the palaeocommunities using multidimensional scaling of the macrofossil data. Replicate data are presented together to show both general trends through the stratigraphy and variability between replicates. Stress levels generally lay between 0.1 and 0.2, which suggest that the MDS analyses are reasonably reliable (Clarke and Warwick 1994. Exceptions to this are indicated below.

Beaulieu:

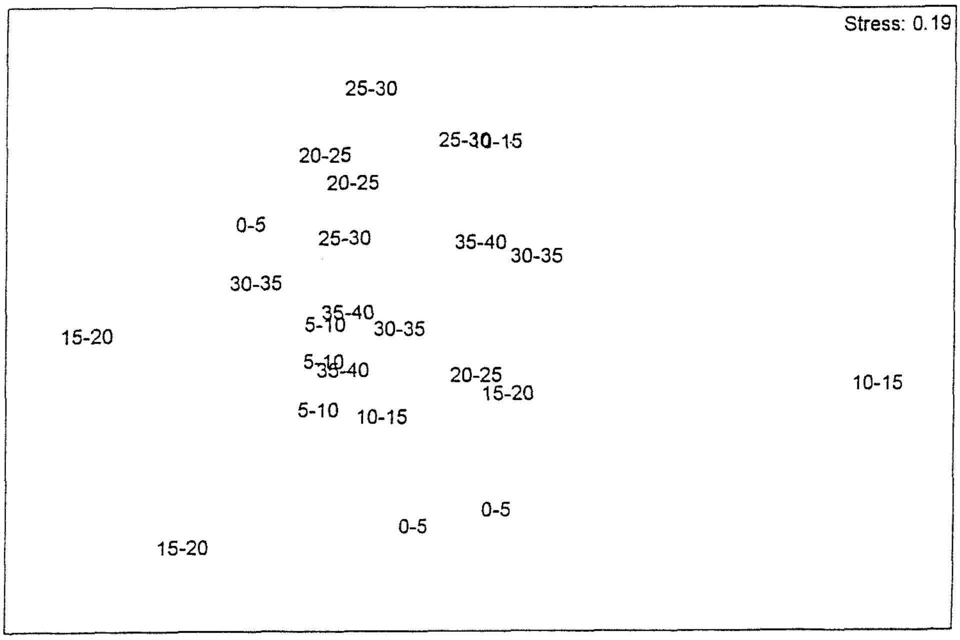
The cores from the lower marsh at Beaulieu (GM1, GM2 and GM3) showed quite a lot of variability between replicates although there is some clustering of replicate material from the lower levels (25 cm and below) (Figure 2.13 (i)). No trends through the stratigraphy were apparent from this analysis of these cores. The middle marsh cores however (GM4, GM5 and GM6) (Figure 2.13 (ii)), demonstrated clear stratigraphic changes, with data from the surface samples grouped at one end of MDS space and progression across the figure to the deeper samples. There was also tight clustering of replicates from the surface levels (e.g. 0-5cm, which was numerically dominated by *S. marina*) and of the deeper samples (20-25 cm and 25-30 cm, with large amounts of *S. maritima*). The groupings were less clear in the middle parts of the core, which might suggest more variability in the marsh system at the time these sediments were deposited. The low stress level (0.08) suggested that the patterns shown by the middle marsh data were very reliable.

Hythe:

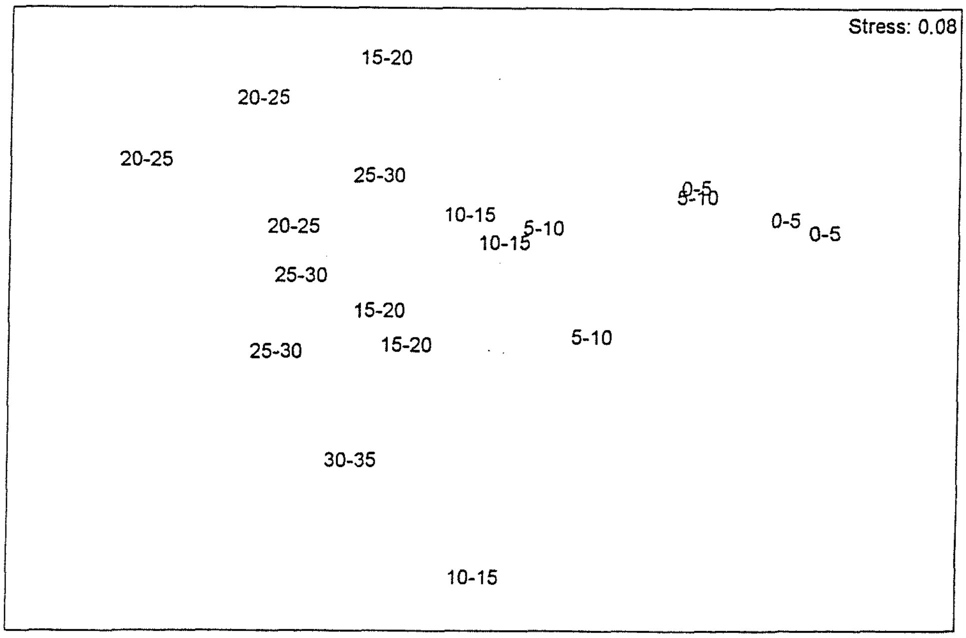
The lower marsh cores from Hythe (H1, H2 and H3) showed very little directional change with depth in MDS space and replicates from the same levels are mostly ungrouped, although there is some clustering of data from deeper levels (e.g. 70-75cm) (Figure 2.14 (i)). The stress level of 0.22 for these analyses made their reliability questionable: this is probably due to the small amount of identifiable material extracted from the Hythe cores. Data from the middle marsh at Hythe (Figure 2.14 (ii)) showed more clustering of replicates, although the data from the middle parts of the core (20-25 cm shows) more variability than the upper or lower layers, with acceptable stress levels.

Bury Farm, Marchwood:

The macrofossil data from the lower marsh at Bury Farm (Figure 2.15 (i)) shows two general clusters: one from the surface layers (0-35 cm) (although there is one outlier from 30-35 cm), and one fairly tight cluster from 40-85 cm. There is some overlapping between the two clusters arising from data from 20-45 m. Data from the middle marsh (Figure 2.15 (ii)) showed two clusters: one loosely grouped set arising from the upper levels (0-20 cm), and another slightly tighter group from the deeper parts of the stratigraphy (20-35 cm). This deeper part was dominated by *Salicornia*, with some *S. marina* in each sample.

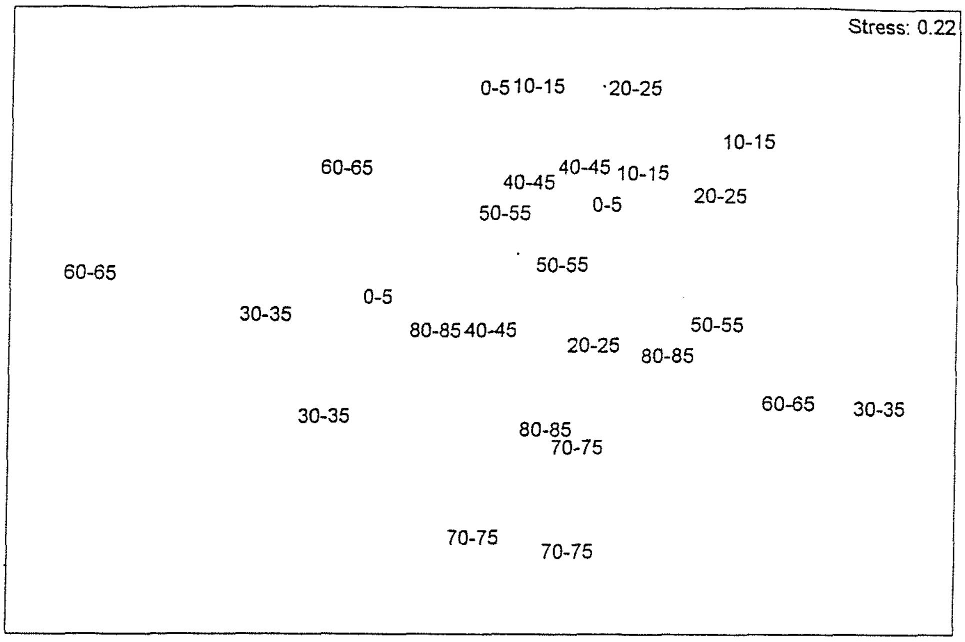


(i) lower marsh, Gins Marsh Beaulieu

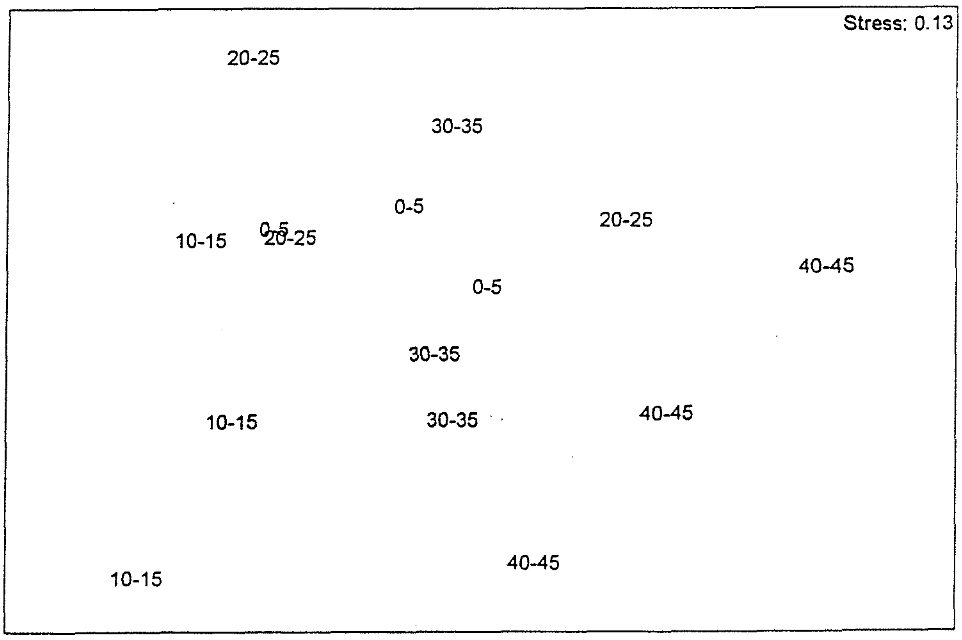


(ii) middle marsh, Gins Marsh Beaulieu

Figure 2.13. Multidimensional scaling (MDS) plot of plant macrofossil data, based on material extracted from saltmarsh cores taken from Gins Marsh, Beaulieu. (i) lower marsh, cores GM1 (core taken 17/12/1996), GM2 (5/9/1997) & GM3 (5/9/1997); (ii) middle marsh, cores GM4 (5/9/1997), GM5 (23/3/1999) & GM6 (23/3/1999). Numbers on the plots represent stratigraphic depths (cm) of the material taken from each of the three replicate cores.

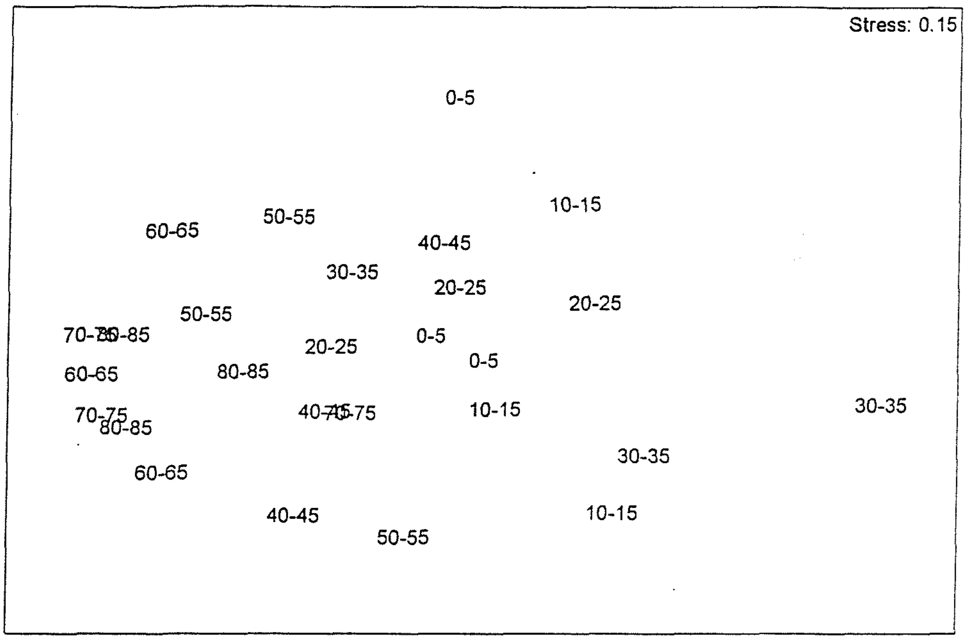


(i) Hythe lower marsh

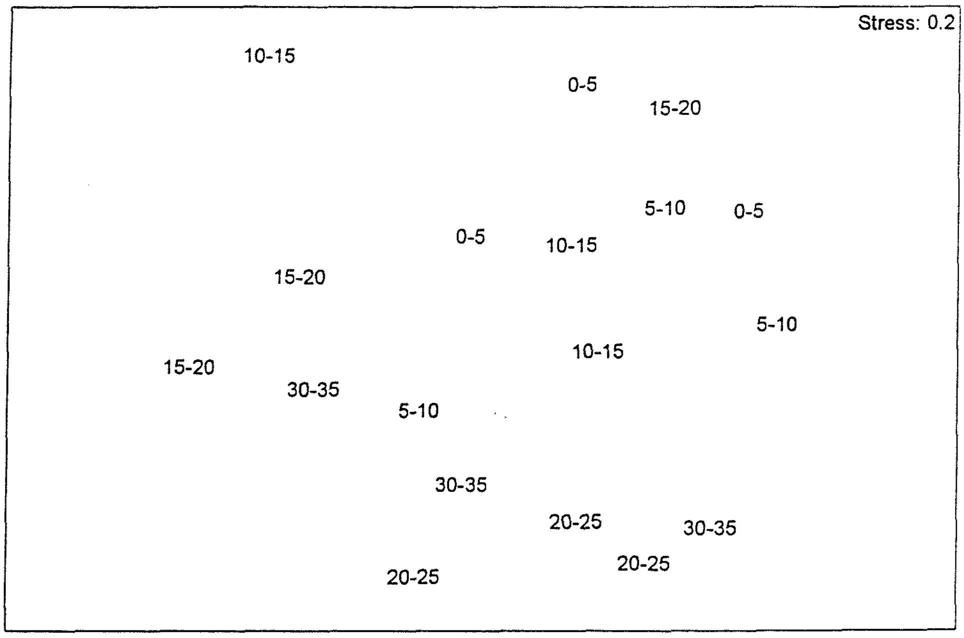


(ii) Hythe middle marsh

Figure 2.14. Multidimensional scaling (MDS) plot of plant macrofossil data, based on material extracted from saltmarsh cores taken from Hythe Marsh, Southampton Water. (i) lower marsh, cores H1 (core taken 24/2/2000), H2 (24/2/2000) & H3 (24/2/2000); (ii) middle marsh, cores H4 (9/11/2000), H5 (9/11/2000) & H6 (9/11/1999). Numbers on the plots represent stratigraphic depths (cm) of the material taken from each of the three replicate cores.



(i) lower marsh, Bury Farm Marsh, Marchwood



(ii) middle marsh, Bury Farm Marsh, Marchwood

Figure 2.15. Multidimensional scaling (MDS) plot of plant macrofossil data, based on material extracted from saltmarsh cores taken from Bury Farm Marsh, Marchwood. (i) lower marsh, cores B1 (core taken 9/11/2000) B2 (9/11/2000) & B3 (9/11/2000); (ii) middle marsh, cores B4 (24/2/2000), B5 (9/11/2000) & B6 (9/11/1999). Numbers on the plots represent stratigraphic depths (cm) of the material taken from each of the three replicate cores.

Discussion

This section contains an interpretation of the data presented here which integrates the historical material and the experimental data presented earlier. These data are used to make inferences on the changes to Solent saltmarsh communities over the last 200 years; and to re-appraise the accepted dates of appearance of the hybrid *Spartina anglica.*

Stratigraphy and accretion rates

The use of a multi-proxy approach allows the estimation of vertical accretion rates over several important temporal scales (table 2.4). The Anthropogenic *Pinus* Rise (APR) gives a stratigraphic date for 1700, 1750 or 1800 (Haskins 1978, Waton 1983, Barber 1981), and it is useful to consider all three dates for interpretation (Long *et al* 1999). A stratigraphic date of 1900 can be reasonably inferred from the ^{210}Pb geochemical information, so it has been possible to estimate accretion rates over three key time-scales: the last 200 to 300 years (depending on which APR date is used); the last 130 years, which in the sites concerned overlaps with documented records of initial *S. anglica* proliferation; and an intermediate period 70 to 170 years before 1870.

The period before 1870-1900 is conventionally assumed to be the pre-*Spartina* period (Goodman *et al* 1959), although the literature search carried out in this project suggests that this date itself may be debatable, at least for interpretation of stratigraphy (see below). The widespread presence of the taxonomically similar *S. alterniflora* (the pollen of which would be very difficult to distinguish from *S anglica/townsendii*) makes use of this as a distinct stratigraphic marker in the pollen profile a questionable exercise. The historical records suggest that the actual date of widespread new (i.e. alien or hybrid) *Spartina* presence in the Solent could be as much as 70 years earlier than the date (1877) when the hybrid was formally identified by the Groves brothers at Hythe (Groves & Groves 1880, 1882). The alien parent species *S. alterniflora* was present in the Southampton region as early as 1829 (Brewis *et al* 1996), and possibly as early as 1816 (Townsend 1883). Furthermore, sterile hybrids between *S. maritima* and *S. alterniflora* were collected in 1815 (Brewis *et al* 1996), although this may not have coincided with geographical spread on any scale. This raises important issues for interpretation of the stratigraphy and reconstruction of the past communities.

Long *et al* (1999) used the *Spartina* pollen rise in Poole Harbour as a chronological marker for *c.* 1890-1900. This is probably reliable for Poole: Hall (1934) reported that, in Britain, *S. alterniflora* was restricted to Hampshire and one site in Sussex during the nineteenth century. Use of *Spartina* pollen as a distinct marker in the Solent region is therefore of less use, unless a wider chronological range (e.g. 1830-1870) is acceptable, and the "recorded hybrid *Spartina* dates" (Table 2.1) are probably inaccurate for stratigraphic interpretation. For the sites in question, I believe that dates of 1850 for Hythe and Marchwood and 1870 for Beaulieu might be more accurate for the *Spartina* pollen rise, although this may not necessarily coincide with the appearance of *Spartina anglica* at these sites.

Table 2.5 The *Spartina* pollen rise and possible stratigraphic dates. H2 and H3 are lower marsh cores; H4 is a middle marsh core. All cores taken in 2000 from Hythe marsh, Southampton Water.

Core	**Stratigraphic level of *Spartina* pollen rise (m)**	**^{210}Pb accretion rate (mm a^{-1})**	***Spartina* date based on ^{210}Pb**	**APR accretion rates (1700/1800) (mm a^{-1})**	***Spartina* date based on limits of APR**
H2	0.65	3.4	1810	2.83-4.25	1760-1847
H3	0.65	3.4	1810	2.67-4	1756-1838
H4	0.35	1.3	1730	1.67-2.5	1790-1860

In this study I found a clear *Spartina* pollen rise was recorded at 0.65m in the Hythe lower marsh cores H2 and H3. Using ^{210}Pb accretion rates from those cores (while accepting that this is well below the limits of accuracy for this method), this would give a date equivalent to 1810AD (+/- 29 years) for the first large-scale appearance of alien (but probably not hybrid) *Spartina.* Early dates for a *Spartina* rise are suggested by the Hythe middle marsh core H4 (Table 2.5), although a stratigraphic level of 0.35m could be interpreted using ^{210}Pb accretion rates as widespread *Spartina* growth as early as 1730, which is most improbable. However, if the overall accretion rate based on the APR is used, the *Spartina* rise could be estimated as being in the period 1790-1860. This does produce interesting correlations with some of the historical information outlined earlier, particularly the reported widespread presence of *S. alterniflora* before 1850, and the presence of hybrid specimens as early as 1815. It should be emphasised, however, that the difficulty of identification of *Spartina* pollen (in comparison with other grasses) makes it a potentially unreliable marker for dating. However, the position at Hythe of the *Spartina* rise (0.65m=1810, based on ^{210}Pb), relative to the APR (0.85m=1700, 1750 or 1800), does confirm the general stratigraphic relationship of these two horizons. However, important questions have been raised by these data about the use of the accepted "first collection" dates (e.g. 1870 at Hythe) for *S. anglica* as reliable stratigraphic dates, at least for sites in the Solent region.

Accretion rates, relative sea-level rise and marsh physiography

It would be expected that accretion rates would have increased since the spread of *Spartina anglica*, since it is known to be very effective at accreting sediment, particularly in the early stages of colonisation (Chapman 1959). Rates are typically over 3 mm a^{-1} (Bird and Ranwell 1964) but some times much higher: as much as 26cm a^{-1} in one site in China has been reported (Chung 1990). Long et al (1999) calculated from stratigraphic evidence that sedimentation rates increased from 1.14 mm a^{-1} to 7.17 mm a^{-1} after establishment of S. anglica in Poole. The pre-*Spartina* period (calculated using the APR) showed much lower rates of accretion (0.84-1.14 mm a^{-1}). Cundy and Croudace (1996) reported ^{210}Pb accretion rates (i.e. effectively post-Spartina) of 3.2- 4.9 mm a^{-1} (mean 4.2 mm a^{-1}) from six sites in the Solent region, although that study did not examine earlier time periods. Accretion rates at lower and middle marsh levels over 0 to130 and 0 to 200-300 years have been calculated for the three sites in my study (Table 2.4) based on the ^{210}Pb information and the APR. The lower marsh at Beaulieu shows an accretion rate of 1.2-1.8 mm a^{-1} over the 200 to 300 year timescale, but has been accreting at 3.3 mm a^{-1} since 1900. However, the marsh was accreting at very low rates (0.15-0.2 mm a^{-1}) in the conventional pre-*Spartina* period, and much faster rates post *Spartina* (3.3 mm a^{-1}). These relative changes are consistent with other studies (e.g. Long et al 1999). The mid-marsh shows the same pattern, although, as would be expected from a more mature part of the marsh systems, accretion rates are lower (Allen 1990). The maps from 1960 (Figure 2.5(i)) suggest that the Beaulieu site has changed a great deal physically since Spartina appeared, and much of it may have been unconsolidated pioneer marsh or mudflat in the earlier period, with little net vertical accretion. The results from the other two sites are less clear: the lower marshes at Hythe and Marchwood do not appear to have accreted any more rapidly since 1900 than before, although if the earlier date for the APR is taken rates have increased. Changes in Southampton Water may be linked to dredging activity associated with commercial shipping. This will have affected sediment supply, particularly at Bury Farm, Marchwood which is adjacent to a "swinging ground" for large container ships to turn (Associated British Ports 2000).

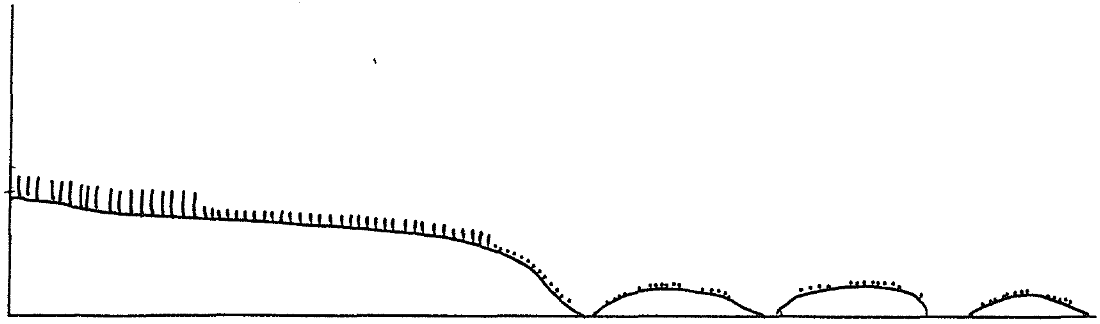
The pattern of increasing accretion rates at Beaulieu, and possible increases at the other sites is therefore consistent with other studies of increasing relative sea levels in Southern Britain in the late Holocene, along with more rapid increases over the last 100 years (Long and Tooley 1995, Cundy and Croudace 1996). However, the exact relationship between short-term saltmarsh accretion rates and sea-level changes is complex, and is complicated by the maturity of the marsh system and *Spartina* "die back" (Gray *et al* 1990). Indeed, the lack of a clear increase in accretion rates in the post-1870 period from Hythe and Marchwood could be a combination of die back (ongoing at these sites), plus the suggested earlier *Spartina* proliferation suggested above (possibly *S. alterniflora* initially), which may have started several decades before the 1900 date derived from ^{210}Pb chronologies. Die back could also explain the horizontal changes at Hythe, where the mudflat area appears to have increased from 1962-1973, which may in part by due to sediment released from marsh erosion (Figure 2.6 (iii)).

Changes in plant communities and zonation

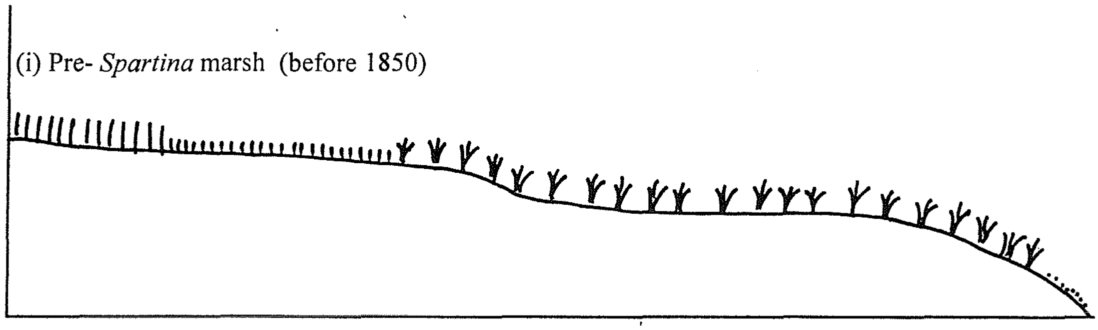
The use of macrofossils for reconstruction of salt marsh palaeocommunities was successful, but with some limitations. The lower marsh sites were generally poor sources of identifiable fossil material (mostly root material was found which cannot be used for reconstruction of surface communities) as roots of some plants (particularly *S. anglica*) can extend over 1m below the surface. However, although the samples were not macrofossil-rich, a largely consistent pattern is shown in the stratigraphy (see below). In addition, the seeds that were the main source of proxy information do not appear to be preserved in a way that is entirely representative of the actual community. For example, very few *Spartina* seeds were found in the samples at any level, although at all sites it is the dominant lower marsh species. This may be either because they are easily broken down (few seeds from any grass species were found compared with, for example, Chenopodaceae, which have a hard surface coat which appears to aid their preservation); or that most seeds are simply rafted away by the tides (large amounts of *Spartina* material can be observed deposited at high marsh levels by autumn and early winter storms). Furthermore, the data suggests more biodiverse communities in recent times, but this could simply be an artefact of the gradual breakdown of the macrofossil material with time.

However, sufficient preserved material was identified to allow reconstruction of the palaeocommunities and to assess changes over the timescales concerned. Figures 2.7 and 2.8 show the macrofossil stratigraphy from the Beaulieu mid and lower marsh cores. Both lower middle marsh data show changes from a pioneer-dominated community in the pre-*Spartina* period to a more mature marsh system with greater biodiversity in the more recent period. This is consistent with Lord Montagu of Beaulieu's evidence to the Royal Commission on Coastal Erosion from 1907 that an unconsolidated marsh system community was much more extensive in the Beaulieu and Lymington marshes; and also that of Groves (1927). The "bulges" in macrofossils from pioneer species (*Salicornia* Spp. and *Suaeda maritima*) do not exactly coincide with the accepted stratigraphic dates for colonisation by *S. anglica* (taken as 1870 on Figures 2.7 and 2.8). However, a larger pioneer community (compared with the present) in the pre-*Spartina* community is indicated. Furthermore, the extension of the "pioneer bulges" into the post-*Spartina* period can be explained by the present-day ecology: *Salicornia* Spp. and *Suaeda maritima* are significant elements of the NVC *S. anglica* community SM6 (Rodwell 2000). Also later *Spartina* die back will have produced gaps for colonisation by pioneers. Furthermore, if we can accept the change to a more diverse community indicated by the macrofossils, this might be explained by the overall expansion of the habitat caused by *Spartina* colonisation. This will have been accompanied by greater spatial diversity with creek edges, pools and disturbed patches and the possible shift to more diverse middle marsh assemblages above the new *Spartina* zone (see below).

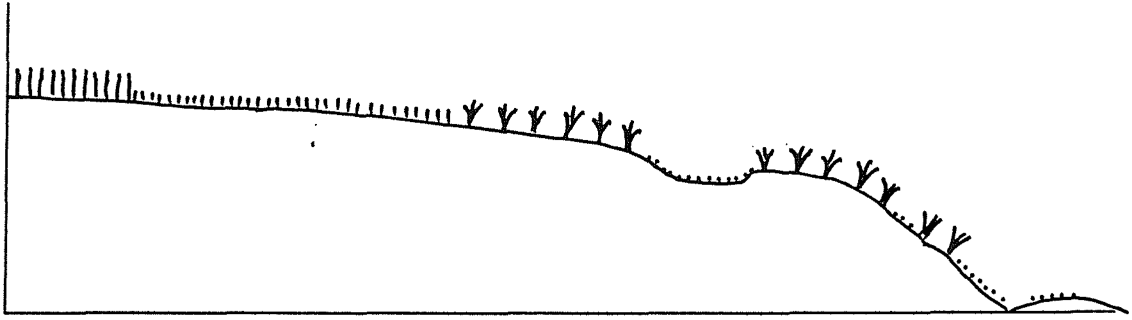
The postulated changes in zonation that have taken place within the framework of the physical changes identified are shown schematically in Figure 2.16. The pre-*Spartina* environment present before *c.*1850 is shown in Figure 2.16 (i). Historical records and maps indicate the extensive pioneer marsh/mudflat system. The exact makeup of the past middle marsh is difficult to discern. Factors such as grazing may have been different then; Bury Farm Marsh was probably used intermittently for cattle grazing in the past (Tubbs 1999). The macrofossil data indicate that broadly the same assemblages were present 150-200 years ago, but the paucity of preserved material prevents any more definite assertions on the community structure. After colonisation (Figure 2.16 (ii)) it is clear from the map data (Figures 2.5 and 2.6) that marsh systems extended horizontally, with a related decline in mudflat. The vertical accretion which accompanied *Spartina* proliferation (Bird and Ranwell 1964) could have reduced the overall tidal exposure of the middle marsh, which will itself have been gradually changing through vertical accretion and succession. It is suggested that the middle marsh limit would gradually have extended up shore (which probably happens anyway in an accreting system, (Pethick 1992)); that the lower limit may have been squeezed by *Spartina* colonisation plus sea-level rise; and that the community may have changed too, in response to these factors and others. The die back stage (Figure 2.16 (iii)), that strictly, is still ongoing, will have been characterised by localised expansions in pioneer habitat. The present day marsh has typically a narrower and more patchy *Spartina* lower marsh than 100 years ago, and a pioneer community which has been squeezed from above by *Spartina* and from below by rising sea levels, and, at Hythe, by erosion.



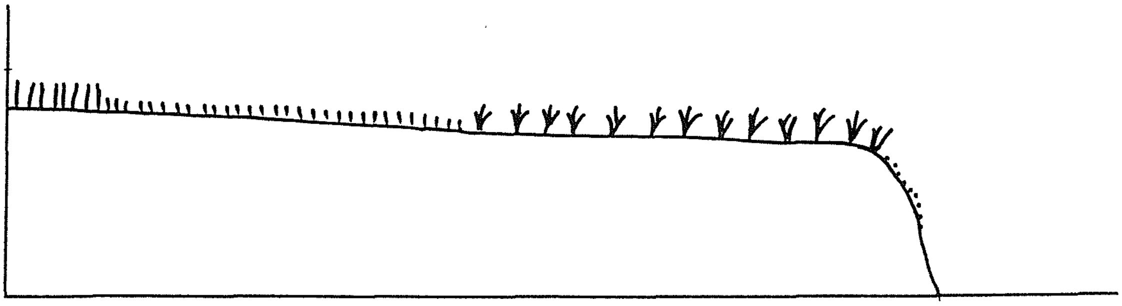
(i) Pre- *Spartina* marsh (before 1850)



(ii) Post colonisation (*c.* 1990)



(iii) Die back phase (*c.* 1940)



(iv) Present day (2001)

||||||||	Upper marsh	ιιιιιιιιι	Middle marsh
Y Y Y Y	*Spartina* marsh	....	Pioneer marsh

Figure 2.16. Schematic diagram of changes in saltmarsh zonation over the last 150-200 years.

Multidimensional scaling analysis of the changes in the palaeocommunities were produced to give additional interpretation of community changes (Figures 2.13-2.15). These reveal some general patterns: there are clear directional changes in palaeocommunity structure as expressed in MDS space in several of the replicate cores (e.g. from the Beaulieu middle marsh cores, Figure 2.13(ii)). Some of the patterns visible on the MDS analyses might relate to the appearance of *Spartina* at the sites. For example, in the Beaulieu middle marsh cores there is clear separation between the surface 0-15 cm (i.e. post-*Spartina*) samples and the deepest 25-35 cm (i.e. pre-*Spartina*) samples. These differences relate to data from the stratigraphic positions of the likely appearance of *Spartina* (in this case at approximately 15.5 cm, based on ^{210}Pb and recorded dates at the site). There is also more variability between replicates from the stratigraphic levels associated with the actual appearance of *Spartina* (10-15 cm and 15-20 cm), possibly reflecting the perturbation of the plant communities (and maybe the spatial variation that accompanied this change) taking place at that period. A similar interpretation of the Hythe middle marsh MDS plot (Figure 2.14 (ii)) is possible. The MDS analysis of the middle marsh cores from Bury Farm, Marchwood (Figure 2.15 (ii)) can be interpreted as showing pre- and post-*Spartina* communities grouped as overlapping but distinct clusters. The groupings of the clusters are consistent with the other stratigraphic data: *Spartina* probably appeared at a time consistent with a stratigraphic level of 21-22 cm, and there is a distinct grouping of all samples from below this level. However, although this interpretation seems consistent with the data I believe that some of the changes suggested by the MDS analysis may be an artefact of the relatively low numbers of macrofossils preserved in these cores and the differential preservation of certain species, rather than community changes themselves.

Development and testing of methodologies

The use of sediment cores for palaeoecological research, and for assessing past trends in relative sea-level is not a new idea, but previous work has tended to rely on single cores and use a single proxy dating technique (e.g. pollen stratigraphy or geochemistry). Although the validity of only using a single core has been tested in terrestrial environments (Turner *et al* 1989) there has been little attempt to validate single core methodologies in intertidal studies. The replicate physical data from this study (stratigraphy radiographs, geochemistry) does appear to largely excuse the use of single core analysis in saltmarsh sediments for geochemical dating, and for producing physical data such as accretion rates.

The same conclusions can be drawn from the palynological data. Lack of replication seems to pose few problems for physical measurements, or for pollen, where a well-mixed "pool" is sampled by the corer. Breakdown, deterioration or bioturbation of pollen grains is a potential problem (Lowe & Walker 1997) (as it is with the macrofossils in this study), but this is likely to be the same in all replicates.

The general community changes that were identified were broadly consistent, and do seem to relate to the changes documented in historical records (see above). However, the macrofossil data did reveal some small differences between replicate cores (macrofossil counts relating to individual species at specific levels in the stratigraphy). For example, core GM1 (Figure 2.7(i)) shows a large *Spergularia* rise at the surface level which did not show up in the replicate cores (GM 2 & GM 3, Figures 2.7 (i) and (iii)). For larger scale biological sampling where variations could be generated by for example, a single seed head being incorporated at a particular point on the marsh surface there are, therefore, potential problems. Some single core data must therefore still be interpreted with some caution, particularly where there is a likelihood of disturbance (e.g. burrowing animals) or reworking of sediments (in mudflat or pioneer saltmarsh, or adjacent to immature creek systems).

The use of multidimensional scaling approaches to interpretation of the macrofossil data did reveal broad community changes, at least based on the macrofossils yielded by the samples. However, as mentioned above, the trends shown must be interpreted with some caution. In almost all of the samples there were more macrofossils (and more species) present in the surface layers compared with the deeper levels in the stratigraphy. Some of the trends visible on these figures could be created by gradual breakdown of biological material rather than by actual changes in past communities.

Limitations

The limitations of the use of macrofossils for community reconstruction in this investigation are discussed in the previous section. Sampling of greater amounts of sediment would have generated more macrofossil material, but this was not possible with the coring equipment used (the modified Russian corer used is a high-volume version of a corer developed for sampling peat bogs). The methods of extraction of macrofossils may be improved: hydrogen peroxide, which was used to deflocculate the clay in the samples, does not, to my knowledge, degrade preserved plant material, and is used as a standard method for this (Long *et al* 1999). It is possible, however, that it could further degrade fragments of material which are already quite broken down and render them unidentifiable. Further information on the breakdown of organic material with depth in cores of this kind (e.g. by loss on ignition) would help interpretation of the community changes which the data seem to indicate.

Additional methods of stratigraphic dating, using appropriate radiochronological techniques (e.g. Caesium-137 or Cobalt-60) would have been useful for interpreting the stratigraphy with greater certainty (Croudace and Cundy 1995). These were not used here, partly because of the additional expense, but also as the stratigraphic relationships between the APR and the ^{210}Pb profile, (plus the further stratigraphic markers such as the rise of *Spartina* itself in the pollen profiles) were considered to be sufficient to validate the information derived.

Further work

The data presented here has raised some important questions about the changes that have taken place in salt marshes in the Southern England over the last 200 years. Further development of methodologies for reconstruction of the past plant communities, using macrofossils and palynology (particularly if it were possible to distinguish with certainty between the pollen of different *Spartina* species), may allow future researchers to shed more light on both the timing and the nature of the transition to a *Spartina*-dominated marsh ecosystem in the Solent region. It would also be useful to explore this important event in other geographical locations to establish whether the changes observed have happened more widely.

Conclusions

This chapter set out to test two related hypotheses:

"Saltmarsh stability before S. anglica *was greater than since."*
The evidence available does not seem to be completely conclusive. Reliable maps are only available as far back as 1850-1870, and the documentary evidence summarised above suggests that *Spartina* (possibly *S. alterniflora* rather than *S. anglica*), was already well–established in some sites. The documentary and experimental evidence does suggest that there was a much larger (and physically unstable) mudflat/pioneer system before *Spartina* became established, and that the appearance of the new species may have stabilised the marsh system (both physically and ecologically). However subsequent die back and sea level rise have resulted in physical destabilisation over the last century, although the changes at the sites investigated here are smaller than documented elsewhere, such as Poole Harbour (Gray and Pearson 1984).

"Community structure and zonation patterns have been disrupted since the establishment of S. anglica*"*
The evidence does suggest a change in community structure (and with it zonation) over the last 200 years in marshes colonised by *S. anglica.* The experimental data supports the historical evidence that an extensive mudflat/pioneer system has been reduced in size and largely replaced with a new plant community, which appears to have stabilised in what is now possibly a more biodiverse system. Other factors (e.g. grazing, changing tidal regimes or weather patterns) are also likely to have contributed to community change.

CHAPTER 3

LOW INTENSITY GRAZING AND BIODIVERSITY ON A SALT MARSH

Introduction

In coastal saltmarsh ecosystems physical factors are widely held to underlie and shape the gross patterns observed as conditions grade from terrestrial to marine (Gray 1992). Biotic factors such as grazing are also recognised as important in shaping their physical, chemical and biological characteristics (Ford and Grace 1998). It has long been recognised that grazers play an important role in determining the composition of plant communities and, in particular, in maintaining their diversity (Tansley and Adamson 1925). Grazing animals can be strong selective agents, choosing palatable and more accessible species or ecotypes; they can also make systems more heterogeneous by maintaining open plant canopies and creating gaps for seedling establishment (Edwards and Gillman 1987). The intensity of grazing has been shown to be important (Reimold *et al* 1975). Grazing at very low intensities does not disturb the equilibrium state (or progress in succession) of the plant community; at the other extreme high intensity grazing, particularly where it forces animals to turn from more nutritious or palatable species to those they would prefer less, seems to reduce diversity (Zeevalking and Fresco 1977).

Both the makeup of the plant community and the physical nature of the plants themselves are effected by grazing animals, particularly when marshes are grazed at high intensities. Two very different types of high intensity herbivory occur: grazing over long periods by domestic animals (typically cattle, sheep or horses) (Ranwell 1961); or seasonally by large numbers of wild animals such as migratory geese (Bazely and Jefferies 1985, 1986; Olff *et al* 1997). In some areas both types of high intensity grazing take place. In the Netherlands, for example, large numbers of overwintering brent geese *Branta bernicla* are able to graze areas where cattle facilitate suitable conditions for them by preventing the dominance of competitive species (Olff *et al* 1997).

High levels of grazing activity can have profound and long-lasting effects on the physical and chemical nature of the marsh and on the salt marsh plant community. Reduction of canopy height by removing biomass alters the light environment, or in the long term maintains an altered light environment (Bakker *et al* 1985, Srivastava and Jefferies 1996, Wilson and Jefferies 1996). This can elevate soil temperature with consequent effects on rates of evaporation and salinity (Crawley 1983, Bertness *et al* 1992, Srivastava and Jefferies 1996, Ford and Grace 1998). 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 grazers are selective (Watkinson *et al* 1993, Olff *et al* 1997). Trampling damages mature plants and directly disrupts seedling establishment, as well as compacting the soil surface, which may also hinder growth of new plants (Reimold *et al* 1975). 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 and 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 and Jefferies 1985, 1986) probably through a combination of changes in the nutrient status 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 (Bazely and Jefferies 1985, Mulder *et al* 1996).

Heavily grazed marshes are typically characterised by a lack of structural diversity and reduced biodiversity as palatable or trampling-intolerant species are usually absent (Bazely and 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 *Festuca rubra*; but with the more typical halophyte species, such as *Plantago maritima* or *Salicornia* spp., largely absent (Beeftink 1979, 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 indeed, thrive, resulting in more diverse plant communities which are not dominated by a single species.

Many saltmarshes 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 south and east England (Gray 1972, Gray and 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*) but usually in lower numbers than in the Netherlands along with resident goose species (e.g. greylag, *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, at least in the UK context, although intense grazing by a single species (geese) has been investigated (e.g. Summers *et al* 1993). Elsewhere in the world attention has usually focused on sites which are grazed intensely by wild animals. In particular, research has focused on the influence of migratory birds such as snow geese (Bazely and Jefferies 1985, 1986) or brent geese (Olff *et al* 1997).

Grazing animals (or their activities) can be considered a 'disturbance' factor, and there may be parallels with Connell's much quoted and widely applied "intermediate disturbance theory" (Caswell 1978, Connell 1978). The applicability of this term to herbivory is itself a subject of some discussion (McGuinness 1987, Bertness 2001, Sousa 2001) (see Chapter 5). Grazers physically disturb plants by consuming them, by trampling on them and by changing their chemical environment (Edwards and Gillman 1987, Bertness 2001). Grazing (or disturbance) on marshes at high intensities produces marshes that are relatively species poor (e.g. in Western Britain) (Gray and Scott 1977b), and those with intermediate levels of grazing (or disturbance) may be expected to be more species rich and more structurally diverse (Zacheis *et al* 2001). Relatively few examples of this are documented: the emphasis of research has been on the impacts of intense grazing. Doody (1992) found, however, that Rockliffe Marsh on the Solway was lightly grazed with a consequently greater structural diversity than other heavily grazed marshes in the region.

Aims

The overall aim of this work was to establish the importance of grazers in marshes that are lightly grazed. This planned to test whether grazers are indeed maintaining the relatively diverse plant communities found at the study site, or whether lack of grazers will lead to long term reductions in biodiversity. This was investigated using experimental exclosures on an area of marsh under light grazing pressure from wild animals.

The specific aim of this experiment was to test the hypothesis that the grazers are acting to maintain these areas of marsh in a particular state and that excluding the grazers will lead to changes from that state. This was achieved by describing and quantifying changes in the plant community when grazers were excluded, by monitoring changes in structure, community composition, biomass and flowering activity.

Specific species were targeted for investigation, in each case testing the null hypothesis that exclusion of grazers did not affect their importance in the community. The species on which the experiment focused were: *Plantago maritima* (*P. maritima* below), which is a palatable species (Bazely and Jefferies 1986, Rowcliffe *et al* 1998 Zacheis *et al* 2001); *Puccinellia maritima* (*Pu. maritima* below), which is a key element of this community and of heavily grazed marshes (Gray and Scott 1977a, 1977b, Beeftink 1979, Rodwell 2000); *Armeria maritima* which is conspicuous in the summer months during flowering but has a low growing habit on these marshes and is not usually grazed (Woodell and Dale 1993); *Limonium vulgare* which is also conspicuous in the summer months during flowering but is also not usually grazed and may be unpalatable (Camp 1999 unpublished); *Salicornia europea* which is a pioneer species which dominates the lowest part of the vegetated saltmarsh but is present in disturbed areas and gaps in the canopy in other zones, and has been shown to be grazed preferentially by brent geese (Rowcliffe *et al* 1998, Rodwell 2000).

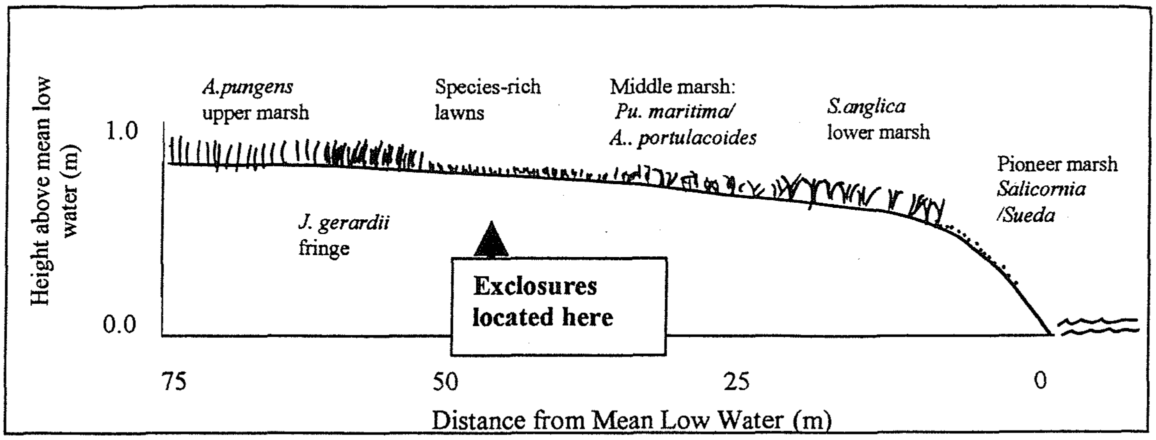
Structural changes and community composition were monitored over the period of the experiment, and the consequent changes in the light environment within the canopy were also determined.

Methods

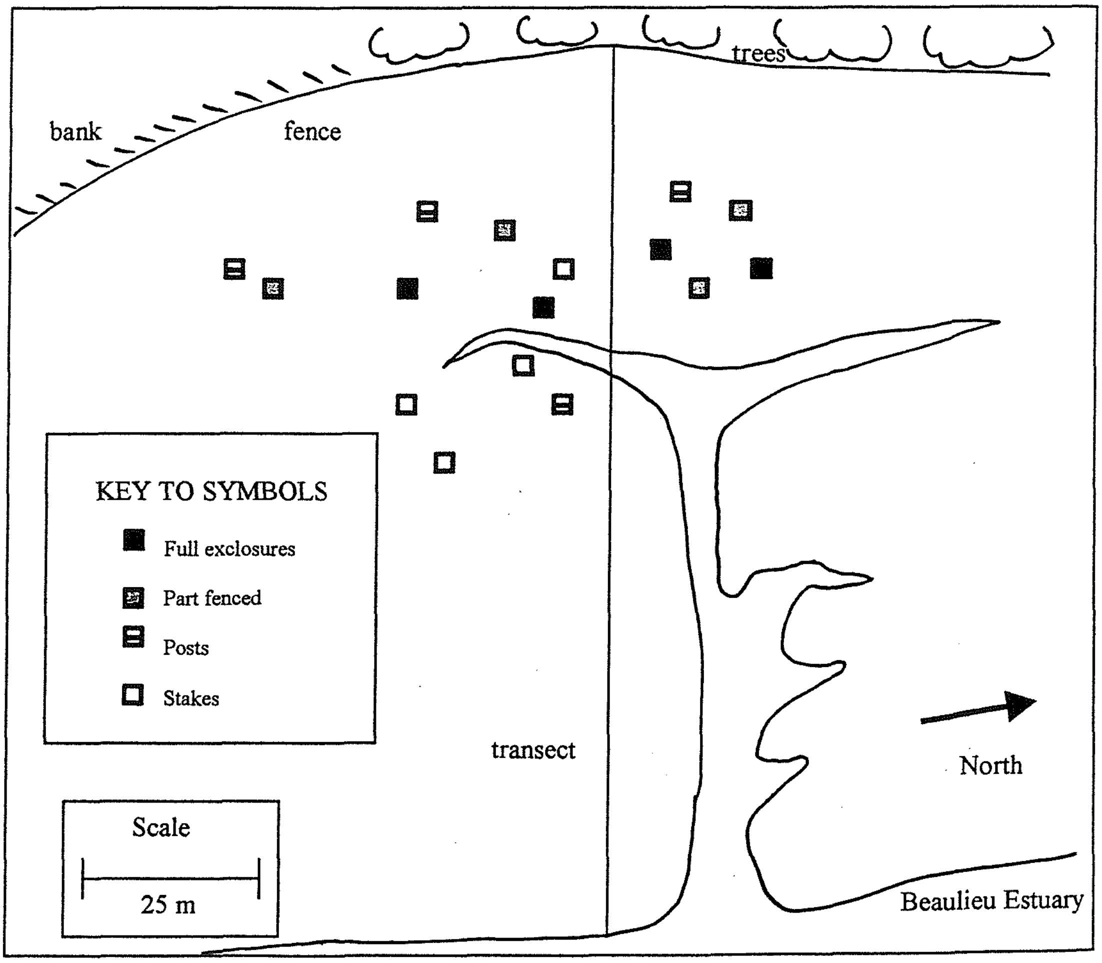
Site Description

The Beaulieu River drains the south-eastern part of the New Forest in Hampshire and is tidal for approximately 10.4km. The Beaulieu Estuary is bordered by extensive salt marshes which are not grazed by domestic animals: they are mainly bounded by woodland enclosures or farmland, and animals of the New Forest Commoners do not generally have access to them. The New Forest is, however, an important site for wild grazing vertebrates including five species of deer, plus rabbits and hares (Putman 1986). The coastal marshes of the New Forest are of international importance for wildfowl, including small numbers of bird species that graze on coastal marshes, such as resident greylag geese (*Anser anser*), the introduced resident Canada geese (*Branta canadensis*) and larger numbers of over-wintering brent geese (*Branta bernicla*) (Burges 2000).

The experimental exclosures which form the basis of this study were constructed on Gins Marsh (Grid Reference SZ 415984; for location maps see Chapter 2, Figure 2.2), which is a mature salt marsh showing 'typical' zonation from a *Salicornia* pioneer zone at the water's edge up to a mature *Agropyron pungens* zone grading into oak woods beyond (Figure 3.1(i)). Just below the *A. pungens* upper marsh zone and the *Juncus gerardii* fringe below it there is a narrow (10-20m wide) band of relatively species rich vegetation that is a maintained as a low growing species rich *Puccinellia maritima* lawn all year round. It is not dominated by any single species but is notable for the density of flowering *Armeria maritima* and *Limonium vulgare* in the early summer (Appendix 3.1, Plate 1). This mid-marsh community could be classified as SM13c, SM13d in the National Vegetation Classification (Rodwell 2000). The activity of grazing animals in the species rich lawns is evident through the presence of faeces from rabbits, deer and wild birds, surface scrapes, mounds for rabbit droppings, and occasional sightings.



(i) Zonation transect of Gins Marsh



(ii) Location of grazing exclosures on Gins Marsh Beaulieu

Figure 3.1 Experimental site maps.

Field experiments and data collection.

In June 1996 four exclosure plots (2.5m x 2.5m) were constructed using 5cm mesh chicken wire and four 1.5 m high wooden fence posts (referred to as exclosures or abbreviated as "Ex" in the descriptions of the results chapter). The wire was dug into the turf to a depth of 0.1m to exclude burrowing animals. Diagonal cross strings were placed between tops of the fence posts to prevent birds landing in the exclosures and to deter deer from jumping in or leaning over the fencing. Three control treatments were established (four replicate plots of each type,): open fenced controls, consisting of four wooden fence posts, fencing on two opposite sides of each plot and cross strings (referred to as part-fenced or "Pf" below); open controls, consisting of four fence posts only (referred to as posts or "Po" below), marked plots using short wooden stakes pushed in to ground level (referred to as stakes or "St" below). These were arranged randomly within the species rich lawns at the study site (Figure 3.1(ii)). During construction of the exclosures care was taken to avoid trampling within the plots, and no data were gathered from a 0.25cm margin adjacent to the edge of each plot to ensure that any disturbance during construction did not affect the data gathered.

Grazing pressure was monitored regularly (monthly where possible) by counting animal droppings in each plot as a measure of the presence of animals. Owen (1971) suggested that as European white-fronted geese (*Anser anser albifrons* Scopoli) defecate every 3.5 minutes, counting droppings is a reliable proxy measure of grazing activity. Droppings cannot easily be sourced in the field to species, so they were broadly categorised as "rabbit" (which might include hares), "bird" (which is likely to be mainly geese but might include ducks) and "deer" (which is likely to be roe deer, although other species are present in the area. At each visit canopy height in each plot was measured at five random points in each plot.

In July 1996 and July 1998 plant surveys of each plot were taken at nine points in 10 random 10cm quadrats (cross-strung) in each plot, with each species present at each point in the upper (10cm or above) the middle (1-10cm) and the lower (0-1cm) recorded. This approach was chosen to quantify structural changes in the plant canopy, which a simple field-based percentage cover approach would not have detected. For clarity of presentation the data are presented as percentages in each canopy level. It was important to investigate at this level of detail to examine the key species sufficiently. The above-ground structure of the plant community is complex and investigating the role of herbivores in this structuring was one of the aims of the experiment. *P. maritima* and *L. vulgare* are major components of the middle canopy; *Pu. maritima* is present in both middle and lower canopies; *A. maritima* is low-growing and only a significant component at ground level; *S. europea* is also low-growing in this part of the marsh. Total counts of flowers of *A. maritima, P. maritima,* and *L. vulgare* were made at the approximate flowering maxima for each species in 1998 and 1999, as these were the most conspicuous flowering species, and also had a clearly defined flowering period compared with, for example *Pu. maritima* and *Salicornia* spp. which continue to flower over most of the summer season. Due to the taxonomic difficulty of identifying the *Salicornia* genus in the field, particularly where it is low-growing in grazed areas, species level identification was not attempted in this study: it is referred to as *Salicornia* below. Total numbers of all flowers of those species selected present, of those species selected, in July 1998 and 1999 were also recorded.

Light levels were recorded using a LT Lutron LX-101 Digital Lux Meter. Readings were between 12.00 and 15.00 during unbroken sunshine at ground level and above the canopy at 10 points in each plot.

Standing biomass was harvested from four randomly selected, 10x10cm squares within each plot in August 1998. Sampling of biomass was destructive and was therefore not possible at time zero (1996). Harvested plant material was washed through a sieve, dried at 70°C to constant weight and then sorted to species and weighed.

Analysis of data

Data were analysed using Microsoft *Excel*, SPSS *Sigmastat* 2.0 and GMAV5 for Windows (Underwood and Chapman 1998). Figures were created using Microsoft *Excel* and SPSS *Sigmaplot* 4.0.

Grazing pressure (faecal counts) was analysed by Kruskal Wallis non-parametric one way ANOVA (using SPSS *Sigmastat* 2.0) on selected periods following construction of the experimental plots. Cochran's Test (see e.g. Underwood 1997, *Experiments in Ecology*, pp. 183-4) was applied prior to all analyses of this kind to check for suitable homogeneity of variances: the grazing pressure data were not suitable for parametric tests even when transformed. Where significant differences between treatment types were indicated by the Kruskal Wallis one way ANOVA, a *post hoc* Dunn's Test was used to evaluate differences between individual treatments. The experimental period was subdivided for analysis into: winter 1996/7, summer 1997, winter 1997/8, summer 1998, winter 1998/9 and summer 1999. Winter was taken to be October to March, summer was taken to be April to September. These periods broadly coincide with the growing/non-growing seasons for the plants, and with the presence or absence of wintering birds in the region. Data were analysed from three randomly selected months in each period.

Canopy structure (height) and community composition (percentage covers and above ground biomass) were analysed (using GMAV5) by nested ANOVA. Student-Newman-Keuls (SNK) Tests (Underwood 1997 pp. 378-80) were applied *post-hoc* to investigate differences between individual elements of the experiment (e.g. different treatments) when significant differences were indicated. Tests were applied where possible to untransformed data. In some cases transformation (e.g. log x+1 for numbers, or arcsine for proportions) was necessary to fulfil the requirements of ANOVA for homogeneity of variances (see e.g. Underwood 1997, pp. 223-224). Where possible, transformation (when used) was applied uniformly across all related data sets (e.g. biomass) to ensure consistency, but this could not be always be applied uniformly across some related data sets as it rendered some of the data too heterogeneous for use of ANOVA.

Biomass data were also analysed using a number of indices as follows:

Margalef Species Richness $d= (S-1)/LOG (N)$

(Where S is the number of species, N is the total number of individuals)

Shannon-Wiener Diversity $H^I= -\Sigma(P_i*LOG_e(P_i))$

Where P_i is the proportion of the *i*th species.

Pielou's Evenness $J^I= H^I /LOG (S))$

H^I is Shannon-Wiener diversity and S is the number of species.

Use of these indices are reviewed in detail by Spellerberg (1991, *Monitoring Ecological Change,* Chapter 6)

Flowering density of whole plots was analysed by one way analysis of variance (ANOVA) (using SPSS *Sigmastat* 2.0) with Tukey Tests applied *post-hoc.* Flowering and community data was also analysed using PRIMER (Plymouth Routines in Multivariate Ecological Research). Hierarchical agglomerative cluster analysis was performed to show the more complex changes that were taking place. This can show 'natural groupings' of samples, by placing those that are more similar to each other closer together in multidimensional space compared with those that are less similar (Clarke and Warwick 1994). The data were analysed using the Bray-Curtis similarity measure, which generates a dendrogram that is used as the basis for the computation of the multidimensional scaling (MDS) algorithm. The MDS algorithm aims to minimise distortion (or "stress") between the similarity rankings in the dendrogram and the distances between data points in "MDS space". Acceptable stress values lie between 0.01 (i.e. a perfect representation of the dendrogram data) and 0.2 (i.e. a potentially useful two-dimensional picture) (Clarke and Warwick 1994).

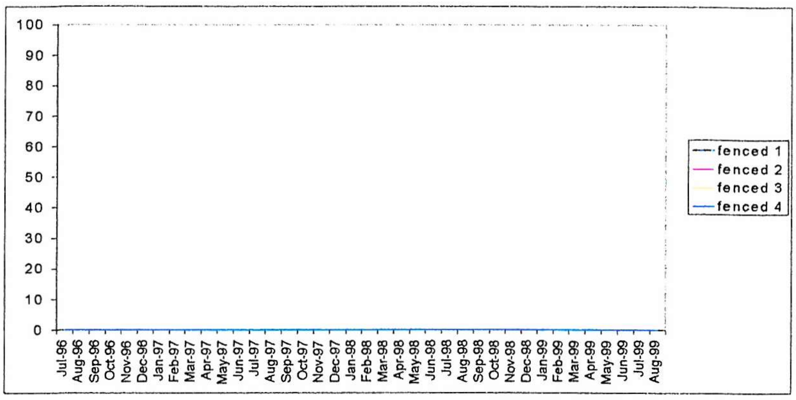
Results

Grazing pressure

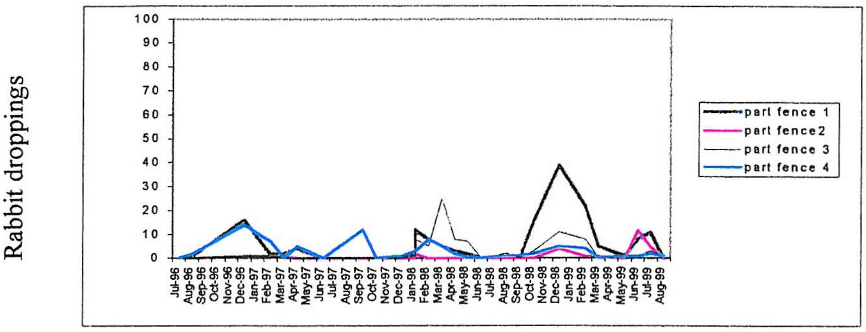
The monthly faecal counts over the period of study are shown in Figure 3.2 (rabbits) and Figure 3.3 (birds). There was no evidence that grazers had entered the experimental exclosure plots: no droppings at all were recorded in them at any sampling visit. However, the control plots had been visited regularly by rabbits and birds, although droppings were not found in all control plots at every visit, indicating considerable spatial or temporal variability in grazing pressure. Very few deer faeces were found although footprints on this marsh were observed regularly. This makes the relative importance of grazing by deer hard to evaluate.

For grazing pressure by rabbits (Figure 3.2), a Kruskal Wallis non-parametric one-way ANOVA on Ranks, showed a significant or highly significant difference between treatment groups in each of all the periods analysed (winter 1996/7 summer 1997, winter 1997/8, summer 1998, winter 1998/9, summer 1999) (Table 3.1). Pairwise multiple comparison procedures (Dunn's Test) revealed that there were differences ($P<0.05$) between the exclosure treatments and all of the controls in winter 1996/7, winter 1998/9 and summer 1999, but could not resolve the differences completely in the other periods. There were no significant differences revealed between the three control treatments.

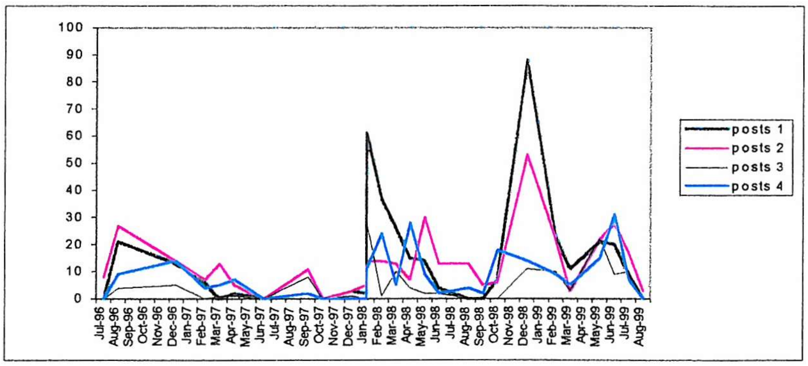
The bird dropping data (Figure 3.3) also showed a significant or highly significant difference between groups (Table 3.1). Dunn's Test showed that the exclosure treatments were significantly different ($P<0.05$) from the three control treatments in winter 1998/9 and summer 1999, and also showed that the stakes controls were significantly different ($P<0.05$) in winter 1997/8. This was the only occasion when a difference of this kind was found. Tests did not fully resolve the differences between treatment types in the other periods but usually showed the exclosures to be different from two of the three control treatments.



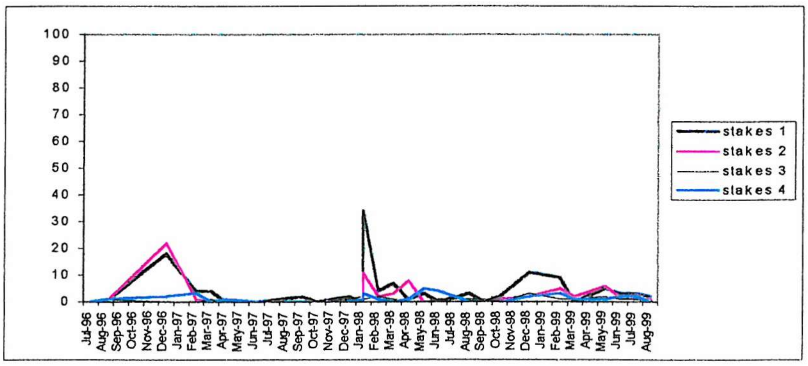
(i) Exclosure



(ii) Part fenced

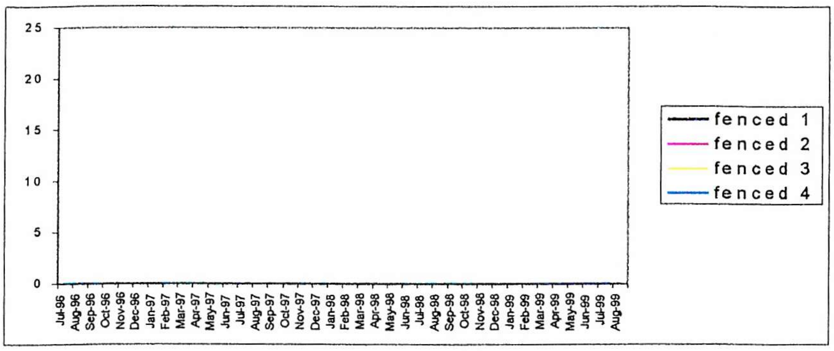


(iii) Posts

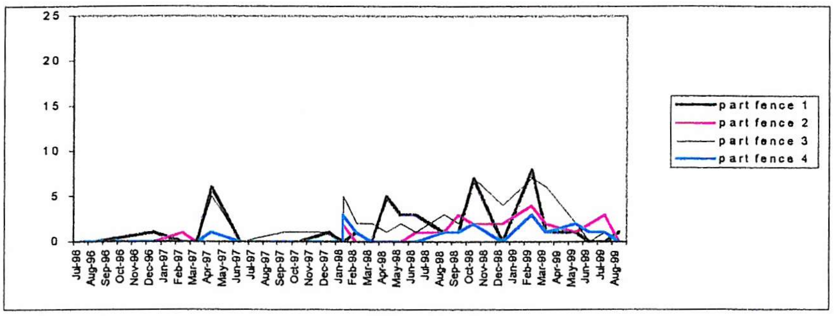


(iv) Stakes

Figure 3.2. Monthly grazing pressure by rabbits (faecal counts per plot at each visit) on exclosure treatment plots. Gins Marsh, Beaulieu, July 1996- August 1999.



(i) Exclosure



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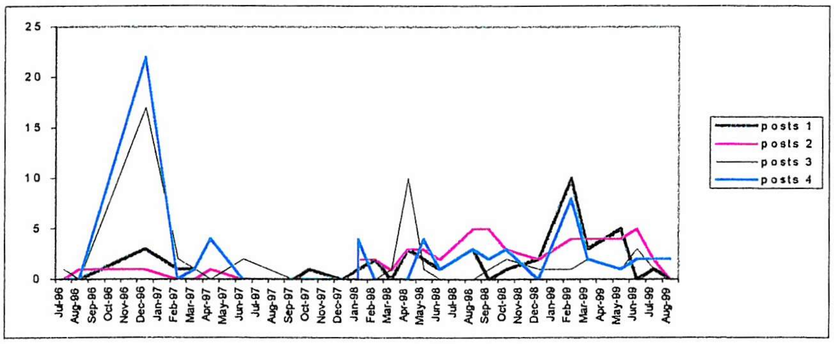
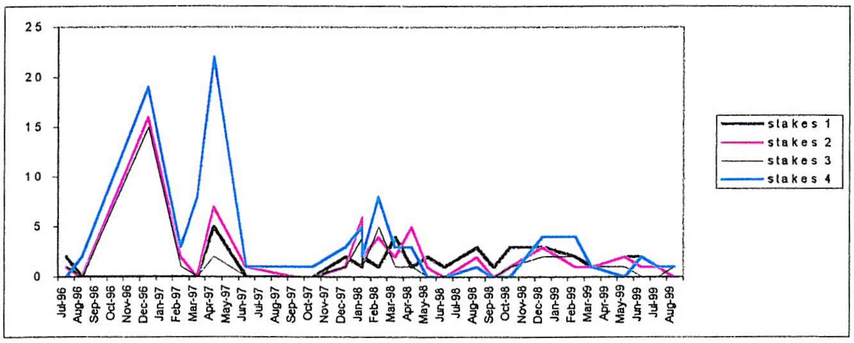


(iii) Posts



(iv) Stakes

Figure 3.3. Monthly grazing pressure by birds (faecal counts) on exclosure treatment plots. Gins Marsh, Beaulieu July 1996- August 1999.

Table 3.1. Analysis of grazing pressure by season (Kruskal Wallis non-parametric one way ANOVA) in grazing exclosures established in June 1996; based on monthly counts of faeces in treatment plots. Gins Marsh, Beaulieu. Data are untransformed.

Grazing pressure (faecal counts)	**Winter 1996/97**		**Summer 1997**		**Winter 1997/8**		**Summer 1998**		**Winter 1998/9**		**Summer 1999**	
	DF	**H**	**DF**	**H**	**DF**	**H**	**DF**	**H**	**DF**	**H**	**DF**	**H**
Rabbits	3	18.5 ***	3	9.4 *	3	29.3 ***	3	19.0 ***	3	26.9 ***	3	22.0 ***
Birds	3	19.2 ***	3	14.34 **	3	21.4 ***	3	19.9 ***	3	29.4 ***	3	38.0 ***

* Denotes significance at $p<0.05$; ** denotes significance at $p<0.01$; ***denotes significance at $p<0.001$. Each season's analysis based on three randomly selected months' data.

The data indicated that the exclosures were fully effective in deterring grazing animals, although the use of the three groups of control treatment was patchy there were no significant differences in the grazing pressure between the three control treatments. The only exception being the grazing of the stakes controls in winter 1997/8 by birds: this was significantly different from the other treatments and controls in this period, but in the context of the full time period of the experiment this is probably of little importance.

Canopy structure

The physical structure of the plant community was changed by the exclusion of grazing animals. Figure 3.4 shows mean canopy height over the experimental period. Structural changes quickly developed in the absence of grazers. There was a rapid separation in height between the exclosure treatments and all three controls, and this persisted through seasonal changes after the first year. The level of separation increased with each growing season.

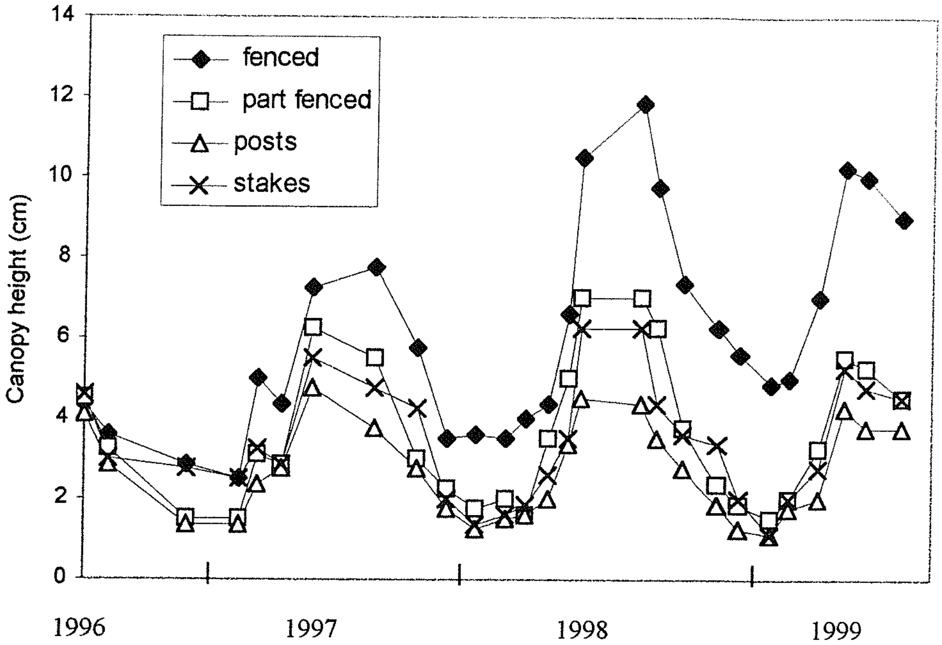


Figure 3.4. Mean canopy height on grazing exclosures, Gins Marsh, Beaulieu, July 1996- August 1999. Data points are pooled means (n=20) of random measurements within experimental plots.

Table 3.2. Analysis of changes in canopy height in grazing exclosures established in June 1996, Gins Marsh, Beaulieu. Nested analysis of variance, n=4 plots. Data are untransformed (Cochran's Test p<0.01).

Source	**DF**	**MS**	**F**	**Calculation of F**
se	1	50.1573	No test	
ye	2	205.4604	No test	
mo(seXye)	12	64.8647	27.68	pl(tr)Xmo(seXye)
tr	3	616.1319	No test	
pl(tr)	12	9.4710	4.04	pl(tr)Xmo(seXye)
seXye	2	1375.8573	No test	
seXtr	3	125.6349	No test	
seXpl(tr)	12	5.7373	2.45	pl(tr)Xmo(seXye)
yeXtr	6	33.1740	No test	
yeXpl(tr)	24	4.2815	1.83*	pl(tr)Xmo(seXye)
trXmo(seXye)	36	4.9.79	2.09	pl(tr)Xmo(seXye)
pl(tr)Xmo(seXye)	144	2.3436	6.69	res
seXyeXtr	6	29.6272	No test	
seXyeXpl(tr)	24	4.4821	1.91	pl(tr)Xmo(seXye)
RES	152	0.3505		
TOT	439			

* Denotes significance at p<0.05; ** denotes significance at p<0.01; ***denotes significance at p<0.001.
The model for this analysis is : X = MEAN + se + ye + mo(seXye) + tr + pl(tr) + seXye + seXtr + seXpl(tr) + yeXtr + yeXpl(tr) + trXmo(seXye) + pl(tr)Xmo(seXye) + seXyeXtr + seXyeXpl(tr) + RES
(Se = season, ye = year, mo = month, tr = treatment, pl = plot)

It was not possible to resolve between-year or between-season differences statistically (Table 3.2). However, month-by-month analysis shows that the differences between treatments developed rapidly and that these differences were, for the most part, sustained. In the second month of the winter season of the first year (winter 1996-7) very significant differences between treatments had developed (SNK procedure, p=0.0106), with the canopy height in the exclosures significantly different from the three controls. In the first part of the following growing season (summer 1997), there were no differences between treatments for the first two months, but after that time the differences were established, with the exclosures differing from the controls in seven of the nine months tested from summer 1997 to winter 1998-9. In the other two months SNK tests also indicated that the exclosures were different from most of the controls, but the tests could not fully resolve those differences.

Community structure and composition

Figure 3.5 shows the total above ground biomass from the harvests of summer 1998. Biomass appeared to increase when grazers were excluded: the exclosures had a higher mean above ground biomass (see below) compared with all of the controls. Nested ANOVA shows that the differences between treatments are highly significant (P=0.0001) Multiple comparison procedures (SNK Test) show that the exclosure treatments were significantly different from all three controls, but no significant differences between control treatments (SNK test, p<0.05, Ex<Pf=Po=St).

The overall changes in the above ground biomass are reflected in the MDS plot (Figure 3.6). This shows distinct clusters based on the mean biomass of each species from the harvests in each plot. The exclosures are clustered near the centre of the plot and the part fenced controls are clustered nearby but separately. The other controls are distributed more randomly in MDS space.

There were broad trends apparent in the diversity of the plots harvested in summer 1998 (Table 3.3). There are also generally lower levels of species richness and species diversity in the exclosures compared with the controls. The differences in species richness (Margalef) are significant (p=0.028), although differences between individual treatment types could not be resolved fully by a *post-hoc* Tukey Test. The differences in Shannon-Wiener Diversity are not statistically significant (one way ANOVA). There are no changes apparent in the overall number of species (11-12 in the exclosures; 10-12 in the controls), so the changes are largely structural.

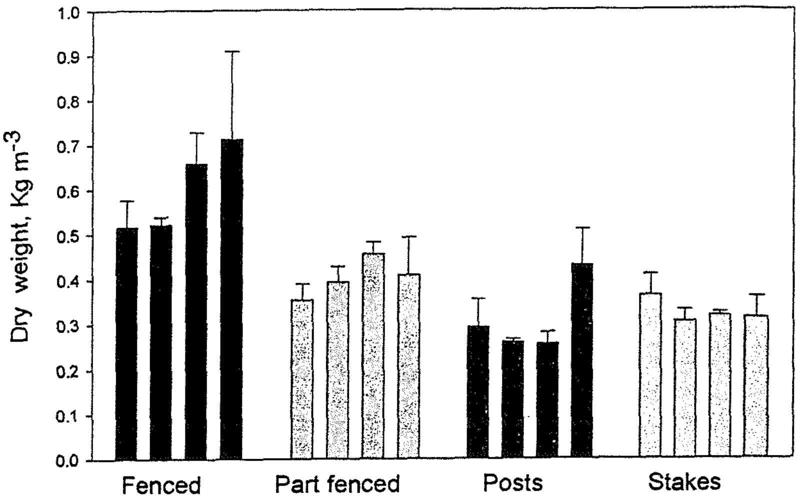


Figure 3.5. Total above ground plant biomassfrom grazing exclosure plots, Gins Marsh, Beaulieu. Plots established July 1996, harvested August 1998 (n=4, bars represent +1 standard error.

Figure 3.6. Multidimensional scaling plot of above ground plant biomass data, from above ground biomass harvests (August 1998) of plots within experimental exclosures; Gins Beaulieu.

Table 3.3. Diversity analysis of mean above ground biomass data from 1998 harvests; exclosure plots, Gins Marsh , Beaulieu.

Plot	**Total species**	**Total mean biomass**	**Species Richness (Margalef)**	**Shannon-Wiener Diversity**	**Pielou's evenness**
Fenced 1	11	5.2	6.1	1.58	0.658
Fenced 2	12	5.2	6.66	1.51	0.607
Fenced 3	12	6.6	5.84	1.42	0.571
Fenced 4	12	7.1	5.6	1.77	0.713
Part fenced 1	12	3.5	8.7	1.64	0.662
Part fenced 2	11	3.9	7.29	1.46	0.61
Part fenced 3	10	4.6	5.94	1.49	0.649
Part fenced 4	11	4.1	7.1	1.47	0.613
Posts 1	11	2.9	9.31	1.77	0.737
Posts 2	11	2.6	10.5	1.49	0.623
Posts 3	11	2.6	10.7	2.07	0.864
Posts 4	10	4.3	6.16	1.57	0.68
Stakes 1	10	3.6	6.97	1.57	0.68
Stakes 2	11	3.1	8.95	1.92	0.8
Stakes 3	11	3.2	8.63	1.84	0.768
Stakes 4	12	3.1	9.63	1.68	0.675

Changes in individual species: percentage cover, biomass and flowering

1996 community data in this section were gathered at the time of construction of the treatment plots (i.e. time zero); and the 1998 data were gathered after three growing seasons.

Plantago maritima

P. maritima appears to proliferate in the absence of grazers, which suggests that they are suppressing its growth at the study site. Figure 3.7 ((i) and (ii)) shows the mean amount of *P. maritima* in the mid-canopy in 1996 and 1998: there were no differences between treatment groups in 1996 (Nested ANOVA, p=0.5397) but the amount of *P. maritima* was greater in the exclosure plots in 1998. Nested ANOVA showed that there were significant differences in the cover of *P. maritima* between treatments in 1998 (nested ANOVA, p=0.0306). Cover was variable however, so the individual differences between treatment types was not fully resolved by multiple comparison procedures (SNK test). *P. maritima* biomass is generally greater in the exclosure plots compared with the controls, although there is an intermediate change in the part fenced controls (Figure 3.7 ((iii)). Nested ANOVA showed that there was a significant difference in the

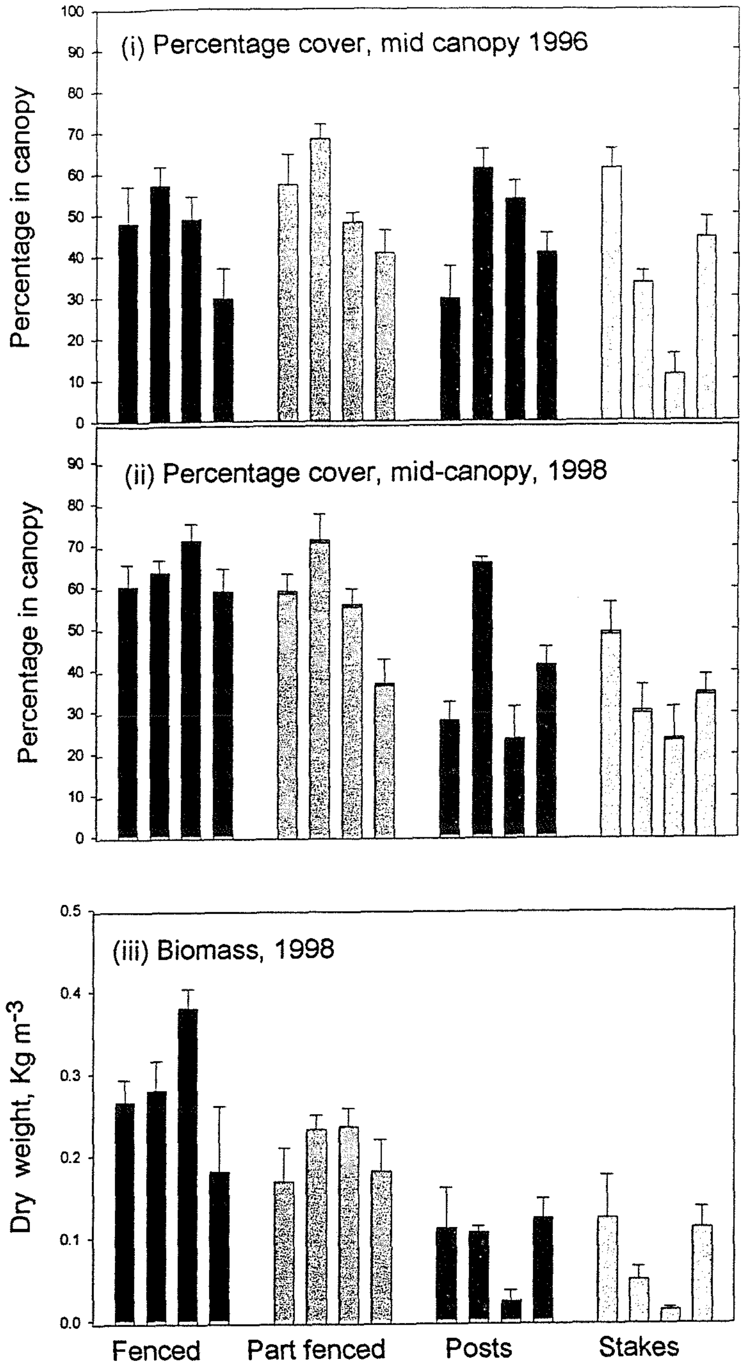


Figure 3.7. *P.maritima* in experimental grazing exclosure plots established July 1996, Gins Marsh, Beaulieu.
(i) percentage cover in mid canopy , field survey July 1996,(n=10), (ii) percentage cover in mid canopy, field survey July 1998, (n=10), (iii) Above ground biomass from harvests in August 1998 (n=4), bars represent +1 standard error.

biomass of *P. maritima* between treatment plots (p=<0.002). Multiple comparison procedures showed no significant difference between the fenced treatment plots and the part fenced controls; and no significant difference between the posts and stakes controls. However there were significant differences between these two groups (exclosures and part fenced vs. posts and stakes) (SNK test, p< 0.05, Ex=Pf>Po=St). *P. maritima* normally flowers at very low levels on this part of the marsh, but by 1998 there was a highly significant increase in flowering observed when grazers were excluded compared with all controls (Kruskal Wallis non parametric one way ANOVA, p<0.0001; SNK test, p< 0.05, Ex>Pf=Po=St). Although *P. maritima* appears to proliferate when grazers are excluded, which suggests that they are suppressing its growth at the study site, the data do not demonstrate this conclusively. There were however, significant changes to flowering levels in this species (Figure 3.8).

Puccinellia maritima

Pu. maritima appears to proliferate when grazers are excluded: these changes were largely structural: *Pu. maritima* appears to grow higher and thus becomes a larger component of the middle canopy, thereby producing greater biomass. Figure 3.9 ((iii) and (iv)) shows the mean percentage of *Pu. maritima* in the middle canopy of the exclosure treatments in 1996 and 1998. In the middle canopy there were no differences between treatment groups in 1996 (nested ANOVA, p=0.3805) although there were some large differences between individual plots. In 1998 there were also no significant differences between treatment plots (nested ANOVA, p=0.4915) although the exclosure plots and the part fenced control plots showed more variability than the posts and stakes control plots. In the lower canopy (Figure 3.9 ((i) and (ii)) the mean percentage of *Pu. maritima* did not vary between treatment types in 1996 (nested ANOVA, p=0.1638). In 1998, however, there were significant differences between treatment types (nested ANOVA, p=0.0197). There were differences between the stakes controls and the full exclosures but the SNK test overall was inconclusive. Figure 3.9 (v) shows the above ground biomass of *Pu. maritima*: this is generally greater in the exclosure plots compared with the controls, Nested ANOVA showed that there was a significant difference in the biomass of *P. maritima*

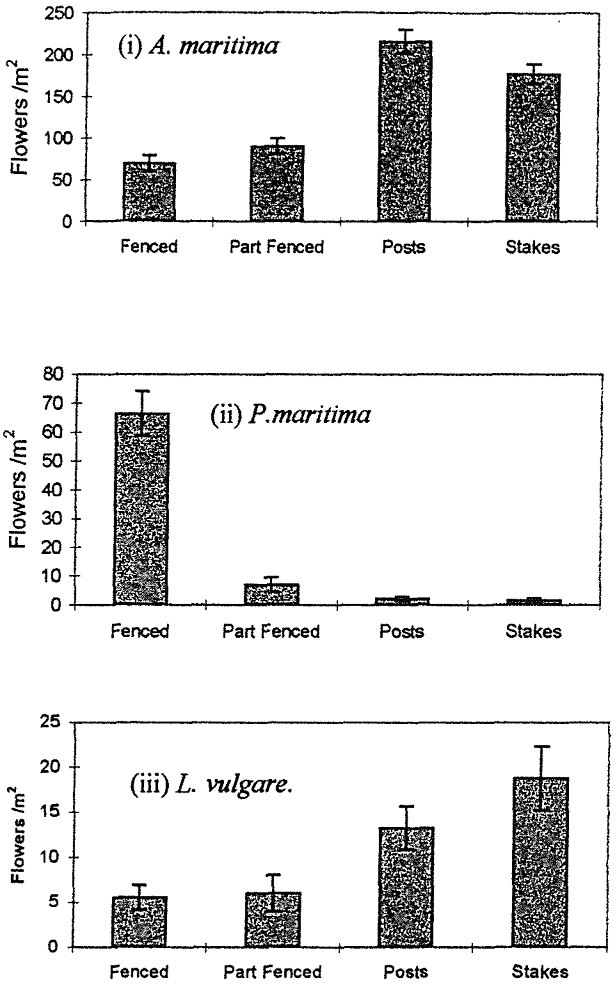


Figure 3.8. Total flowers in grazing exclosures, Gins Marsh , Beaulieu, July 1998 (n=4, error bars = +/- one standard error). (i) *A. maritima* (ii) *P. maritima* (iii) *L. vulgare.*

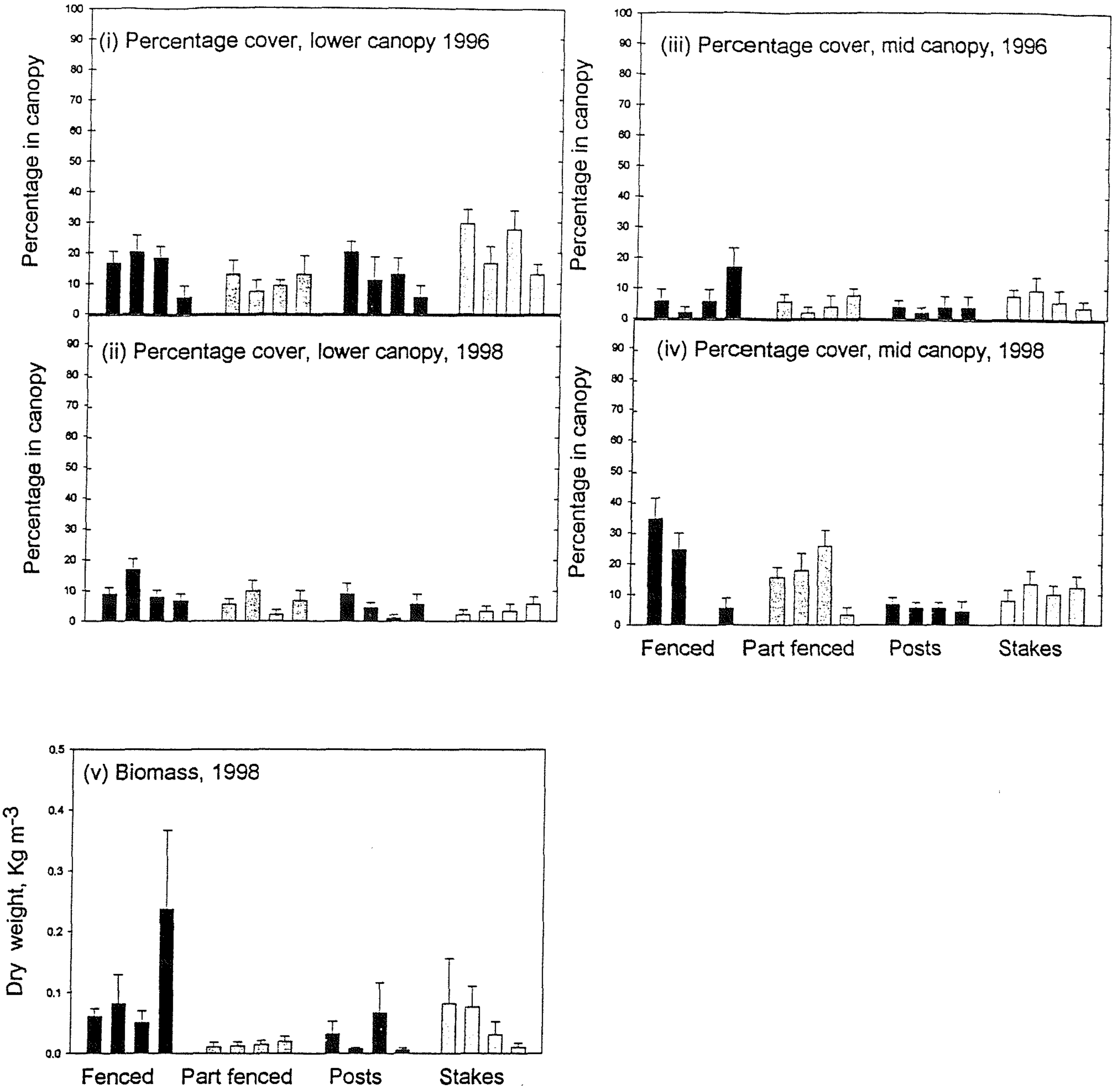


Figure 3.9 *Pu maritima* in experimental grazing exclosure plots established July 1996, Gins Marsh, Beaulieu.
(i) percentage cover in lower canopy , field survey July 1996,(n=10), (ii) percentage cover in lower canopy, field survey July 1998, (n=10), (iii) percentage cover in mid canopy , field survey July 1996,(n=10), (iv) percentage cover in mid canopy, field survey July 1998, (n=10), (v) Above ground biomass from harvests in August 1998 (n=4). Bars represent +1 standard error.

between treatments plots (p=<0.0257). Multiple comparison procedures (SNK test) could not fully resolve the differences between treatment types.

Armeria maritima

Figures 3.10 (i) and (ii) shows the mean percentage of *A. maritima* in the lower canopy of the exclosure treatments in 1996 and 1998. Exclusion of grazers appears to reduce the amount of this species in the plant community although differences are not clearcut: clear patterns may be difficult to demonstrate because of spatial variability. There were no differences between treatment groups in 1996 (nested ANOVA, p=0.5735) but the amount of *A. maritima* was reduced in the exclosure plots in 1998. There were significant differences in the amount of *A. maritima* between treatments (nested ANOVA, p=0.0129). The individual differences between treatment types were less clear and were not fully resolved by an SNK test. However, this procedure did indicate that the stakes and posts controls were different from the exclosures but not from the part fenced controls. Additionally, the part fenced controls themselves were not significantly different from the fenced exclosure treatment plots. Figure 3.10 (iii) indicates that the above ground biomass of *A. maritima* was reduced in the exclosure treatments in 1998, but these differences were not statistically significant (nested ANOVA, P=0.137). There were reductions in flowering of *A. maritima* (Figure 3.8 (i); Appendix 3.1, Plate 1 and 2). Flowering density in the exclosures was significantly reduced compared with the control treatments (one way ANOVA, p<0.001). Flowering also declined less in the part fenced controls, which suggests the effects of the grazing animals in these controls were at an intermediate level between the fully exclosed treatments and the other two controls (Tukey Test, p<0.05, Ex<Pf<Po=St).

Limonium vulgare

Figures 3.11 (i) and (ii) shows the percentage of *L. vulgare* in the mid-canopy of the exclosure treatments in 1996 and 1998. Changes in this species following exclosure appear to be minor: exclusion of grazers may produce minor structural changes but no overall change in plant growth. There were no differences between treatment groups in 1996 (p=0.3560). The amount of *L. vulgare* in the mid-canopy seemed to be reduced in 1998 compared with the controls (Figure

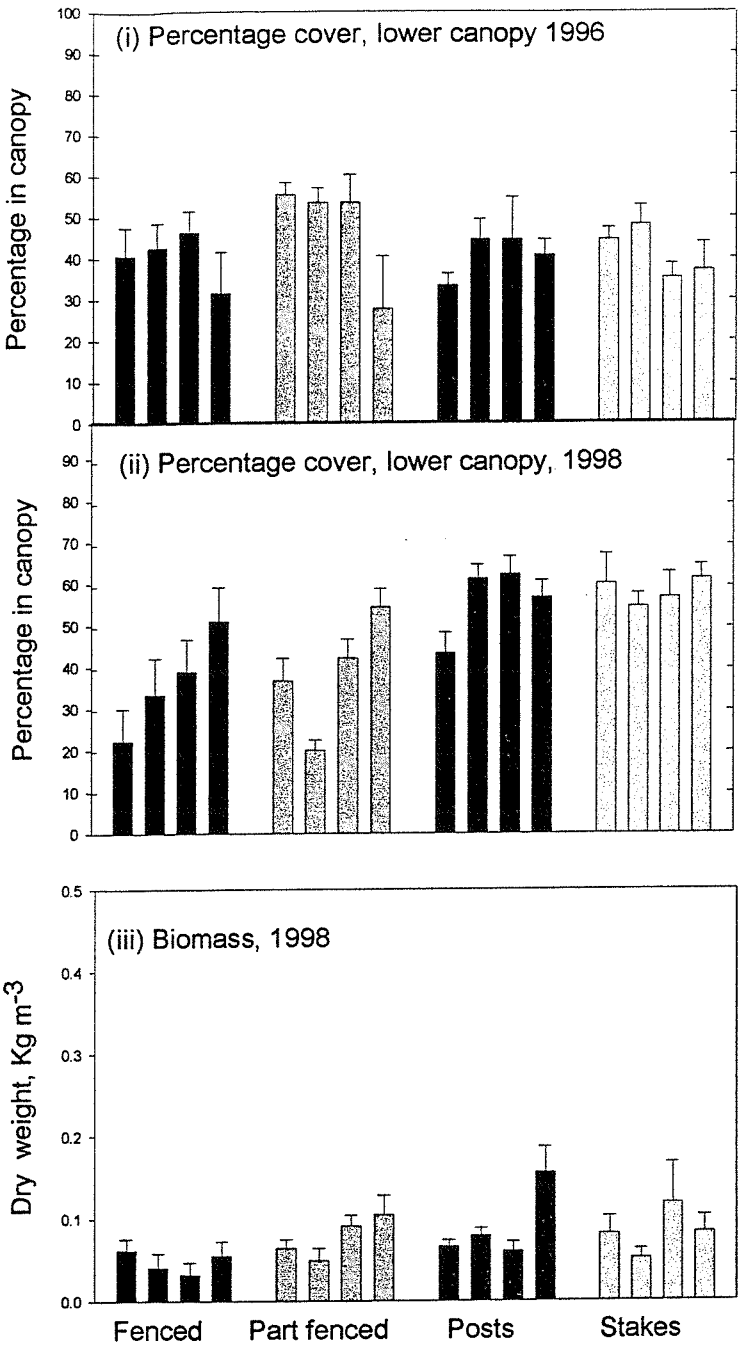


Figure 3.10. *A. maritima* in experimental grazing exclosure plots established July 1996, Gins Marsh, Beaulieu.
(i) percentage cover in lower canopy , field survey July 1996,(n=10), (ii) percentage cover in lower canopy, field survey July 1998, (n=10), (iii) Above ground biomass from harvests in August 1998 (n=4), bars represent +1 standard error.

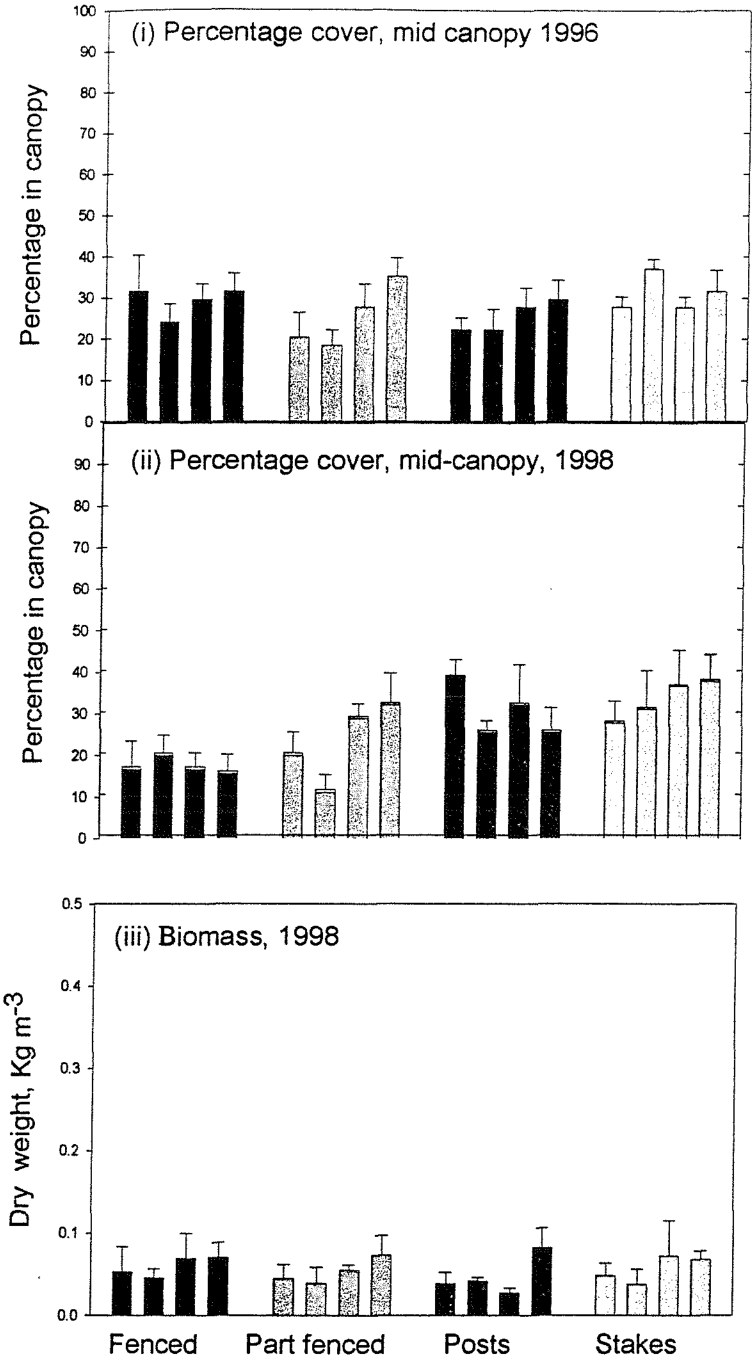


Figure 3.11. *L. vulgare* in experimental grazing exclosure plots established July 1996, Gins Marsh, Beaulieu.
(i) percentage cover in mid canopy , field survey July 1996,(n=10), (ii) percentage cover in mid canopy, field survey July 1998, (n=10), (iii) Above ground biomass from harvests in August 1998 (n=4), bars represent +1 standard error.

3.11 (ii)), and there were significant differences between treatments (Nested ANOVA, p=0.0476), but SNK tests could not fully resolve differences between treatment types. Figure 3.11 (iii) show the above ground biomass of *L. vulgare*: there are no differences between treatment types (Nested ANOVA, p=0.7856). There was a significant reduction in flowering density of *L. vulgare* in the exclosure plots (Figure 3.8 (iii)) (Kruskal Wallis non parametric one way ANOVA, p<0.001). As in the case of *A. maritima,* flowering density in the part fenced controls did not significantly decrease (SNK test, p<0.05, Ex=Pf<Po=St). It is possible that the flexible stems of *L. vulgare* give it some advantage through trampling resistance, but this advantage is lost when the animals are excluded.

Salicornia spp.

Salicornia spp. appear to be suppressed by removal of grazers. In the lower canopy the mean percentage of *Salicornia* did not vary between treatment types in 1996 (Figure 3.12 (i)) (nested ANOVA showed differences between treatment, p=0.420, but SNK tests did not show any differences between treatments). The data from this year suggests that the distribution of *Salicornia* in the plots at the start of the experiment was patchy: several of the plots had a mean percentage of *Salicornia* of 10-20% but several had less than 5% and one had none at all. In 1998, however, there were highly significant differences in the percentage of *Salicornia* in the lower canopy between treatment types (Figure 3.12 (ii)) (nested ANOVA, p=0.0003): multiple comparison tests showed that there were no differences between the posts/stakes control plots; and differences between the full exclosures/ part fenced controls plots (SNK test, p<0.01, Ex=Pf<Po=St). There were however no significant differences between the biomass of *Salicornia* in different treatment types in 1998 (nested ANOVA, p=0.1211), although there was generally less of this species in the exclosures compared with the controls. Biomass levels of this species were very low: it is a succulent plant with a very high water content so dry weight is probably less representative of its relative importance in the community than percentage cover.

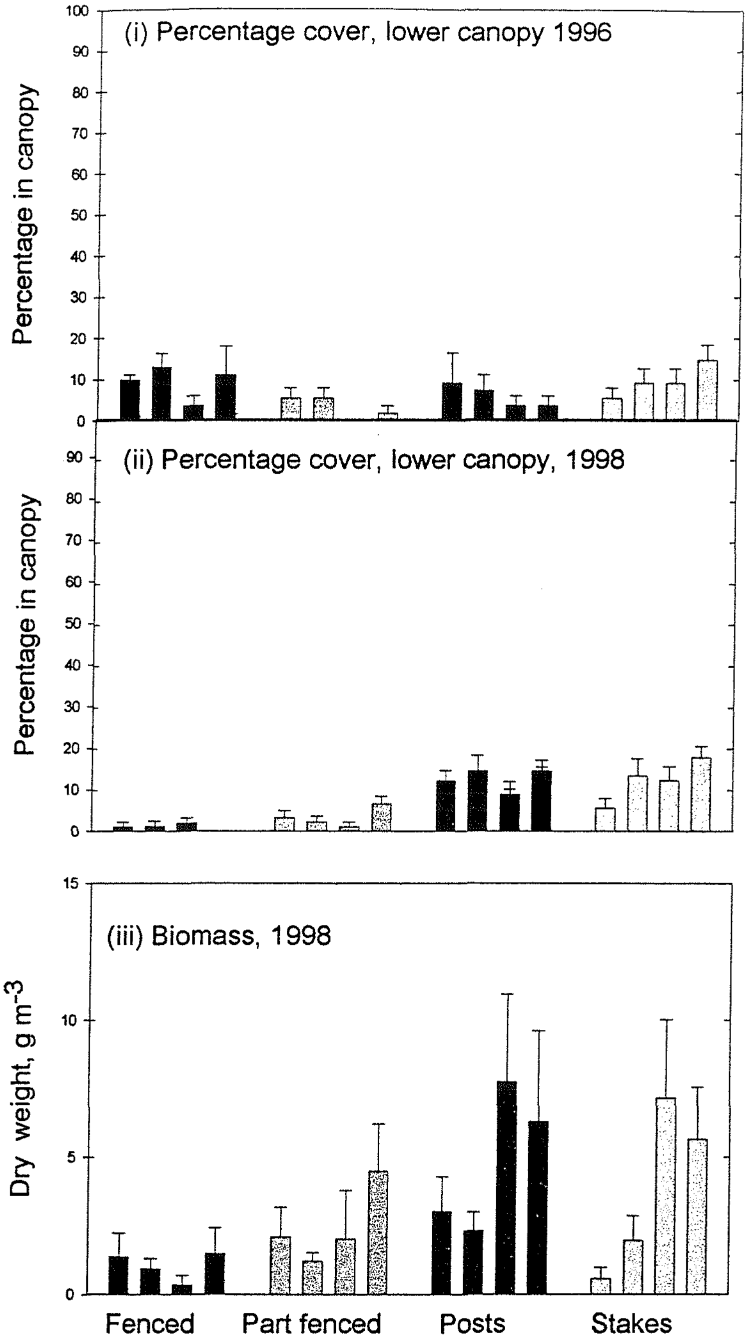


Figure 3.12. *S. europea* in experimental grazing exclosure plots established July 1996, Gins Marsh, Beaulieu.
(i) percentage cover in lower canopy , field survey July 1996,(n=10), (ii) percentage cover in lower canopy, field survey July 1998, (n=10), (iii) Above ground biomass from harvests in August 1998 (n=4), bars represent +1 standard error.

Table 3.4. Analyses of survey data for saltmarsh plant species in grazing exclosures, Gins Marsh Beaulieu; (i) percentage cover from non-destructive sampling surveys in July 1996 and July1998, (ii) biomass data from harvests in August 1998.

(i)Percentage cover (1996 and 1998)

Source of variation	df	***P. maritima*** **mid-canopy**		***A. maritima*** **lower canopy**		***Pu. maritima:*** **mid-canopy**		***Pu. maritima:*** **lower canopy**		***L. vulgare*** **mid-canopy**		***Salicornia*** **spp. lower canopy**	
		MS	**F**	**MS**	**F**	**MS**	**F**	**MS**	**F**	**MS**	**F**	**MS**	**F**
Treatment, 1996	3	8.54	0.76	2.37	0.69	0.20	1.12	0.86	2.03	1.50	1.19	0.63	3.73
Treatment 1998	3	60.1	4.18 *	3.03	5.52 *	0.20	0.85	3.09	4.84 *	1.53	3.56 *	3.56	14.18 ***

(ii)Biomass (1998)

Source of variation	df	*P. maritima*		*A. maritima*		*Pu. maritima:*		*L. vulgare*		*S. europea*	
		MS	F	MS	F	MS	F	MS	F	MS	F
Treatment	3	2.34	9.17 **	0.19	2.23	0.67	4.44 **	0.04	0.36	0.04	2.38

(i) n = 10 samples from within each plot, all data are arcsine transformed , Cochran's Test NS, except 1996 *L. vulgare* and *A. maritima* where untransformed data was used; *L. vulgare* Cochran's Test NS, *A. maritima* Cochran's Test C+0.24, p<0.05
(ii) n= 4 samples from within each plot, data are untransformed except *P. maritima* and *Pu. maritima* which are transformed Ln (*x*+1), Cochran's Test NS.
* Denotes significance at p<0.05; ** denotes significance at p<0.01; ***denotes significance at p<0.001.
The model for these analyses is : X = MEAN + Tr + Pl(Tr) + RES
(Tr = treatment, Pl = plot)

Light levels

Light levels were reduced more within the plant canopy (i.e. at ground level) in the exclosure plots than in the controls (Figure 3.13) in 1998. This would be expected in the higher growing plant canopy that had developed by that time (Figure 3.4). Nested ANOVA showed that there were very significant differences in light levels at ground level between treatment types (P=0.003). Reductions in the exclosure plots compared with all control treatments were significant (SNK test, p<0.05, Ex<Pf=Po=St). It is likely that these differences were due to the changes in physical structure and height of the canopies. This may be the main factor responsible for the changes in coverage and flowering of *A. maritima* (see

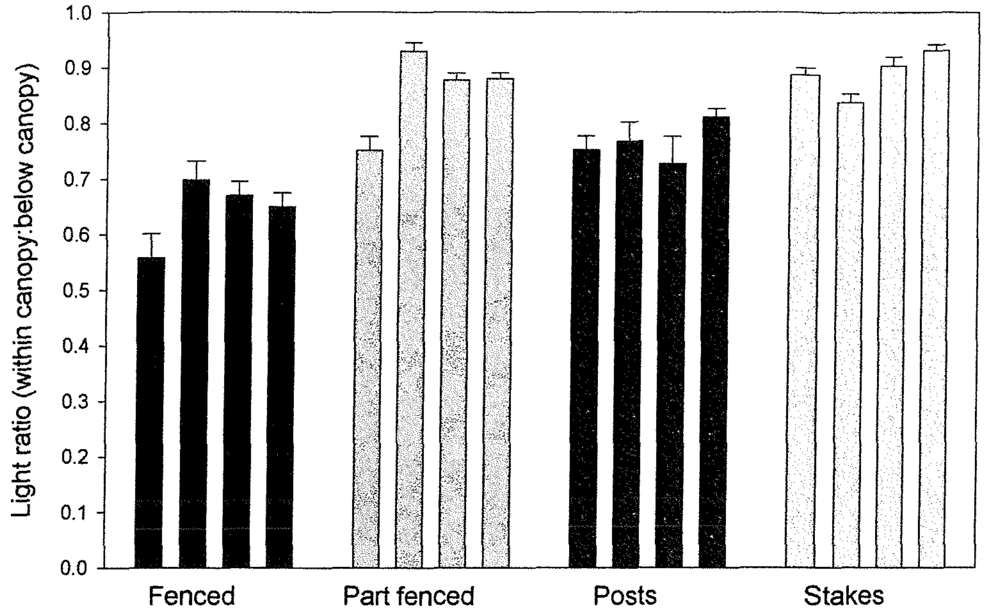


Figure 3.13. Light level ratios (ground level light level: above canopy light level) in grazing exclosures, Gins Marsh, Beaulieu, August 1998 (n=10)

below). There were differences between replicate plots in the exclosures and the part fenced controls (plot 1 was different from the other 3 in each treatment), but not between plots in the other two control treatments. This suggests that the effects of grazing in suppressing vertical plant growth were uniform over the posts and stakes controls.

Figures 3.14 and 3.15 show the relationship between the light ratio and the level of flowering density of *A. maritima.* The data from 1998 (Figure 3.14) appeared to show a significant linear relationship between the flowering density and the light ratio (R^2=0.61, $P<0.001$). The 1999 data (Figure 3.15) also showed such a relationship (ratio (R^2=0.56, $P<0.001$), but inspection of the figures reveals a possible threshold level at a ratio of approximately 0.7 (i.e. 70% of light reaching plants growing largely in the lower canopy).

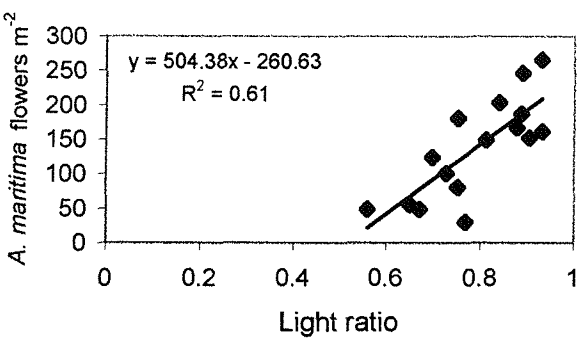


Figure 3.14. *A. maritima* flower density against light ratio (ground level light level: above canopy light level) in exclosure plots and controls. Gins Marsh, Beaulieu, July 1998. Each point represents the mean (n=10) light ratio in one experimental plot.

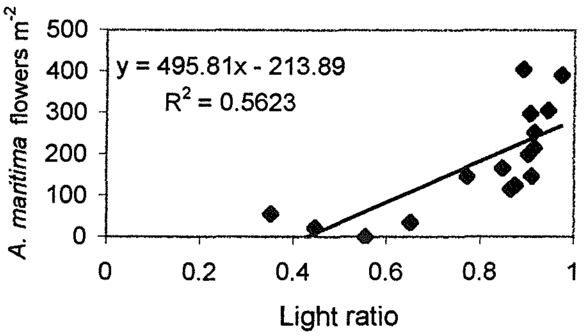


Figure 3.15. *A. maritima* flower density against light ratio (ground level light level: above canopy light level) in exclosure plots and controls. Gins Marsh, Beaulieu, July 1999. Each point represents the mean (n=10) light ratio in one experimental plot.

Discussion

Methodology and Limitations

There are some problems with the procedural controls used. The part fenced controls appear to act as deterrents to the grazing animals, particularly birds (Figures 3.2 and 3.3). Although this was not reflected in the grazing pressure data it may explain the clustering of the part fenced controls on the MDS plot (Figure 3.6). The posts-only controls, which were included to test for an effect caused by that component of the exclosure, seemed to work to attract one group of grazers (rabbits), possibly because the rabbits may feel less visually apparent to potential predators when next to a wooden post (Figure 3.2). It is also possible that the positioning of some exclosures, although random with respect to position in the zone of the marsh may have led to some user preference on the part of the grazers, for example due to the relative proximity of the refuges of the rabbits. None of these differences proved to be statistically significant, but perhaps a randomised block design would have been more robust.

There are also difficulties in recording changes in structure and composition of the plant communities. Three "tiers" of canopy were surveyed at each annual survey, it is quite possible that some species were under-recorded by the methods used. For example, *S. europea* plants did not grow to their full potential size in the grazed areas, and due to their erect growth habit they would have been recorded less than the prostrate *A. maritima*. Also, for similar reasons, it was not possible to distinguish between seedlings and mature *S. europea* plants, which remained very small compared with mature plants elsewhere on the marsh. Measuring biomass deals with the problems of recording changes in overall composition, at least in terms of dry weight, but does not reflect changes in structure or take into account the differing water contents between, for example the succulents *A. tripolium* and *S. europea*, and the woody shrub *A. portulacoides*.

It is worth noting that the communities under investigation here (and come to that almost any plant community) are themselves a product of herbivory as a selective force. Edwards and Gillman (1987) made the point that exclusion of herbivores may not actually demonstrate the role of herbivory on that community. The system has been very much shaped by herbivory, in selecting species and ecotypes that can tolerate grazing or can compete with tolerant species (Zacheis 2001). However the experiment can still demonstrate importance of herbivory in influencing the present composition of the plant community.

Grazer selectivity, disturbance and facilitation

The data presented here show that grazers are acting selectively, in that they are suppressing the more palatable and competitive *P. maritima.* This selection is probably driven by palatability and physical accessibility. In the case of the co-dominants *P. maritima* and *A. maritima* the changes which followed exclosure construction (Figures 3.9 and 3.10) can be explained by this. *P. maritima* is a major food source (Rowcliffe 1998) and is presumably therefore palatable as well as nutritious, and easy for grazers to access due to its upright growth habit. *A. maritima* may or may not be palatable (occasional flowers were observed to have been grazed) but its very low prostrate habit renders it almost inaccessible to rabbits, geese or deer unless they expend energy to dig or grub out the surrounding substrate. However, the overall effect of grazing animals observed on the plant community is caused by physical disturbance as well as by grazing itself. At a structural level this can be seen by the large residual canopy heights of the full exclosure plots compared with the controls (Figure 3.4), even through the winter months (Appendix 3.1; Plate 3). These canopies included dead flowers of grasses and *P. maritima* , which would have otherwise been grazed, but also dead flowers of *L. vulgare*, which would not (see below), but presumably would have been broken by trampling and washed away by the tide. This residual dead material is likely to be reducing light levels at ground level through the winter months, and therefore reducing the energy available to low growing plants (e.g. *A. maritima*) for photosynthesis for survival through the winter and growth and flowering in the spring.

Trampling resistance is also probably responsible for maintaining flowering densities of *L. vulgare* (Figure 3.8(iii)), which is known to be avoided by grazers (Summers *et al* 1993, Rowcliffe 1998). Trampling by sheep has been shown to increase species diversity in the middle and upper marsh (Bakker 1985, Bakker *et al* 1985). Although my experiment cannot completely separate the separate roles of trampling and grazing, the changes in both abundance and flowering of *L. vulgare* do suggest that trampling is of importance in maintaining the structure of the community.

Grazers are known to facilitate the activities of other species, for example cattle have been shown to maintain a short sward suitable for grazing by geese (Olff *et al* 1997). In the marshes studied here there is some grazing activity all year round. In this system both major grazer groups (rabbits and geese) may facilitate the other. Rabbits are present all year round but only appear to use the marsh frequently from the late winter to early summer, whereas small numbers of resident geese (and with it their activity on the marshes) are swelled by the arrival of the migratory brent geese in the autumn. If one or other group was not present, the vegetation structure could change to the more rank growth that rapidly developed in the full exclosure plots. A lower sward is more accessible to both rabbits and geese, but it is also made up of younger, more nutritionally profitable growth (Gray and Scott 1977b, Davy and Bishop 1991). Indeed, areas of high *Pu. maritima* biomass are usually avoided by grazing geese because of the relatively low nutrient quality of the older plant material (Rowcliffe 1998). It is therefore quite possible that the changes, which took place rapidly in the exclosures, could prove to be persistent over quite long time scales. The grazers would be likely to avoid these areas of higher biomass unless it was disturbed by external factors such as tidal debris or ice (which would, in effect set back or restart the process of succession). Bigger grazers, such as cattle, may also be able reverse the changes. Bazely and Jefferies (1986) found that grazing activity was low two years after fences were removed from exclosures which had been erected five years earlier, so it is clear that the grazers are playing a major role in maintaining the communities that they exploit.

Biodiversity and genetic structure

At the low levels studied in this experiment, grazing acts as a patchy disturbance factor, both in time and space. Grazing pressure data (Figures 3.2 and 3.3) showed a great deal of variation between individual plots, between months and between seasons. The irregular nature of the grazing pressure may be a key element in producing the levels of both structural and biological diversity present. *Salicornia* spp. are annuals whose natural zone is the unstable pioneer area between properly vegetated marsh and unstabilised mudflat. In the upper and middle marsh these species only usually colonise gaps, and in Gins Marsh these gaps are scarce and are mostly generated by animal scrapes or trampling. In a similar way, tidal debris allows opens *S. europea* to persist in the upper parts of New England marshes by creating gaps by smothering of the dominant species at those levels. At time zero (1996) there was variability between all of the different plots before the exclosures were constructed, but in 1998 this variability had reduced in the exclosure plots, with the mean percentage cover of *Salicornia* spp. declining from 5-10% to less than 3%. *Salicornia* spp. also declined in the part fenced plots, which the animals generally used less, but was still present, with a similar patchy distribution, in the posts and stakes controls. The small gaps colonised by *Salicornia* spp. can also be used for germination of other plants, either from seeds within the soil or brought in by the tide. At the low levels of grazing pressure operating in this study the marsh system could be viewed as unsaturated with herbivores: grazers can operate selectively, and, to an extent randomly, as wherever they land or walk to, they are likely to find palatable plant material. In a heavily grazed marsh the system is close to saturation: selective pressure on palatable species is much more intense and uniform, so a less diverse system results. Heavily grazed marshes in the UK tend to have fewer gaps: heavy grazing and trampling pressure usually produces a tight grass sward, typically of *Pu. maritima* and where gaps are created, seedlings of more palatable species are usually grazed before they become established (Gray and Scott 1977b, 1980).

The activities of grazing animals on the study site appear to be maintaining the mid-marsh plant communities in a state of arrested (or slowed) succession. The community which the grazers are maintaining is a relatively species-rich short sward, with abundant flowering of *A. maritima* and no dominance by any single species (Appendix 3.1, Plates 1 and 4). The physical structure of the exclosed communities shifted towards a more homogeneous community dominated by grasses (*Pu. maritima* and *F. rubra*). Similar observations have been made in other studies of grazers on saltmarshes (Ellison 1987, Hik *et al* 1992, Rowcliffe *et al* 1998). The increases in abundance of *P. maritima* may represent an intermediate stage in successional change towards a relatively species-poor sward dominated by grasses.

The changes in flowering rates by *A. maritima* and *P. maritima* when grazers were exclosed have implications for the genetic structure of the populations present in grazed salt marshes. On the grazed middle marsh *A. maritima* flowers abundantly but flowering densities declined when the grazers were excluded, as did the abundance of the plants themselves and their biomass (Figure 3.10). This is an interesting indirect effect, as the grazers do not actually consume *A. maritima.* These changes were driven by the structural changes which took place in the exclosures: a change to a higher growing community (Figure 3.4) reduced light levels at ground level for the low-growing *A. maritima* (Figure 3.15), which in turn reduced its photosynthetic activity, so less resources were available for growth or reproduction. It appears that once a certain threshold of light penetration is reached (c. 70%), this begins to have impacts on the resources available to *A. maritima.* The data suggest that at this level of shading the initial impacts (e.g. after two years) are small, but increase with time as resources are depleted further. It is possible that the long term activities of grazers have selected a population of low-growing *A. maritima.* It would be interesting to compare the genetic structure of such populations with, for example, populations growing on steep rocky cliffs which are inaccessible to large grazers.

Meanwhile, the activity of grazers renders the populations of *P. maritima* on the middle marsh almost entirely dependent on clonal growth for reproduction. This has been observed in *Pu. maritima* where grazed areas are occupied by extensive clones with less morphological variability than in ungrazed areas (Gray and Scott 1980). Consumption of biomass, and possibly consumption of the few flowers that are produced, reduces seed set to very low levels at the study site. When grazers are excluded, there is a rapid increase in observed flowering (and subsequent seed production). This change may prove to be short term, as the successional processes which the grazers have previously delayed, produces a shift to a grass-dominated community, which could itself shade out the *P.*

maritima, along with any seedlings which develop from the initial increased seed production. In the grazed community, however it is possible that local genetic bottlenecks could be developing with clonal growth the only significant means of reproduction for *P. maritima.*

The structural changes which followed exclosure will have other impacts on biodiversity: seeds will lack gaps for germination which the activities of animals produce, and where seeds do germinate seedlings are more likely to be shaded out by the denser canopy of older plant material above. Two results of this seem clear: the community as a whole will reduce in diversity, and the increase in biomass and seed production by *P. maritima* is likely to be short lived.

The changes in the community in the absence of grazers are shown in Figure 3.16. The present community is maintained as a SM13 *Puccinellietum maritimae* salt marsh, *Limonium vulgare-Armeria maritima* subcommunity; General Salt Marsh (Tansley 1911 and Chapman 1934). Exclosure of grazers has switched this to a *Plantago maritima-Armeria maritima*; sub-community *Plantaginetum* (Chapman 1934). It seems probable that over a period of perhaps 4-5 years cessation of grazing would lead to a SM13 community with *Puccinellia maritima* dominant: *Puccinellietum (Glycerietum) maritimae* (Tansley 1911). In the longer term (maybe a decade or more) it is likely that succession will continue, resulting in expansion of the existing SM16 *Festuca rubra* salt marsh community *Juncetum gerardii*, with *Juncus gerardii* dominant, which may be suppressed to a narrow fringe at present by the grazing, trampling and competition.

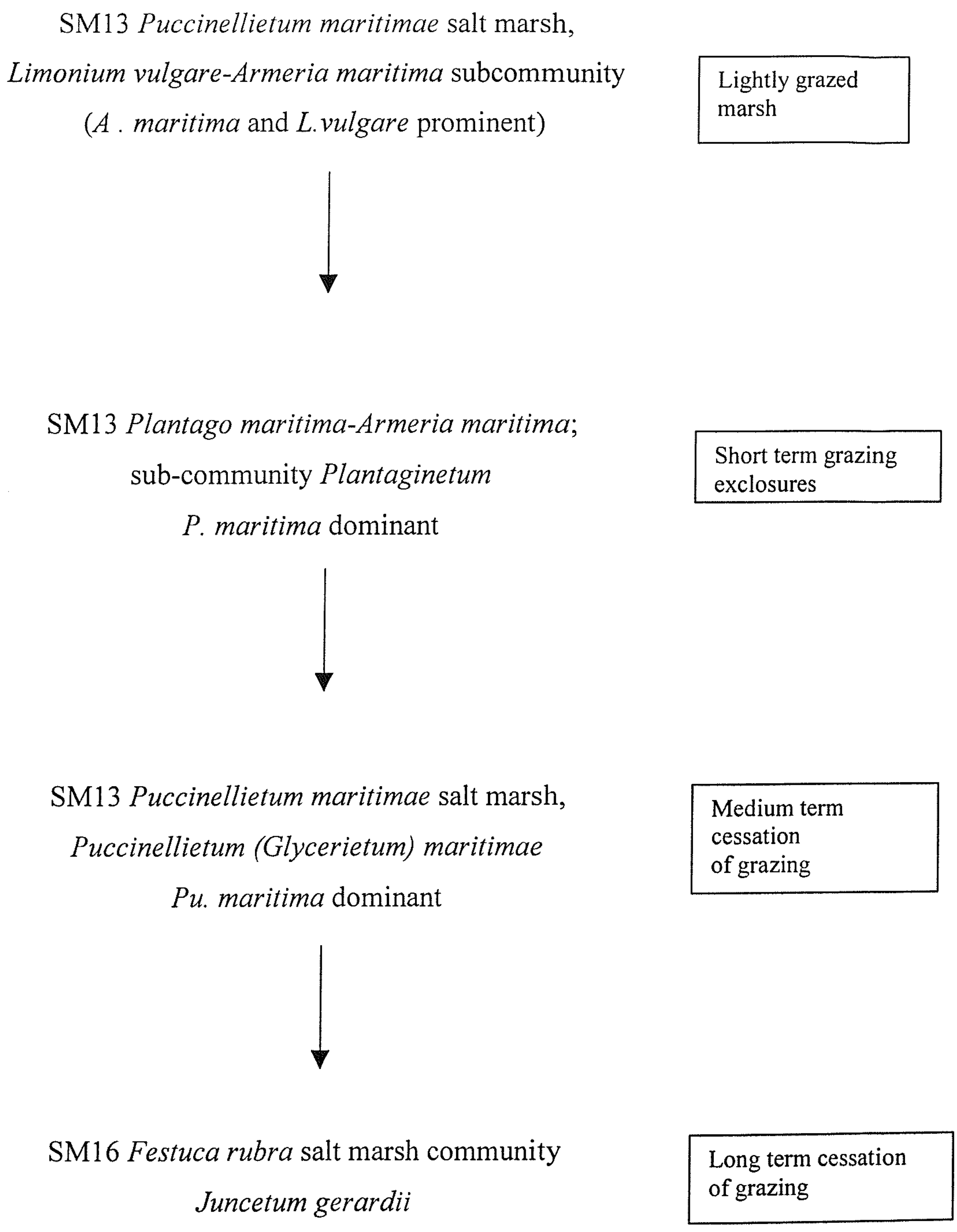


Figure 3.16 Changes in the Gins Marsh saltmarsh community under altered grazing regimes. Plant communities after Rodwell (2000).

Intermediate disturbance revisited

Figure 3.17 shows how differing levels of grazing pressure can fit into the wider ideas of intermediate disturbance and diversity (e.g. Connell 1978).

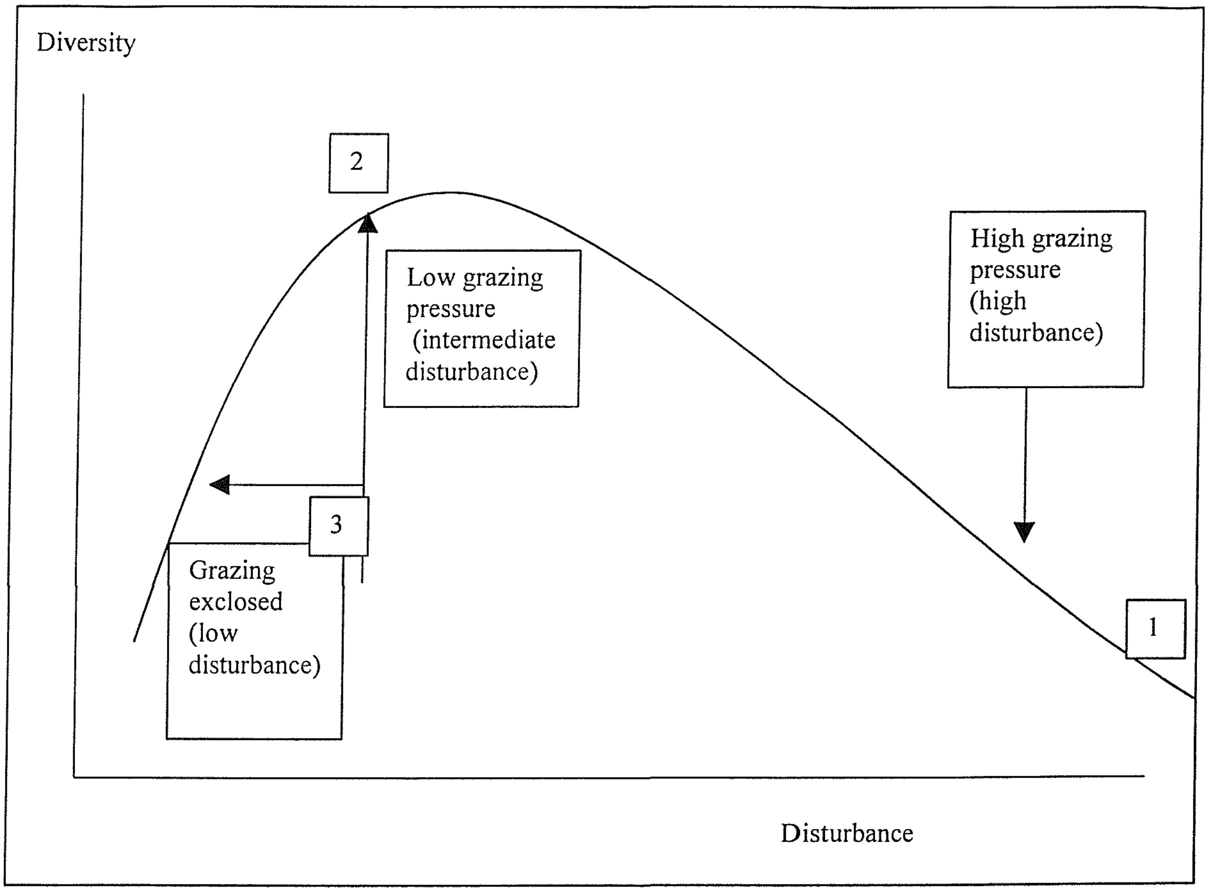


Figure 3.17. Effects of different levels of grazing on plant species diversity, interpreted as levels of disturbance (after Connell 1978). Numbers correspond the the different states shown on Figure 3.18.

A typical heavily grazed domestic grazing marsh would have a low level of diversity dominated by a tight low turf of grazing-tolerant plants such as *Pu. maritima,* with little of the characteristic saltmarsh halophyte plants (*State 1* on Figure 3.18: (Rodwell 2000)). High levels of diversity will be present where grazers are present in low numbers, as on the marsh studied here (*State 2* in Figure

3.18). In this case there is no single dominant species, and maintenance of a low sward means competition for light is not a major factor in suppressing mid-successional species. Disturbance by grazers probably encourages more community diversity. Succession is thus retarded at a high diversity stage, although evidence from this study suggests that elimination of grazers leads to reduced diversity (Table 3.3).

When grazers are excluded the system changes to a less diverse community dominated by more competitive species: a persistent, taller, closed canopy develops and lack of physical disturbance combines with low light levels to prevent establishment of any new species (*State 3* in Figure 3.18). The competitive relations between plants are probably set by long term grazing, and removal of this pressure disrupts the balance of the community (Zacheis *et al* 2001). Furthermore, the resulting taller growth is less palatable (Van der Wal *et al* 2000) so grazing pressure would be unlikely to increase again unless some other factor (e.g. frost damage, different grazers or more intense grazing pressure) intervened. Where the other environmental variables in the system remain unchanged (i.e. in the absence of other disturbance factors), switches to this state are more likely to be irreversible than a switch from *State 2* to *State 1* where a reduction in grazing pressure could see a return back to the more diverse state. This may be a useful way of managing grazing marshes for biodiversity, although in the context of the UK intensive domestic grazing on marshes has declined in recent years as profitability has reduced.

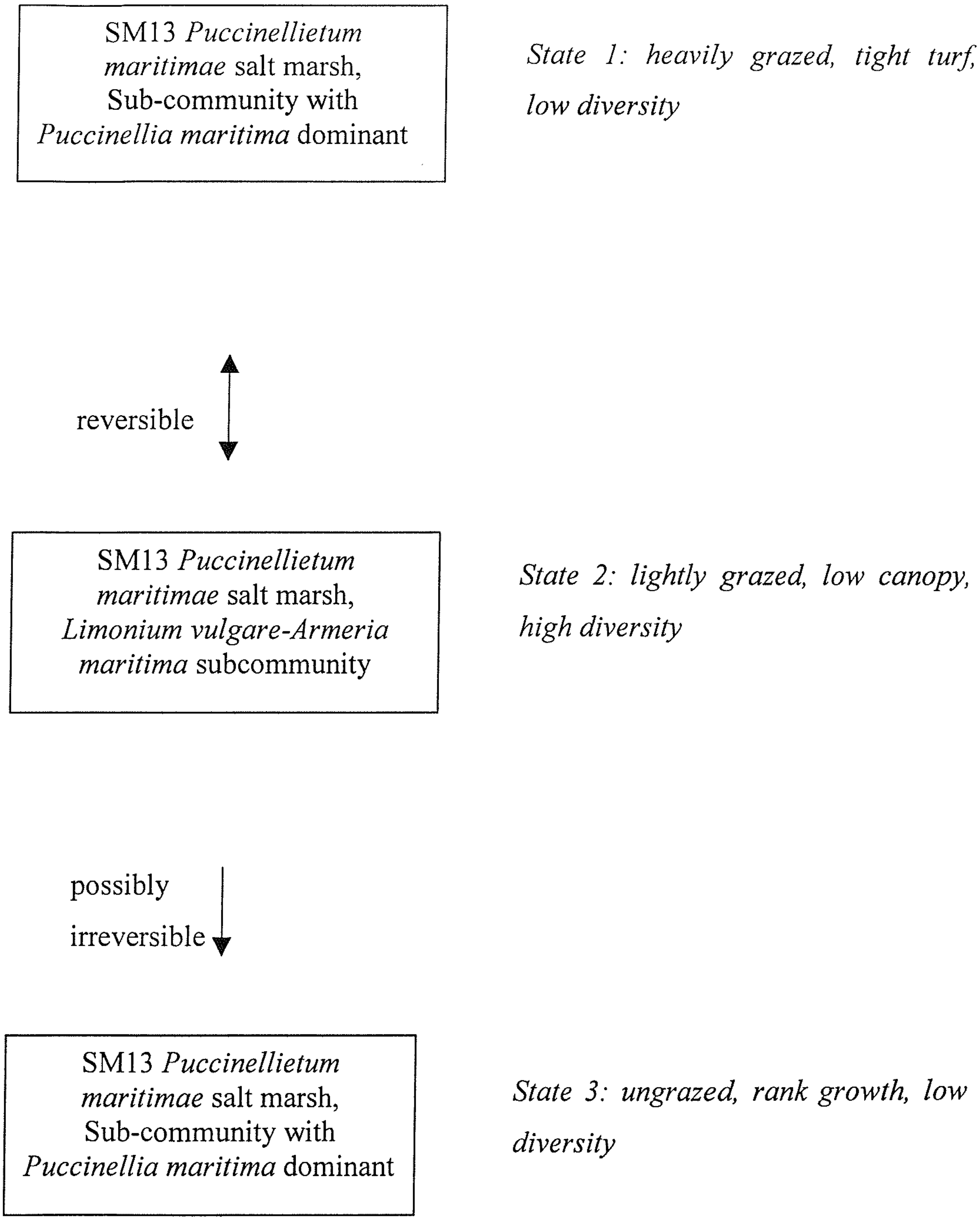


Figure 3.18. Community changes at different levels of grazing pressure. Plant communities after Rodwell (2000).

Conclusions

This experiment has demonstrated that grazers are instrumental in maintaining the diverse plant communities on the upper marsh at Gins Marsh, Beaulieu, so the original hypothesis can be accepted. Some of the changes were structural, and to an extent, predictable. Higher canopy growth and, overall, increased biomass were observed, as expected, in the exclosure plots. Specific species were investigated as the major part of the experiment. Exclusion of grazers produced significant changes: increases to the growth of palatable species (*P. maritima, Pu. maritima.*) and indirect effects which led to reduction of *A. maritima* and *Salicornia* spp. *A. maritima* had reduced due to shading, the annual *Salicornia* spp. had probably declined due to lack of gaps created by grazers for colonisation. Flowering of the species observed also changed in the absence of grazers: flowering by the two most conspicuous flowering plant species in the community, *A. maritima* and *L. vulgare* declined significantly, possible due to shading by increased growth of species previously suppressed by grazers. The palatable *P. maritima*, which does not usually flower on this marsh (or flowers are suppressed by grazers) flowered profusely where grazers were excluded.

CHAPTER 4

THE ROLE OF COMPETITION AND FACILITATION IN MAINTAINING SALT MARSH PLANT ZONATION

Introduction

Community ecologists have traditionally investigated the patterns observed in assemblages of living things, and tried to explain those patterns by developing an understanding of the mechanisms and processes which have generated them (e.g. Connell 1972, Grime 1979). The organisms that make up those communities are often arranged along physical gradients. As our knowledge has developed it has become clear that many of the processes apply to any system where conditions vary spatially.

Much work has been carried out on rocky shores, where community structure is usually easy to recognise (Lewis 1964, Stephenson and Stephenson 1971). Physical factors, such as height relative to the tide, salinity, and temperature dictate the patterns which are observed, and superimposed on this are, for example, variations in wave exposure or shelter (Raffaelli and Hawkins 1996). Zonation is often patchy with space-occupying organisms arriving and colonising largely by chance, often occupying gaps generated by random disturbance events (Sousa 2001, for review). There are also variations on larger scales: different organisms occur in different regions, with their distribution a reflection of their adaptation to the physical conditions but also their evolutionary and biogeographical history (Stephenson and Stephenson 1971).

The same patterns can be observed on other gradients in physical conditions: on mountainsides (Whittaker and Niering 1975, Vasquez and Givnish 1998); on mires where nutrient levels vary (Wheeler and Proctor 2000); along gradients of differing substrate depth (Belcher *et al* 1995) and on salt marshes, which have much in common with rocky shores but as sheltered, soft sediment environments.

Saltmarshes also have many characteristics of their own which make them useful places to learn more about the underlying causes of ecological patterning (Bertness 1992, Gray 1992, Huckle *et al* 2000).

The roles of physical and biological factors in determining zonation

Zonation of plant communities has long been held to be fundamentally driven by gradients of physical conditions. Plants have differing levels of physiological tolerance to stressful conditions such as, for example, extremes of elevation (Whittaker 1957) temperature (Bazzaz 1979), aridity (Orshan 1963), waterlogging (Bertness *et al* 1992*)*, or salinity (Gray and Scott 1978b). A very general rule has been developed in which the most competitively able organisms are the least capable of tolerating more stressful conditions, and the less competitive species are thus displaced to more stressful habitats (Levine *et al* 1998); and this seems to apply across a range of natural ecosystems (see below). In effect, a plant can be either an effective competitor or be a good stress-tolerator, but not usually both at the same time (Grime 1979), as there are always fitness trade-offs between the two qualities. This system of trade-offs has been identified as important in generating the zonation patterns we see, even though physical conditions are usually the over-riding driving force in dictating community structure or dictating the range at which species may survive (Gray 1992).

The role of biotic factors should not be discounted, however. In many ecosystems the importance of the balance between the physiological tolerance and the competitive ability of living organisms has been clearly demonstrated. This has been considered in many different ecosystem types, for example rocky shores (Connell 1972), mangroves (Ellison and Farnsworth 2001), freshwater ponds (Grace and Wetzel 1991), and in saltmarshes (Bertness 1991, Pennings and Calloway 1992). There is consensus amongst these authors that the spatial patterns and, in particular, the boundaries between different populations is the product of this balance of trade-offs, but also that the abiotic or physical factors are more important in setting boundaries at the more stressful end of the scale. Meanwhile the biotic interactions, such as competition and facilitation, become increasingly more important where physical conditions are more benign. This has been synthesised as the 'competitive-physiological-exclusion' concept (CoPE concept) by Bockelmann and Neuhaus (1999), in which plant populations are excluded from a particular habitat either by competition (usually with other plant species) or by physical conditions that they are unable to tolerate.

Saltmarsh zonation: manipulative experiments

Saltmarshes often show clear zonation, with distinct plant communities present at different elevations (e.g. Adam 1980, Gray 1992, Rodwell 2000). Because species tend to occupy a particular vertical level, zonation has generally been ascribed to tidal influences (Gray 1992) and tide-related physical parameters such as salinity and waterlogging (Gray and Scott 1977b). However, the spatial patterning which is observed is frequently complex, and the role of biotic interactions, particularly competition (Bertness and Ellison 1987), and herbivory (Ford and Grace 1998), but also facilitation (Bertness and Shumway 1993, Bertness and Hacker 1994), have received some attention over the last decade or so in studies using experimental manipulations in the field.

One of the earliest experimental manipulation of this kind was undertaken by Stalter and Batson (1969), who set out to investigate why certain species grow at particular marsh levels. They transplanted selected North American saltmarsh species, and showed that several species can grow in other zones. They ascribed most of the reasons for the zonation they observed to be due to tidal factors, although they did speculate that interspecific competition could be in additional factor.

In one of a series of experiments in New England saltmarshes, Bertness and Ellison (1987) found that the lower marsh dominant *Spartina alterniflora* was restricted to lower elevations by the presence of more competitive upper marsh species such as *Juncus gerardii* and *Spartina patens*. Bertness (1991) used transplant experiments to show that *J. gerardii* competitively excluded *S. patens* and the pioneer grass *Distichlis spicata* from highest parts of the upper marsh, although when neighbouring plant growth was excluded both of these species grew successfully at higher levels than usual. Pennings and Calloway (1992) found that flooding, salinity and competition interacted to determine plant zonation patterns on a marsh in southern California, but using the physical parameters they measured, the middle marsh was the least physically stressful , and at it was at this level that competition seemed to be most important in determining spatial patterns.

There are however exceptions to this general rule: Bockelmann and Neuhaus (1999) found that the upper marsh grass *Elymus athericus* was limited at its *lower* boundary by competition with the dwarf shrub *Atriplex portulacoides.* In this case *E. athericus* was found to be competitively excluded from a high stress habitat, a result at odds with the CoPE model suggested by the same authors' review of many other zonation studies (Bockelmann and Neuhaus 1999). The authors were unable to offer a possible mechanism for their findings: both species have similar salinity tolerances, both have comparable "phalanx" growth strategies (Bertness and Ellison 1987) and both have similar nutrient requirements. These exceptions echo those found on rocky shores where competition or grazing have been shown to set the upper limits of some algal species (Underwood 1980, Hawkins and Jones 1992, Raffaelli and Hawkins 1996, review)..

Competition....for what?

Much of the literature to date has examined the relative roles of physical tolerance and competition on plant zonation, but while many of the earlier studies identified competition as an important factor, they did not demonstrate what resources the plants were actually competing *for.* One experiment investigating this was the work of Groves and Williams (1975) who showed the relative importance of root and shoot competition between *Trifolium subterraneum* and *Chondrilla juncea.* This showed that plants compete with the above ground growth of neighbours for light, but also with below ground growth for nutrients and water. More recent studies have begun to examine this issue in the context of saltmarshes. Initial studies focussed on competition for light by above ground growth, and growth strategies. Ellison (1987) suggested that competition for light by *Salicornia europea,* when growing amongst taller growing perennial species, was more important than competition for nutrients. Light penetration to the marsh surface can be reduced by more than 90%, which both limits seedling success and compromises the survival chances of lower growing species (Bertness and Ellison 1987). Bertness (1991) suggested that the reason for the dominance of *J. gerardii* over *D. spicata* was the early growth of *J. gerardii*, by which it "pre-emptively displaces" its competitors by taking over 50% of available light; but also its "phalanx" root growth which, once established, excludes the less dense "guerrilla" runners of the potential competitor species. Castellanos *et al* (1994) showed that *Arthrocnemum perenne* reduced light penetration to the lower growing *Spartina maritima* by 97% which prevented it recolonising areas which may be otherwise physically suitable. Furthermore, the C3 species *A. perenne* starts growing earlier in the year than the C4 species *S. maritima* and also has a dense root mat which inhibits growth of the *S. maritima* runners.

More recently, there have been attempts to evaluate the importance of competition for nutrients amongst competitor species. Bockelmann and Neuhaus (1999) (see above) tested whether competition for nutrients was a factor in explaining the unexpected spatial relationship they had found between *E. athericus* and *A. portulacoides* by nitrogen-fertilising treatment plots, but did not find that it was a significant factor. However, Levine *et al* (1998) suggested that the trade-offs of the CoPE model are largely nutrient controlled, i.e. that the supply and availability of nutrients can act to dictate the competitive relations across physical gradients. They suggest that competition for light can dictate competitive outcomes among salt marsh plants, but only when nutrients are not a limiting factor. They demonstrated this by fertilising plots of *J. gerardii*, *S. alterniflora* and *S. patens*. Their results showed that when nutrients were enriched the competitive relations found in previous studies (Bertness and Ellison 1987, Bertness 1991) were reversed compared with normal marsh conditions, i.e. the species which had previously been displaced to the lower zones became dominant over the upper marsh dominants.

Facilitation and positive interactions

I have focussed so far on how competition for resources can influence spatial patterning and zonation. However, work over the last ten years has identified the importance of positive interactions between different species in a plant community; and this work has begun to clarify the role of these associations in zonation and succession.

Bertness (1991) found that hypersaline bare patches in the upper marsh are initially colonised by two salt-tolerant lower marsh species, *S. patens* and *D. spicata.* Growth of these species reduces soil salinity and facilitates invasion by the dominant upper marsh species *J. gerardii.* The competitive subordinates act in this case to ameliorate the harsh hypersaline conditions, and then subsequently succumb to succession. A similar relationship was identified by Castellanos *et al* (1994), where tussocky growth of *Spartina maritima* colonised poorly-drained areas of a lagoon system in Spain, and were later replaced by *Arthrocnemum perenne* as the tussocks broke down. In this case *S. maritima* tussocks provided a favourable layer of oxidising sediment for *A. perenne* to colonise, whereas the rest of the zone was strongly reducing and only suitable for *S. maritima.*

Positive interactions can also operate in a more simple way than this. It is a long established ecological idea that under physically stressful conditions neighbouring plants can act together to buffer one another against, for example, the wind or the tide (e.g. Clements *et al* 1916). Bertness and Hacker (1994) showed that both direct and indirect positive interactions between *J. gerardii* and the perennial shrub *Iva frutescens.* The two species grow together in the middle marsh in New England. Bertness and Hacker used a combination of transplant and removal techniques to show that the presence of neighbouring plants at lower marsh levels enhanced the performance of both species. *I. frutescens* is intolerant of high salinity levels, and the presence of neighbouring *J. gerardii* in the middle marsh maintains lower salinity levels simply by casting some shade and preventing evaporation. In the upper marsh relations between neighbours were all competitive. They suggested that this shows that interactions between plants change from negative at the upper end of the marsh to positive at the lower, more stressful end. These associations can even operate at another trophic level: when neighbouring *J. gerardii* are removed, *I frutescens* is colonised by twice as many aphids (Hacker and Bertness 1995)

In this experiment I aimed to clarify some of the factors which produce some of the spatial patterning in saltmarshes in Southern England. I focused on the zonation of two species that are important components of these ecosystems, namely *Spartina anglica* and *J. gerardii. S. anglica* first appeared in Southampton Water in the second half of the nineteenth century and caused profound physical and ecological changes, which continue to this day (see Chapter 2), and are still not fully understood (Lambert 1964, Gray *et al* 1991, Tubbs 1999). In Southern England *S. anglica* often grows as monospecific stands in the lower marsh zone, where it is highly competitive; but it is only found in the upper marsh in pools or at the edges of creeks. Like the American *Spartina* species studied by Bertness (1991 a & b) it is a rapid coloniser of suitable substrates and has a 'guerrilla' or runner root morphology. It is a true halophyte with salt glands on the leaves. (van Diggelen *et al* 1986). The rush *J. gerardii* does not possess any outright halophyte characteristics and is usually found as a narrow fringe in the upper marsh, and is not usually found at lower levels (Rodwell 2000). The two species are not usually found growing together.

Aims

In particular, the experiment described here aimed to establish the relative importance of physical and biological factors (competition and facilitation) in setting the generally observed spatial patterns of the two species. To achieve this an upper marsh species (*J.gerardii*) was transplanted to the lower marsh, and a lower marsh species (*S.anglica*) was moved to the upper marsh. Different treatments of the transplants were established to evaluate the importance of interactions with neighbouring plants. Plant success was measured by measuring growth (height and above/below ground biomass) and reproductive success (seed or fruit production).

More formally, the null hypotheses to be tested were that:
Transplantation to the upper marsh does not affect the success of *S. anglica.*
Transplantation to the lower marsh does not affect the success of *J. gerardii.*
Interactions between neighbouring plants do not affect success of *S. anglica* or *J. gerardii.*

Methods

Site description

Sims Wood Marsh (Grid Reference SU 411008) is situated on the eastern shore of the Beaulieu Estuary, on land owned by the Exbury Estate. The marsh displays distinct zonation from a *Salicornia* pioneer zone at the marsh edge up to a mature *Elymus pycnathus* zone grading into oak woods beyond (Figure 4.2; Appendix 3.1, Plate 5). Just below the *E. pycnathus* upper marsh zone there is a *Juncus gerardii* fringe 3-5 m wide. The community here is NVC SM16 *Festuca rubra* salt-marsh community *Juncetum gerardii* (Warming 1916), sub-community with *J. gerardii* dominant (Rodwell 2000).

Below this, there is a zone of species rich middle marsh that grades into an NVC SM6 *Spartina anglica* salt marsh community *Spartinetum townsendii* (Tansley 1916, Rodwell 2000). This is bordered at the edge of the marsh by a narrow pioneer zone of NVC SM8 Annual *Salicornia* salt marsh community *Salicornietum europaeae.*

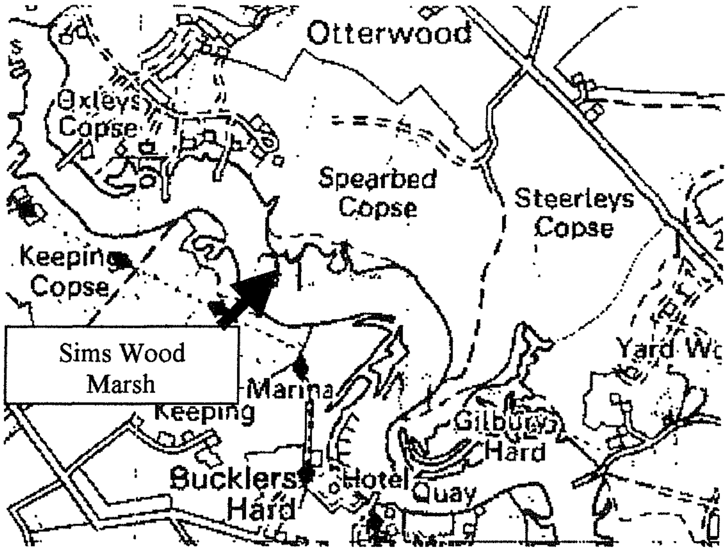


Figure 4.1. Beaulieu Estuary, showing location of experimental site at Sims Wood Marsh, (not to scale).
(Crown Copyright www.multimap.com, accessed 26/04/2001)

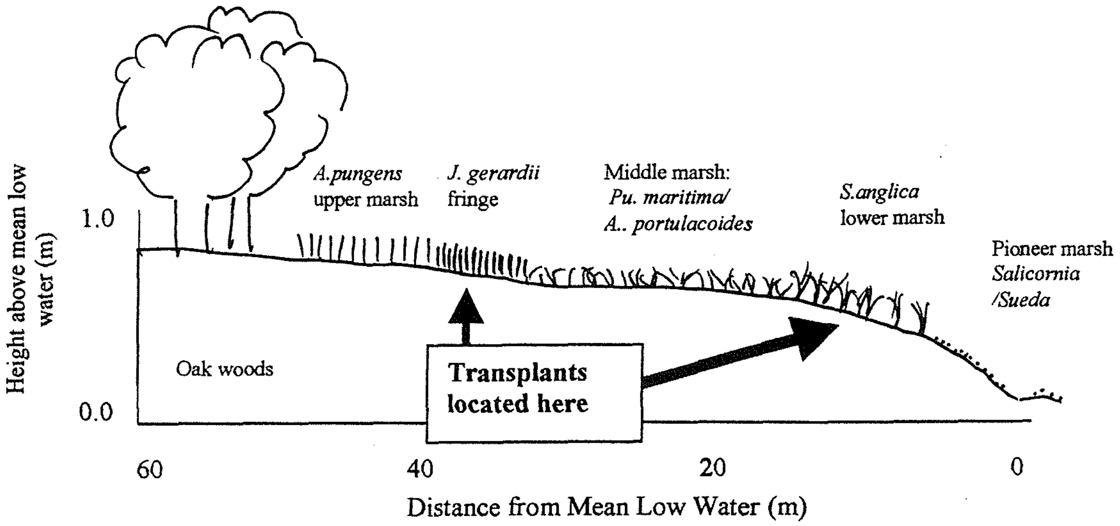


Figure 4. 2. Zonation transect of Gins Marsh, showing transplant locations between lower marsh (*S.anglica*) and upper marsh (*J. gerardii*).

Experimental design

Plants were transplanted within their own ambient substrate, so the experimental design used tested just for the effect of location on plant success, with or without the effects of neighbouring plants rather than additionally testing for the effect of substrate type.

Blocks of saltmarsh substrate (0.25m x 0.25m, by 0.25m deep) with all intact above ground vegetation were excavated using a sharp spade. *J. gerardii* has a 'turf' or "phalanx" root morphology extending up to 0.25 m below ground (Bertness & Ellison 1987). *S. anglica* has a "runner" or guerrilla morphology (Caldwell 1957) which can extend several metres horizontally, and over a metre below ground, without a dense root mat. *S. anglica* runners were cut during transplantation but as the process took place before active growth had started regeneration of damaged runners was expected. Eleven transplants of each treatment were moved between the lower zone (*S. anglica*) and the upper marsh (*J. gerardii* fringe). Lateral controls (transplanted within their own zone) were also established to check for effects of transplanting. Untransplanted plots were also marked to act as untreated controls to check for background changes during the experimental period. Neighbouring above ground plant growth was removed by clipping the surrounding 0.15m of vegetation with sheers and scissors at ground level regularly through the whole trial: monthly throughout the year and fortnightly from April to August. Reciprocal transplants were carried out to minimise damage to the marsh, but also to minimise the time taken to transplant: transplants were never out of the ground for more than 30 minutes. Both of the transplant zones are almost monocultures. Other species were removed with care by hand. In the following sections "up marsh" refers to *S. anglica* transplants being moved to the *J. gerardii* zone; "down marsh" refers to *J. gerardii* transplants being moved to the lower marsh zone). Treatment and control types are summarised in table 4.1.

Table 4.1 Transplant treatments and controls for *S.anglica* and *J. gerardii*. Sims Wood Marsh, Beaulieu.

***S. anglica* transplants:**	***J. gerardii* transplants:**
Up marsh: with neighbou rs	Down marsh: with neighbours
Up marsh: without neighbours	Down marsh: without neighbours
Lateral controls (within zone) with neighbours	Lateral controls (within zone) with neighbours
Lateral controls (within zone) without neighbours	Lateral controls (within zone) without neighbours
Untransplanted control	Untransplanted controls

Transplant plots and controls were established in March/April 1996. These were taken from the *S. anglica* lower marsh zone and the *J. gerardii*-dominated upper mid marsh zone (referred to as upper marsh in this chapter). There is approximately 0.28m difference in elevation between these two zones. This effectively means that the lower (*S. anglica*) zone is inundated twice daily (although coverage is not total during neaps), and the upper (*J. gerardii*) zone is only inundated 4-5 times per month on average. Plots were monitored for three years until they were harvested in August 1998 .

Productivity and growth

The height of ten randomly selected culms ground level to the highest point) was measured at the same time as fruit and seeds were counted each summer. Fruit (*J. gerardii)* production and seed (*S. anglica*) production were recorded at the same time. Data for *J. gerardii* fruit were gathered in late June/early July; and for *S. anglica* seeds in late September. Individual plants are hard to distinguish, so 10 culms were selected at random within each plot and all fruit or seeds were counted. Where less than 10 culms produced fruit or seeds all of those present were counted.

Plots were harvested (above and below ground) in July (*J. gerardii*) and September (*S. anglica*) 1998. The whole plot was not harvested, but the central 0.1x.0.1m (0.25 cm deep) of each transplant was taken to minimise edge effects.

Below ground material was washed to remove all substrate. Below and above ground material were dried at 60°C for 24 hours or to constant weight.

Data analysis

The data were analysed by analysis of variance where the assumptions were met, and where this was not possible despite transformation, non-parametric tests (Kruskal-Wallis one way analysis of variance on ranks) were performed (e.g. Underwood 1997). Appropriate *post-hoc* tests were used to establish which treatment types were different when significant differences were indicated. Microsoft Excel, SPSS SigmaStat and SPSS SigmaPlot were used for analysis and data presentation.

Plant interactions were further analysed using the Relative Neighbour Effect (RNE) index (Markham and Chanway 1996). This is a modified version of the Relative Competitive Intensity (RCI) Index (Wilson & Keddy 1986, Belcher *et al* 1995). The RNE gives a measure of plant performance in the presence or absence of neighbours, and is set in the context of the maximum plant performance (with or without neighbours). The result is a score within a range from -1 to +1: negative values indicate performance has been facilitated by neighbours, positive values indicate that performance has been reduced by competition with neighbours.

$$\mathrm{RNE} = (P_{-\mathrm{N}} - P_{+\mathrm{N}}) / x$$

Where P is the performance of plants (e.g. biomass) in the presence (+N) and the absence (-N) of neighbours; and x is the $P_{-\mathrm{N}}$ or $P_{+\mathrm{N}}$, whichever is the greater.

Mean biomass values for each treatment were used for calculating RNE. To prevent propagation of errors in generating Standard Errors for the data, standard errors for RNE were calculated as follows (P.J.Shaw, pers. comm.):

For the standard errors of each figure,
$\mathrm{D} = (\mathrm{A}-\mathrm{B}) / \mathrm{B}$, or $\mathrm{D} = \mathrm{C} / \mathrm{B}$

Where D = Std. Error of RNE, A = Std. Error of P_{-N} , B = Std. Error of P_{+N} , and C = A - B

$\Delta C = \sqrt{\Delta A^2 + \Delta B^2}$

$\Delta D = D\sqrt{(\Delta C / C)^2 + (\Delta B / B)^2}$

$\Delta D = D\sqrt{((\Delta A^2 + \Delta B^2)/ (A-B)^2) + (\Delta B/B)^2}$

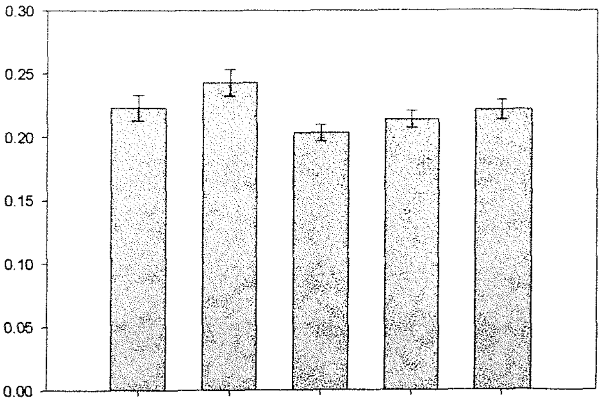
Results

Plant growth

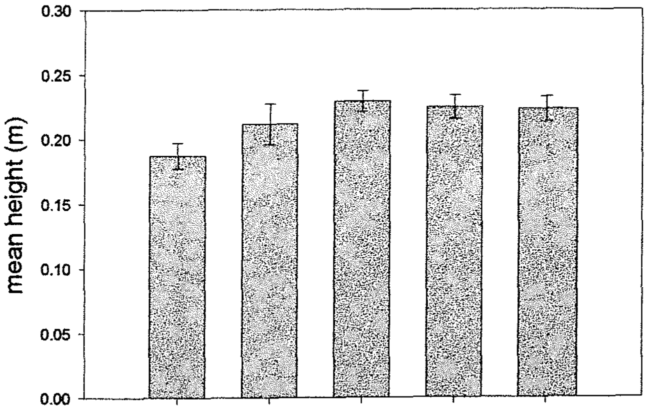
In 1996 and 1997 there were no significant changes to the heights of the *S.anglica* treatment plots (Figure 4.3 (i) and (ii)). In 1998 (Figure 4.3 (iii)). there were significant differences between treatment groups (ANOVA, P=0.002). The height of plants in the up marsh transplants with neighbouring growth intact was significantly different from that in all other treatment groups. There were no other significant differences between groups (Table 4.2). This suggests that the presence of neighbouring plant growth would be detrimental to the success of *S. anglica* plants colonising the upper marsh, but also indicates that *S.anglica* can succeed in the physical conditions there if biotic interactions are reduced.

Table 4.2. *S.. anglica* transplants, analysis of mean heights at growth maximum, 1998, All Pairwise Multiple Comparison Procedures (Tukey Test).

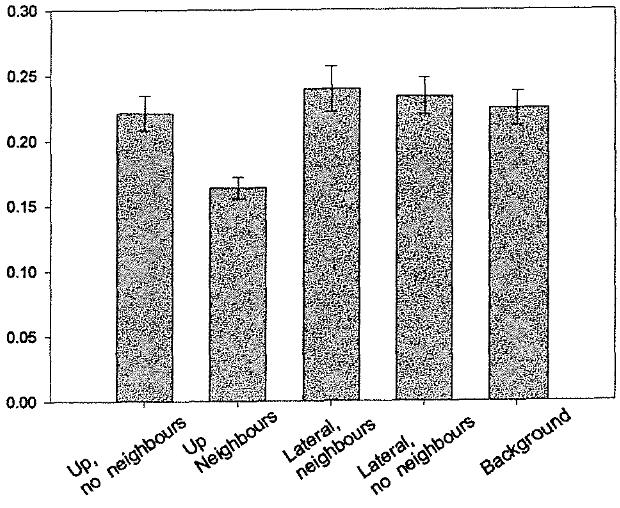
Comparison	**p**	**q**	**P**	**P<0.05**
Lateral control no neighbours vs. Up marsh, no neighbours	5	5.542	0.003	Yes
Lateral control no neighbours vs. Up marsh, neighbours	5	1.335	0.878	No
Untransplanted vs. Lateral control, no neighbours	5	1.068	0.942	No
Lateral control, no neighbours vs. Lateral control, neighbours	5	0.401	0.999	No
Lateral control, neighbours vs. Up marsh, neighbours	5	5.141	0.006	Yes
Lateral control, neighbours vs. Up marsh, no neighbours	5	0.935	0.964	No
Untransplanted vs. Lateral control, neighbours	5	0.668	0.990	No
Untransplanted vs. Up marsh, neighbours	5	4.473	0.021	Yes
Untransplanted vs. Up marsh , no neighbours	5	0.267	1.000	No
Up marsh, no neighbours vs. up marsh, neighbours	5	4.206	0.035	Yes



(i) 1996



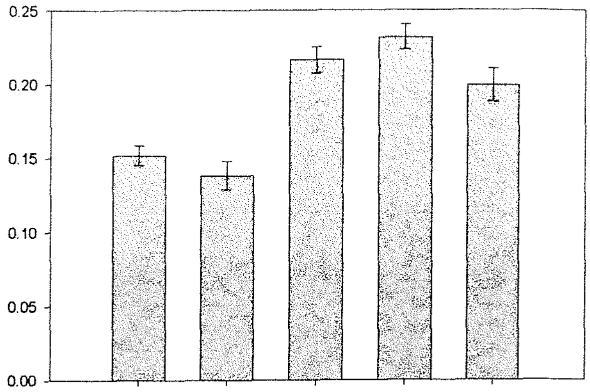
(ii) 1997



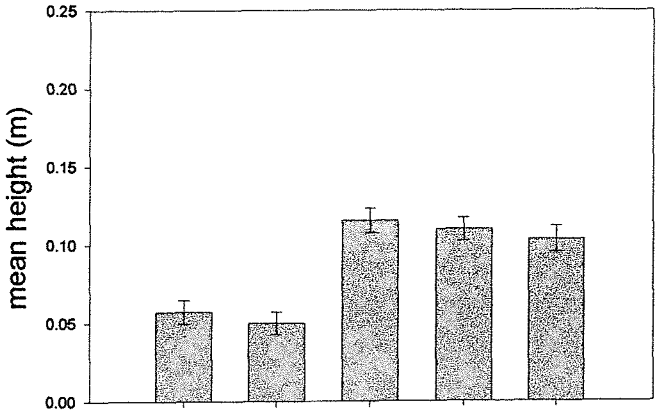
(iii) 1998

Figure 4.3 Mean height of *S. anglica* plants in transplant plots, Sims Wood Marsh, Beaulieu, September 1996, 1997 and 1998. (n=11, error bars represent +/- one standard error).

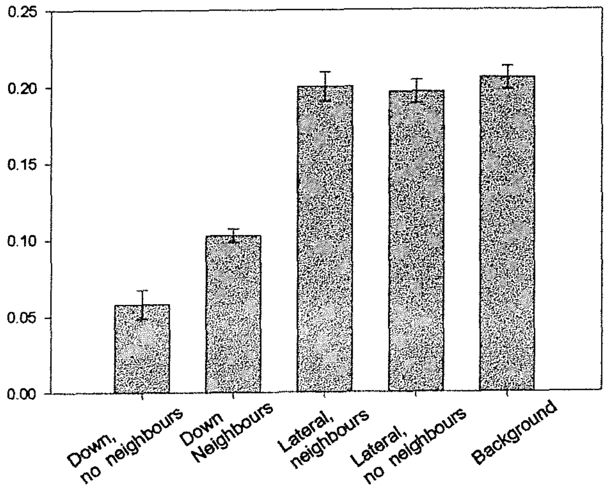
J. gerardii was also significantly affected by transplantation to a different zone: both down marsh treatments showed significantly reduced growth heights in 1996, 1997 and 1998 (Figures 4.4 (i) (ii) and (iii)). One way ANOVA of the data in each of the three years showed significant differences between treatments (P=<0.001). *Post-hoc* tests (Tukey tests) on each year's data showed that the two down marsh treatments were significantly different from the other within zone treatments (Tables 4.3, 4.4 and 4.5). The only deviation from this trend was that the 1996 down marsh transplants with neighbouring growth were not significantly different from the untransplanted "background" control treatment. Furthermore, in 1998 the down marsh transplant with no neighbouring plant growth grew to a significantly lower height than the down marsh transplant with neighbouring growth. This suggests that the presence of neighbouring plants adjacent to *J. gerardii* in the harsh physical conditions of the lower marsh zone does assist its growth, although conditions were unsuitable for it to survive in the long term with or without the presence of neighbouring plants.



(i) 1996



(ii) 1997



(iii) 1998

Figure 4.4 Mean height of *J. gerardii* plants in transplant plots, Sims Wood Marsh, Beaulieu, July 1996, 1997 and 1998. (n=11, error bars represent +/- one standard error).

Table 4.3 *J. gerardii* transplants, analysis of mean heights at growth maximum, 1996, All Pairwise Multiple Comparison Procedures (Tukey Test).

Comparison	p	q	P	**P<0.05**
Lateral control no neighbours vs. Down marsh, no neighbours	5	8.029	<0.001	Yes
Lateral control no neighbours vs. Down marsh, neighbours	5	4.666	0.015	Yes
Untransplanted vs. Lateral control, no neighbours	5	1.411	0.855	No
Lateral control, no neighbours vs. Lateral control, neighbours	5	1.018	0.951	No
Lateral control, neighbours vs. Down marsh, no neighbours	5	6.952	<0.001	Yes
Lateral control, neighbours vs. down marsh, neighbours	5	3.648	0.090	No
Untransplanted vs. Lateral control, neighbours	5	0.477	0.997	No
Untransplanted vs. Down marsh , no neighbours	5	5.820	0.001	Yes
Untransplanted vs. Down marsh , neighbours	5	2.871	0.267	No
Down marsh, no neighbours vs. down marsh, neighbours	5	3.091	0.202	No

Table 4.4 *J. gerardii* transplants, analysis of mean heights at growth maximum, 1997, All Pairwise Multiple Comparison Procedures (Tukey Test).

Comparison	p	q	P	**P<0.05**
Lateral control, neighbours vs. Down marsh, no neighbours	5	8.041	<0.001	Yes
Lateral control, neighbours vs. down marsh, neighbours	5	6.054	<0.001	Yes
Untransplanted vs. Lateral control, neighbours	5	1.711	0.746	No
Lateral control, no neighbours vs. Lateral control, neighbours	5	1.297	0.889	No
Lateral control no neighbours vs. Down marsh, no neighbours	5	6.668	<0.001	Yes
Lateral control no neighbours vs. Down marsh, neighbours	5	4.757	0.012	Yes
Untransplanted vs. Lateral control, no neighbours	5	0.521	0.996	No
Untransplanted vs. Down marsh , no neighbours	5	5.516	0.003	Yes
Untransplanted vs. Down marsh , neighbours	5	3.844	0.065	No
Down marsh, no neighbours vs. down marsh, neighbours	5	1.634	0.776	No

Table 4.5 *J. gerardii* transplants, analysis of mean heights growth maximum, 1998, All Pairwise Multiple Comparison Procedures (Tukey Test).

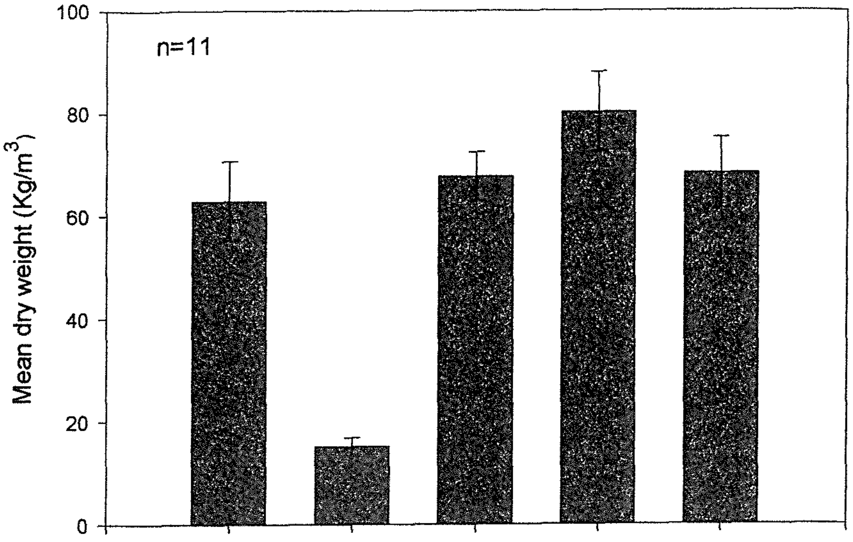
Comparison	**p**	**q**	**P**	**P<0.05**
Untransplanted vs. Down marsh , no neighbours	5	18.585	<0.001	Yes
Untransplanted vs. Down marsh , neighbours	5	12.223	<0.001	Yes
Untransplanted vs. Lateral control, no neighbours	5	1.082	0.940	No
Untransplanted vs. Lateral control, neighbours	5	0.649	0.991	No
Lateral control, neighbours vs. Down marsh, no neighbours	5	17.899	<0.001	Yes
Lateral control, neighbours vs. down marsh, neighbours	5	11.574	<0.001	Yes
Lateral control no neighbours vs. Down marsh, no neighbours	5	0.433	0.998	No
Lateral control, no neighbours vs. Lateral control, neighbours	5	17.441	<0.001	Yes
Lateral control no neighbours vs. Down marsh, neighbours	5	11.141	<0.001	Yes
Down marsh, no neighbours s vs. down marsh, neighbours	5	5.650	0.002	Yes

Harvested Biomass

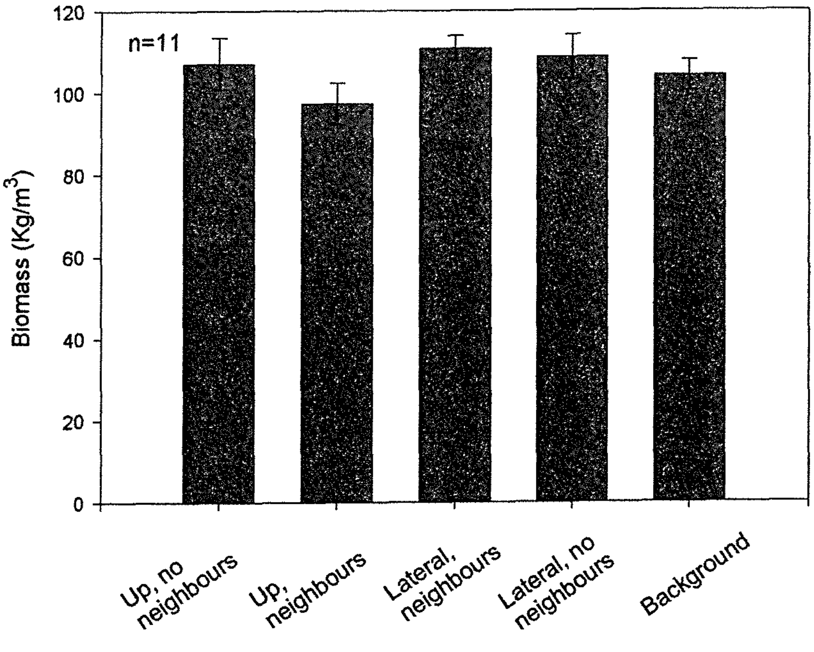
Figure 4.5 (i) and (ii) show the above and below ground biomass for the *S. anglica* transplants at the final harvests in summer 1998. There are significant differences between above ground biomass values for the different groups (Kruskal-Wallis One Way ANOVA on Ranks, P<0.001). Multiple Comparison Procedures (Dunn's Test) shows that the up marsh transplants with neighbouring plant growth intact are significantly different from all other treatments, but that there are no differences between the other treatment groups (Table 4.6). There were no significant differences in below ground biomass (Figure 4.5 (ii)) although the mean value for the up marsh transplant with neighbours was less than all other treatment groups (ANOVA, P=0.353).

Table 4.6 *S. anglica* transplants above ground biomass (1998 harvests): All Pairwise Multiple Comparison Procedures (Dunn's Method).

Comparison	**P<0.05**
Lateral control no neighbours vs. Up marsh, neighbours	Yes
Lateral control no neighbours vs. up marsh, no neighbours	No
Lateral control, no neighbours vs. Lateral control, neighbours	No
Untransplanted vs. Lateral control, no neighbours	No
Untransplanted vs. up marsh , neighbours	Yes
Untransplanted vs. up marsh , no neighbours	No
Untransplanted vs. Lateral control, neighbours	No
Lateral control, neighbours vs. up marsh, neighbours	Yes
Lateral control, neighbours vs. up marsh, no neighbours	No
Up marsh, no neighbours vs. up marsh, neighbours	Yes



(i) above ground



(ii) below ground

Figure 4. 5. Biomass of *S. anglica* transplant plots, Sims Marsh, Beaulieu (harvested September 1998). Error bars represent +/- one standard error.

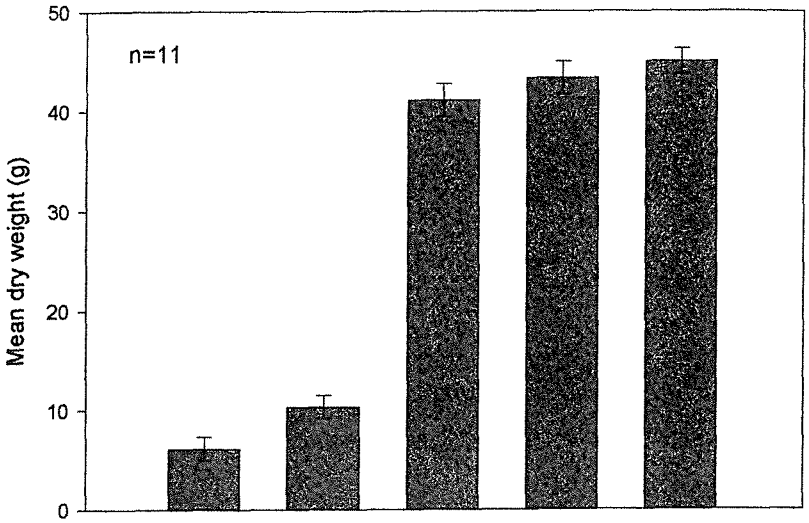
The *J. gerardii* transplants (Figure 4.6 (i) and (ii)) also show changes due to the treatments. There were significant changes in above ground biomass between treatment groups (ANOVA, P<0.001). A Tukey Test showed that the above ground biomass of both down marsh treatment groups (with and without neighbours) was significantly different from the other groups (Table 4.7). Below ground biomass (Figure 4.6 (ii)) was significantly different between treatment groups (ANOVA P=0.002). A Tukey Test showed that the below ground biomass of the down marsh treatment group without neighbours was significantly different from the other groups (P<0.050) (Table 4.8).

Table 4.7 *J. gerardii* transplants, above ground biomass (1998 harvests), All Pairwise Multiple Comparison Procedures (Tukey Test).

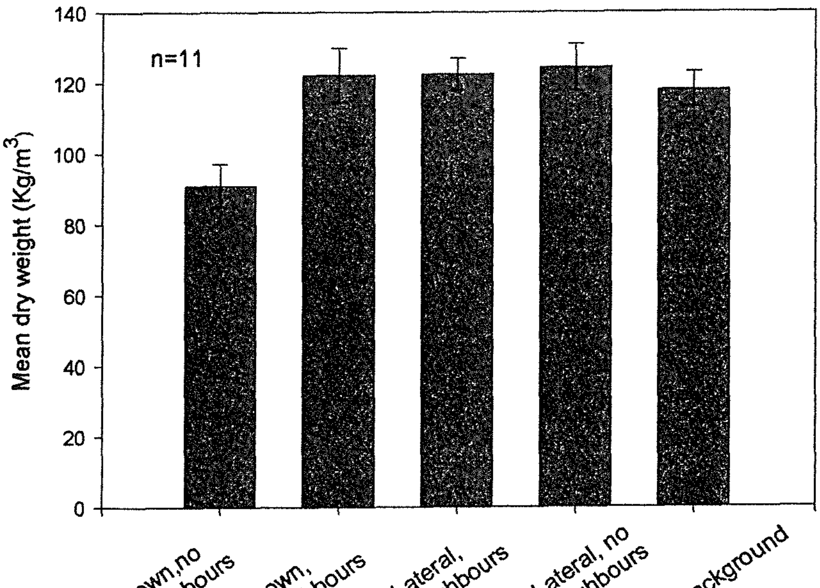
Comparison	p	q	P	**P<0.05**
Untransplanted vs. Down marsh , no neighbours	5	27.386	<0.001	Yes
Untransplanted vs. Down marsh , neighbours	5	24.432	<0.001	Yes
Untransplanted vs. Lateral control, no neighbours	5	2.712	0.322	No
Untransplanted vs. Lateral control, neighbours	5	1.166	0.922	No
Lateral control, neighbours vs. down marsh, no neighbours	5	26.220	<0.001	Yes
Lateral control, neighbours vs. down marsh, neighbours	5	23.266	<0.001	Yes
Lateral control, no neighbours vs. Lateral control, neighbours	5	1.546	0.809	No
Lateral control no neighbours vs. down marsh, no neighbours	5	24.674	<0.001	Yes
Lateral control no neighbours vs. down marsh, neighbours	5	21.720	<0.001	Yes
Down marsh, no neighbours vs. down marsh, neighbours	5	2.954	0.241	No

Table 4.8 *J. gerardii* transplants, below ground biomass 1998 harvests, All Pairwise Multiple Comparison Procedures (Tukey Test).

Comparison	p	q	P	**P<0.05**
Lateral control no neighbours vs. down marsh, no neighbours	5	5.382	0.004	Yes
Untransplanted vs. Lateral control, no neighbours	5	1.020	0.951	No
Lateral control no neighbours vs. down marsh, neighbours	5	0.342	0.999	No
Lateral control, no neighbours vs. Lateral control, neighbours	5	0.287	1.000	No
Lateral control, neighbours vs. down marsh, no neighbours	5	5.095	0.006	Yes
Untransplanted vs. Lateral control, neighbours	5	0.733	0.985	No
Lateral control, neighbours vs. down marsh, neighbours	5	0.0546	1.000	No
Down marsh, no neighbours vs. down marsh, neighbours	5	5.041	0.007	Yes
Untransplanted vs. Down marsh , neighbours	5	0.678	0.989	No
Untransplanted vs. Down marsh , no neighbours	5	4.363	0.026	Yes



(i) above ground



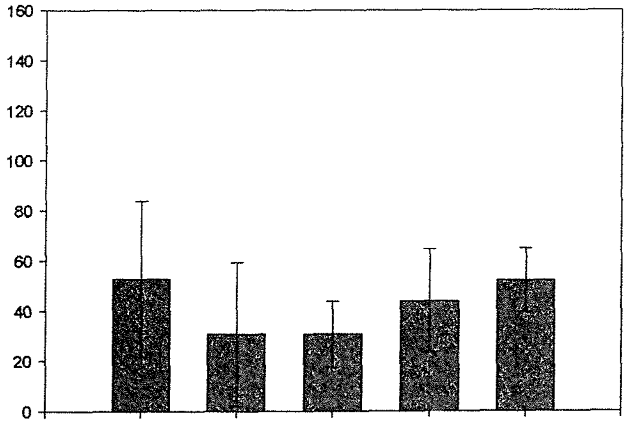
(ii) below ground

Figure 4.6 Biomass of *J.gerardii* transplant plots,
Sims Marsh, Beaulieu (harvested July 1998). Error bars represent +/- one standard error.

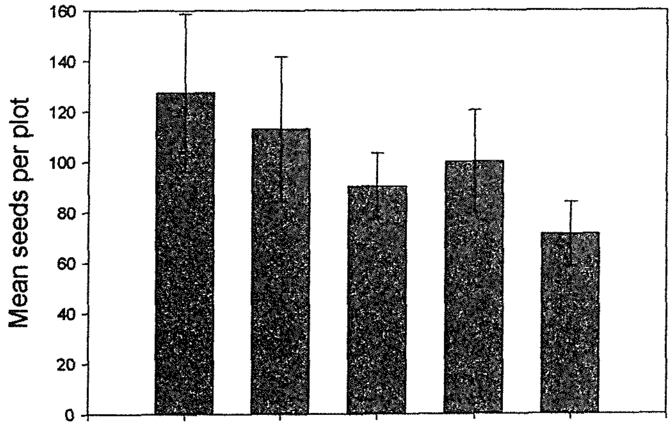
Overall, the clearest changes have taken place in above ground biomass. *S. anglica* biomass in the transplants up the marsh with neighbouring growth is significantly reduced, probably due to competition for light with other plants already established the upper marsh zone (such as *J. gerardii*), which start to grow earlier in the year. This is explored further in the Discussion section. The reduction in *J. gerardii* biomass in both down marsh treatments is likely to be due to its poor tolerance to the physical stresses associated with regular tidal inundation at lower marsh levels. Changes in below ground biomass are likely to be less clear because of residual biomass that was accumulated before transplanting.

Seed production

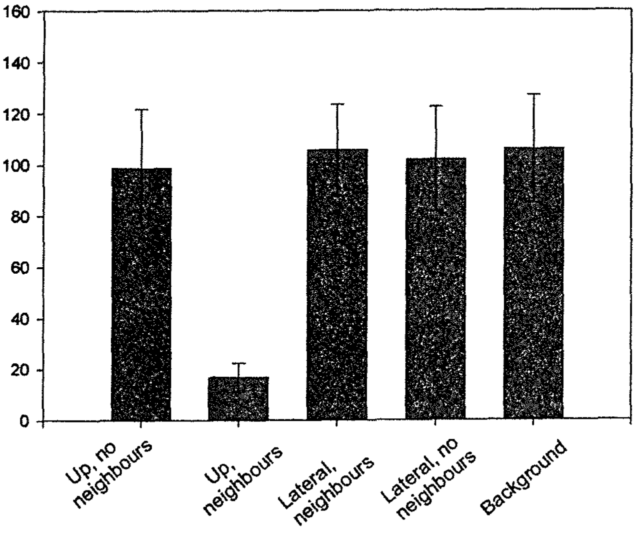
Figures 4.7 (i), (ii) and (iii) shows the annual seed production of the *S. anglica* plots in each growing season. There were no significant differences between treatments in 1996 and 1997. In 1998 there was a significant difference in seed production (ANOVA, P=0.005) between treatment types. *Post-hoc* tests showed that there was a significant reduction in seed production in the up marsh transplant with neighbours (Tukey Test, Table 4.9), but no other differences between treatments. This suggests that *S. anglica* is capable of growing in the physical environment of the upper marsh, but that biotic interactions with neighbouring plants limit its reproductive success at that level.



(i) 1996



(ii) 1997



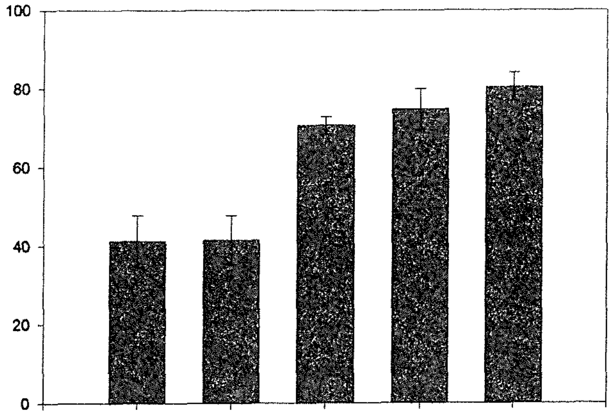
(iii) 1998

Figure 4.7. Annual seed production of *S. anglica* transplant plots. Sims Marsh , Beaulieu, 1996-1998. Data based on seeds counts on 10 randomly selected plants in each transplanted plot. (n=11, error bars represent +/- one standard error).

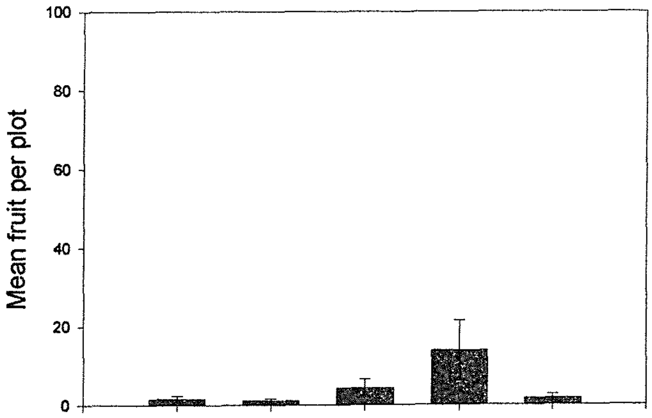
Table 4.9 *S. anglica* transplants, seed production, 1998, All Pairwise Multiple Comparison Procedures (Tukey Test).

Comparison	p	q	P	P<0.05
Untransplanted vs. up marsh , neighbours	5	4.761	0.012	Yes
Untransplanted vs. up marsh , no neighbours	5	0.393	0.999	No
Untransplanted vs. Lateral control, no neighbours	5	0.214	1.000	No
Untransplanted vs. Lateral control, neighbours	5	0.0146	1.000	No
Lateral control, neighbours vs. up marsh, neighbours	5	4.746	0.013	Yes
Lateral control, neighbours vs. up marsh, no neighbours	5	0.379	0.999	No
Lateral control, no neighbours vs. Lateral control, neighbours	5	0.199	1.000	No
Lateral control no neighbours vs. up marsh, neighbours	5	4.547	0.019	Yes
Lateral control no neighbours vs. up marsh, no neighbours	5	0.180	1.000	No
Up marsh, no neighbours vs. up marsh, neighbours	5	4.368	0.026	Yes

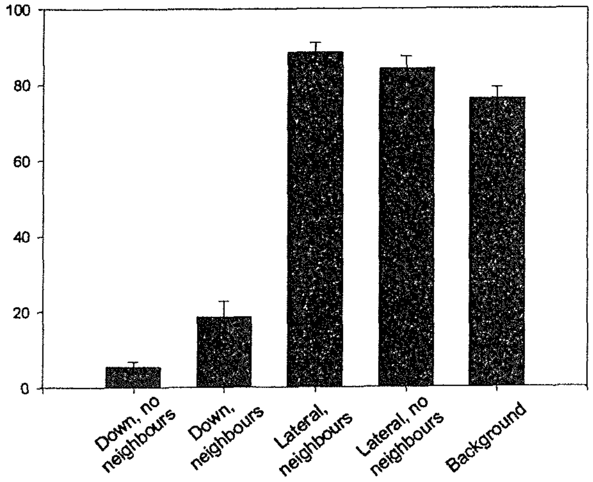
Figure 4.8 (i), (ii)and (ii) shows the fruit production in *J. gerardii* transplant plots in each growing season (1996, 1997 & 1998). There was very low fruit yield in any of the plots in 1997. There were storms in spring 1997 and it is possible that these disrupted plant growth and seed production. There were no significant differences between treatment types in 1997 (Kruskal Wallis- one way ANOVA, P=0.882). However there were changes in fruit production in down marsh transplants in both 1996 and 1998. In 1996 there were significant differences between treatment groups (ANOVA. P=<0.001). A *post-hoc* Tukey Test showed that both down marsh transplant groups (with and without neighbours) were significantly different from the other treatments, but there was no difference between the down marsh transplants themselves (Table 4.10).



(i) 1996



(ii) 1997



(iii) 1998

Figure 4.8. Annual fruit production of *J. gerardii* transplant plots. Sims Marsh , Beaulieu, 1996-1998. Data based on fruit counts on 10 randomly selected plants in each transplanted plot. (n=11, Error bars represent +/- one standard error).

Table 4.10 *J. gerardii* transplants, fruit production, 1996, All Pairwise Multiple Comparison Procedures (Tukey Test).

Comparison	p	q	**P**	**P<0.05**
Untransplanted vs. Down marsh , no neighbours	5	7.751	<0.001	Yes
Untransplanted vs. Down marsh , neighbours	5	7.697	<0.001	Yes
Untransplanted vs. Lateral control, no neighbours	5	1.942	0.647	No
Untransplanted vs. Lateral control, neighbours	5	1.133	0.929	No
Lateral control, neighbours vs. Down marsh, no neighbours	5	6.618	<0.001	Yes
Lateral control, neighbours vs. down marsh, neighbours	5	6.564	<0.001	Yes
Lateral control, no neighbours vs. Lateral control, neighbours	5	0.809	0.979	No
Lateral control no neighbours vs. Down marsh, no neighbours	5	5.808	0.001	Yes
Lateral control no neighbours vs. Down marsh, neighbours	5	5.754	0.002	Yes
Down marsh, no neighbours vs. down marsh, neighbours	5	0.0539	1.000	No

In 1998 there were also significant reductions in fruit production between treatments (Kruskal-Wallis one way ANOVA on ranks, P=<0.001). There were significant reductions in fruit yield in both down marsh treatments compared with the within zone treatments although Dunn's Test did not fully resolve the differences between individual treatments (See Table 4.11). The *post-hoc* test does not indicate a difference between fruit production in the two down marsh transplants themselves.

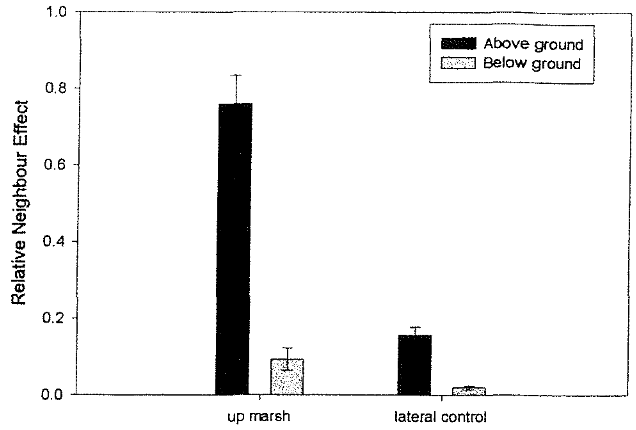
Table 4.11 *J. gerardii* transplants, fruit production, 1998, All Pairwise Multiple Comparison Procedures (Dunn's Test).

Comparison	**P<0.05**
Lateral control no neighbours vs. down marsh, no neighbours	Yes
Lateral control no neighbours vs. down marsh, neighbours	Yes
Untransplanted vs. Lateral control, no neighbours	No
Lateral control, no neighbours vs. Lateral control, neighbours	No
Lateral control, neighbours vs. down marsh, neighbours	Yes
Lateral control, neighbours vs. down marsh, no neighbours	Yes
Untransplanted vs. Lateral control, neighbours	No
Untransplanted vs. Down marsh , no neighbours	Yes
Untransplanted vs. Down marsh , neighbours	No
Down marsh, no neighbours vs. down marsh, neighbours	No

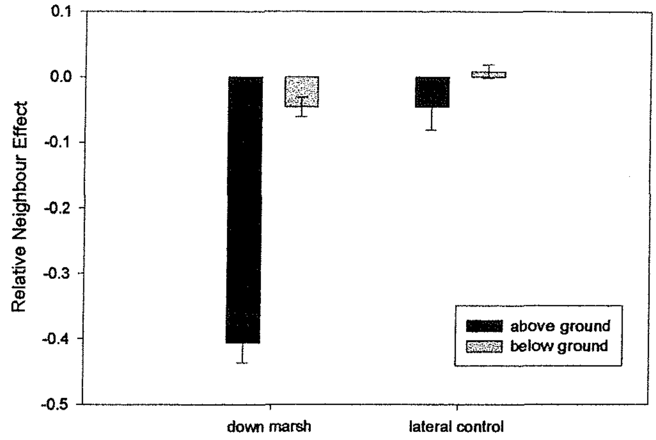
Relative Neighbour Effect

Figure 4.9 shows the relative neighbour effect indices for the two species in the upper and lower marsh. There are positive RNE scores for *S. anglica* in the upper marsh, indicating that *S. anglica* (Figure 4.9(i)) faced strong competition from neighbouring plant growth, that has particularly large impact on above ground biomass. There were also small competitive effects on *S. anglica* in the lower marsh, and most of this would be intraspecific as it is very much the dominant species in that zone.

J. gerardii transplants showed strongly negative RNE in the lower marsh (Figure 4.99(ii)). This is evidence that neighbouring plant growth assists the success of the transplants moved to the lower marsh.



(i) *S. anglica*



(ii) *J. gerardii*

Figure 4.9. Plant interactions in transplant plots. (i) *S. anglica*, (ii) *J. gerardii* Relative Neighbour Effects (mean RNE) index for above and below ground biomass from harvests in 1998. Error bars show +/- one standard error, adjusted for propogation of errors.

Discussion

Limitations of the experiment

The results of this experiment are mostly unequivocal: the project design and the use of a range of treatment types and controls has produced some clear-cut results including strong evidence positive interactions both between conspecifics and between different species of saltmarsh plants.

However, in assessing the factors which affect zonation patterns, it would be preferable to measure variables along a complete transect from high marsh to low marsh. This experiment only gathered data in the lower part of the upper marsh, and the lower marsh, leaving the middle part of the marsh (where *S. anglica* is present but less frequently than at lower levels) untested. The discussion below explores the issue of a continuum of interactions between plants, operating along a gradient of physical harshness down the marsh, and any inferences about the middle part of these continua must remain speculative until more work of this kind is carried out on a finer scale. In addition, there are always limitations to any experiment carried out on a single site.

Furthermore, recent work (e.g. Levine *et al* 1998) has added to our knowledge of the role of nutrients in setting zonation patterns in saltmarshes. The results of this study are discussed below in the context of this work, but it would be interesting to explore this further in the field.

Relative importance of physical and biotic factors

My experiments have gone some way to characterise the importance of physical and biotic factors in setting the zonation patterns of *S. anglica* and *J. gerardii.*

The results show that *S. anglica* is poorly–equipped to deal with the competitive environment in the upper marsh: after three growing seasons in the presence of neighbouring growth, seed production, above ground biomass and maximum height were all significantly reduced. (Figures 4.3, 4.5 & 4.7). Had the plots been left for another growing season it seems possible that some of the *S. anglica* transplants to the upper marsh, with neighbouring growth, would have died. The RNE data (Figure 4.9) confirms the importance of competition, with high values given for the upper marsh transplants. A *Spartina* transplant plot with surrounding competition removed, still growing well after three years, is shown in Appendix 3.1 Plate 6. A positive RNE score was also given in the lower marsh, so competition (mainly intraspecific competition in this zone) could also limit plant success at lower marsh levels. This may be a small but important factor in the die back process (Goodman and Williams 1961, Gray and Pearson 1984), which is still not fully understood. Dense stands of *S. anglica* are observed to degenerate, and this has been ascribed to reducing conditions around the roots. If the plants were additionally stressed by intraspecific competition (albeit at a fairly low level) this could also contribute to the degeneration of the *S. anglica* in areas affected by die back.

S. anglica is a fast-growing, vigorous competitor within its own zone, utilising its halophytic characteristics to tolerate the saline conditions, its fibrous architecture to reinforce it against tidal forces, and its runner ('guerrilla') root morphology to colonise bare patches of substrate which are not fully stabilised (Scholten & Rozema 1990, Thompson *et al* 1991). When it is transplanted up the marsh these characteristics do not give it any advantage over other plant species. Conditions are usually less saline (except in bare patches), tidal influences are reduced and many of the resident species (e.g. *J. gerardii*) have dense root mats which its runners cannot penetrate. Furthermore, its C4 physiology adds to its disadvantages with respect to its potential C3 competitors. Indeed, the parent species *S. maritima* is at the extreme northern limit of its range in the British Isles (Hubbard 1992). The early seasonal growth of *S. anglica* is limited by low temperatures (C4 is more typical of tropical plants) and leaf growth is slow below 9-10 °C, so it is slow to emerge compared with most upper saltmarsh plants (Long 1983). *S .anglica* often does not start growing until mid-May in southern England, by which time *J. gerardii* is already close to maximum height, as are other high marsh plants such as *A. pungens*. There is a clear parallel here with the relationship between *J. gerardii* and *D. spicata* identified by Bertness (1991)

Access to light for photosynthesis is probably the driving force in limiting the success of *S. anglica* in the upper marsh but one other factor, that of nutrient uptake, which I did not quantify in this experiment, is also probably of importance. *S. anglica* has been shown to grow well in non-saline conditions (Long & Mason 1983, pp. 47-48). In the field, *S. anglica* is only usually present in the upper marsh in bare patches or pools (Appendix 3.1, Plates 6 and 7). The upper marsh at the study site is characterised by a thick and almost continuous blanket of vegetation, and is not disturbed at all by human beings. I did find that *S. anglica* had colonised a bare patch in a poorly drained area generated, in part, by my own trampling when tending the experimental plots (Appendix 3.1, Plate 7). *S. anglica* does not produce much fertile seed in most years, and tends to propagate by vegetative fragments being carried to suitable areas for them to take hold (Caldwell 1957). It can probably take advantage of bare patches in the upper marsh because such gaps are often rendered hypersaline by evaporation (Bertness & Hacker 1984). Hypersaline conditions limit the initial success of upper marsh plants such as *J. gerardii*, so initially *S. anglica* will be able to succeed. As *S. anglica* grows, however, the soil conditions will become less saline as *S. anglica* excretes salt through its leaves, and surface insolation will be reduced by shading. Surrounding growth of upper marsh species will develop by the bare patch and, at the same time, below ground invasion, through the phalanx of root mats, will also occur. *S. anglica* will be thus be outcompeted in just a few growing seasons.

The *J. gerardii* transplants have also shed some light on the factors that set the bounds of its distribution on a marsh. The results show a reduction in success of plants transplanted down the marsh (as measured by seed production and height) in the first growing season (1996), that appears to deteriorate further with time (Appendix 3.1, Plates 9 and 10). By the third growing season (1998), when the plots were harvested, there was an interesting differentiation between the two down marsh transplant treatment types. While both down marsh treatments had significantly reduced success compared with the within zone transplants and the controls (Fig 4.4, 4.6 and 4.8), by all measures by 1998, the below ground biomass and maximum heights of plots with neighbouring growth, were significantly larger than the plots with neighbouring growth removed. The strongly negative RNE index scores for both above and below ground biomass confirm the view that facilitation is a key factor here in extending the lower limit of *J. gerardii* within the zonation of a salt marsh. The RNE scores for *J. gerardii* in the upper marsh are close to zero, which indicates that biotic factors (competition & facilitation) are less important to *J. gerardii* plants growing in their 'optimum' conditions.

J gerardii simply does not have the physiological ability to tolerate regular, deep inundation and the physical and chemical stresses that come with it. Indeed, many of the plants in the down marsh treatment plots were in very poor condition by 1998 and probably would not have survived much longer. However, facilitation by surrounding plants seems to have helped it to survive at lower levels. The lower below ground biomass in the plots without neighbours suggests that these plots were expending more resources just to survive, and they had little left for growth or production of propagules.

The experiment has reaffirmed the validity of the CoPE concept as a theoretical explanation for zonation studies, as suggested by Bockelmann and Neuhaus (1999). Abiotic factors do control the lower distribution boundaries along gradients of increasing physical stress. I have shown, however that positive interactions between neighbouring plants, in this case simply through plants gaining some physical protection from neighbours, is important in extending the lower limit of some intertidal species by ameliorating the harsh conditions. This confirms the early ideas of Clements (1916) and adds to the evidence of other positive interactions in saltmarshes produced by Bertness and Hacker (1994) and Castellanos *et al* (1994).

The CoPE concept also suggests that at upper limits in a saltmarsh competition is of more importance. In effect what is suggested here is that biotic interactions switch at some point down a gradient of physical stress from negative (competition) to positive (facilitation), It would be an interesting exercise to identify the position of this boundary, if it exists, although in the case of this experiment I have at least identified biotic interaction gradients ranging from neutral to highly positive (in the case of *J. gerardii*) and from highly negative to slightly negative (*S. anglica*). This expansion of the concept is shown schematically in Figure 4.10. This scheme could be related to Grime's (1979) ideas on plant strategies. He suggested that competitive plants would dominate where conditions for plant growth are generally favourable, that is disturbance is rare and resources are plentiful. A tolerant strategy (e.g. halophyte physiology in saltmarshes) would assist plants in more harsh or environments. However, the role of resources on this continuum may not be as clear-cut as this (see below).

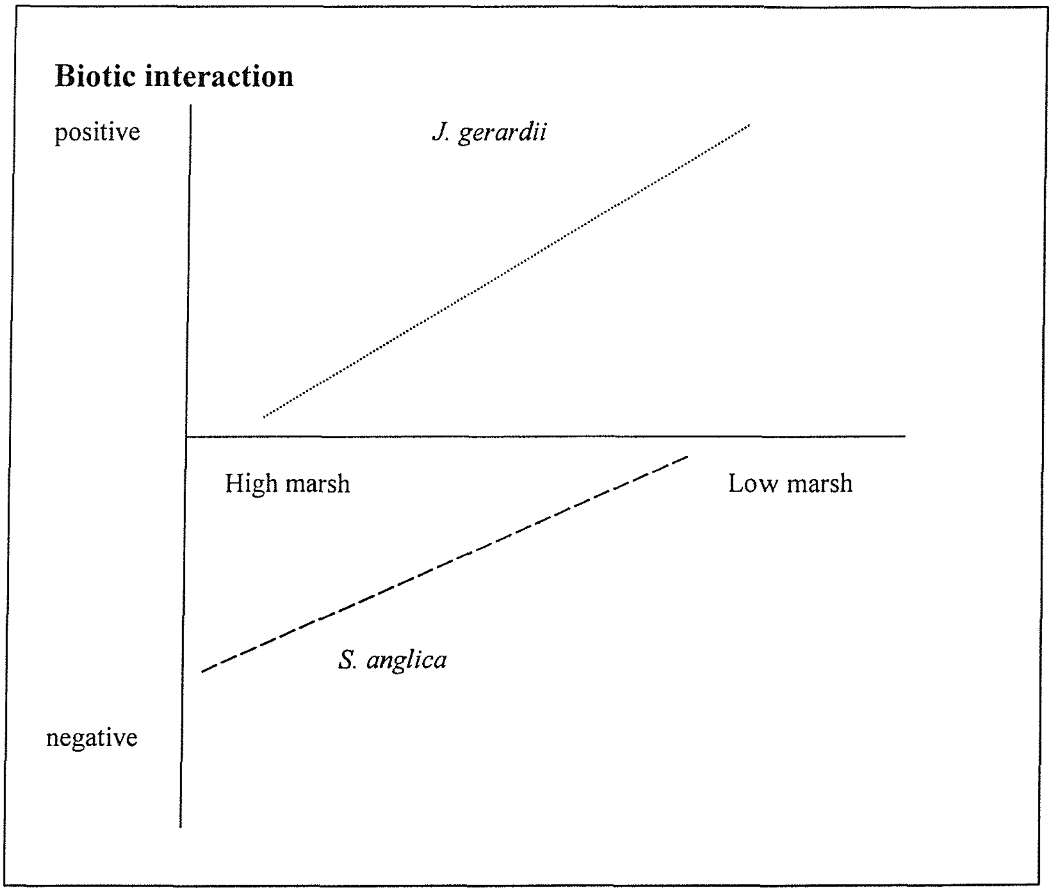


Figure 4.10. Schematic representation of the importance of biotic interactions of *J. gerardii* and *S. anglica* along a marsh gradient. The biotic interactions investigated in this experiment (competition with neighbouring plants for above ground space and light), as measured by the Relative Neighbour Effect, were used for this representation.

Light, nutrients and plant zonation

Grime (1979) suggested that the competitive strategy would lead to dominance in a crowded population living in an environment that was undisturbed and rich in resources. The upper salt marsh plant community is crowded, and the habitat is relatively undisturbed (except by, for example, the occasional large piece of timber debris or tidal wrack rafted onto the marsh by storm tides). However, resources are not as plentiful as might be expected. There is clearly competition for light, and this seems to be a driving factor in excluding *S. anglica* from the upper marsh. Indeed, the dominance of *J. gerardii* in this zone is in part due to its early emergence relative to its competitors and the thick canopy of vegetation that it produces, which will act to prevent much establishment of seedlings below it. Immediately above the *J. gerardii* community is a dense *A. pungens* community, which in which the dominant grass has a tall and persistent canopy which shades out almost all other plants.

Light is only one resource for which there is competition. Levine *et al* (1998) hypothesised that light dictates the competitive outcome among marsh plants where nutrients are not a limiting factor, but that where nutrients were added to a system, competitive hierarchies were disrupted. They found that when nutrient levels were enhanced the zonation patterns broke down, and the poor competitors which survived, through strategies which assist survival in harsher conditions, were able to outcompete the 'resident' competitors. The key to this could be root morphology. The dense and fine root mat *J. gerardii* (which also gives other competitive advantages in excluding runners of potential competitors), and the overall high below ground biomass, that is produced by *J. gerardii* probably acts as a much more efficient absorber of nutrients than the runners of *S. anglica*, that are designed more for spread and survival within a less stable environment.

Levine *et al* (1998) went on to suggest that addition of nitrogen to a saltmarsh ecosystem could disrupt entire zonation patterns. Growth of salt marsh plants has been shown to be nitrogen-limited (Valiela and Teal 1974). Some plants with halophyte characteristics may increase their salt-tolerance by producing osmotically active nitrogen-based compounds: addition of nitrogen to the system allows plants to use some of these extra resources for growth (Stewart and Lee 1974, Van Wijnen and Bakker 1999). Bertness and Ellison (1987) suggested that interspecific competition was a major determinant of typical zonation patterns in salt marsh plant communities, so if competitive relations were altered by addition of available nitrogen the whole nature of saltmarsh ecosystem could change. The established problem of eutrophication in UK rivers and estuaries (Moss 1998) could already be leading to changes in the 'natural' zonation patterns we see through enabling Grime's 'toleraters' to become 'competitors'. The Beaulieu Estuary is relatively unpolluted (Environment Agency 1999, Hydes 2001), as it drains an area with little intensive agriculture and a small population; but there are already estuaries in southern England which are heavily eutrophic, and much of the intertidal at these sites are dominated by low marsh species such as *S. anglica.* Langstone Harbour, Hampshire, and Chichester Harbour, Sussex, are two good examples of this (Haynes 1982, Cassels, unpublished, 1997). This could, of course, be seen as a somewhat speculative generalisation. The wide expanses of *S. anglica* marshes at these locations may well originate from other factors: coastal squeeze through the effects of rising sea levels, coastal defence and reclamation has already led to a reduction in suitable habitat for upper marsh communities (Pye and French 1993). However, the conservation impacts of these changes, especially if they are pollution-driven, are only too clear.

Conclusions

Returning to the original hypotheses of this experiment:

"Transplantation to the upper marsh does not affect the success of S. anglica."
This hypothesis has clearly been disproved: in an unmanipulated upper marsh *S. anglica* is outcompeted by other species which are better adapted to the competitive conditions.

"Transplantation to the lower marsh does not affect the success of J. gerardii.*"*
J. gerardii. cannot tolerate the harsh conditions in the lower marsh, although the presence of neighbouring plants seems to prolong its survival at lower levels. The hypothesis is rejected.

"Interactions between neighbouring plants do not affect success of S. anglica *or* J. gerardii."
The experiment has demonstrated the importance of positive interactions between neighbouring plants. These appear to operate to extend the downward limit of plants from the upper marsh (*J.gerardii*). Intraspecific competition affects the success of *S. anglica* at higher marsh levels, and may set its upper limit. The hypothesis is rejected.

CHAPTER 5

DISCUSSION

The experiments that are the basis of this thesis have investigated elements which contribute to the spatial patterning observed in saltmarshes, namely biotic interactions between plants, the role of new species in perturbing existing plant communities and the importance of grazing pressure. Each of these can have effects that can operate on varying temporal and spatial scales. Saltmarshes are 'long term' ecosystems: the marsh systems in the Solent region have been characteristic of the area since the last Ice Age (West 1980, Tomalin 2000a), although their present extent is now much less (around 10%) than in the past (Tubbs 1999, Associated British Ports 2000). The physical factors which have shaped them have operated on widely varying timescales, both large (e.g. progressive sea level change 10,000 years) and small (e.g. a storm event or a landslip, or a single daily tidal cycle) (Long and Tooley 1995). This thesis has focussed on several biological factors that can be viewed in the same way: they can operate over varying scales, both temporally and spatially. The effects of these combined, multiple, fluctuating factors (both physical and biological) create and maintain the diverse and heterogeneous natural systems that are the coastal marshes of Southern England, as elsewhere in the world.

In this final discussion I expand on the main themes that recur throughout the thesis: spatial pattern, grazing and diversity and the impact (and future) of *Spartina anglica*.

Pattern and process in a changing world

Saltmarshes are characteristically zoned, in a similar way to other ecological systems which exist on physical gradients, such as rocky shores (Raffaelli and Hawkins 1996) or montaine communities (Whittaker and Niering 1975). These patterns are largely set by the variation in physical factors, such as tidal inundation (Jeffries 1977), exposure (Gray 1992), or salinity (Gray and Scott 1977b).

However, the typical zonation pattern can often only be observed over a marsh system as a whole. A remotely sensed image may be used to demonstrate clear changes in vegetation zones as communities shift from halophyte to terrestrial away from the shore, but to an observer standing on that shore the patterns can be less immediately obvious (Appendix 3.1, Plate 11). Pioneer plants such as *Salicornia* spp. may dominate the lowest part of the marsh, but they may also be found in disturbed patches in the upper marsh (Bertness and Ellison 1987, Cassells unpublished 1997); a lower marsh species, such as *S. anglica*, may dominate extensive areas of the lower marsh, but will also be present on creek edges and within pools at higher levels (Hill 1990) (Appendix 3.1, Plate 6); tussocky growth in the lower marsh may be colonised by species more representative of higher levels (Castellanos *et al* 1994); long lived terrestrial species, such as oaks, may be observed persisting above a non-terrestrial ground flora and tidal debris (Tomalin 2000b).

It has been established over the years that the physical factors are the main driving forces underlying the gross patterns (e.g. Gray 1992), but they act in concert with each other and with a range of lesser elements (both physical and biological) to determine the patterns within the marshes themselves. The relative importance of all of these factors is very hard to fully quantify. Some of the factors are continuous or, at least predictable, such as tides; but others can operate randomly and quite unpredictably. Examples include: a storm (Long and Tooley 1995); a piece of driftwood or tidal debris being deposited on the shore (Bertness and Ellison 1987) (Appendix 3.1, Plates 12 and 13); the chance arrival of a large flock of migrant grazing birds (Zacheis *et al* 2001); the anthropogenic (but nonetheless random) appearance of a new competitive plant species (Lambert 1964). Moreover, these factors can operate on small or large scales, within space and time, varying in intensity as they do so. Clearly this type of variation is not peculiar to either saltmarshes or other coastal ecosystems: the great diversity of natural life on earth is driven by this self-same combination of the predictable and the random. However, study of this within a system dictated fundamentally by largely measurable physical gradients allows us to understand more about the effects of the other factors involved.

The range occupied by a plant down the shore is the product of physical and biological factors. The study by Gray (1992) of the distribution of *S. anglica* clarified the over-riding importance of physical factors in setting the upper and lower limits (see Chapter 1). Prediction of these limits is possible with over 90% accuracy based on just four physical variables (spring tidal range, estuary area, fetch and latitude). However, it is the interaction between these variables and the other physical and biological variables, operating on all of the species present, which give the marsh system its fine grain patterning.

My transplant experiment in Chapter 4 identified both negative and positive interactions, both interspecifically, and intraspecifically, which helped to set the upper and lower limits of the two species investigated (*J. gerardii* and *S. anglica*). Competition has been emphasised, until recently, as an important biotic factor contributing to zonation patterns, but recognition of the role of positive interactions (e.g. the concept of facilitation) can be traced back to the earliest days of ecology as a science (Clements *et al* 1926). This has gained some attention recently, with saltmarshes proving to be useful environments for investigation (e.g. Bertness 1991, Castellanos *et al* 1994, Callaway and Pennings 2000); but also streamside communities (Levine, J.M. 2000), rocky shores (Leonard 2000) tundra (Sammul *et al* 2000), subalpine meadows (Callaway *et al* 2000) and deserts (Tielborger and Kadmon 2000). The effectiveness of a plant as a competitor will vary against the backdrop of the other factors operating upon it. Even within a small area of marsh there will be variations in tidal exposure, substrate organic or water content, salinity or the availability of above ground space and light. The success of a plant at a particular time and place will depend on the product of its own species-specific strategies and tolerances, its own abilities as dictated by its genotype, and the forces to which it is exposed (Grime, 1977, Gray and Scott 1980, Huiskes 1990).

These tolerances and abilities appear to be fixed: my own field observations would suggest that *Juncus gerardii* would always be successful at a boundary between the upper and middle marsh zones, but that it would be outcompeted at higher elevations and unable to survive harsher conditions lower down the marsh.

However, the environment is not unchanging. Each individual plant (and each generation of a species) will succeed or fail partly due to chance events, but also due to its effectiveness (or the effectiveness of individuals of that species) against the selective pressures applied to it (Endler 1986, Ridley 1993). The result of this will be gradually changing tolerances of a plant species to the physical and biological factors that set the zonation patterns. But of course, this is an 'arms race' and the other species competing for space and resources will also be battle hardened by continuing selective pressures (Endler 1986, Primack and Kang 1989). Genetic differentiation along physical gradients in salt marshes has received some attention to date: Antfingler (1981) found evidence of minor differences along salinity gradients; Davy and Smith (1985) found some evidence of genetic differentiation in different marsh communities. Gray and Scott (1980) suggested that much of the wide phenotypic variation of *Pu. maritima* in Britain is genetically determined, and that grazing has produced characteristic forms with a prostrate growth habit. Gray *et al* (1979) found a wider variation in forms of *Pu. maritima* in lower marsh sites compared with those in upper marsh communities. They suggested that this could be due to the more open canopy of the lower marsh allowing more different forms to persist, while only those with a more competitive (or on grazing marshes, grazing-tolerant) strategy could survive in the closed community at higher marsh levels.

It is possible, however, that competitive relations, plant success and hence zonation patterns could change if physical conditions themselves change more rapidly than the adaptive capacities of the species making up the zonation patterns. In the case of a short term, permanent event, such as a landslip, which immediately and permanently alters the physical system, new patterns will develop based on the tolerances of the species present or those capable of colonising the changed system. Some changes might be less abrupt but still quite rapid in onset and long-term. Scientific consensus is that we are in the midst of a period of rapid climate change, with regional temperatures set to rise by between 1.4°C and 5.8°C during the present century (Hulme 2000, www.epa.gov/globalwarming), with consequences for relative sea levels over much of the world. This could make a significant difference to the factors that currently set the limits for *S. anglica.* Gray's model (1992) included latitude as the second most important factor in setting the upper limit of *S. anglica*, but clearly latitude itself encompasses a range of physical variables, including temperature and climate. There is already a body of evidence suggesting that spring in the British Isles (Hossell *et al* 2000) and the Northern Hemisphere (Schneider and Root 1996; Schwartz and Reiter 2000) now starts earlier and is warmer than a few decades ago). If the spring and summer temperatures warmed conditions would become more favourable for the C4 metabolism of *S. anglica*, allowing it to grow with greater vigour, but also, crucially, earlier in the year (Long 1983). In Chapter 4, I suggested that the relatively late start to the annual growing season of *S. anglica* could be a major factor in its lack of competitive success at higher marsh levels. Upper marsh plants like *J. gerardii*, with a temperate C3 physiology (Long 1983) can emerge early and appear to gain a significant advantage over late emergers such as *S. anglica* by taking available above ground space and light. In a warmer world (or a warmer southern England), would *S. anglica* be able to extend its range up the marsh? In the context of rising sea levels (squeezing the upper marsh back) and warmer temperatures, will conditions favour *S. anglica* even more? This scenario, in the context of rising sea levels, was proposed by Huiskes (1990), who suggested that an extended and much less differentiated lower marsh, composed mostly of *S. anglica*, would result. I make some suggestions for possible futures for *S. anglica* towards the end of this chapter.

Grazing and pattern

Chapter 3 of this thesis studied the effects of excluding wild grazers from parts of a saltmarsh. The most obvious effects of grazers on coastal marshes are long term and operate over the scale of whole ecosystems (Reimold *et al* 1975). Extensive areas of saltmarsh in Western Britain have been grazed by domestic sheep and cattle for centuries, and this long term, high intensity grazing has generated and maintained marsh systems of low floral diversity which are dominated by a few grazing tolerant plants such as *Pu. maritima* (Gray 1972). In my work I have examined a marsh system which was grazed lightly by wild animals, and was relatively diverse compared with any domestically grazed marsh, of which there is only one in the Solent region, at the head of the Test estuary (Tubbs 1999). My experimental site (Gins Marsh) was on the banks of the Beaulieu Estuary in the New Forest, and the land use in this area has been well documented since the Norman invasion in the 11th century (Tubbs 1999). It is possible that most of the factors effecting the plant communities I studied here, over three growing seasons, had been largely unchanged for many decades; and that those communities have been resilient enough to recover from short term damage caused by, for example, the hard winter of 1963, or the disturbances caused by the embarkation for the D-Day landings in 1945 (although *S. anglica*, of course, has certainly produced significant long term changes). New Forest Commoners' animals have not been traditionally given access to the banks of the Beaulieu River, partly because of the hazardous mudflats, but also because most of the waterside is privately owned by the Beaulieu and Exbury Estates. Furthermore the palaeoecological evidence and documentary sources identified in Chapter 2 suggests that the area of upper marsh studied was already well established, and, perhaps, relatively biodiverse over a hundred years ago, before the local invasion of lower elevations by *Spartina*.

Most of my work was on marshes which were largely unchanged over a relatively long time-scale, on which there may have been consistent light grazing pressure from rabbits, hares, geese and deer for over a hundred years, or quite possibly much longer. In this context, exclusion of the grazers from small experimental plots produced quite striking results. The well-established plant community at Gins Marsh rapidly showed significant changes in structure, composition and diversity in just three growing seasons (with structural changes in just a few months (Figure 3.4); with signs that one of the characteristic species (*A. maritima*), was becoming out-competed by other species that had previously been suppressed by the low levels of grazing activity. Furthermore, evidence in the literature supports field observations that that these changes were likely to be quite persistent, as the nutritional quality of the plants diminishes with the structural changes which were taking place (Davy and Bishop 1981, Olff *et al* 1997, Rowcliffe *et al* 1998). This is an example of the short term removal of a long term factor leading to possible long term changes. At present the grazing exclosures are still in place and will remain so until the changes observed appear to have largely ceased. At that stage removal of the exclosure might be worthwhile, to examine the potential for the system to recover to its previous state.

Could a natural phenomenon have the same effects on the marsh plant communities as the exclosures? Instinctively it seems unlikely that the several species of grazers could be excluded or cease to use the marsh. Myximatosis and haemorragic viral disease have periodically reduced rabbit numbers in England, but they have usually recovered within a short time (Thomas 1963). Migratory geese are protected under the Wildlife and Countryside Act (1981) and the European Habitats Directive (European Union 1992), even though they are agricultural pests in some areas. However, my exclosure experiment suggests that even a relatively short period of reduced grazing could lead to long term changes to the plant community. Other work has confirmed the importance of wild grazers facilitating grazing for each other by grazing at different times of the year (Olff *et al* 1997). Furthermore human disturbance, in the context of the Solent, is an increasing threat. Pleasure-boating on the Beaulieu has grown rapidly in recent years, even during my brief period of fieldwork I have observed landowners with access to the shore extending existing jetties into large slipways for use by bigger boats, even on Gins Marsh itself, which is part of a National Nature Reserve. It is easy to envisage human activity around the Beaulieu marshes reaching a threshold where grazing wildlife was reluctant to use the upper marsh as a food resource, with the result that the diverse upper marsh community is lost.

The role of grazers as disturbance factors was also discussed in Chapter 3. It was suggested that the low-intensity grazing operating at Gins Marsh could be interpreted in the context of the widely quoted intermediate disturbance theory (Connell 1978). The term disturbance has been used to include a huge range of factors that disrupt or damage living organisms, and free resources for colonisation or occupation. Floating logs (Dayton 1971), storm waves (Paine and Levin 1981), moving boulders (Sousa 1979), smothering sediment (Underwood 1998) are examples of disturbance factors on rocky shores. On salt marshes the effects of sediment (Zedler 1983), ice (Redfield 1972), freshwater flooding (Zedler 1983), and hypersalinity (Zedler 1983) on living systems have been studied. There is a lack of agreement about whether grazing actually constitutes a genuine form of disturbance. McGuiness (1987) and Sousa (2001) suggest that applying the term disturbance to all sources of damage, such as predation, herbivory and parasitism is not valid, and according to Sousa *"has little heuristic value and often muddles discussion and models of the phenomenon"*. However Bertness (2001) takes a different view, and includes foraging by animals as a natural disturbance of saltmarshes along with ice (Redfield 1972), debris (Bertness and Ellison 1987), fire (Ford and Grace 1998) and sediments (Gough and Grace 1998). Tidal debris is of less importance in Solent marshes, but a clear drift line is usually visible, sometimes with large pieces of driftwood or litter (Appendix 3.1, Plates 12 and 13).

The actions of grazers are complex. Hulme (1996) suggests that the complexity of the effects of grazing can go beyond most normal forms of disturbance. However I take Bertness's view that much of what they do does constitute a disturbance factor (Bertness 2001). In addition to physically removing photosynthetically active plant material (Crawley 1983); they eat flowers and seeds (Olff *et al 1997*); they can grub up tubers or root material (Zacheis *et al* 2001); they make scrapes or burrows and can compact the soils (Ford and Grace 1998); they create mounds by defecating (Ford and Grace 1998); and they cycle nutrients rapidly back into the soil (Bazeley and Jefferies 1986). In the context of a single seed being carried by the tide and deposited on the shore, a small deer hoof print through low-growing vegetation into soft mud represents an opportunity for germination and seedling establishment. In the case of pioneer species such as *Salicornia* spp., this is one of the few opportunities the species has to colonise above the lowest (and physically harshest) part of the marsh. In my exclosure experiment *Salicornia* spp. declined from being widespread but patchily distributed at the start of the experiment to much reduced but largely more evenly spread numbers in the exclosed plots by the third year of the trial (Figure 3.12). This possibly reflected the decline in suitable microhabitats (generated by the disturbance of grazing animals) for seedling establishment. A parallel can be drawn with the work of Bertness and Ellison (1987), who found at their sites in New England, USA, that *Salicornia europea* was only present in bare patches created by tidal debris rafted onto the upper marsh, as it was unable to colonise the soft substrate at the lower end of the marsh.

In the context of the Solent marshes, disturbance by grazers has allowed *Salicornia* to maintain a foothold in the upper marsh. Documentary evidence, and the palaeoecological studies presented here (Chapter 2) suggest that pioneer habitat for species such as *Salicornia europea* were much more widespread 200 years ago, before the appearance of *Spartina.* Furthermore, many of the marshes in Southern England (most notably Hythe), where *Spartina anglica* was first recorded) are now eroding and the pioneer zone is absent, with just a steep cliff of eroding substrate at the tidal edge.

Spartina anglica and the dynamic marsh system

Despite the constancy of many of the factors affecting the nature of coastal marshes in the region (see above), the marshes of the Solent are very different from those of 200 years ago. The palaeoecological work and literature review carried out for this thesis (Chapter 2) suggests a past system with more extensive mudflat and pioneer marsh, sea levels at more than 40-50 mm below those of the present day (Cundy and Croudace 1996, Bray *et al* 2000). Lord Montagu of Beaulieu (1907) and J. Groves (1927) both recalled estuaries which had changed enormously in their lifetimes, following the spread of hybrid *Spartina.* Undoubtedly the marshes of the 21st century are different from 200 years ago; it seems likely that they will be different again in another 200 years time.

The present day zonation and patterning of the saltmarsh plant communities in Southern England is largely dominated by *S. anglica.* It is present in the lower levels of most saltmarshes in Southern England, usually in extensive stands, much of which is monoculture or near-monoculture of a species with very little genetic variation (Charman 1990, Gray, *et al* 1991). Data presented in Chapter 2 suggests that it has significantly "squeezed" the pioneer community (which is further squeezed by sea level rise and erosion at many locations). Beyond this information, it has not been possible to characterise much of the composition of the pre-*Spartina* plant community. The evidence presented here does not suggest that the present plant communities are less biodiverse, indeed the opposite may be true. At any rate, the extended physical size of most marshes post-*Spartina* has allowed similar range of plant species to survive the changes which the appearance of *S. anglica* brought about.

The wider impacts of *Spartina* on biodiversity are not usually much considered compared at least with the physical and ecological changes. Loss of mudflat could have had serious implications for wading birds, and wildfowl such as Brent geese feed on pioneer marsh species and sea grass (*Zostera*) beds, which are believed to have declined post-*Spartina* (Chapman 1959, Doody 1992). It is uncertain what the conservation impacts of this have been, particularly when the appearance of *Spartina* has coincided with a time of major wildfowling activity in the late Victorian era; and data sets of bird numbers from that period until the early 1970's (when nationwide counts began), are probably not reliable. There is little conclusive evidence of effects on wading birds with the exception of the dunlin *Calidris alpina*. Dunlins feed on open mud at the higher end of tidal flats. There is evidence that dunlins have reduced significantly both nationally and in the Solent region, and loss of mudflat is likely cause (Tubbs 1999). There is little doubt that extensive feeding areas for wading birds have been lost: Hubbard and Stebbings (1967) estimated that on the south coast of England alone 12044 ha of tidal flats have been covered in largely monospecific *Spartina* stands since the late 1800s. There has been some response to this, for example, *S. anglica* swards have been restored to mudflats on the Lindisfarne National Nature Reserve to improve the availability of macrobenthic fauna to shorebirds (Frid *et al* 1999).

Spartina clearly caused significant changes, over a scale encompassing whole estuaries, regions, and even continents (Doody 1982, Chung 1990). Whatever the precise impacts of the appearance of *Spartina* on coastal marshes have been (and it is hoped that this thesis adds a little to that information), it seems that this new species may be a factor which fluctuates or may reduce in importance when considered over long timescales. The rapid expansion of *Spartina* was followed within a few decades by the onset of die back (see Chapter 1 for an account of the mechanism of this process), and this process is ongoing still. Some marshes have experienced extensive die back, with former *Spartina* stands restarting the process of succession from mudflat and on to pioneer marsh (Doody 1984, Farrer, unpublished 1997); others have extensive pans within declining *Spartina* stands.

This process is taking place against a background of regional sea level rise and global climate change, with consequent erosion at marsh edges, most notably in the Solent region at Hythe.

The longer term fates of *Spartina* and *Spartina* marshes are unclear. The die back process is continuing, and although in general most marshes in this region are eroding, some sites appears to be largely in balance, with new stands developing where conditions for accretion allow. It seems unlikely that over a timescale of a further 200 years *S. anglica* will disappear, although its hybrid ancestry and genetic uniformity could threaten it (Raybould *et al* 1991). The great majority of *Spartina* stands are heavily infected with the ergot fungus *Claviceps pupurea.* While not killing the plants, this probably reduces their vigour, and almost certainly reduces their ecological fitness by reducing potential setting of seeds, although they do not usually produce much viable seed because of their hybrid sets of chromosomes (Gray *et al* 1991). This has spread rapidly since it was first recorded on *Spartina* in Europe during the 1960s: infection rates in flowering heads of 90% are now common (Gray *et al* 1991).

Four speculative scenarios for the future of *S. anglica*, are possible:

(i) An ergot-resistant *Spartina* could evolve. *Spartina* is currently under huge selective pressure through the high incidence of ergot, and any mutation with resistant characteristics would potentially be at an advantage, not least by being able to set more seed.
(ii) *Spartina* could succumb to either a new parasitic disease or a more virulent form of ergot: genetically uniform species are always threatened by disease outbreaks- the best documented example being the spread of potato blight during the nineteenth century. Widespread loss of *Spartina* marshes would produce dramatic effects in coastal and estuarine ecosystems, with huge volumes of sediment released and major implications for shipping and coastal defence.
(iii) *Spartina* may yet be a beneficiary of climate change: its C4 photosynthesis may give it improved competitive ability at higher levels of the marsh than it can currently occupy.

(iv) *Spartina* could reach some sort of stable level in marsh communities, with much -reduced stands compared with 60 years ago (themselves squeezed by sea level rise and erosion), but still as a significant component of the lower marsh.

Whatever the outcome, one of the original premises put forward in Chapter 1 still stands: saltmarshes are dynamic systems, and the *Spartina* story (though still incomplete) has illustrated that their dynamic nature can extend over timescales of hundreds of years.

Further Work

This thesis is inevitably limited in its scope, and has focused on just a few elements that contribute to the patterning of plant communities on salt marshes. It would always be desirable to examine more factors, more species, with greater replication, in multiple sites. The emphasis of the work has very much been on the plants themselves, their success or failure and their inter- (and intra-) relations. There is certainly scope for more manipulative ecological experiments in the marsh systems I have studied. Examination of other species from other marsh zones may shed light about the position on a marsh where, species by species, competition exceeds the importance of physiological tolerance, and the point at which positive interactions cease to outweigh lack of tolerance.

Recently authors have focussed on the importance of nutrients in competitive relations, and in the context of problems of eutrophication of estuarine and coastal waters in Southern England, further work on this field could be very valuable. The role of nutrients and nutrient cycling was also not addressed in the grazing experiments, although some authors have highlighted the importance of this (Bockelmann and Neuhaus 1999, Van Wijnen and Bakker 1999, Keddy *et al* 2000).

There is also still much to be learned about the palaeoecological history of marshes through the onset of *Spartina*, and before. The methodologies developed for this thesis were loosely successful, and it would be interesting to develop better ways of reconstructing past communities, possibly with different methods and alternative proxy indicators, such as Foramenifera or testate amoebae. Palaeoecologists have tended to avoid coastal environments, but this work suggests they have untapped potential for research. The thesis has also integrated work on a variety of timescales and disciplines- a rarity in much ecological research. The use of palaeoecology to develop ideas which might be investigated or validated with short term field experiments could be a very useful (and novel) approach for future research.

APPENDICES

Appendix 1 Plant Species and Authorities

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Appendix 1, Table 1. Plant species names.

Species	**Common Name**
Agropyron pungens (Pers)	Sea Couch
Agrostis stolonifera L.	Creeping Bent
Armeria maritima (Mill.)	Thrift or Sea Pink
Aster tripolium L.	Sea Aster
Atriplex patula L.	Common Orache
Atriplex portulacoides L.	Sea Purslane
Carex distans L.	Distant Sedge
Carex extensa Good	Long-bracted Sedge
Cochlearia anglica L.	English Scurvy-grass
Festuca rubra L.ssp. rubra	Red Fescue
Glaux maritima L.	Sea Milkwort
Juncus gerardii LOISEL	Saltmarsh Rush or Mud Rush
Juncus maritimus LAM.	Sea Rush
Limonium vulgare	Common Sea Lavender
Plantago maritima L.	Sea Plantain
Phragmites australis (Cav.) Trin. ex Steudel	Common Reed
Puccinellia maritima (Huds) Parl.	Common Salt-Marsh-Grass
Salicornia europea L.	Common Glasswort
Salicornia perenne (Mill)	Perennial Glasswort
Scirpus maritimus L.	Sea Club-rush
Spartina alterniflora Lois	Smooth Cord Grass
Spartina anglica C.E. Hubbard	Common Cord Grass
Spartina maritima (Curt.) Fernald	Cord Grass
Spartina x *townsendii* H. & J. Groves	Townsend's Cord Grass
Spergularia marina L.	Lesser Sea-spurrey
Suaeda maritima L. Dumort	Annual Seablite
Triglochin maritima L.	Sea Arrowgrass

Appendix 2.1 Historical records and data sources

Archives and information sources

Cartographic Unit, Department of Geography, University of Southampton
Centre For Environmental Sciences Library and Reference Collection, University of Southampton
City of Southampton Central Library
Geodata Unit *Spartina* Archive Collection, University of Southampton
Hartley Library, University of Southampton: Cope Collection and Parliamentary Papers Collection
Wessex Medical Library (Biological Sciences section)
www.oldmaps.co.uk Accessed September 2000

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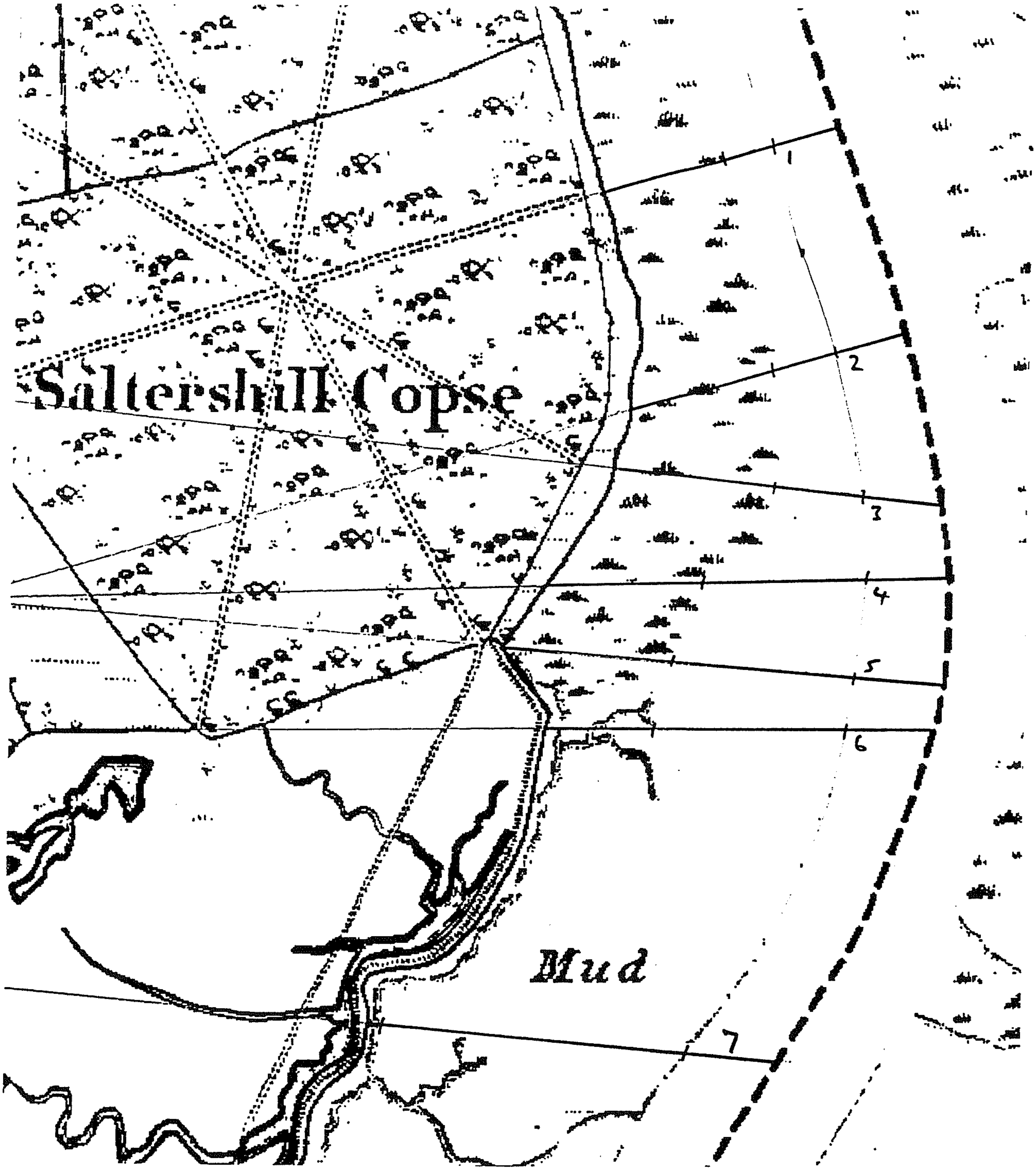
Maps

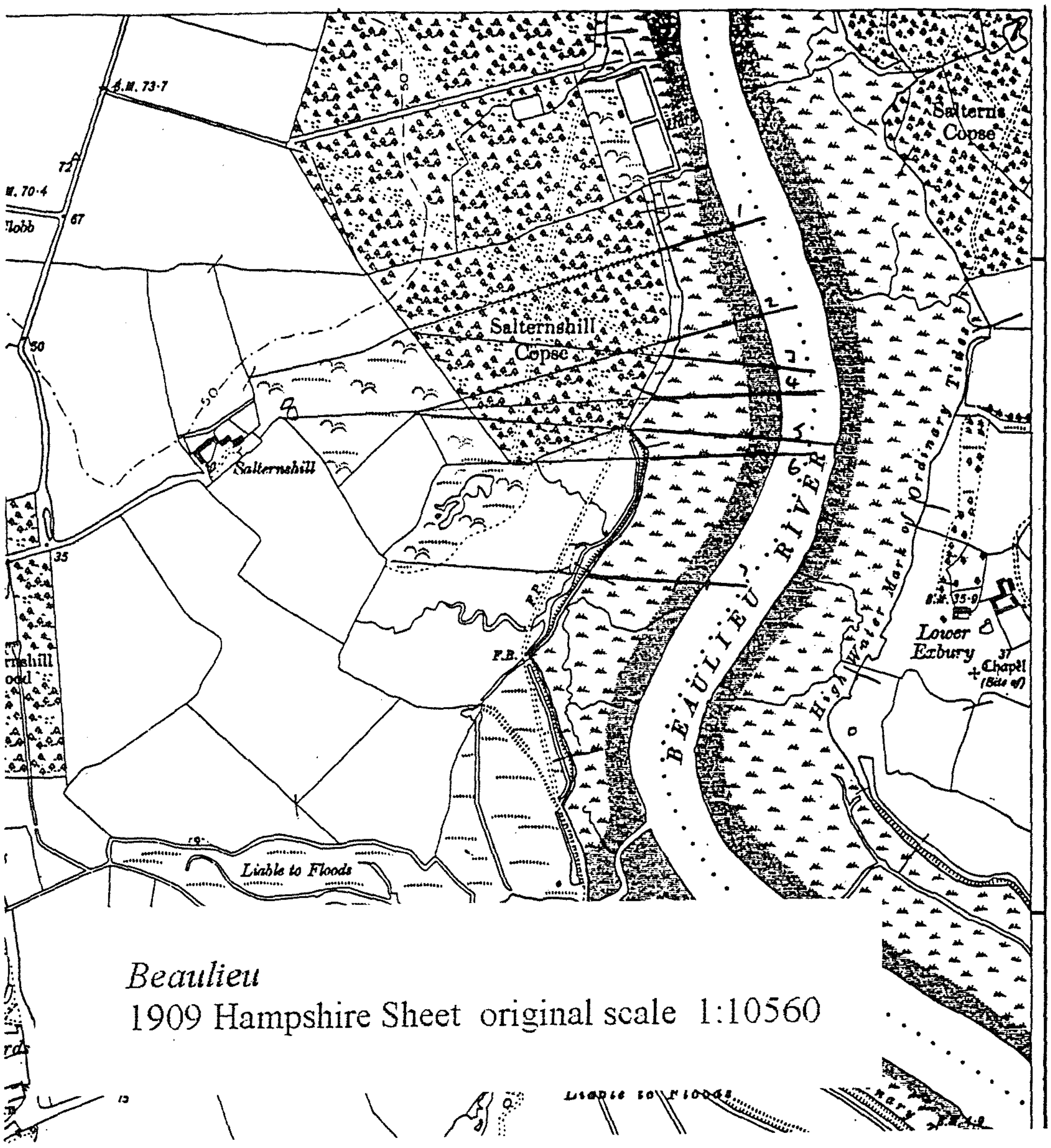
Ordnance Survey Maps:
1870 County Series, original scale 1:10560.
(Image from http://www.old-maps.co.uk/ (Landmark Information Group))
1909 Hampshire Sheet
1910 Hampshire Sheet LXV SW,
1931 Hampshire Sheet LXV SW,
1898 Hampshire Sheet LXV SW,
1965 Sheets SU3811 & SU3711.
1973 Sheet SZ49NW

Richardson, T. , King, W. Driver A. and Driver W. (1789). *A plan of His Majesty's forest called the New Forest in the County of Southampton, 1789* (*"Driver's map of the New Forest"*). William Faden, London.

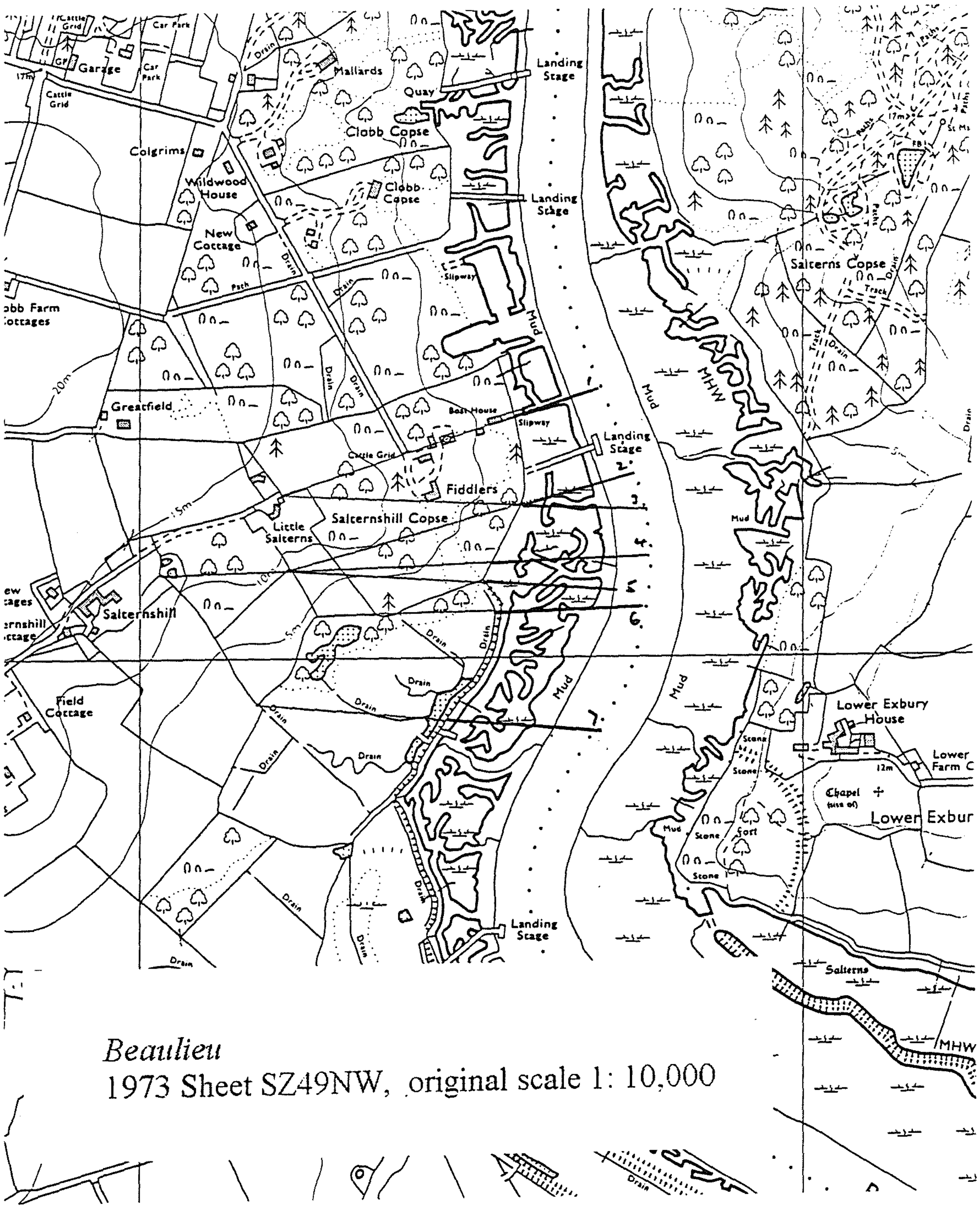
Appendix 2.2 **Transects on Historical Maps**



Beaulieu
1870 County Series, original scale 1:10560.



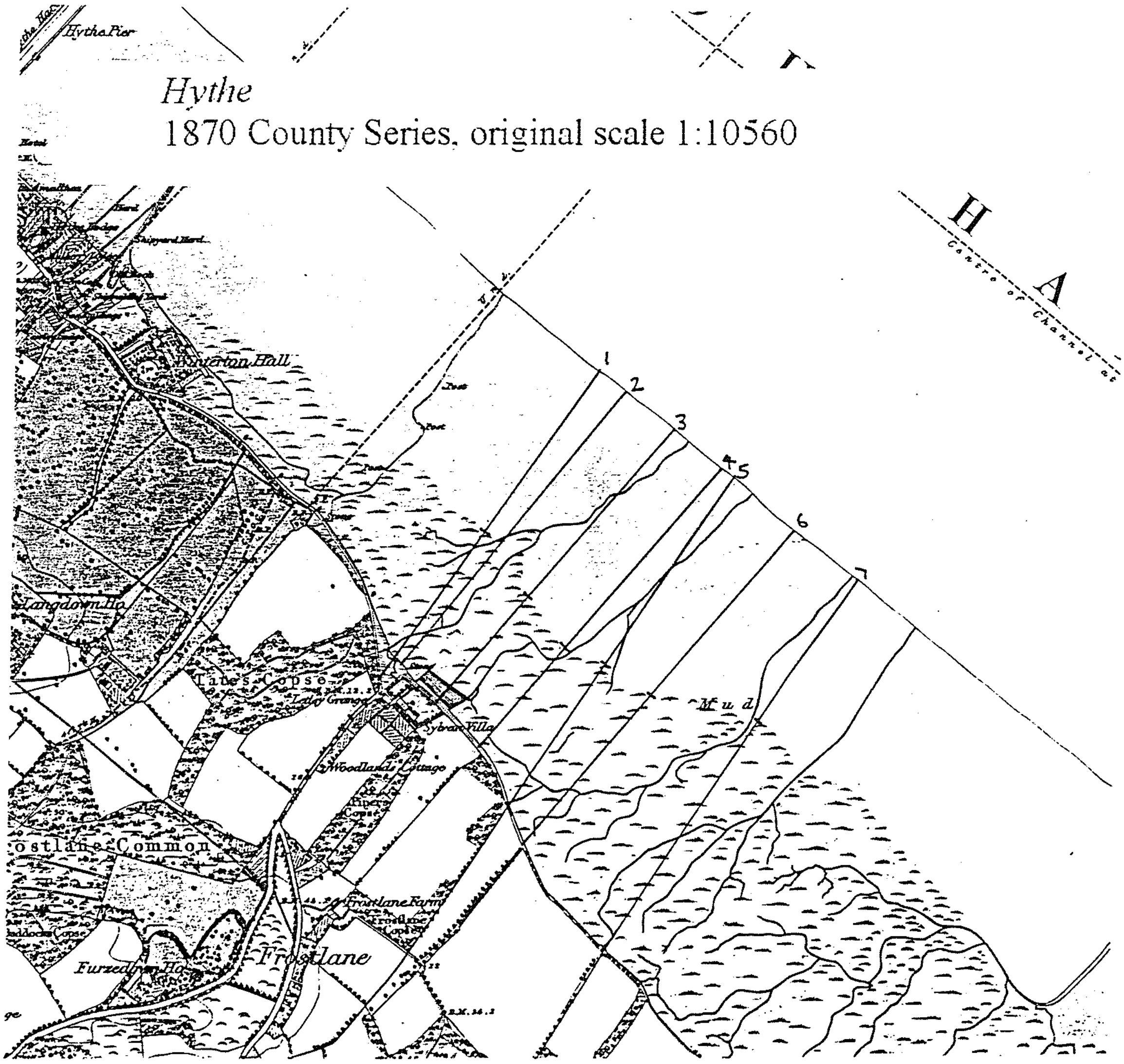
Beaulieu
1909 Hampshire Sheet original scale 1:10560



Beaulieu

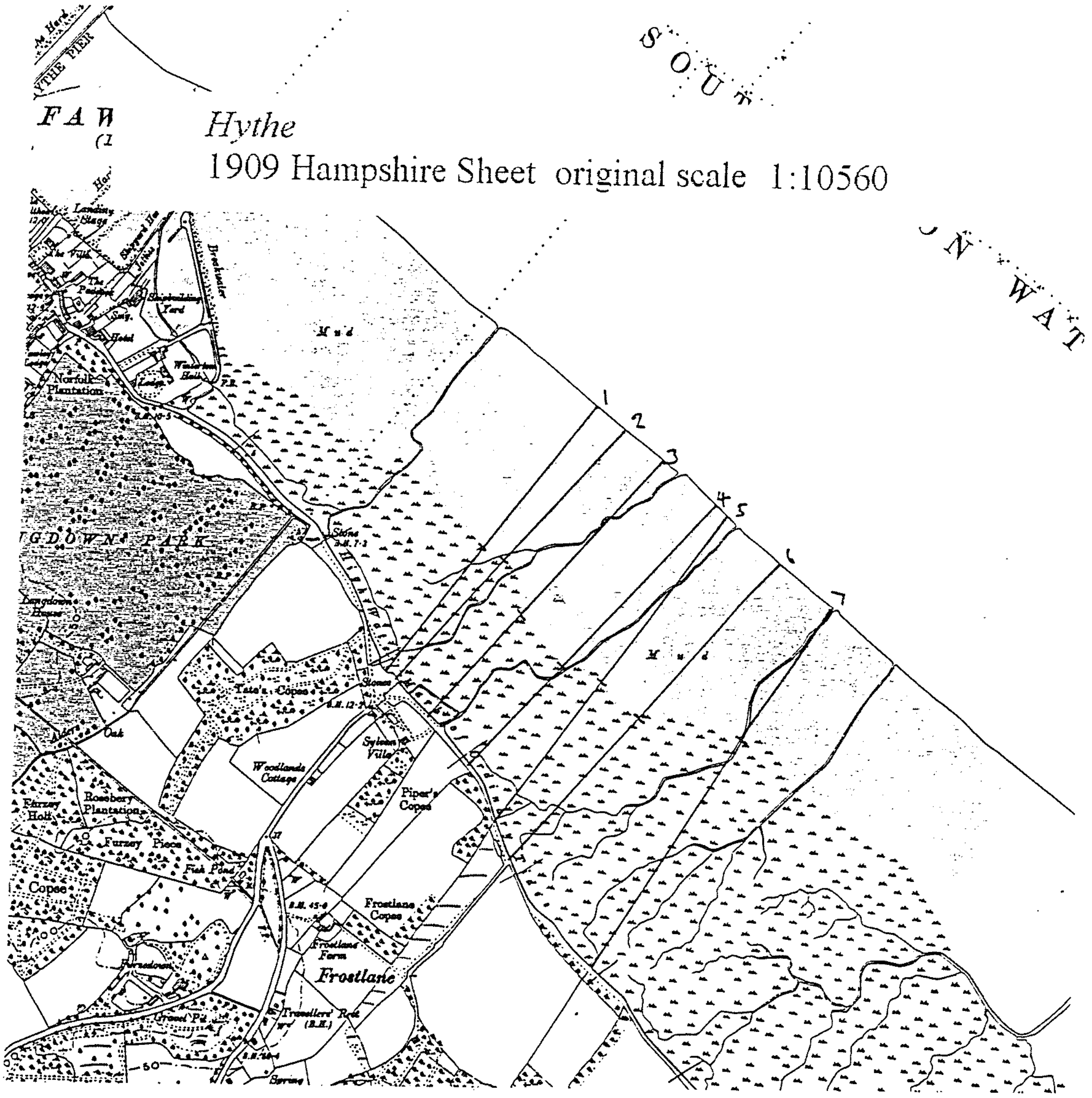
1973 Sheet SZ49NW, original scale 1: 10,000

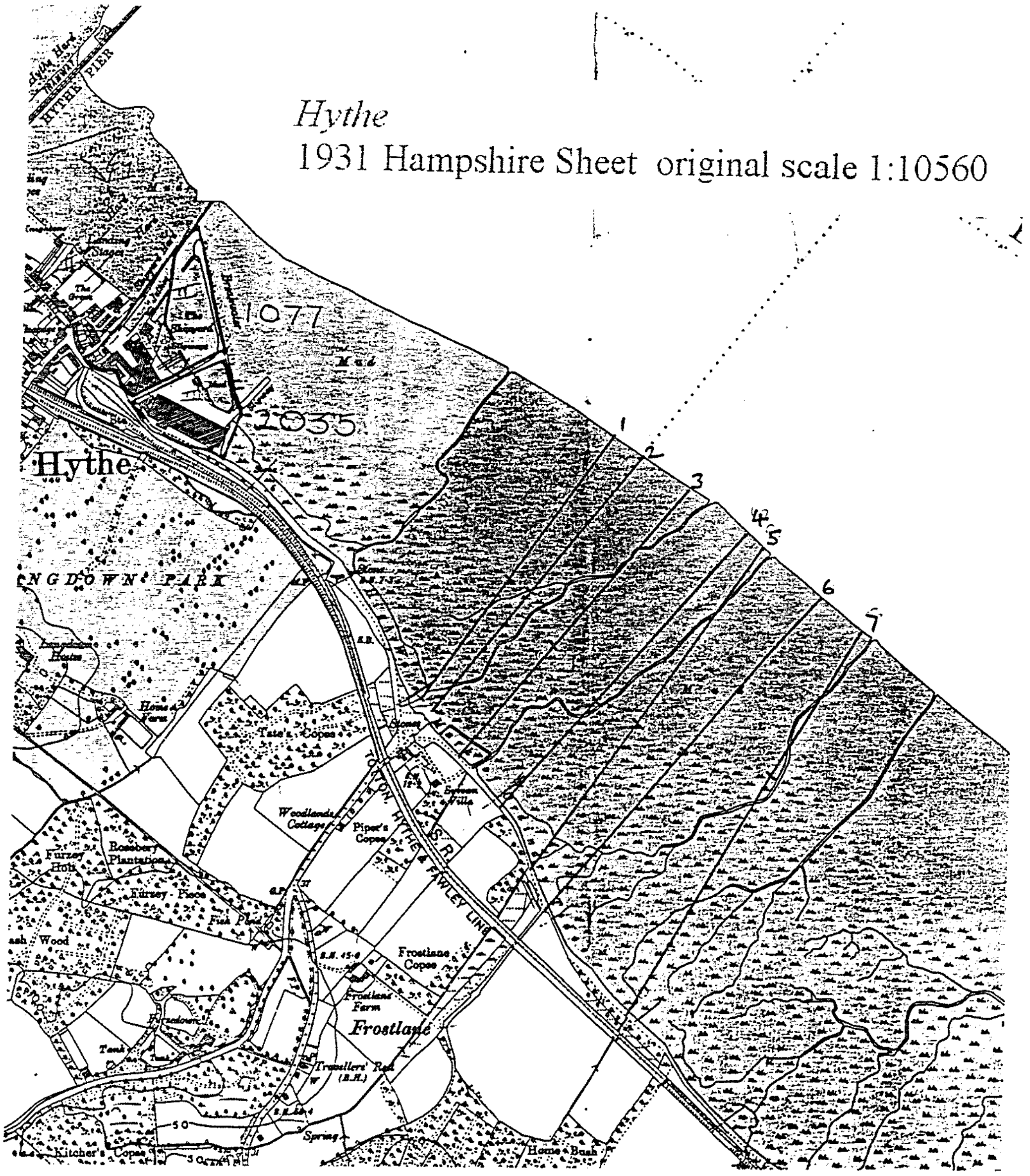
Hythe
1870 County Series, original scale 1:10560



Hythe

1909 Hampshire Sheet original scale 1:10560





Hythe
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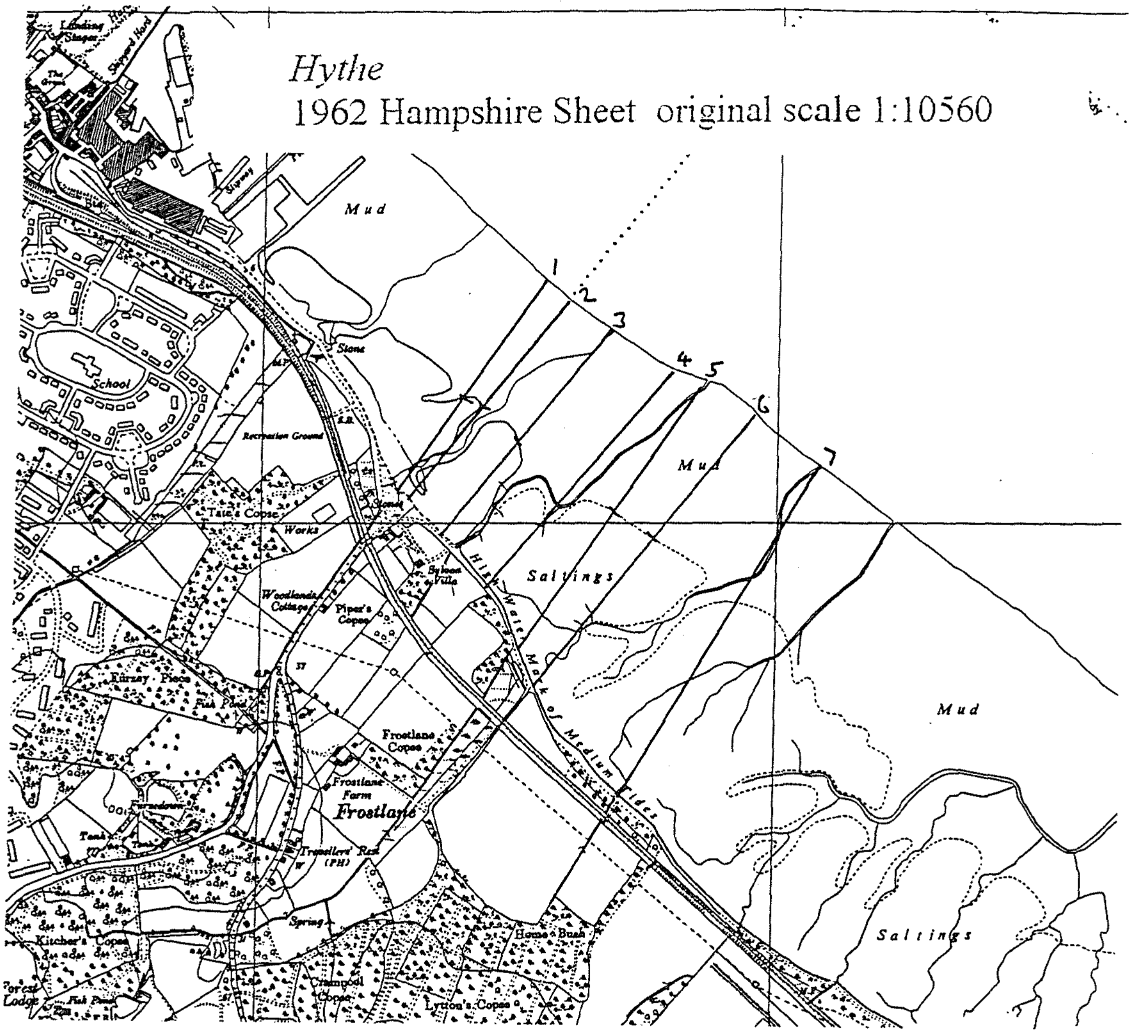
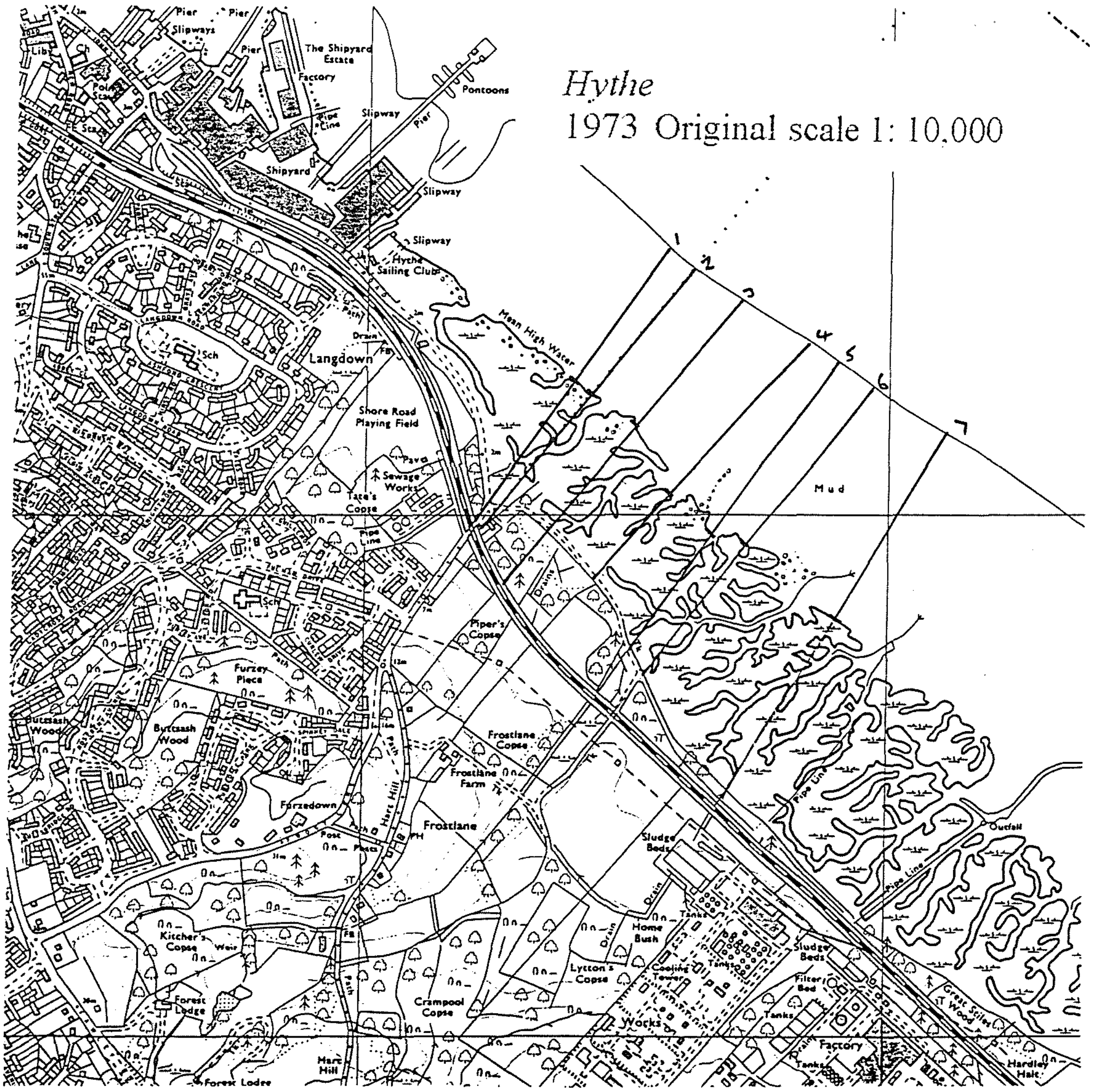
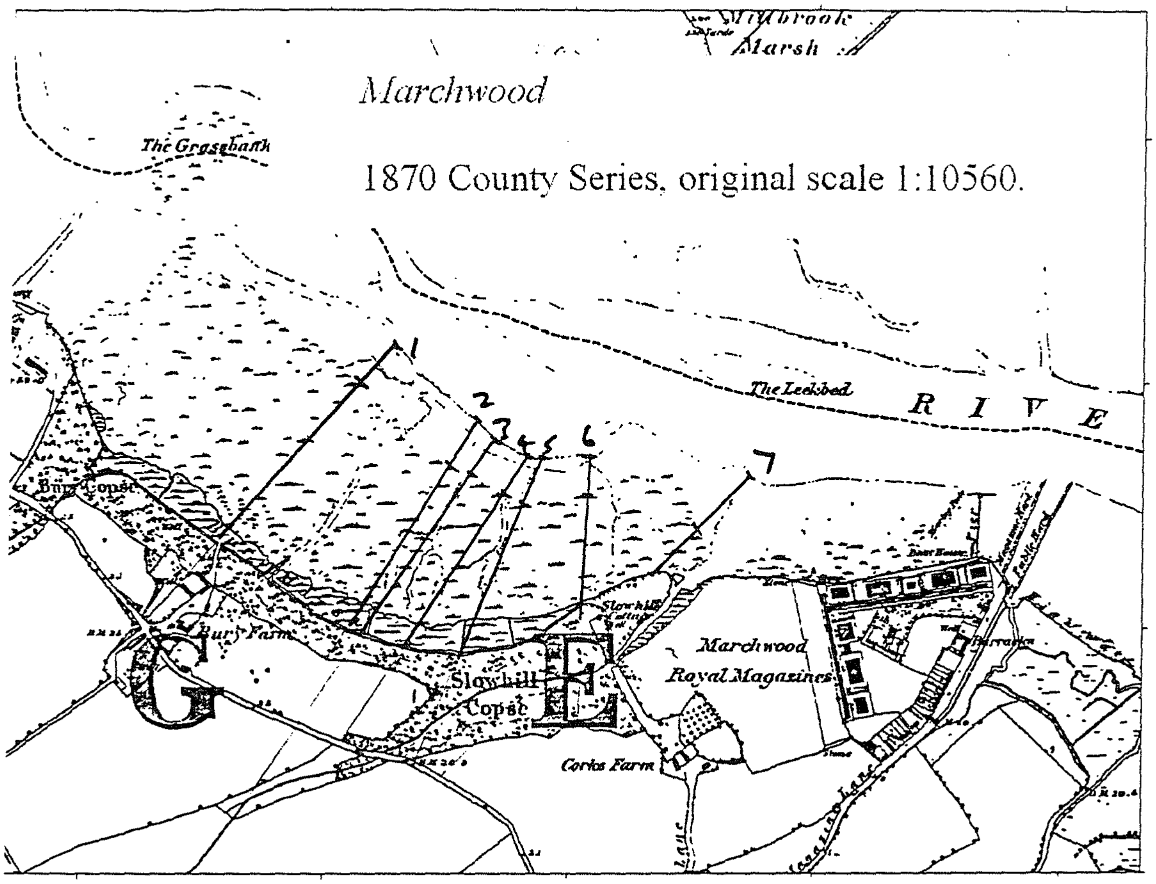


Hythe

1962 Hampshire Sheet original scale 1:10560

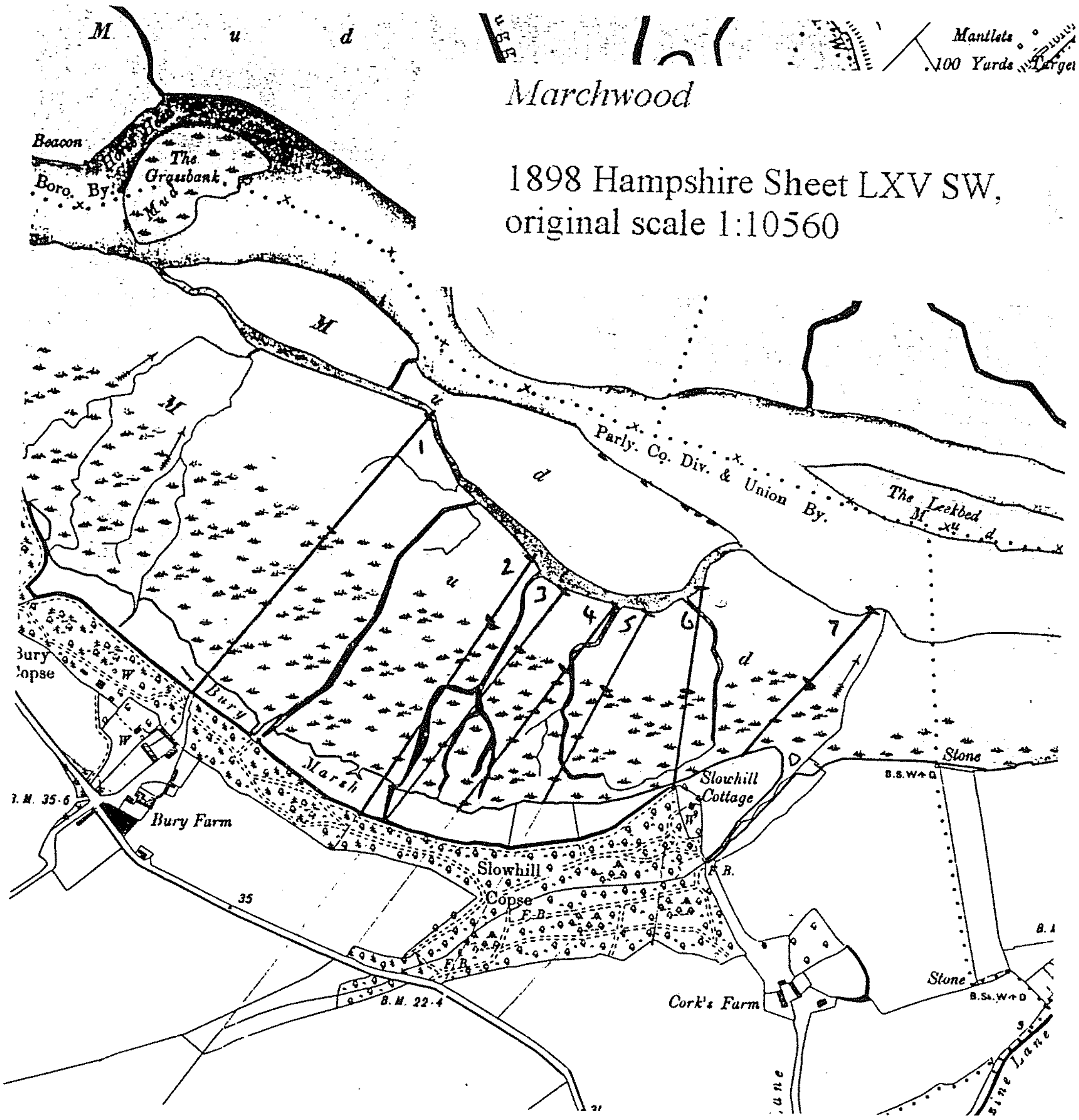


Hythe
1973 Original scale 1: 10,000



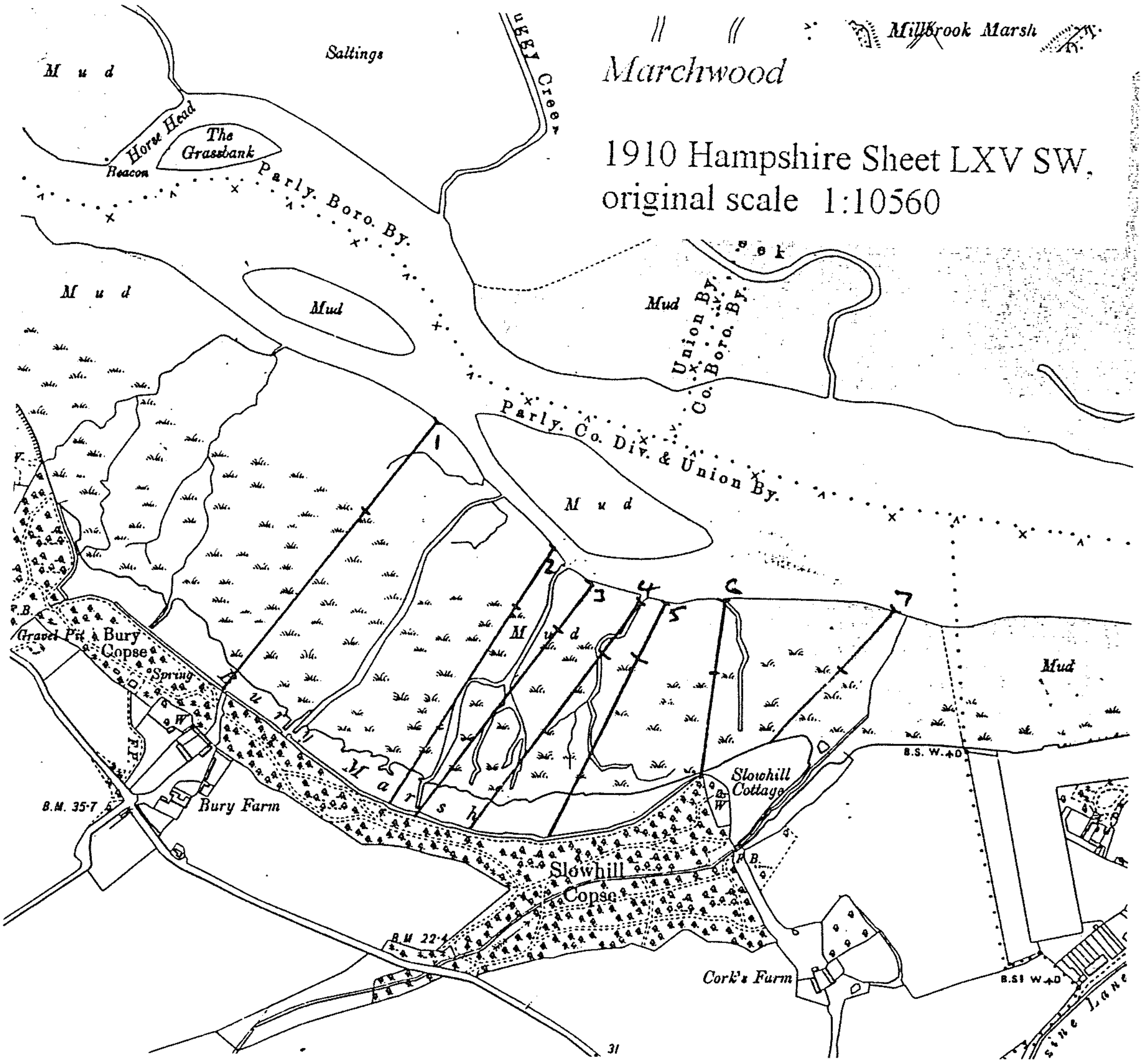
Marchwood

1870 County Series, original scale 1:10560.

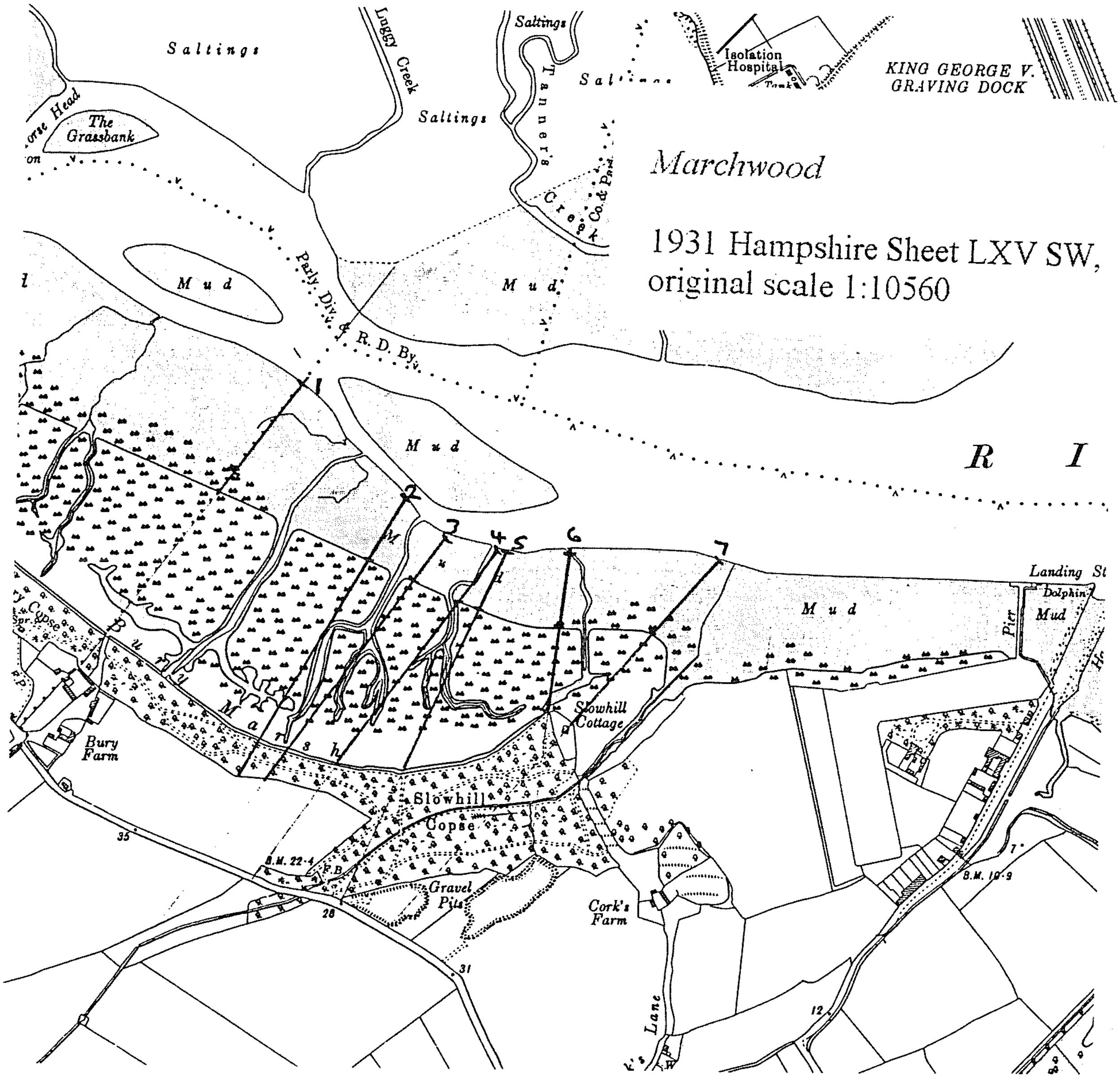


Marchwood

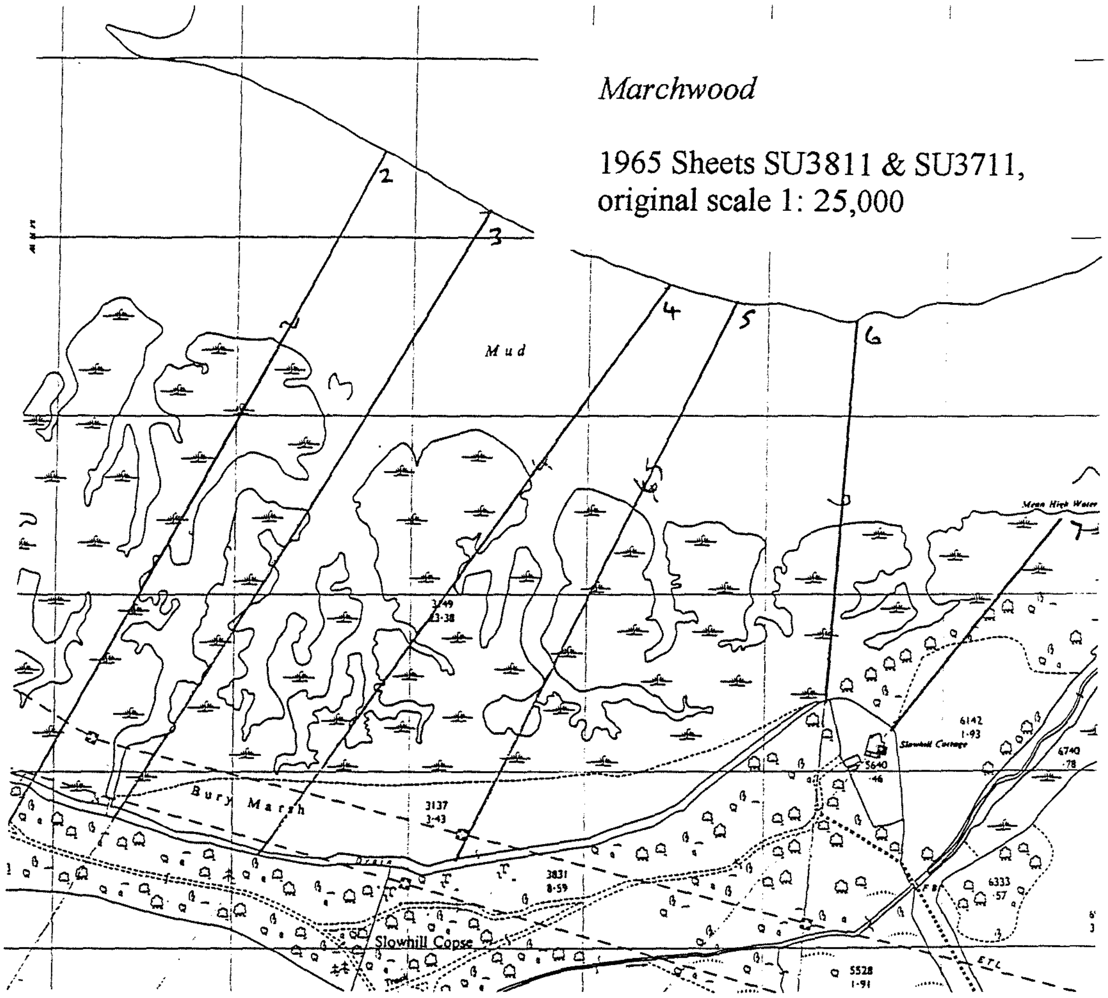
1898 Hampshire Sheet LXV SW,
original scale 1:10560



1910 Hampshire Sheet LXV SW,
original scale 1:10560


Marchwood

1931 Hampshire Sheet LXV SW, original scale 1:10560



Marchwood

1965 Sheets SU3811 & SU3711, original scale 1: 25,000

Appendix 2. Pollen Laboratory Methods

UNIVERSITY OF SOUTHAMPTON: DEPARTMENT OF GEOGRAPHY

PALAEOECOLOGY LAB: POLLEN PREPARATION SCHEDULE

A: SOLUTION OF CARBONATES AND HUMIC COMPOUNDS

1. Using a clean spatula place a small quantity of sediment (c.½ cm^3) in a clean, labelled 15 ml or larger test tube. If sediments are suspected or known to be calcareous add a few ccs of 10% HCL; if normal acid peats go to stage 4 below. Add 2-5 exotic pollen tablets.
2. When reaction, if any, is complete cap the tubes and centrifuge at 3,000 rpm for 3 minutes, ensuring first that tubes are balanced by being filled to the same level. This applies throughout the schedule.
3. Carefully decant; i.e. pour away liquid from tube, retaining residue. Do it in one smooth movement. Unless noted to the contrary all chemicals may be decanted into the fume cupboard sink with water running continuously.
4. Add a few ccs of 10% KOH to test tube, mix on vortex mixer, top up KOH to within 3 cm of top of tube and place in boiling water bath in fume cupboard for 10 minutes (up to 20 mins if samples dirty).
5. Using a little distilled water, wash residue through a fine (180 micron) sieve sitting over a 400 ml beaker. Sieve the beaker contents through a 10µm sieve. Clean test tubes with distilled water and refill with contents of sieve. NB be especially careful in keeping sieves, beakers and test tubes in correct number order.
6. Centrifuge and decant as often as necessary.
7. Add distilled water, centrifuge and decant. Repeat procedure until brown stain removed from supernatant liquid. **(Two treatments with KOH and two sievings are much more effective than increasing the time at stage 4).**

B: HYDROFLUORIC ACID TREATMENT

NB HF burns are painful and slow to heal - read the safety notices before using! Rubber gloves, face protection (visor) and an apron must be worn over your lab coat. This procedure is unnecessary for highly organic samples.

(a) Add a small amount of distilled water to residue and mix thoroughly.
(b) Add c.5 ml of 40% HF to test tube and place in water bath for about 30 minutes. Time required will vary greatly with quantity of silicates present; for very siliceous samples repeat steps a & b. Samples can be left for 1-2 days in cold HF if much silicate present, and then treated to another dose of hot HF.
(c) Centrifuge and carefully decant **into the labelled collector vessel, not down the sink**.
(d) Add dilute HCL, mix and put in boiling water bath for 3-5 minutes - do not boil the HCL. (This removes colloidal silica, etc).
(e) Centrifuge and decant.
(f) Add distilled water, mix, centrifuge and decant. Repeat.

C: ACETYLATION

8. Add glacial acetic acid, mix, and centrifuge. Decant into fume cupboard sink with water running during and after.
9. Repeat.
10. Make up acetylation mixture, freshly, just before it is required. Using a measuring cylinder mix acetic anhydride and conc. sulphuric acid in proportions of 9:1 by volume. Measure out acetic anhydride, using automatic pipette first, then add conc. H_2SO_4 carefully, stirring to prevent heat build-up. Stir again just before use.
11. Add a few cc to sample, mix and fill tube about ½ or ⅔ full.
12. Put in boiling water bath for no more than 1-3 minutes. (Stirring is unnecessary since acetylation should not be carried on for longer than 3 minutes as it destroys some pollen types. Never leave glass rods in tubes as steam condenses on the rods and runs down into the mixture reacting violently).
13. Centrifuge and decant **into large (3 litre) beaker of water in fume cupboard**. This "quenches" the reaction mixture; the beaker may be emptied down the sink diluting further with plenty of running water
14. Add glacial acetic acid, mix, centrifuge and decant.
15. Add distilled water and 1 cc 10% KOH (and 1 drop of detergent (Teepol) if material is clumping together), mix, centrifuge and decant.

D: MOUNTING IN SILICONE FLUID

This is a longer, more refined technique than using glycerol or glycerine jelly and has the important advantage of not altering pollen grain size overmuch. Also, as silicone fluid is practically non-volatile the slides never dry out and do not need sealing.

16. Add distilled water, mix, centrifuge and decant.
17. Add 1 cc distilled water, 5 cc 100% ethanol and 1-2 drops of safranin or other stain. Do not over-stain as the grains will be difficult to identify and the staining cannot be reversed! Mix, top up with ethanol, centrifuge and decant.
18. Add 100% ethanol, mix, centrifuge and decant.
19. Add c. 1 cc of toluene and pour from test tubes into labelled glass vials. Repeat to wash all pollen from test tube and balance vials carefully. Seal with polythene tops.
20. Carefully lower vials into centrifuge using forceps, and spin at no more than 750 rpm for 10 minutes.
21. Carefully decant into beaker containing tissues in fume cupboard - leave this to evaporate for 24 hours with the fan running - post an Unattended Experiment notice on the outside of the lab door in the holder provided.
22. Add silicone fluid (viscosity MS 200/2,000 cs.), 2-6 drops, and mix well with a small disposable rod - pollen grains may otherwise clump together. Do not add too much silicone fluid!
23. Allow excess toluene to evaporate from the vials - 24 hours in fume cupboard as above.
24. Make up slides. Fix cover slip with varnish at corners - no need to seal.

Professor Keith Barber, October 2000

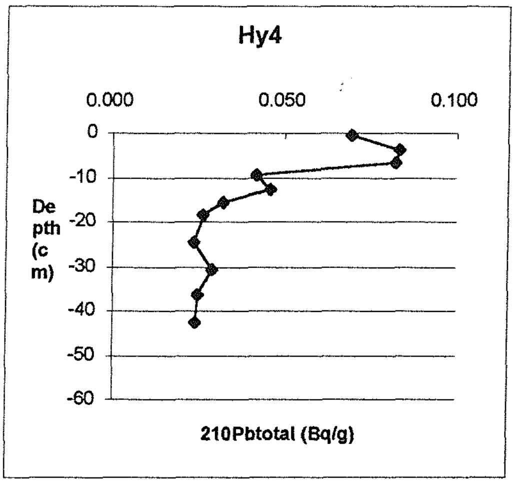
Appendix 2.4. Lead-210 (^{210}Pb) dating of salt marsh cores

^{210}Pb dating: rationale and methodology.

^{210}Pb (half-life = 22.3 years) is a naturally-produced radionuclide that has been extensively used in the dating of recent sediments. Dating is based on determination of the vertical distribution of ^{210}Pb derived from atmospheric fallout (termed unsupported ^{210}Pb, or ^{210}Pb$_{excess}$), and the known decay rate of ^{210}Pb (see Appleby and Oldfield 1992 for further details of the ^{210}Pb method). ^{210}Pb activity was determined by a proxy method through alpha spectrometric measurement of its grand daughter nuclide ^{210}Po. The method employed is based on Flynn (1968), using double acid leaching of the sediment with ^{209}Po as an isotopic tracer followed by autodeposition of the Po isotopes in the leachate on to silver discs. Discs were counted for a minimum of 400000 seconds, and detection limits are 0.1Bq/kg. The supported ^{210}Pb activity was estimated using the ^{210}Pb activity in mineralogically-similar, older (pre-1850) sediments from the study areas (0.011 Bq/g, Cundy and Croudace 1996), or by subtraction of the value of constant ^{210}Pb activity at depth. Sediment accretion rates were determined using the "simple model" of ^{210}Pb dating (e.g. Robbins 1978), where the sedimentation rate is given by the slope of the least squares fit for the natural log of the ^{210}Pb$_{excess}$ activity versus depth. The 95% confidence interval on the sediment accumulation rate is also shown. It should be noted that the sediment accumulation rate estimated for each core could be improved by analysis of ^{137}Cs activities, to corroborate the ^{210}Pb-derived rate.

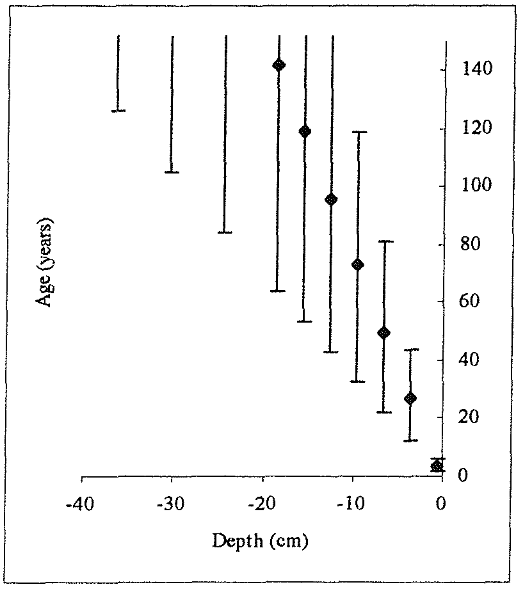
Core H4

Sample depth (cm)	Sample mass (g)	Po-210 activity (Bq/g)	Counting error (%)
-0.5	1.39	0.069	3.35
-3.5	1.41	0.083	3.66
-6.5	1.17	0.082	3.48
-9.5	1.30	0.041	3.91
-12.5	1.20	0.046	4.02
-15.5	0.98	0.032	4.36
-18.5	1.12	0.026	4.36
-24.5	0.88	0.024	4.86
-30.5	1.55	0.029	3.96
-36.5	1.58	0.025	4.42
-42.5	1.37	0.024	4.45



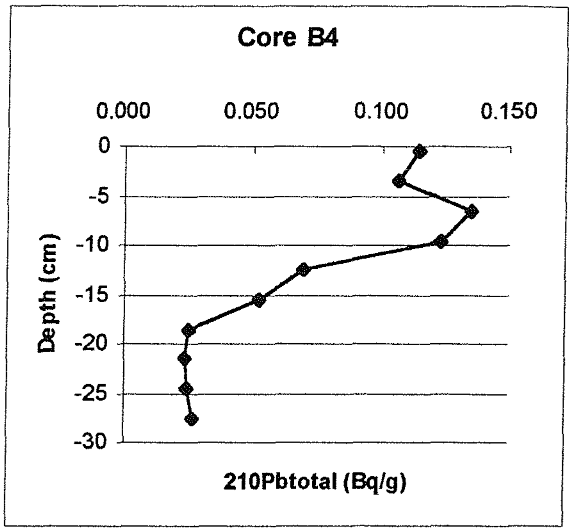
Sediment accretion rate, based on simple model of ^{210}Pb dating, = 1.3 mm per year
(95% confidence interval = 0.8 – 2.9 mm/y).

Age-depth graph for H4 core, based on simple model (error bars shown are calculated using the 95% confidence interval on the gradient of the linear regression fit of $\ln^{210}Pb_{excess}$ vs. depth).

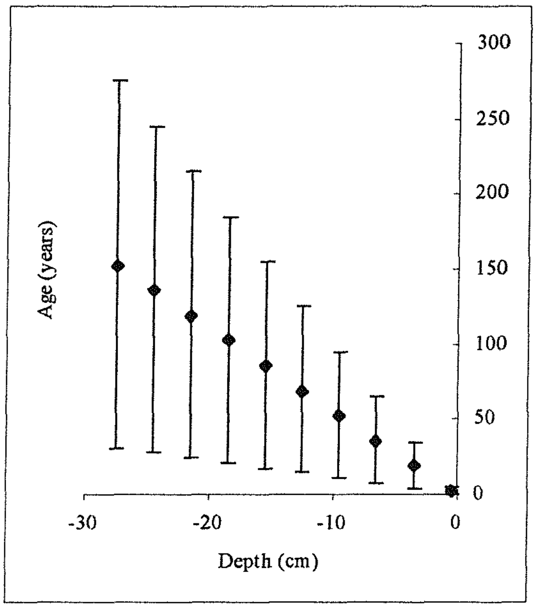


Core B4

Sample depth (cm)	Sample mass (g)	Po-210 activity (Bq/g)	Counting error (%)
-0.5	0.3107	0.114	6.87
-3.5	0.6155	0.107	6.40
-6.5	0.4662	0.135	8.09
-9.5	0.8688	0.123	7.38
-12.5	1.2753	0.069	4.16
-15.5	1.0004	0.052	3.13
-18.5	1.9148	0.026	1.54
-21.5	1.1719	0.024	1.43
-24.5	1.1248	0.025	1.49
-27.5	1.2433	0.027	1.60



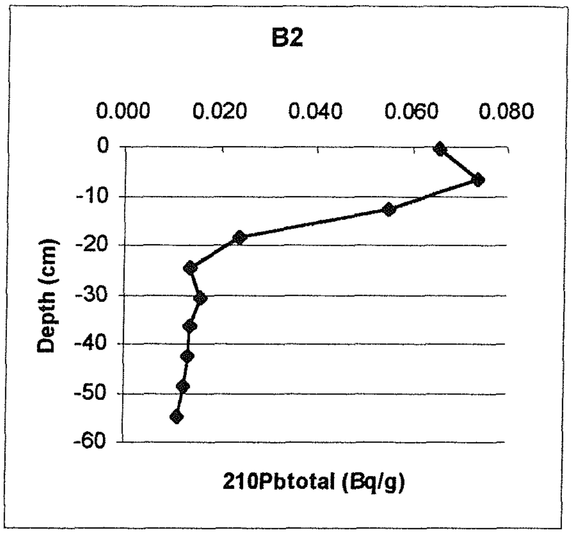
Sediment accretion rate, based on simple model of ^{210}Pb dating, = 1.8 mm per year (95% confidence interval = 1.0 – 8.8 mm/y).



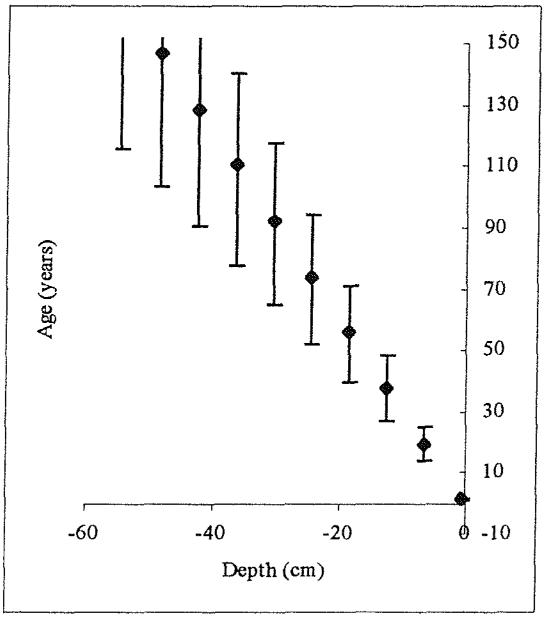
Age-depth graph for B4 core, based on simple model (error bars shown are calculated using the 95% confidence interval on the gradient of the linear regression fit of $\ln^{210}\mathrm{Pb}_{\mathrm{excess}}$ vs. depth).

Core B2

Sample depth (cm)	Sample mass (g)	Po-210 activity (Bq/g)	Counting error (%)
-0.5	1.057	0.066	3.53
-6.5	1.39	0.073	3.47
-12.5	0.91	0.055	4.15
-18.5	1.85	0.024	4.13
-24.5	2.071	0.014	5.45
-30.5	1.922	0.016	3.95
-36.5	2.083	0.014	4.41
-42.5	1.984	0.013	4.91
-48.5	1.759	0.013	5.10
-54.5	1.723	0.011	4.63



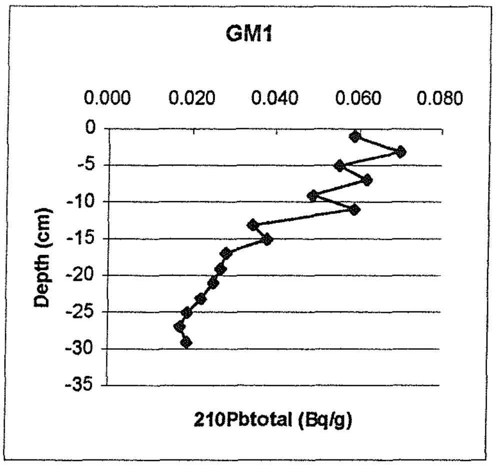
Sediment accretion rate, based on simple model of ^{210}Pb dating, = 3.3 mm per year (95% confidence interval = 2.6 – 4.7 mm/y).



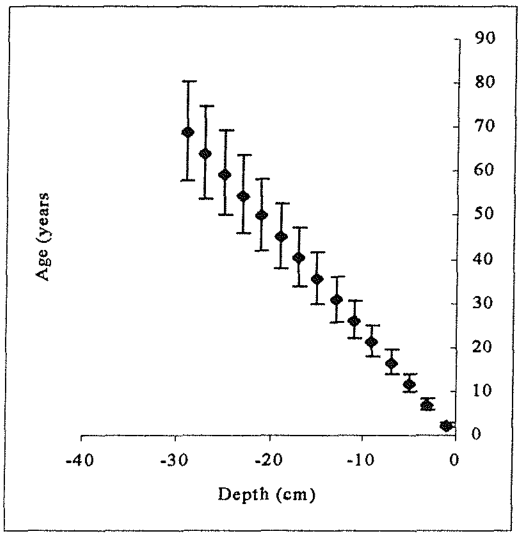
Age-depth graph for B2 core, based on simple model (error bars shown are calculated using the 95% confidence interval on the gradient of the linear regression fit of $\ln{}^{210}\mathrm{Pb}_{\mathrm{excess}}$ vs. depth).

Core GM1

Sample depth (cm)	Sample mass (g)	Po-210 activity (Bq/g)	Counting error (%)
-1	3.05	0.059	2.40
-3	3.55	0.070	2.27
-5	3.34	0.055	2.29
-7	3.39	0.062	2.72
-9	3.41	0.049	2.41
-11	3.36	0.059	2.31
-13	3.54	0.035	2.31
-15	3.13	0.038	2.38
-17	3.12	0.028	2.39
-19	3.79	0.027	2.52
-21	3.08	0.025	2.40
-23	3.26	0.022	2.80
-25	3.14	0.019	2.94
-27	3.76	0.017	2.62
-29	3.15	0.019	2.69



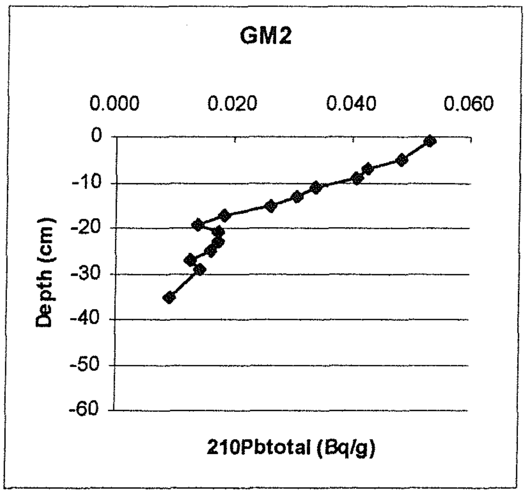
Sediment accretion rate, based on simple model of ^{210}Pb dating, = 4.2 mm per year (95% confidence interval = 3.6 – 5.0 mm/y).



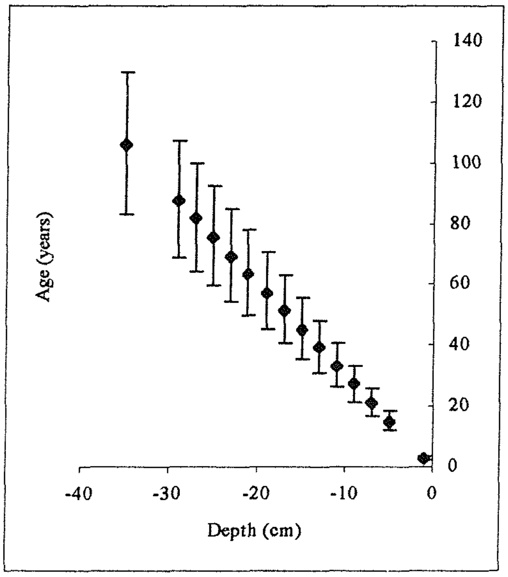
Age-depth graph for GM1 core, based on simple model (error bars shown are calculated using the 95% confidence interval on the gradient of the linear regression fit of $\ln^{210}\mathrm{Pb}_{excess}$ vs. depth).

Core GM2

Sample depth (cm)	Sample mass (g)	Po-210 activity (Bq/g)	Counting error (%)
-1	3.12	0.053	1.74
-5	3.1	0.048	2.06
-7	3.04	0.042	1.77
-9	3.12	0.041	1.78
-11	3.14	0.034	1.75
-13	3.09	0.031	1.99
-15	3.01	0.026	1.94
-17	3.16	0.018	2.17
-19	3.07	0.014	2.34
-21	3.06	0.017	2.06
-23	3.12	0.017	2.07
-25	3.03	0.016	2.43
-27	3.03	0.013	2.67
-29	3.04	0.014	2.24
-35	3.01	0.009	2.63



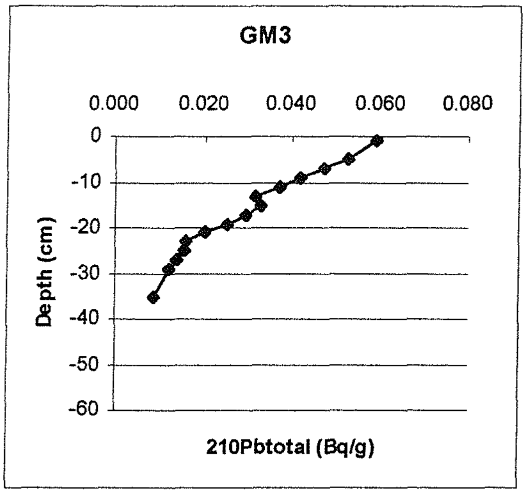
Sediment accretion rate, based on simple model of ^{210}Pb dating, = 3.3 mm per year (95% confidence interval = 2.7 – 4.2 mm/y).



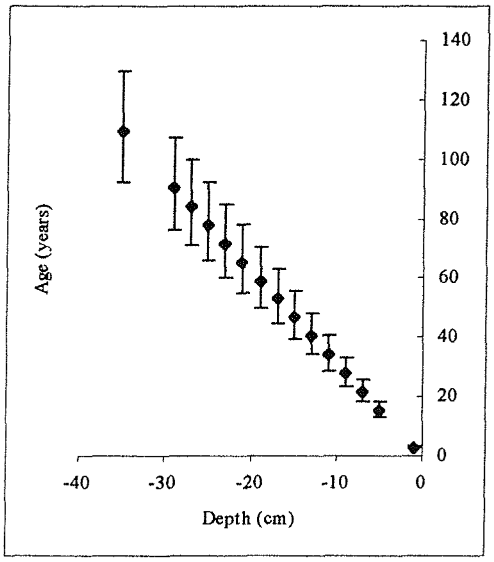
Age-depth graph for GM2 core, based on simple model (error bars shown are calculated using the 95% confidence interval on the gradient of the linear regression fit of ln^{210}Pb$_{excess}$ vs. depth).

Core GM3

Sample depth (cm)	Sample mass (g)	Po-210 activity (Bq/g)	Counting error (%)
-1	3.07	0.059	2.39
-5	3.13	0.053	2.17
-7	3.06	0.047	2.39
-9	3.15	0.041	2.29
-11	3.17	0.037	2.40
-13	3.06	0.031	2.62
-15	3.06	0.033	2.29
-17	3.06	0.029	2.41
-19	3.08	0.025	2.53
-21	3.08	0.020	2.54
-23	3.1	0.016	2.58
-25	3.2	0.015	3.14
-27	3.05	0.014	3.01
-29	3.21	0.012	2.86
-35	3.1	0.009	3.06



Sediment accretion rate, based on simple model of ^{210}Pb dating, = 3.2 mm per year
(95% confidence interval = 2.7 – 3.8 mm/y).



Age-depth graph for GM3 core, based on simple model (error bars shown are calculated using the 95% confidence interval on the gradient of the linear regression fit of $\ln^{210}Pb_{excess}$ vs. depth).

References:

Appleby P.G. and F.Oldfield (1992) Applications of ^{210}Pb to sedimentation studies. In: Ivanovich M. and Harmon R.S. (eds) *Uranium-series disequilibrium. Applications to earth, marine and environmental sciences.* 2nd Edition, Oxford Science, Oxford.

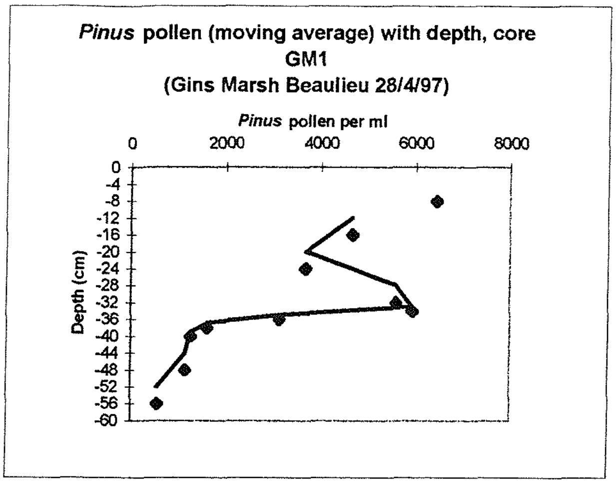
Cundy A.B. and I.W.Croudace (1996) Sediment accretion and recent sea level rise in the Solent, southern England: inferences from radiometric and geochemical studies. *Estuarine, Coastal and Shelf Science*, 43, 449-467.

Flynn W.W. (1968) Determination of low-levels of polonium-210 in environmental materials. *Analytica Chimica Acta*, 43, 221-227.

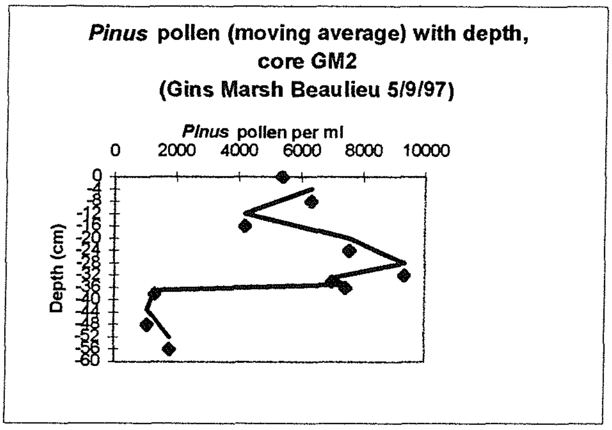
Robbins J.A. (1978) Geochemical and geophysical applications of radioactive lead. In: *The Biogeochemistry of Lead in the Environment Part A* (Nriagu J.O. Ed.) Elsevier/North Holland Biomedical Press pp 285-293.

Appendix 2.5. Anthropogenic *Pinus* Rise Figures

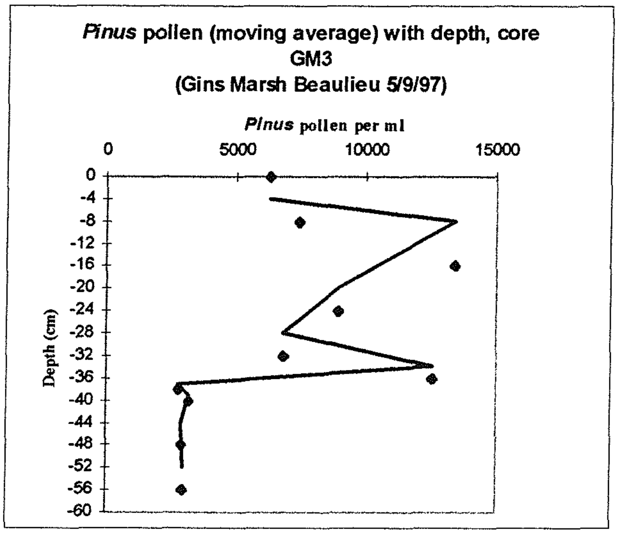
(i) *Pinus* pollen (moving average) with depth, core GM1
(Gins Marsh Beaulieu 28/4/97)
(ii) *Pinus* pollen (moving average) with depth, core GM2
(Gins Marsh Beaulieu 5/9/97)
(iii) *Pinus* pollen (moving average) with depth, core GM3
(Gins Marsh Beaulieu 5/9/97)
(iv) *Pinus* pollen (moving average) with depth, core GM4
(Gins Marsh Beaulieu 23/3/99)
(v) *Pinus* pollen (moving average) with depth, core GM5
(Gins Marsh Beaulieu 23/3/99)
(vi) *Pinus* pollen (moving average) with depth, core GM6
(Gins Marsh Beaulieu 23/3/99)
(vii) *Pinus* pollen (moving average) with depth, core H1(Hythe 24/2/2000).
(vii) *Pinus* pollen (moving average) with depth, core H2 (Hythe 24/2/2000).
(ix) *Pinus* pollen (moving average) with depth, core H3 (Hythe 24/2/2000).
(x) *Pinus* pollen (moving average) with depth, core H4 (Hythe 6/9/2000).
(xi) *Pinus* pollen (moving average) with depth, core H5 (Hythe 6/9/2000).
(xii) *Pinus* pollen (moving average) with depth, core H6 (Hythe 6/9/2000).
(xiii) *Pinus* pollen (moving average) with depth, core B1 (Bury Farm, Marchwood 6/9/2000).
(xiv) *Pinus* pollen (moving average) with depth, core B2 (Bury Farm, Marchwood 6/9/2000).
(xv) *Pinus* pollen (moving average) with depth, core B3 (Bury Farm, Marchwood 6/9/2000).
(xvi) *Pinus* pollen (moving average) with depth, core B4 (Bury Farm, Marchwood 6/9/2000).
(xviii) *Pinus* pollen (moving average) with depth, core B5 (Bury Farm, Marchwood 6/9/2000).
(xviii) *Pinus* pollen (moving average) with depth, core B6 (Bury Farm, Marchwood 6/9/2000).


Pinus pollen (moving average) with depth, core GM1
(Gins Marsh Beaulieu 28/4/97)
Pinus pollen per ml
0
2000
4000
6000
8000
Depth (cm)
0
-4
-8
-12
-16
-20
-24
-28
-32
-36
-40
-44
-48
-52
-56
-60

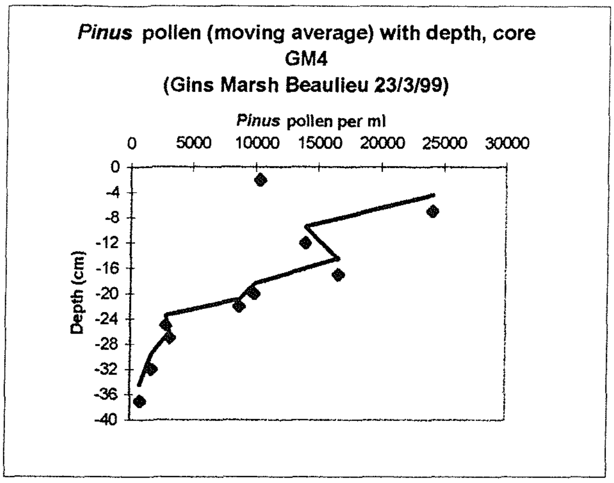
(i)


Pinus pollen (moving average) with depth, core GM2
(Gins Marsh Beaulieu 5/9/97)
Pinus pollen per ml
0
2000
4000
6000
8000
10000
Depth (cm)

(ii)

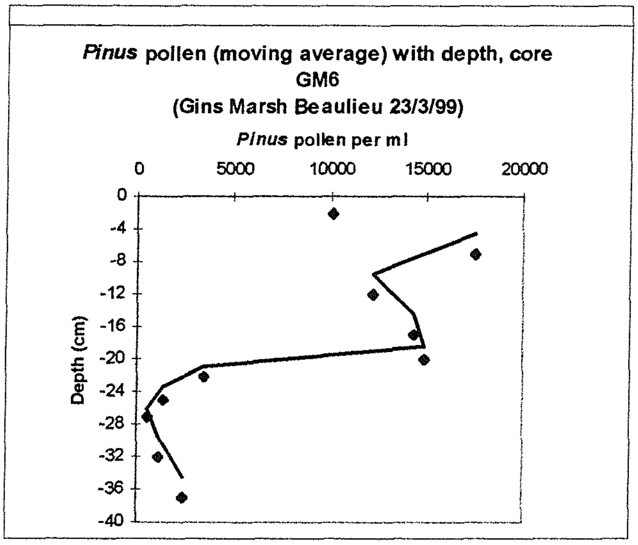

Pinus pollen (moving average) with depth, core GM3
(Gins Marsh Beaulieu 5/9/97)
Pinus pollen per ml
0
5000
10000
15000
Depth (cm)
0
-4
-8
-12
-16
-20
-24
-28
-32
-36
-40
-44
-48
-52
-56
-60

(iiii)

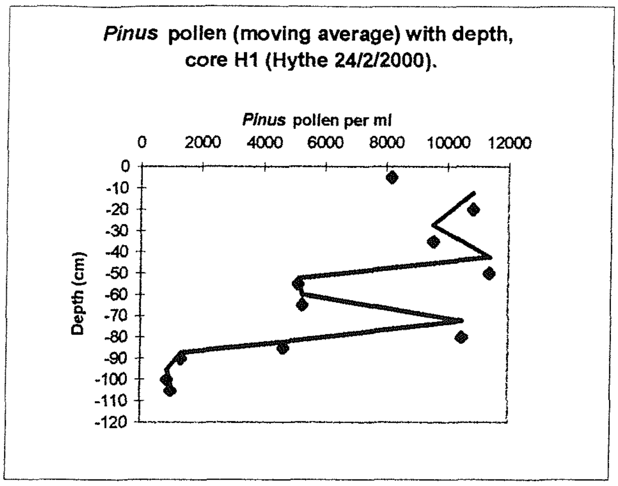

Pinus pollen (moving average) with depth, core GM4 (Gins Marsh Beaulieu 23/3/99)
Pinus pollen per ml
0
5000
10000
15000
20000
25000
30000
Depth (cm)
0
-4
-8
-12
-16
-20
-24
-28
-32
-36
-40

(iv)

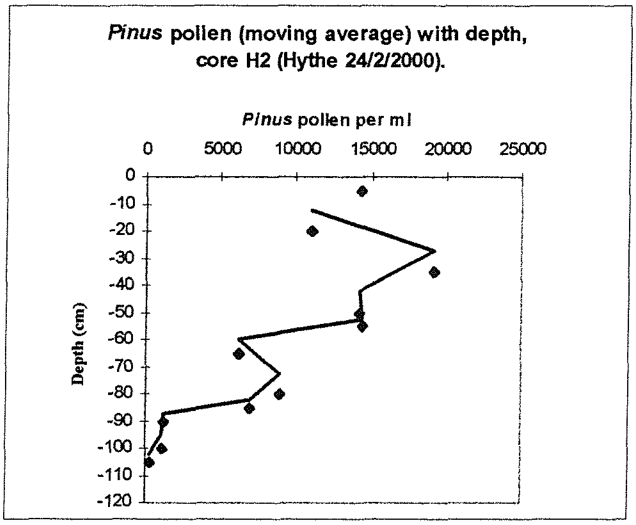
(v)


Pinus pollen (moving average) with depth, core GM6 (Gins Marsh Beaulieu 23/3/99)
Pinus pollen per ml
0
5000
10000
15000
20000
Depth (cm)
0
-4
-8
-12
-16
-20
-24
-28
-32
-36
-40

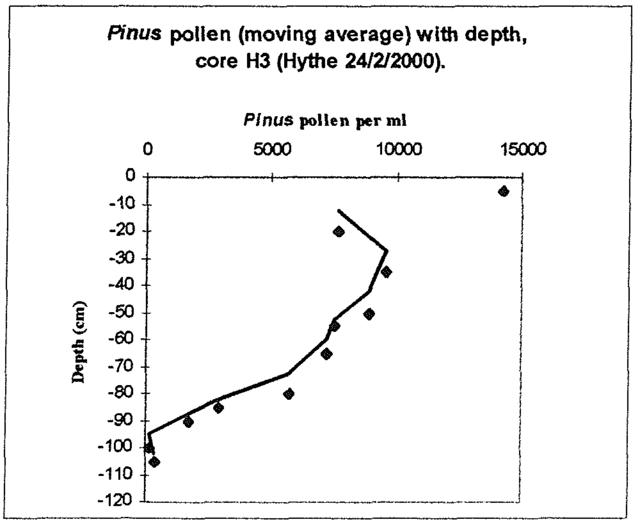
(vi)


Pinus pollen (moving average) with depth, core H1 (Hythe 24/2/2000).

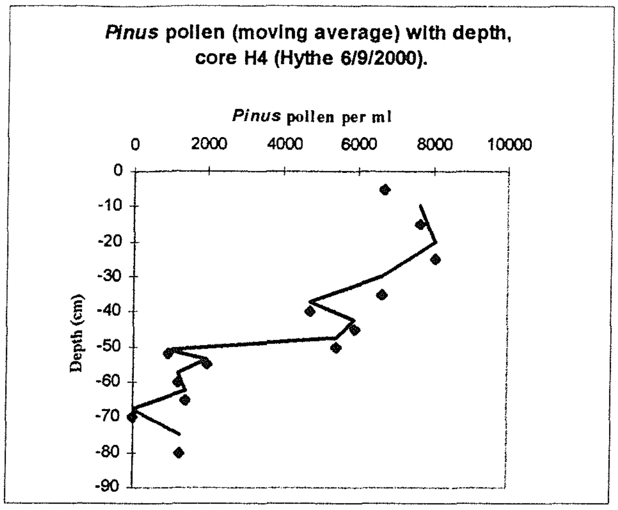
(vii)


Pinus pollen (moving average) with depth, core H2 (Hythe 24/2/2000).

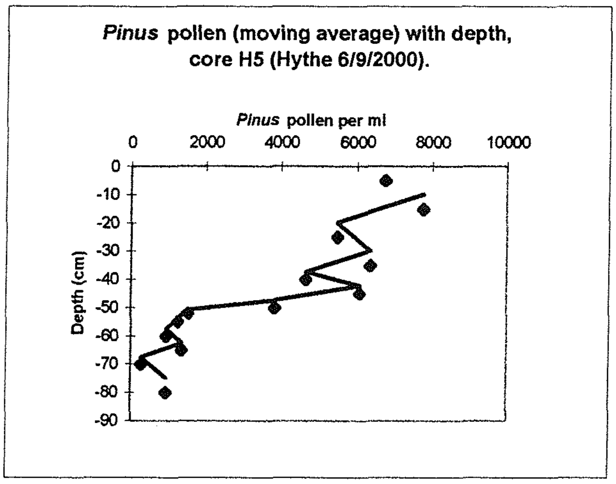
(viii)


Pinus pollen (moving average) with depth, core H3 (Hythe 24/2/2000).

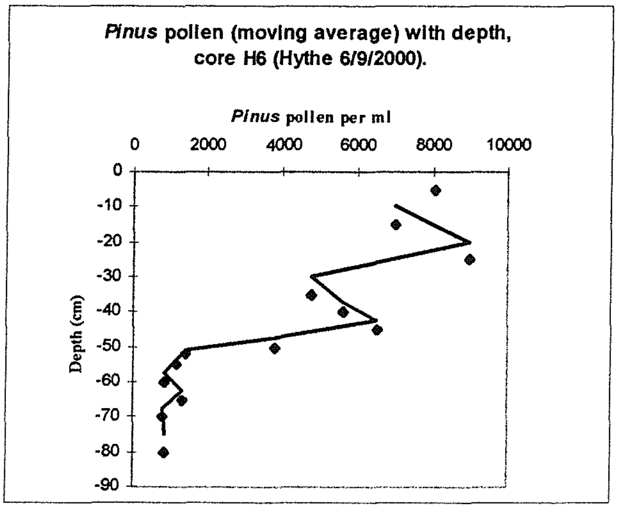
(ix)


Pinus pollen (moving average) with depth, core H4 (Hythe 6/9/2000).
Pinus pollen per ml
0
2000
4000
6000
8000
10000
Depth (cm)
0
-10
-20
-30
-40
-50
-60
-70
-80
-90

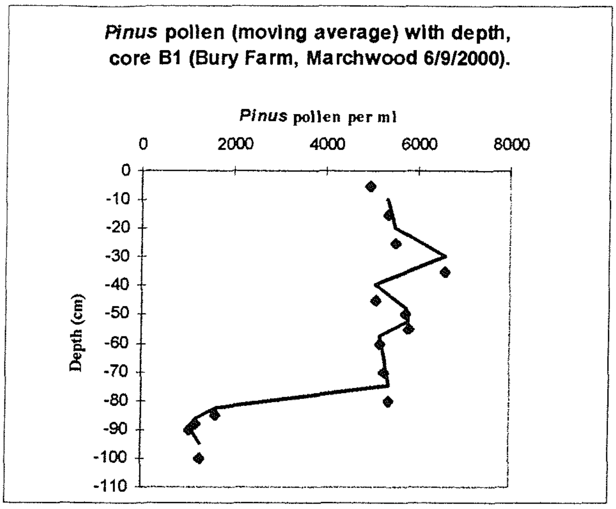
(x)


Pinus pollen (moving average) with depth, core H5 (Hythe 6/9/2000).
Pinus pollen per ml
0
2000
4000
6000
8000
10000
Depth (cm)
0
-10
-20
-30
-40
-50
-60
-70
-80
-90

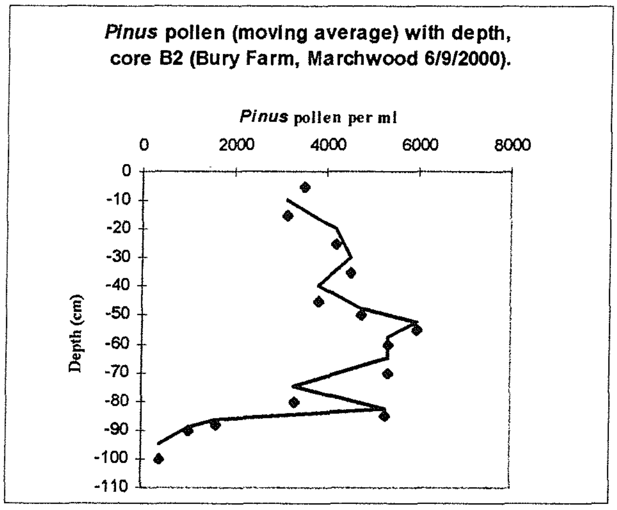
(xi)


Pinus pollen (moving average) with depth, core H6 (Hythe 6/9/2000).
Pinus pollen per ml
0
2000
4000
6000
8000
10000
Depth (cm)
0
-10
-20
-30
-40
-50
-60
-70
-80
-90

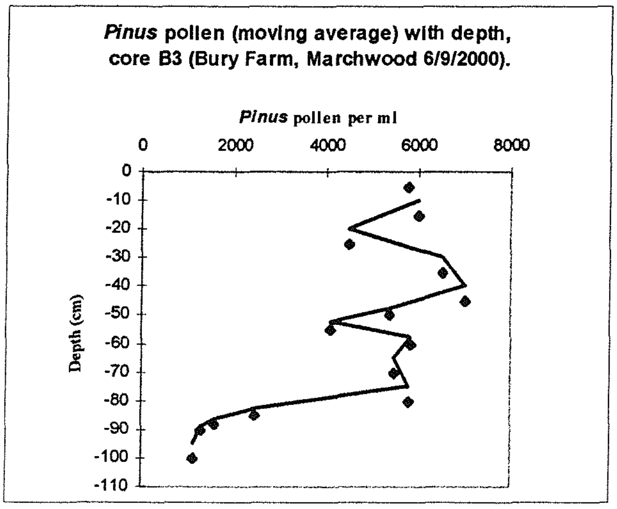
(xii)


Pinus pollen (moving average) with depth, core B1 (Bury Farm, Marchwood 6/9/2000).
Pinus pollen per ml
0
2000
4000
6000
8000
Depth (cm)
0
-10
-20
-30
-40
-50
-60
-70
-80
-90
-100
-110

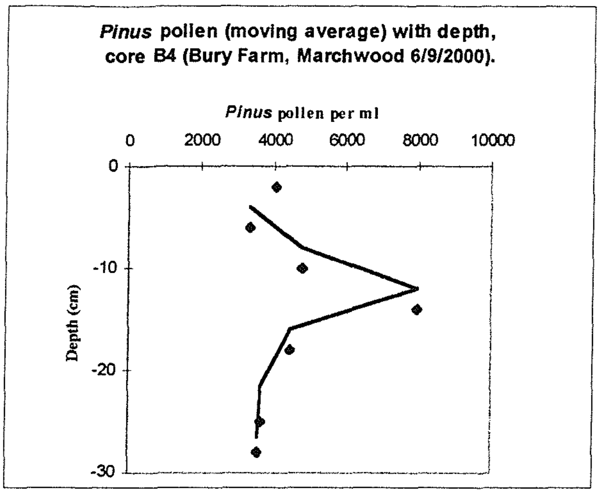
(xiii)


Pinus pollen (moving average) with depth, core B2 (Bury Farm, Marchwood 6/9/2000).
Pinus pollen per ml
0
2000
4000
6000
8000
Depth (cm)
0
-10
-20
-30
-40
-50
-60
-70
-80
-90
-100
-110

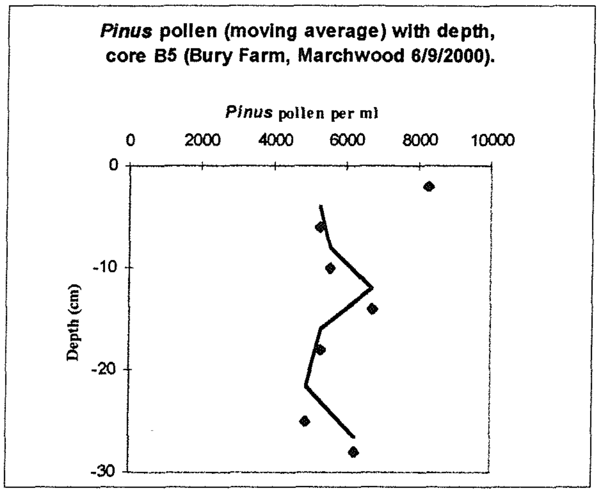
(xiv)


Pinus pollen (moving average) with depth, core B3 (Bury Farm, Marchwood 6/9/2000).
Pinus pollen per ml
0
2000
4000
6000
8000
Depth (cm)
0
-10
-20
-30
-40
-50
-60
-70
-80
-90
-100
-110

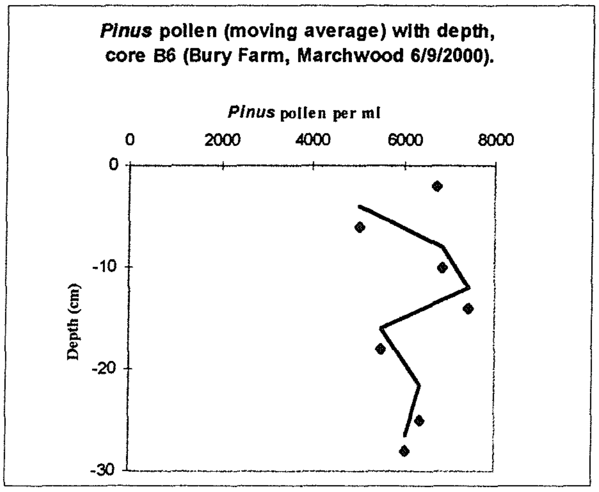
(xv)



(xvi)



(xvii)



(xviii)

Appendix 3.1 Plates

Plate 1. Species rich lawns, with *A. maritima* in flower, at Gins Marsh, Beaulieu (June 1998).

Plate 2. Experimental exclosure plot, with *A. maritima* in flower, at Gins Marsh, Beaulieu (June 1998).

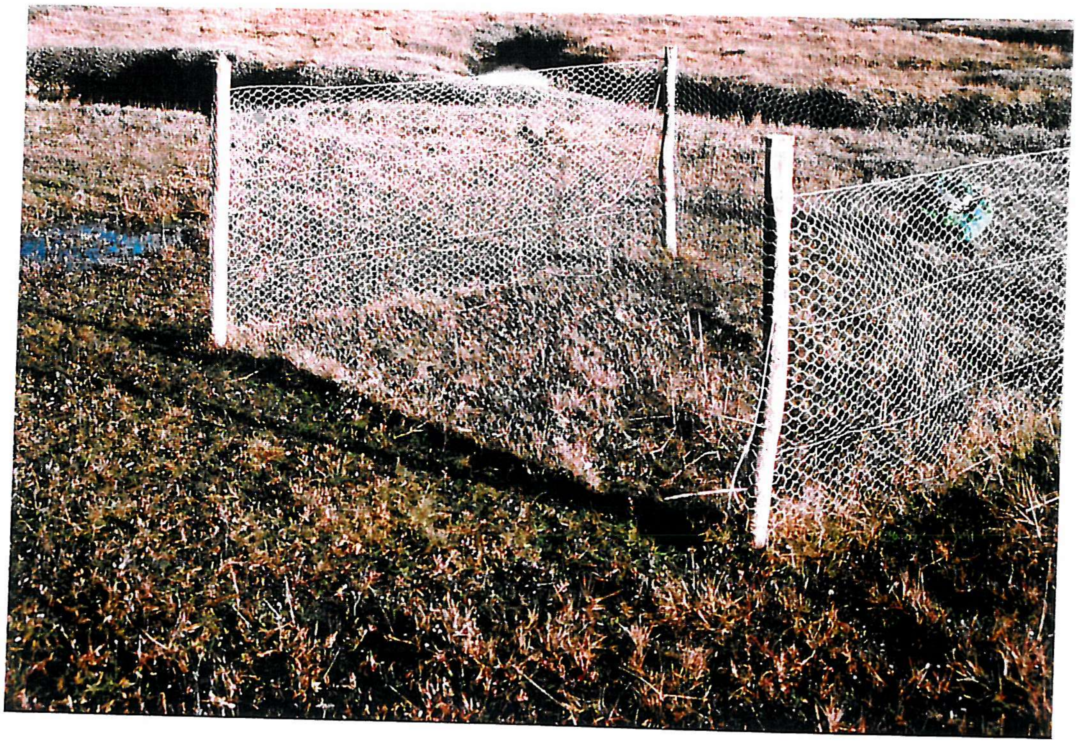


Plate 3. Residual canopy in winter, in grazing exclosure at Gins Marsh, Beaulieu (January 1997).

Plate 4. Posts control plot at Gins Marsh, Beaulieu (June 1997).

Plate 5. Saltmarsh zonation at Sims Wood Marsh, Beaulieu (March 1996). The *J. gerardii* zone is the brown fringe on the right. *S. anglica* occupies the area near the water.

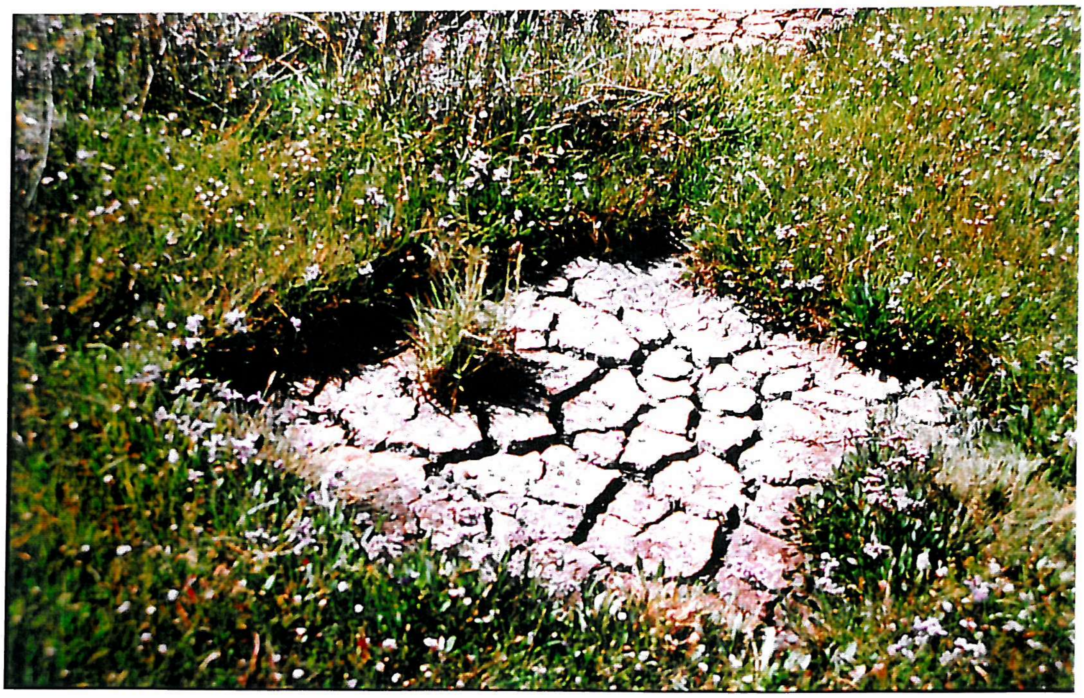


Plate 6. *S. anglica* growing in a pool in the upper marsh (temporarily dry). Sims Wood Marsh, Beaulieu, July 1997.

Plate 7. *S. anglica* colonising a disturbed patch in the upper marsh at Sims Wood Marsh, Beaulieu (March 1996).

Plate 8. *Spartina anglica* transplant plot with surrounding competition removed, in the third growing season. Sims Wood Marsh, July 1998.

Plate 9. *J. gerardii* transplant plot with neighbouring growth removed, in the first growing season (August 1996), Sims Wood Marsh, Beaulieu .

Plate 10. *J. gerardii* transplant plot with neighbouring growth removed, in the third growing season (August 1998), Sims Wood Marsh, Beaulieu.

Plate 11. Patchy zonation of plant communities, Gins Marsh, Beaulieu, June 1996.

Plate 12. Tidal debris on the drift line, Sims Wood Marsh, Beaulieu, May 1997.

Plate 13. Large tidal debris on the drift line, Sims Wood Marsh, Beaulieu, September 1997.

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