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# The Role of Soil and Vegetation Processes in the Control of Organic and Mineral Fluxes in Some Western European Salt Marshes

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## ABSTRACT

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Comparative studies of salt marsh productivity, the pool of nutrients in marsh soils, and the associated fluxes of nutrients, sediments and organic matter have been made in the UK, The Netherlands, Portugal and France. These have shown contrasting relationships between the functional maturity of a marsh and the direction and magnitude of associated fluxes. Actively-extending marshes tend to be flood-dominated systems and net importers of sediment and organic matter, while exporting mineral nutrients. Marshes that are not extending, however, are usually ebb-dominated, net exporters of organic matter and even sediment. These latter marshes can best be regarded as 'mature' or, if they are showing signs of decay, as 'over-mature', in contrast to the 'immature' marshes that are still growing.

Soil available phosphorus ($PO_4$-P) concentrations measured ranged from 15 to 200 mg/kg, and influenced the primary productivity of the marsh. $PO_4$-P concentrations are themselves partly controlled by the origin and amount of sedimentation on the marsh surface. In contrast, soil inorganic nitrogen showed a strong seasonal trend, with minimum concentrations, related to plant uptake, occurring in early summer.

The breakdown of organic matter, both above and below the soil surface, appears more rapid in a healthy mature marsh than in a degenerating marsh, and physical processes in the creeks are more pronounced. Low levels of soil microbial activity, immobilization of mineral nitrogen and the slow breakdown of plant litter would seem to characterize degenerating 'over-mature' marshes. Despite these factors, there was little or no difference in the Net Aerial Primary Productivity (300–800 g $m^{-2}$ $y^{-1}$) measured at two marshes, one of each type, in the UK.

**ADDITIONAL INDEX WORDS:** *Salt marshes, nutrient fluxes, soils, sediments, primary productivity, ecosystem function.*

## INTRODUCTION

Salt marshes occur on the upper parts of the inter-tidal zone. Their soils are composed of fine-grained sediments carried in by tidal action and then stabilized by the development of vegetation cover. The growth of this vegetation cover increases the rate of sediment accretion by slowing water flow over the marsh. Where salt marshes exist, there are usually mud flats occupying the lower part of the inter-tidal zone.

Until relatively recently, salt marshes were viewed as little better than derelict land, and were often built upon, used as rubbish tips, or excavated to form marinas. That perception has now changed and, in addition to their conservation value, they are now seen as important for sea defence, for wildfowling, as nurseries for fish, and as sources of organic matter and nutrients for adjacent ecosystems, some of which include shell-fish and birds. Salt marshes also act as pollution filters. Geese and, in some places, sheep and cattle graze the marsh. Monetary value can be given to all these attributes (KING and LESTER, 1995). For instance, it has long been accepted that salt marsh in front of a clay sea wall offers considerable protection to that wall from wave action. It is thus possible to reduce both the height and maintenance of a wall protected by salt marsh, and the cost savings (both capital and maintenance) can be quantified for different widths of marsh (NRA, 1992).

Salt marshes are best regarded as processors of organic and mineral material of estuarine and coastal origin. The marsh soils, sediments, fauna and flora provide reserves of nutrients and organic carbon, which are cycled both within the marsh, and between marsh, mudflat and coastal waters. In addition, there are inputs from adjacent terrestrial habitats. Aerial inputs of nitrogen can contribute up to 4 g N $m^{-2}$ $yr^{-1}$ in the UK (GOULDING, 1990), and up to 4.5 g N $m^{-2}$ $yr^{-1}$ in The Netherlands (KOERSELMAN and VERHOEVEN, 1992).

Salt marshes erode and accrete in cycles driven by tides, weather and the sediment supply, and can respond to changes in sea level provided that there is an adequate supply of sediment and landward migration is not restricted (PETHICK, 1992). Salt marshes have been built by the import

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of sediment, but there is always a considerable dynamic sediment flux within the marsh, with erosion in one part being balanced by accretion in another part.

The vegetation of salt marshes shows a marked zonation from the pioneer zone, which is covered by each tide, through the lower marsh, which is covered only by spring tides, and the middle marsh, to the upper marsh, which is covered only for short periods by the highest of spring tides (BOORMAN *et al.,* 1994a).

The impact of natural and anthropogenic environmental changes on the salt marsh ecosystem can only be predicted accurately by understanding the functioning of the ecosystem. Changes in the functioning may affect the value of the salt marsh in terms of its roles in sea defence, in supporting inshore fisheries, and in its high intrinsic value for nature conservation. Salt marshes are biologically and chemically active (ODUM and DE LA CRUZ, 1967). They were once thought to be net exporters of organic matter and nutrients (TEAL, 1962; ODUM, 1969, 1980), and this idea became formalized in the 'outwelling theory' or 'outwelling hypothesis'. However, it often remains unclear what are the net effects of the various cycles, of nutrients, of organic matter and of sediments, in relation to the marsh as a whole (NIXON, 1980). The functional aspects of salt marshes can best be studied in one of two ways. They can be studied at the ecosystem level dealing with energy flows (MITSCH and GOSSELINK, 1993), or they can be seen as transition zones between terrestrial and marine environments (HANSEN and DI CASTRI, 1992; DAME *et al.,* 1992; CHILDERS, 1994).

This paper investigates the relationships between salt marshes and adjacent ecosystems, estuaries and coastal waters, and examines the likely effect on these relationships of environmental changes, such as climate change and sea level rise. Findings from the first stage of the work have already been presented (LEFEUVRE *et al.,* 1993; ASJES and DANKERS, 1994; BETTENCOURT *et al.,* 1994; BOORMAN *et al.,* 1994a, 1994b; DAME and LEFEUVRE, 1994). This paper reviews these findings in the light of further studies.

## STUDY SITES

Salt marshes can be subdivided on the basis of their state of development. This may range from growing and extending laterally to degenerating in the extent and density of the vegetation. In these functional terms, marshes can be regarded as being 'immature' while they are still developing, 'mature' when they have reached a degree of stability and 'over-mature' when they show signs of degeneration (BOORMAN *et al.,* 1994a). Study sites (Table 1) were selected to represent different functional types of salt marshes in four countries (the UK, France, The Netherlands and Portugal). Sample points were selected randomly within the different vegetation zones, and the marshes were monitored between 1990 and 1995.

Table 1. *Summary of the details of the study sites.*

| Country | Site | Area (ha) | Tidal Range (m) | Marsh Type | Functional Maturity |
|---|---|---|---|---|---|
| UK | Tollesbury | 26 | 4.3 | Estuarine | Over-mature |
| UK | Stiffkey | 38 | 4.8 | Barrier | Mature |
| France | Mont St Michel | 6 | 11.0 | Foreland | Immature |
| Portugal | Mira | 2 | 3.4 | Estuarine | Mature |
| Portugal | Pancas | 5 | 3.8 | Estuarine | Mature |
| Netherlands | Ameland | 4 | 2.1 | Barrier | Mature |
| Netherlands | Groningen | 10 | 2.1 | Foreland | Immature |
| Netherlands | Waarde | 1 | 4.9 | Estuarine | Over-mature |

The area quoted is that of the study area, usually only a small part of the whole site. Tidal range is the difference between Mean High Water Spring Tide and Mean High Water Neap Tide

There were two main sites in the UK. One was at Tollesbury in Essex, forming part of the estuary of the river Blackwater (BOORMAN *et al.,* 1994a), and the other was at Stiffkey (Figure 1) on the north Norfolk coast (HAZELDEN and LOVELAND, 1996), on an extensive area of coastal fringing marsh. At Tollesbury the salt marsh is very dissected, with sinuate creeks bordering both London Clay (Eocene) upland and reclaimed marsh. The salt marsh here has a limited pioneer zone and appears to be over-mature, as it is degenerating with signs of erosion in many places. The sediment is a silty clay with around 58% clay and 40% silt; water movement through this sediment is very slow and the soils are often anaerobic within 30 cm depth. The area is important for shell-fish and inshore fisheries. Within the study site, ten sampling sites were selected randomly on the lower marsh (*Puccinellia maritima* (Hudson) Parl. and *Halimione portulacoides* (L.) Aellen) and ten on the pioneer marsh (*Aster tripolium* (L.) and *Salicornia* spp.). There is little middle or upper marsh at Tollesbury.

Contrastingly, the study site at Stiffkey is part of a broad strip of marshland (about 1 km wide) fringing the north-facing coast, and protected from the sea by a combination of shingle ridge, sand dunes and offshore sand banks. The salt marsh, mainly middle and upper marsh, is much less dissected than at Tollesbury. It is developed on stratified deposits which range from clay to sand, but which commonly contain between 25 and 45% clay and around 50% silt; sediment on levées has up to 20% fine sand. The sandy layers are relatively permeable and so allow some lateral water movement. Sampling sites were selected randomly, with a number of sites in each of three vegetation zones (*Limonium vulgare* Miller, *Halimione portulacoides* (L.) Aellen in the middle marsh and *Elymus pycnanthus* (Godron) Melderis in the upper marsh) chosen to reflect the overall species composition of the marsh. Seven sites were selected in the *Limonium* zone, three in the *Halimione* and two in the *Elymus.*

Limited studies were carried out at three further sites in the UK (HAZELDEN and LOVELAND, 1996). Northey Island and North Fambridge, both in Essex (Figure 1), were once reclaimed marsh (polder), which reverted to salt marsh following breaches in the sea wall in 1897 which were not repaired. Reclaimed marsh, just landward of the sea wall by the Tollesbury marsh, and now grassland, was sampled to provide comparative microbiological data.

The French sites were at the eastern end of Mont Saint Michel Bay (Figure 2), and range from pioneer to upper marsh (LEFEUVRE *et al.,* 1994). One site was grazed intensively by sheep and the other ungrazed. Since most of the marshes investigated during this project were not used for

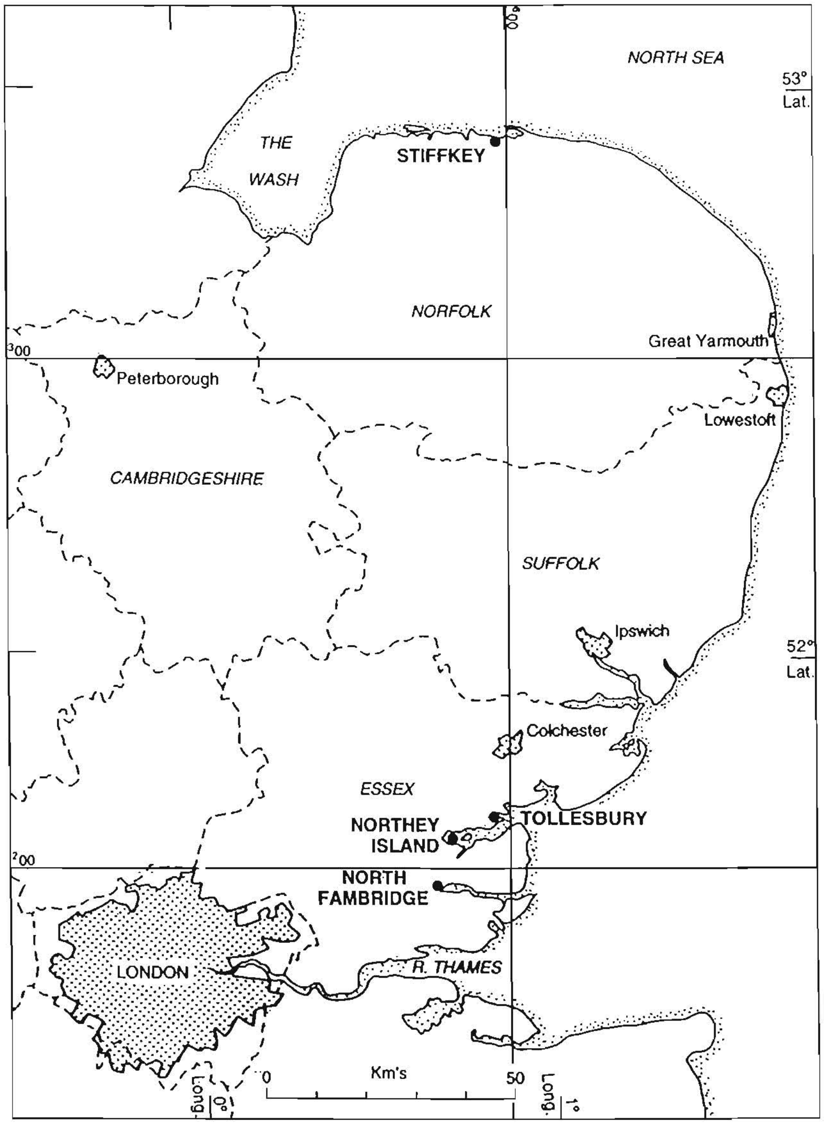

Figure 1. Location of the salt marsh study sites in the UK.

grazing, only the ungrazed marsh is discussed in this paper. Two Portuguese marshes were studied (Figure 2), one in the Mira Estuary (BETTENCOURT *et al.*, 1994) and one at Pancas on the south side of the Tagus Estuary (BETTENCOURT, 1996). Three sites have been investigated in The Netherlands (DANKERS, 1996), one on Ameland, one north of Groningen, and the third at Waarde in the Westerschelde (Figure 2).

The soils on all the marshes (HAZELDEN and LOVELAND, 1996) are saline Typic Hydraquents (SOIL SURVEY STAFF, 1975), or Unripened Gley Soils (AVERY, 1980) developed in mainly fine-textured estuarine or marine alluvium. At Mont Saint Michel, the soils are more sandy. On the highest ground and towards the landward edge of the marsh, particularly at Mont Saint Michel and Ameland, there are soils with partially ripened upper horizons which resemble the Typic Fluvaquents (SOIL SURVEY STAFF, 1975) or Alluvial Gley Soils (AVERY, 1980) found on reclaimed marsh (polders). Both ripened and unripened soils are classified as Gleyo-Salic Fluvisols by FAO-UNESCO (1990).

## METHODS

### Sampling

Bulk samples of soil, generally to 20 cm depth, were taken to determine mineral nutrients. Sampling was carried out monthly in the UK and France during the growing season, and three or four times a year in the Netherlands and Portugal. At each of the randomly selected sampling sites, three randomly selected sub-sites were sampled and these samples bulked for analysis.

Samples were taken from the UK sites in March and July/August 1994 in order to assess microbiological activity. Three

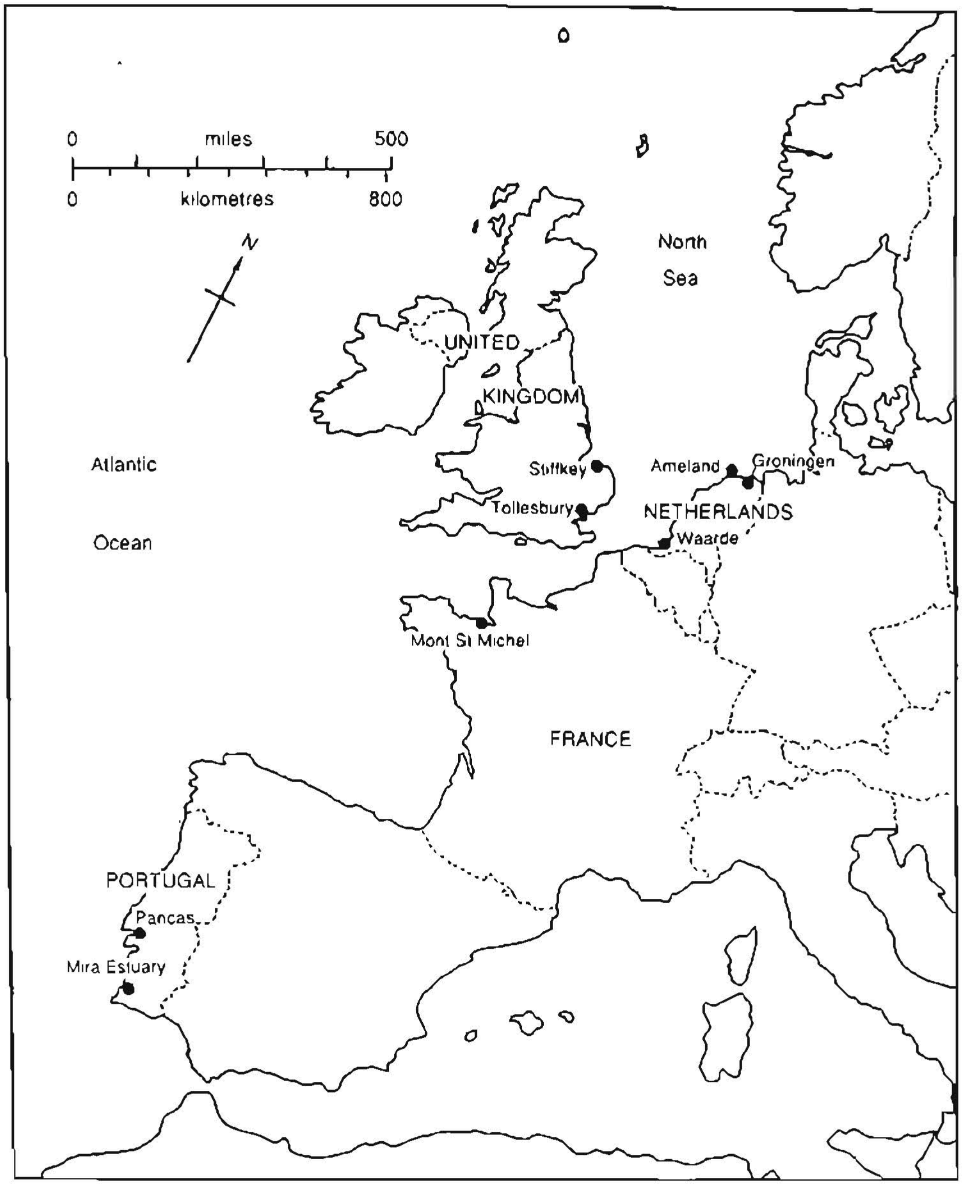

Figure 2. Location of the salt marsh study sites in the Netherlands, France and Portugal.

samples were collected from each of five of the sampling sites within the pioneer and lower marsh at Tollesbury and from the *Limonium* zone in the middle marsh at Stiffkey. For comparison, five samples were also collected from Northey Island, and five from reclaimed marsh adjacent to the Tollesbury site. The samples were incubated and analyses separately. Generally, samples were taken to 30 cm depth. In the pioneer zone at Tollesbury, however, strongly anaerobic soil often occurs within 30 cm depth, and so samples to 15 cm were used.

Samples to 20 cm depth were also collected in the UK and France for field incubation (ENO, 1960; GORDON *et al.*, 1987), in order to assess the mineralization and immobilization of nitrogen. This technique incubates the soil sample in its natural environment but isolated from the effects of plant uptake and leaching. Samples were collected in June 1994 from three sites in each of the pioneer marsh and lower marsh at Tollesbury; and from six sites at Stiffkey, three in the *Limonium* zone and two in the *Halimione* (middle marsh), and one in the *Elymus* (lower marsh). One part of the sample was taken away for analysis, and the other was wrapped loosely in a polythene bag and reburied in the soil. This second sample was collected after 15 days incubation. In France, this exercise was repeated four times a year, with samples from three sites in each of the vegetation zones incubated for 30 days.

Interstitial soil pore water samples were collected monthly during the growing season from the UK sites in order to determine dissolved mineral nutrients. The water was collected using ceramic porous pot samplers at 40 cm depth (GROSSMAN and UDLUFT, 1991; HAZELDEN and LOVELAND, 1996). Three samplers were installed at the apices of a triangle, 1.5 m apart, at each of five sampling sites within the lower marsh at Tollesbury, and at three sites in the *Limonium* zone, one in the *Halimione* and one in the *Elymus* zone at Stiffkey. For sampling, these were evacuated to a partial vacuum of 70 kPa, and left for the minimum time necessary to achieve an adequate sample for analysis (50–100 ml), commonly about an hour. It is important that only a small sample is taken since removal of soil water affects the soil hydrology (GROSSMAN and UDLUFT, 1991). Samples were analyses separately.

Primary production was determined by cutting sample quadrats according to the method of Smalley (LINTHURST and REIMOLD, 1978). Each month during the growing season 30 replicate quadrats were cut at each of the two marsh types at Tollesbury, and 36 quadrats at Stiffkey. The level of replication and the quadrat size (0.1 $m^2$) were selected, following an initial trial, to give standard errors in monthly biomass of less than 10%. Oven dry (80°C) weights of living and standing dead biomass, and of litter, were determined for each species.

The rate of decomposition of litter on the marsh surface at Stiffkey and Tollesbury was studied by the use of litter bags. Polypropylene bags 150 × 150 mm with a mesh size of 2 mm were filled with fresh litter collected on the site and roughly corresponding to 2 g dry weight per bag. The fresh to dry weight ratio of the fresh litter was determined for each site. The bags were placed on the marsh surface for 7 time periods of up to 300 days. At each time period 9 bags were collected from each site and the dry weight of the remaining material was determined.

Tidal data were recorded and water samples were taken in the main creek every 30 minutes during each of the tidal cycles. Water velocities were measured at three depths within the creek and a mean (arithmetic) calculated. Water samples were pumped from 1 m intervals down the water column, and analyses for coarse organic material (> 50 μm), total nitrogen, $NH_4$-N, $NO_3$-N and $NO_2$-N, total phosphorus, chlorophyll-a and suspended sediment.

The water discharge was calculated by taking the average current speed with the mean cross-section area of the water during a time interval (normally half an hour but 10 minutes during the turn of the tide). Multiplying the volume by the mean concentration of a particular substance during the same half hour gave the transport load of that substance. By summing these periods an exchange figure for each flood and ebb tide was obtained, and a net tidal flux estimated. Net tidal fluxes were expressed on an area basis to allow for the differences in size between the Tollesbury and Stiffkey sites (38 and 26 hectares respectively).

Changes in the surface level of each in the salt marsh study sites at Stiffkey and Tollesbury were monitored by means of three rows of four 2 m long mini-transects. At each transect the surface level at 20 points was measured in relation to an aluminium bar placed across pairs of fixed points, which were anchored at 80 cm depth. The network thus consisted of a total of 240 points at each site and the levels were recorded approximately monthly from May 1993.

## Analytical Methods

Soil ammonium-nitrogen and nitrate-nitrogen were determined by steam distillation from a 2 M potassium chloride extract, and nitrite-nitrogen spectrophotometrically. Soil available phosphorus ($PO_4$-P) was extracted with 0.5 M sodium hydrogen carbonate solution and determined colorimetrically as the blue molybdate complex (MAFF/ADAS 1986). Soil nutrient analyses are expressed as mg/kg on an oven-dry basis.

For the pore and tidal creek waters, total nitrogen was determined by Kjeldahl digestion using a copper-selenium catalyst followed by steam distillation, and total phosphorus was determined as the blue molybdate complex after an alkali digest (SMITH and BAIN 1982). The dissolved nutrients, $NH_4$-N, $NO_3$-N and $PO_4$-P, were analyzed either by ion chromatography, or by steam distillation ($NH_4$-N and $NO_3$-N), and colorimetrically as the blue molybdate complex ($PO_4$-P) (MAFF/ADAS 1986). $NO_2$-N was determined spectrophotometrically. Coarse organic matter in tidal water was collected from a water sample of 50 litres filtered over a plankton net (50 μm) (DANKERS *et al.*, 1984). Sediment from the water was separated, where appropriate on a 0.45 μm glass-fibre filter, but generally there was too little sediment to analyze separately. Chorophyll-a was determined spectrophotometrically after extraction in an aqueous solution of acetone.

Soil microbial biomass was determined by the fumigation-extraction carbon method of VANCE *et al.* (1987). Samples were incubated for 10 days at 55% of their water holding capacity before fumigation in de-alcoholised chloroform and extraction (soil equal to 25 g dry weight was used) in 100 ml of 0.5 M $K_2SO_4$. The addition of HgO during digestion was found to be essential to prevent the reaction of halides, which are abundant in these soils, with the chromate digestion solution; without HgO, the apparent level of microbial biomass measured was typically 2 to 3 times higher than its true value.

Dehydrogenase activity values were determined by the method of HILL *et al.* (1993) as a measure of soil microbial activity. This measure of biological activity can give erroneously large values in highly reducing conditions due to the chemical, as well as the biological, reduction of tetrazolium chloride (TTC) into triphenyl formazan (TPF). A pilot test confirmed that chemical reduction could have accounted for 35–55% of the observed production of TPF in some of the Tollesbury pioneer zone samples, and these results have been omitted in calculating the mean values.

Measurements of soil nitrogen were made following both field incubation (ENO, 1960; GORDON *et al.*, 1987), and laboratory incubation (ISO, in press) of soil samples. The concentrations of $NH_4$-N and $NO_3$-N before and after incubation give an assessment of the extent of nitrification and ammonification (gross mineralization) occurring in the soil. In the laboratory, nitrogen mineralization and nitrifying potential were determined using a modification of the standard ISO method (ISO, in press). This recommended incubation of the soil at

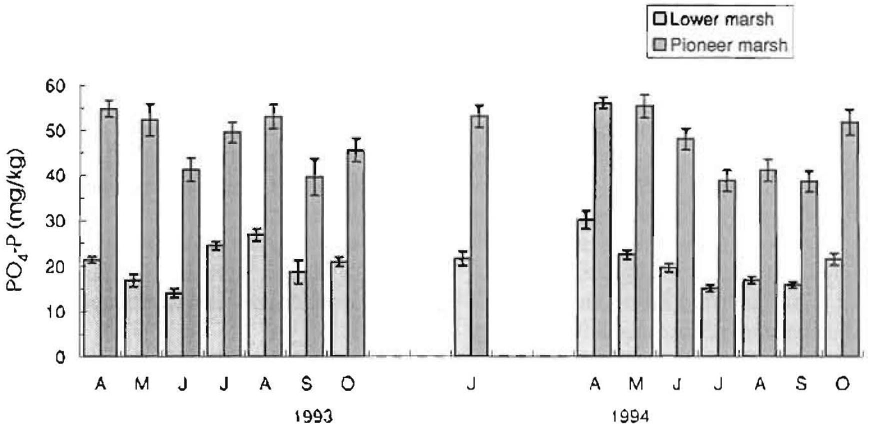

Figure 3. Mean monthly soil available phosphorus ($PO_4$-P) concentrations at Tollesbury, UK (±SE, n = 10).

40 to 60% of the maximum water holding capacity for 21 days at 25°C. This procedure was followed for the Tollesbury reclaimed marsh soils, but is considered inappropriate for salt marsh soils since they are unlikely ever to dry to this extent. Consequently, these soils were incubated at 80% of their maximum water holding capacity, which represented a median value of their water content when sampled.

All the data were examined by analysis of variance (ANOVA) and linear regression analysis using Systat for Windows v. 6.0, Microsoft Excel v. 5.0 and Minitab v. 9.2. The microbiological data were examined using one-way ANOVA followed by multiple range tests, using Tukey's HSD Test to obtain 95% confidence intervals for site means.

## RESULTS

### Soil Phosphorus

The mean monthly values of soil available phosphorus ($PO_4$-P) from the pioneer zone at Tollesbury were significantly higher ($p < 0.001$) than those from the lower marsh by a factor of more than 2 (Figure 3). 88% of the variance in $PO_4$-P concentration was accounted for by vegetation zone and date of sampling, most by vegetation. Overall mean concentrations were 47.9 ± 0.8 mg/kg and 20.4 ± 0.5 mg/kg (±SE, n = 150) for the pioneer zone and lower marsh respectively.

Soil available phosphorus levels at Stiffkey were comparable with those on the lower marsh at Tollesbury. Overall mean concentrations were 21.2 ± 1.2, 20.4 ± 1.2 and 16.8 ± 1.1 mg/kg for the *Limonium, Halimione* and *Elymus* zones (±SE, n = 105, n = 45, n = 30) respectively.

At Northey Island and North Fambridge, which were once agricultural and have reverted to salt marsh following extensive damage to the sea walls in 1897, there were much higher concentrations of available P than at either of the other two UK sites. Mean concentrations here in lower marsh soils were 75.4 ± 2.1 and 87.5 ± 2.5 mg/kg (±SE, n = 42, n = 25) respectively.

The mean available phosphorus concentrations in October 1993 for all the marsh soils studied during this project are shown in Figure 4 (available phosphorus was not measured in the French soils); the relative values remained similar throughout 1993 and 1994. There was a wide range of values; lowest concentrations were in the Mira marsh with an overall mean of 13.8 ± 1.5 mg/kg (±SE, n = 12), and largest concentrations at Waarde with 146.1 ± 7.7 (±SE, n = 32) in The Netherlands.

### Soil Ammonium-Nitrogen

Inorganic nitrogen in the salt marsh soils examined was dominantly $NH_4$-N. Soil $NO_3$-N concentrations were much smaller and showed no seasonal pattern, and there was virtually no $NO_2$-N present.

Mean monthly concentrations of soil ammonium-nitrogen, at both Stiffkey (Figure 5) and Tollesbury, generally fell in early or mid summer and recovered in autumn and winter as plant growth declined. Most of the variation at Stiffkey was explained by sampling date ($r^2 = 0.532$, $p < 0.001$), and there was no significant difference between vegetation zones. At Tollesbury, $NH_4$-N concentrations in the pioneer marsh soils were generally slightly higher than those for the lower marsh ($p = 0.025$). Overall mean concentrations were 22.8 ± 1.8 and 17.2 ± 1.6 mg/kg, respectively (±SE, n = 150).

$NH_4$-N concentrations appeared to follow a similar pattern in soils from the Dutch and the Portuguese marshes, declining in the summer, but with fewer measurements than in the UK, it was not possible to confirm this trend. Overall mean concentrations at Ameland, Groningen and Waarde were 28.4 ± 2.8, 24.0 ± 3.6 and 27.1 ± 3.2 mg/kg respectively (±SE, n = 32, n = 20, n = 32). There were differences between vegetation zones in the Ameland marsh soils with overall mean concentrations of 12.9 ± 1.5, 26.4 ± 3.3 and 51.1 ± 5.4 mg/kg (±SE, n = 8, n = 16, n = 4) in the *Salicornia, Puccinellia* and *Elymus* zones respectively. Mean $NH_4$-N concentrations measured in the Portuguese soils were of the same order as above.

The soils at Mont Saint Michel were very different, however, with only small amounts of $NH_4$-N and no seasonal pattern. Concentrations ranged from 2.9 ± 0.1 mg/kg in the low-

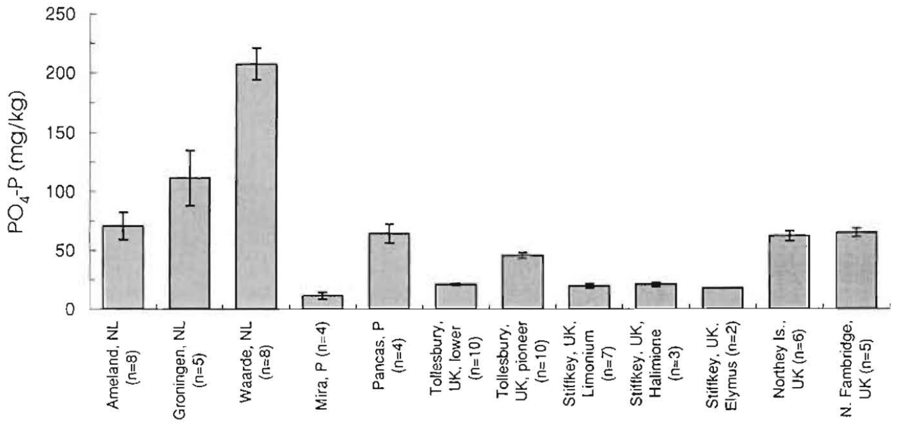

Figure 4. A comparison of mean soil available phosphorus levels at all sites in October 1993 (±SE).

er marsh to 4.5 ± 0.3 mg/kg in the middle marsh soil (±SE, n = 99).

### Soil Pore Water Exchanges

These were only investigated at the UK sites. At both Tollesbury and Stiffkey, concentrations of nutrients in soil water samples were consistently very low (Table 2). PO$_4$-P concentrations were generally of the same order as in adjacent tidal creeks (around 0.07 mg Total P l$^{-1}$).

Nitrogen, however, gave different results. Concentrations of NO$_3$-N in pore waters were much smaller than those of NH$_4$-N (Table 2). This situation was reversed in the tidal creeks where mean NO$_3$-N levels (0.71 ± 0.05 mg NO$_3$-N l$^{-1}$, ±SE, n = 243) were much higher than those of NH$_4$-N (0.10 ± 0.02 mg NH$_4$-N l$^{-1}$, ±SE, n = 243). There was virtually no NO$_2$-N in either pore or creek waters. Mean NH$_4$-N concentration in the pore water samples at Tollesbury was remarkably constant and significantly larger than at Stiffkey ($p < 0.001$).

### Microbiological Activity

Although the mean soil microbial biomass figures ranged from 838 to 1904 μg C g$^{-1}$ (Table 3), there were no significant differences between any of the UK sites. Mean dehydrogenase activity was greatest at Stiffkey, and showed significant variation ($p = 0.05$), being much greater in August (716 μg TPF g$^{-1}$ d$^{-1}$) than in March (421 μg TPF g$^{-1}$ d$^{-1}$) (Table 3). Lowest values came from the reclaimed marsh at Tollesbury, and from the lower marsh at Tollesbury.

None of the soil samples incubated in the laboratory, or in the field at Stiffkey, showed any significant net mineralization or immobilization. During field incubation for 15 days at Tollesbury, however, there was immobilization of ammonium-nitrogen (Table 4), giving a net nitrogen immobilization in June 1994 of around 30 mg N kg$^{-1}$ 15d$^{-1}$ in the pioneer marsh and 20 mg N kg$^{-1}$ 15d$^{-1}$ in the lower marsh.

In the French marsh soils, between June 1994 and the end of 1995, there was net nitrogen mineralization. Overall mean net mineralization ranged from 4.2 ± 1.0 mg N kg$^{-1}$ 30d$^{-1}$ in

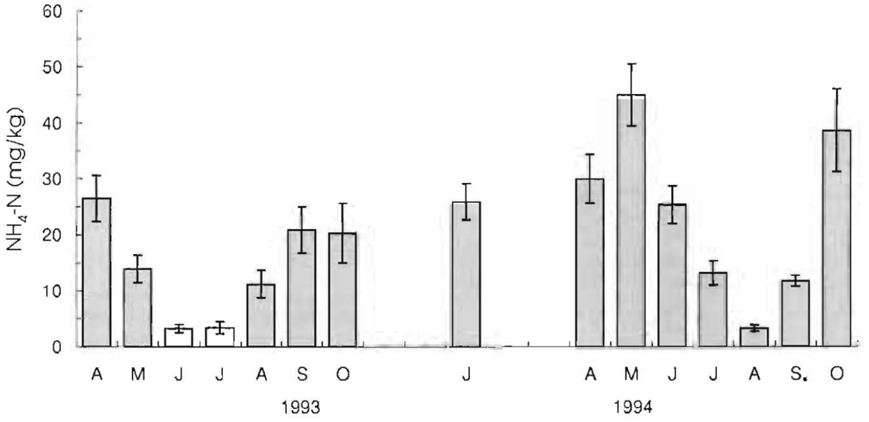

Figure 5. Mean monthly soil ammonium-nitrogen (NH$_4$-N) concentrations at Stiffkey, UK. There was no significant difference between vegetation zones so mean values are for the marsh as a whole (±SE, n = 12).

Table 2. *Overall mean concentrations of $PO_4$-P, $NO_3$-N and $NH_4$-N in soil pore waters.*

| | $PO_4$-P | $NO_3$-N (mg/l) | $NH_4$-N |
|---|---|---|---|
| Tollesbury | 0.02 ± 0.01 | 0.14 ± 0.03 | 1.50 ± 0.10 |
| Stiffkey | 0.03 ± 0.01 | 0.02 ± 0.05 | 0.25 ± 0.07 |

± SE, n = 105

the upper marsh to 15.8 ± 1.0 mg N kg$^{-1}$ 30d$^{-1}$ in the middle marsh (±SE, n = 54).

The nitrifying potential of the UK salt marsh soils (19–73 $\mu g\ NO_{3^-}/NO_{2^-}\ g^{-1}\ 21d^{-1}$) was of the same order as that measured in the reclaimed marsh soils under grassland (33 $\mu g\ NO_{3^-}/NO_{2^-}\ g^{-1}\ 21d^{-1}$), and there were no significant differences between marsh sites or sampling dates.

## Organic Matter Production

There is considerable variation in the measured Net Aerial Primary Productivity (NAPP) for the main types of marsh vegetation found at the UK sites, as defined by marsh zone and dominant plant species (Table 5). Data from the French site (Bouchard, 1996), Dutch sites (Dankers, 1996) and Portuguese sites (Bettencourt, 1966) are included in this table for comparison. Part of the reason for this variation in NAPP is the difference in $PO_4$-P concentrations in the marsh soils (Figure 6).

## Plant Litter and Decomposition

The initial rates of litter decomposition were high with at least 20% of the initial dry weight being lost within the first ten days, but with slower rates thereafter (Figure 7). At Tollesbury it was difficult to follow the decomposition after 80 days as the loss of the plant material by decay was obscured by the growth of algae on the material remaining. However, that the rate of decomposition was faster at Stiffkey than at Tollesbury.

The decomposition rates at Stiffkey were similar to those at Mont Saint Michel Bay where it was shown that the microfauna accounted for approximately a half of the decomposition process (Bouchard, 1996). The rates of breakdown in the marshes at Pancas, Portugal (Bettencourt, 1996 report) were intermediate between those of Tollesbury on the one hand and those of Stiffkey and of Mont Saint Michel Bay on the other hand, despite much higher average temperatures in Portugal. The low rates of decomposition can probably be explained by the prevailing low surface moisture levels resulting from the hot dry summers.

Table 3. *Microbial biomass and dehydrogenase activity.*

| Site and Date Sampled | Microbial Biomass ($\mu$g C g$^{-1}$) | Dehydrogenase Activity ($\mu$g TPF g$^{-1}$ d$^{-1}$) |
|---|---|---|
| Stiffkey (15/3/94) | 838$^{a}$ | 421$^{b}$ |
| Stiffkey (3/8/94) | 1,904$^{a}$ | 716$^{c}$ |
| Tollesbury (Lower) (10/3/94) | 953$^{a}$ | 126$^{a}$ |
| Tollesbury Lower (5/7/94) | 958$^{a}$ | 138$^{a}$ |
| Tollesbury Pioneer (5/7/94) | 1,566$^{a}$ | 275$^{ab}$ |
| Tollesbury Reclaimed (16/8/94) | 990$^{a}$ | 83$^{a}$ |
| Northey Is. (16/8/94) | 1,372$^{a}$ | 231$^{ab}$ |

Differences between sites were determined using one-way ANOVA followed by multiple range tests, using Tukey's HSD Test to obtain 95% confidence intervals for site means. Mean (n = 5) with the same superscript letter are not significantly different at this level

Table 4. *Mean mineralisation/immobilisation following 15 days field incubation at Tollesbury, UK.*

| | Date | Lower Marsh | Pioneer Marsh |
|---|---|---|---|
| $NO_3$-N (mg/kg) | 21/6/94 | 4.5 ± 1.4 | 1.7 ± 0.4 |
| | 5/7/94 | 3.5 ± 0.6 | 1.6 ± 1.1 |
| $NH_4$-N (mg/kg) | 21/6/94 | 24.6 ± 5.3 | 36.3 ± 10.0 |
| | 5/7/94 | 3.9 ± 2.3 | 5.2 ± 2.6 |

± SE, n = 3

## Water Transport of Nutrients and Organic Matter

At Tollesbury, the tidal water volume was between 3 × $10^5$ and 5 × $10^5$ m$^3$, and virtually all tides cover most of the marsh. With an area of about 40 hectares, this corresponds to an average depth at high water of 0.75–1.25 m across the whole of the marsh. Tidal velocities were relatively low at Tollesbury, but the ebb velocity was generally higher than that of the flood. Mean peak velocities were 0.44 m/s and 0.36 m/s for the ebb and flood respectively. The velocity increased

Table 5. *Net Aerial Primary Productivities (NAPP) found in these studies.*

| Zone | Dominant Species[1] | NAPP Range g m$^{-2}$ yr$^{-1}$ (DW) | Location |
|---|---|---|---|
| Pioneer marsh | *Salicornia* | 249–849 | Netherlands |
| | | 368–625 | Tollesbury, UK |
| | | 233 | France |
| | *Suaeda* | 1,032 | France |
| | *Spartina* | 1,493–1,553 | Netherlands |
| | | 946 | Portugal |
| Lower marsh | *Puccinellia* | 457–701 | France |
| | | 317–657 | Tollesbury, UK |
| | | 355–428 | Netherlands |
| | *Arthrocnemon p.* | 860 | Portugal |
| Middle marsh | *Puccinellia* | 645–824 | Netherlands |
| | | 458 | Stiffkey, UK |
| | | 417 | France |
| | *Halimione* | 1,582–1,708 | France |
| | | 631 | Stiffkey, UK |
| | | 769–2,771 | Portugal |
| | *Arthrocnemon f.* | 3,180 | Portugal |
| | *Arthrocnemon p.* | 767 | Portugal |
| Upper marsh | *Elymus* | 362–1,260 | Netherlands |
| | | 375 | Stiffkey, UK |
| | | 1,266–1,386 | France |

Data for The Netherlands from Dankers (1996) for France from Bouchard (1996) and for Portugal (Bettencourt 1996 report).

[1] Species and authority: *Arthrocnemon f.* = *Arthrocnemon fruticosum* (L.) Moq., *Arthrocnemon p.* = *Arthrocnemon perenne* (Miller) Moss, *Puccinellia* = *Puccinellia maritima* (Hudson) Parl., *Elymus* = *Elymus pycnanthus* (Godron) Melderis, *Halimione* = *Halimione portulacoides* (L.) Aellen, *Salicornia* = *Salicornia europaea* L. agg., *Spartina* = *Spartina anglica* C.E. Hubbard and *Suaeda* = *Suaeda maritima* L.

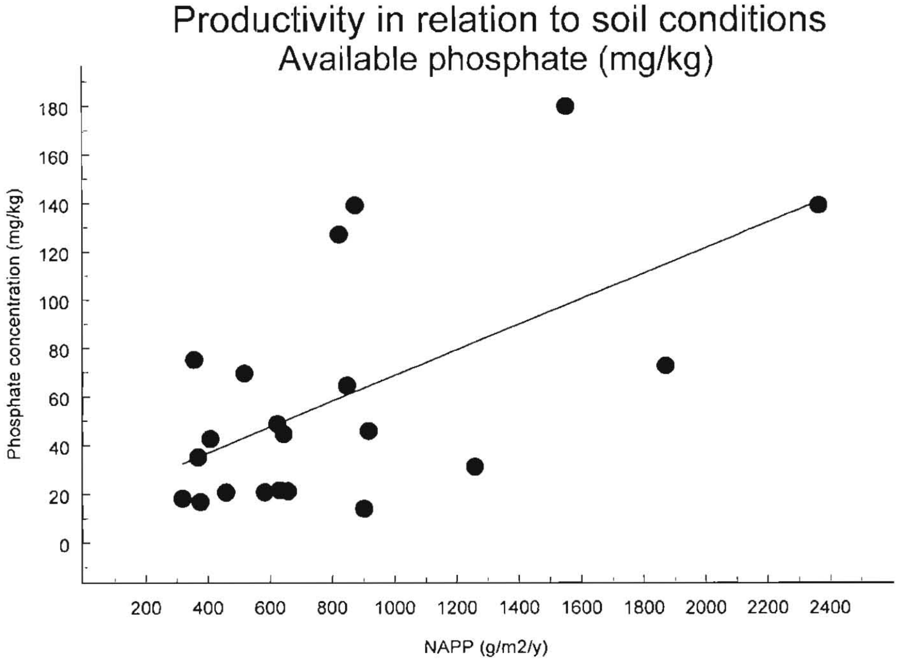

Figure 6. Relation between Net Aerial Primary Productivity and soil available phosphorus ($PO_4$-P) concentrations at sites in the UK and the Netherlands with fitted regression line ($r^2 = 0.35$, $p = 0.01$).

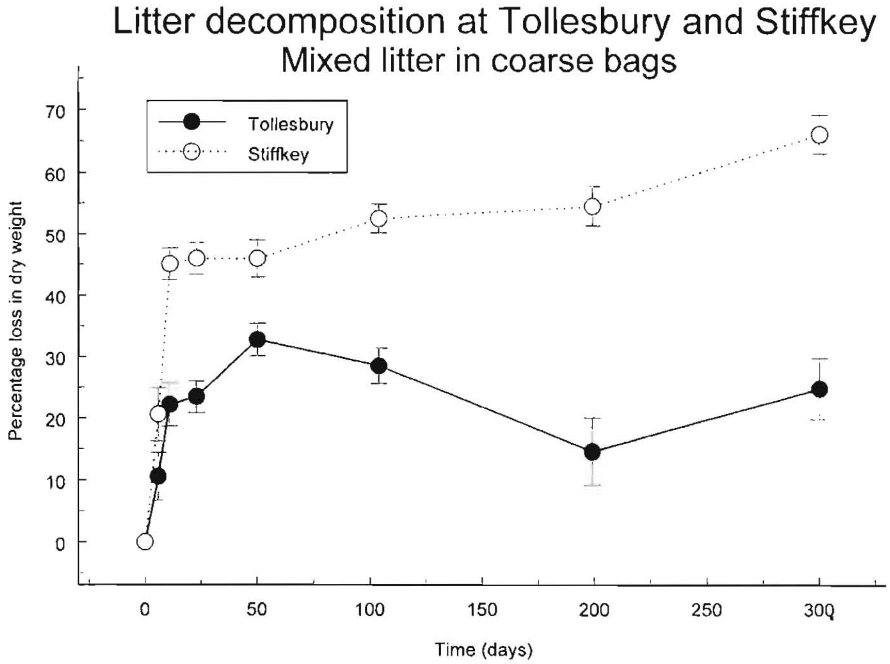

Figure 7. Litter decomposition at Tollesbury and Stiffkey expressed as the percentage weight loss (±SE) of mixed litter in coarse bags left on the marsh surface for periods of up to 300 days.

Table 6. *Four tidal exchanges at Tollesbury, UK, showing exchanges during the flood and ebb tides.*

| Date of observations[1] | | 21.07.94 | 21.06.94 | 28.07.94 | 06.09.94 |
|---|---|---|---|---|---|
| Maximum water level (m OD) | | 2.38 | 2.42 | 2.51 | 2.75 |
| Peak velocity (m/s) | Flood | 0.35 | 0.32 | 0.36 | 0.40 |
| | Ebb | 0.48 | 0.34 | 0.41 | 0.51 |
| Water volume ($m^3 \times 10^3$) | Flood | 434 | 322 | 434 | 491 |
| | Ebb | 301 | 321 | 411 | 506 |
| Particulate matter (tonnes) | Flood | 12.20 | 4.78 | 3.56 | 2.49 |
| | Ebb | 2.00 | 4.18 | 3.44 | 3.16 |
| Total nitrogen (kg) | Flood | 1,070 | 774 | 1,034 | 1,092 |
| | Ebb | 508 | 786 | 1,027 | 816 |
| Nitrate-nitrogen (kg) | Flood | 358 | 696 | 340 | 296 |
| | Ebb | 202 | 786 | 409 | 313 |
| Total phosphorus (kg) | Flood | 70.9 | 50.3 | 134 | 49.0 |
| | Ebb | 72.2 | 40.5 | 106 | 62.0 |

[1]Figures are arranged in order of increasing tidal height

steadily during the flood tide reaching a maximum at, or soon after, half tide, whereas on the ebb the peak velocity was reached rather earlier in the cycle while the water was still running off the surface of the higher marsh (BOORMAN *et al.*, 1994b). There were quite large exchanges (Table 6) of nitrogen (500–1000 kg per tide), mainly in the form of nitrate-nitrogen, though in no clear direction (Table 7). Exchanges of phosphorus were smaller (40–100 kg per tide) and irregular with no clear net flux (Table 7).

At Stiffkey, the water volume moving with each tide is between $1 \times 10^4$ and $15 \times 10^4$ $m^3$. With an area of 26 hectares, this corresponds to an average depth across the marsh of 0.04–0.58 m. Tides below around 2.0 m O.D. cover very little of the main surface of the marsh. Tidal velocities are much higher than at Tollesbury, and there was much greater difference between the spring and neap tides (Table 8). With neap tides that only flood a limited area of the marsh surface, the flood velocities were higher than the ebb (0.28–0.38 m/s and 0.15–0.18 m/s, respectively). Spring tides, however, covered most of the marsh surface and the ebb tide was dominant; peak flood velocity was around 0.6 m/s, peak ebb 0.7–1.3 m/s.

At Stiffkey, nutrient exchanges and fluxes are smaller (Tables 8 and 9), even when the relative sizes of the sites are taken into account (Tollesbury 40 ha, Stiffkey 26 ha). Total nitrogen exchanges at Stiffkey are from 20–290 kg per tide (equivalent to 30–450 kg per tide at Tollesbury). The size of the exchange is variable and so is the direction of the net flux. Nitrate-nitrogen forms a lower proportion of the total nitrogen load than at Tollesbury (28% compared with 48%). The phosphorus exchanges, like those for nitrogen, are lower in absolute terms at Stiffkey (equivalent to about 2–30 kg per tide).

The exchanges of nitrogen observed at the two UK sites were similar to those observed in The Netherlands where there were only small net differences for all forms of nitrogen (BOORMAN, *et al.*, 1994a). In contrast in Mont Saint Michel Bay there were generally net exports of all forms of nitrogen. In the Mira, Portugal, there were small imports of nitrate nitrogen associated with low background levels of all forms of nitrogen (BOORMAN *et al.*, 1994a). In both The Netherlands and Portugal there were only very small exchanges of phosphate although there was no data available on exchanges of phosphate from either the French site or the highly eutrophic Pancas site in the Tagus estuary.

Chlorophyll-a levels were very low (<0.01 mg/l) in the tidal waters at both Stiffkey and Tollesbury, so analyses were discontinued.

Table 7. *Net fluxes per tide for each of the tides shown in Table 6.*

| Component | | | | | |
|---|---|---|---|---|---|
| Date[1] | 21.07.94 | 21.06.94 | 28.07.94 | 06.09.94 | |
| Particulate matter ($g/m^2$) | | +25.4<br>* | +1.51<br>n.s. | +0.30<br>n.s. | −1.67<br>n.s. |
| Total nitrogen ($g/m^2$) | | +1.40<br>n.s. | −0.03<br>n.s. | +0.02<br>n.s. | +0.69<br>n.s. |
| Nitrate-nitrogen ($g/m^2$) | | +0.39<br>n.s | −0.23<br>n.s. | −0.17<br>* | −0.04<br>n.s. |
| Total phosphorus ($g/m^2$) | | <±0.01<br>n.s. | +0.02<br>n.s. | +0.07<br>* | −0.03<br>n.s. |

[1]Figures are arranged in order of increasing tidal height
+ = import, − = export
*—significant at 95% confidence interval, n.s.—not significant

Table 8. *Four tidal exchanges at Stiffkey, UK, showing exchanges during the flood and ebb tides.*

| Date of observations[1] | | 19.07.94 | 26.07.94 | 23.06.94 | 08.09.94 |
|---|---|---|---|---|---|
| Maximum water level (m OD) | | 1.99 | 2.52 | 3.01 | 3.27 |
| Peak velocity (m/s) | Flood | 0.38 | 0.28 | 0.61 | 0.64 |
| | Ebb | 0.15 | 0.18 | 0.72 | 1.30 |
| Water volume ($m^3 \times 10^3$) | Flood | 12.4 | 21.6 | 117 | 114 |
| | Ebb | 10.5 | 21.4 | 109 | 148 |
| Particulate matter (tonnes) | Flood | 0.20 | 1.33 | 0.94 | 1.38 |
| | Ebb | 0.09 | 0.34 | 1.63 | 3.45 |
| Total nitrogen (kg) | Flood | 41.9 | 40.6 | 262 | 171 |
| | Ebb | 19.7 | 63.7 | 199 | 285 |
| Nitrate-nitrogen (kg) | Flood | 8.54 | 10.0 | 46.3 | 95.3 |
| | Ebb | 6.13 | 12.3 | 63.1 | 67.6 |
| Total phosphorus (kg) | Flood | 1.14 | 6.90 | 18.8 | 2.48 |
| | Ebb | 1.16 | 5.22 | 9.37 | 1.97 |

[1] Figures are arranged in order of increasing tidal height

## Sediment Transport and Deposition

Normally, turbidity at Tollesbury was low; the mean suspended solids was 17.9 mg/l. Mean measured sediment input was 2.6 tonnes or 6.4 g/m$^2$ per tide (Table 6). This corresponds to an annual input of 4.7 kg/m$^2$. The sediment load was largely unaffected by tidal velocity (Figure 8), and the input of significant quantities of sediment only occurred when there was sufficient wave action to stir up the mud on the outer flats at the start of the flood.

The mean suspended sediment load at Stiffkey was also low (22.6 mg/l), but somewhat higher than at Tollesbury. However, there were much higher maxima at Stiffkey, in excess of 150 mg/l, and the sediment load was closely related to the tidal velocity (Figure 7). There was a mean measured sediment export of 1.6 g/m$^2$; however, this figure was not thought to be representative (see discussion).

At Stiffkey, there was a short pulse of relatively high velocity (and turbid water) as the tidal front moves up the creek (Figure 9); this was of short duration, 10–20 minutes and, because the volume of water at this stage was relatively small, the overall impact of this is also small. With the higher tides, there is a similar, although larger, peak velocity during the early stages of the ebb (Figure 10).

The network of levelled transects showed that notable accretion occurred at both Stiffkey and Tollesbury in April 1994 and again in December 1994/ January 1995; however, erosion occurred at both sites during October 1994. Overall it appeared that Stiffkey was accreting at 3.08 mm/yr compared with 4.27 mm/yr at Tollesbury (Figure 11).

These accretion rates are relatively low compared with 12 mm in 10 months recorded in the *Spartina* zone, the 24 mm in the *Puccinellia* zone or the 43 mm in the pioneer *Salicornia* zone in the sites at Groningen in the Netherlands. Accretion rates in the Pancas marshes are similar to the Dutch figures at an estimated 32 mm/yr. No data on vertical accretion rates are available for Mont Saint Michel Bay but, given the high rates of horizontal extension of the marshes, vertical accretion rates are likely to be similar to those observed in the Netherlands and Portugal.

## DISCUSSION

The small concentrations of $PO_4$-P in the lower marsh at Tollesbury compared to the pioneer marsh reinforce the conclusions of our previous work (BOORMAN *et al.*, 1994a) in suggesting that the pool of soil available phosphorus may be close to permanent exhaustion in the lower marsh, and that this limits plant growth. Sediment currently being deposited on the lower marsh apparently does little to replenish the reserves; it may be that this sediment is simply material being recycled. With the amount of total P in adjacent coastal

Table 9. *Net fluxes per tide for each of the tides shown in Table 8.*

| Component | | | | | |
|---|---|---|---|---|---|
| Date[1] | 19.07.94 | 26.07.94 | 23.06.94 | 08.09.94 | |
| Particulate matter (g/m$^2$) | | +0.44<br>* | +3.82<br>* | −2.71<br>n.s. | −7.96<br>* |
| Total nitrogen (g/m$^2$) | | +0.9<br>n.s. | −0.09<br>n.s. | +0.24<br>* | −0.44<br>* |
| Nitrate-nitrogen (g/m$^2$) | | +0.01<br>n.s. | −0.01<br>* | −0.06<br>* | +0.11<br>* |
| Total phosphorus (g/m$^2$) | | −0.01<br>* | +0.01<br>n.s. | +0.04<br>n.s. | −0.01<br>* |

[1] Figures are arranged in order of increasing tidal height
+ = import, − = export
*—significant at 95% confidence interval, n.s.—not significant

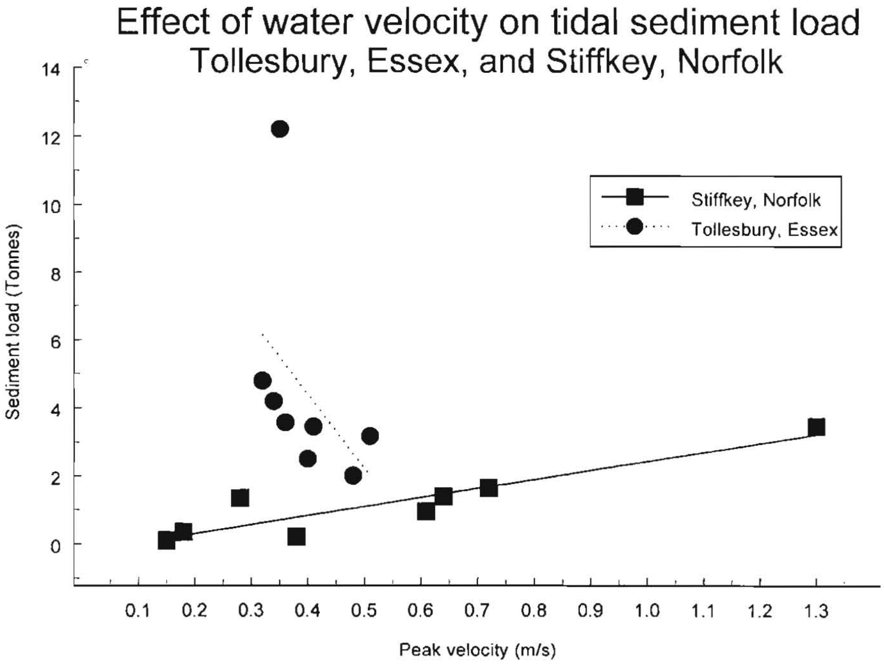

Figure 8. Relation between tidal sediment load (tonnes) and peak water velocity (m s$^{-1}$) at Tollesbury, Essex and Stiffkey, Norfolk with fitted regression lines (Stiffkey $r^2 = 0.85$, $p < 0.001$, Tollesbury $r^2 = 0.21$, n.s.).

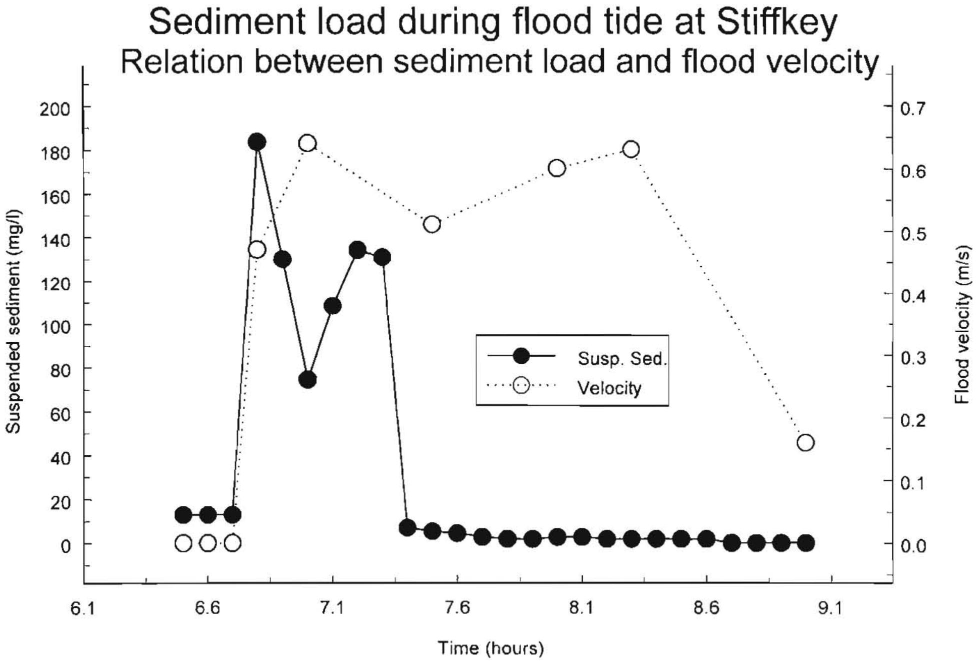

Figure 9. Suspended matter (mg/l) as a function of time (hours) and velocity of the tidal flow (m/s) during the morning flood tide at Stiffkey on 8th September 1994.

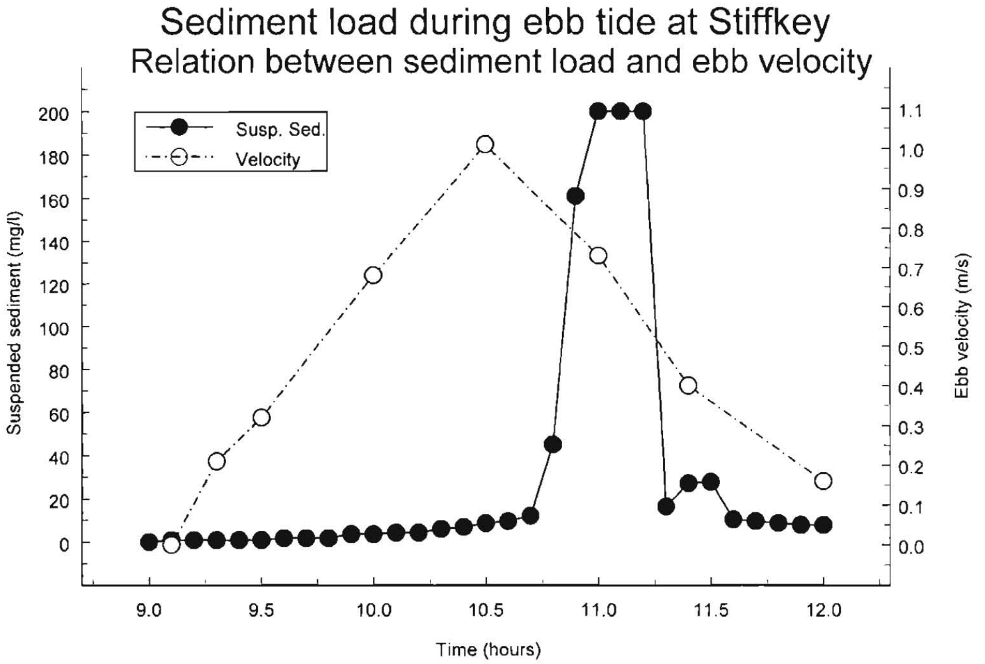

Figure 10. Suspended matter (mg/l) as a function of time (hours) and velocity of the tidal flow (m/s) during the morning ebb tide at Stiffkey on 8th September, 1994.

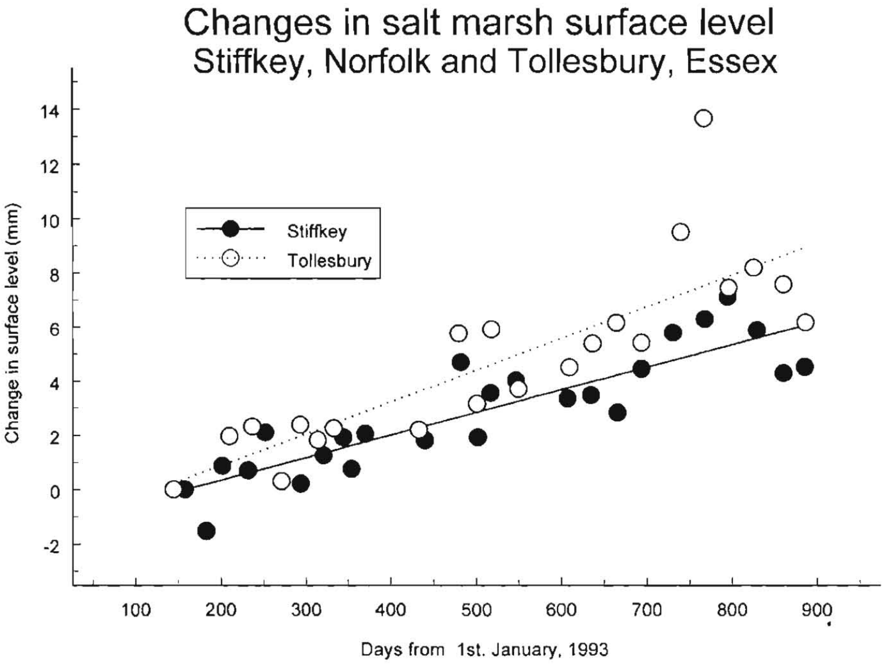

Figure 11. Changes in salt marsh surface level with time at Tollesbury and Stiffkey. Each point represents the mean of 240 readings at each site. Rates of accretion at Stiffkey = 3.08 mm/y ($r^2$ = 0.77, $p < 0.001$) Tollesbury = 4.27 mm/y ($r^2$ = 0.69, $p < 0.001$).

waters only around 0.07 mg/l, there is no other ready source of replenishment. At Stiffkey, concentrations in soils of the *Elymus pycnanthus* zone (upper marsh) are the lowest, much as would be expected since this plant colonises the coarser-textured levées. The large concentrations of $PO_4$-P at Northey Island and North Fambridge are most likely caused by new sediment coming onto the marshes; since 1897 around 0.6 to 1 m of fresh sediment has been deposited on these sites. At Waarde, the large concentrations are probably the result of pollution in the estuary.

Soil available nitrogen, including ammonium-nitrogen and nitrate-nitrogen, is an important control of plant growth in salt marshes (VALIELA and TEAL, 1979a, 1979b). Inorganic nitrogen in the salt marsh soils examined was dominantly $NH_4$-N. $NH_4$-N is produced in soil from the microbial decay of plant and other organic litter, and, during the growing season, the $NH_4$-N produced, and the $NO_3$-N resulting from nitrification, is rapidly taken up by vegetation (ADDISCOTT *et al.,* 1991). Soil $NH_4$-N concentrations at both Stiffkey (Figure 5) and Tollesbury declined in spring and early summer, and only increased again as plant growth slowed in late summer and early autumn. Although there were no significant differences between soil $NH_4$-N concentrations in the vegetation zones at Stiffkey, there were at Tollesbury, reflecting the wetter, more anaerobic, environment in the pioneer zone.

Soil $NH_4$-N concentrations in the marsh soils at Mont Saint Michel are much smaller than those at any of the other sites. This is largely a reflection of the coarser textured, and so more aerobic, soil.

BOORMAN *et al.* (1994a) demonstrated a relationship between the concentration of soil $NH_4$-N and the amount of plant litter. This relationship could be important in the salt marsh ecosystem, as a high storm tide can strip out the litter and deposit it elsewhere, leaving the marsh depleted of the organic debris from which nutrients are mineralized. Such storm tides may well become more frequent and more pronounced with sea level rise and a changing climate.

There are opportunities for nutrient exchange between tidal creek water and soil/sediment pore water. The hydraulic conductivity of clayey marsh soils such as at Tollesbury and Stiffkey is very low (RANDS, 1984), and there is little water movement except along root and faunal channels. This 'mobile' water drains out under gravity or is readily displaced by a flood tide, and it was primarily this water which was of interest, and which was extracted by the porous pot suction samplers (GROSSMAN and UDLUFT, 1991).

$PO_4$-P concentrations in pore waters in the UK marshes were generally of the same order as in adjacent tidal creeks, thus providing little evidence for significant direct fluxes of $PO_4$-P. Concentrations of $NH_4$-N were higher in the more anaerobic environment of the pore water than in the creek water. Mean $NH_4$-N concentration in the pore water samples at Tollesbury was remarkably constant and larger than at Stiffkey, suggesting that the soils were more anaerobic at the former site. Total dissolved inorganic nitrogen (DIN) was represented by $NO_3$-N plus $NH_4$-N, as there was virtually no $NO_2$-N in these waters. Thus, the pore water (Table 2) at Tollesbury contained more DIN that the tidal creek water, while the situation was reversed at Stiffkey. These figures suggest the potential for an export of DIN from the marsh soil at Tollesbury, and an import to Stiffkey.

Soil microbial biomass levels in the UK marshes fell within the range expected for soils beneath meadows (500–1000 $\mu$g C ml$^{-1}$ soil), and were higher than values beneath arable soils (200–500 $\mu$g C ml$^{-1}$ soil) (T. HILL, 1995 *pers. comm.*). The dehydrogenase activity (Table 3) suggested that there was more microbiological activity in soils of the healthy and actively-growing mature marshes such as Stiffkey, and less in those of over-mature marshes, such as the lower marsh at Tollesbury.

Field incubation of soil at Tollesbury identified immobilization of mineral nitrogen as the dominant process. This was due to the strong demand for N caused by the death and microbial decay of roots following sampling. In general terms, the decay of plant material with a C:N ratio greater than 25 will tend to immobilize nitrogen, at least initially. If the C:N ratio is less than 25, then mineralization begins immediately (ADDISCOTT *et al.,* 1991). In contrast, mineralization was the dominant process in the marshes around Mont Saint Michel, reflecting the coarser textured soil and a more aerobic environment.

The nitrifying potential of the marsh soils was measured under wetter conditions (incubated at 80% of maximum water holding capacity) than would normally be used for the reasons discussed in the methods section above. It was feared that this may have inhibited activity. However, the nitrifying potential measured in the salt marsh soils was of the same order as that measured in the reclaimed marsh soils under grassland, which were incubated at the more usual 50% of maximum water holding capacity.

Salt marsh plants are highly productive commonly producing around 1 kg m$^{-2}$ yr$^{-1}$ of organic matter above ground (BOORMAN *et al.,* 1994a). This productivity is partly influenced by the soil available phosphorus content. The plants produce at least an additional 50% below ground in rhizomes and roots (HEMMINGA *et al.,* 1996), although earlier studies suggested a much higher below-ground biomass and production (GROENENDIJK and VINK-LIEVAART, 1987). Algal mats are a significant factor in both the English and Portuguese salt marshes, and have been discussed elsewhere (BOORMAN *et al.,* 1994a). Although they do not appear to affect the overall productivity of the system, they affect the salt marsh in various ways, by trapping sediment, by inhibiting seed germination and seedling growth, and also through nutrient take-up during their growth and nutrient-release during their decay.

Decomposition of litter from the salt marsh vegetation was more rapid at Stiffkey than at Tollesbury. This may, in part, be attributed to the Stiffkey marshes being at a higher level and therefore subject to shorter periods of tidal inundation. While previous studies indicated that significant quantities of organic matter could be exported (BOORMAN *et al.,* 1994a), the bulk of the organic matter produced by a salt marsh remains on the surface of the marsh where it is subsequently broken down. A detailed study of *Halimione portulacoides* showed that at three sites in Mont Saint Michel Bay, with an average standing dead production of 670 g m$^{-2}$ yr$^{-1}$, 73%

of this ended up as litter on the marsh surface while 27% was exported from the site (Bouchard 1996).

Fluxes of sediment and nutrients were calculated on the basis of the weights of a component imported or exported on each tide (Tables 6 and 8). Since these values relate to marsh catchments of different areas, tidal budgets were calculated on the basis of the weights of components per square metre (Tables 7 and 9), imported or exported, and thus these can be compared directly from site to site. There were discrepancies between ebb and flood volumes, and these have been discussed previously (BOORMAN *et al.*, 1994a). The small size of the nutrient fluxes at Stiffkey can be partly explained by the higher level of marsh reducing the opportunities for nutrient exchange.

The high sediment load at Stiffkey on the ebb tide of the 8th September 1994 can be explained by the high ebb velocities reached (up to 1.3 m/s, see Table 8). However, these velocities were only reached in parts of the main creek, and the sediment export represented was very largely from the bed of the creek and did not represent erosion of the marsh surface. Thus, the mean export figure of 1.6 g/m$^2$ must be taken as representing a much higher figure from a limited area. Excluding this high export figure based on a very high tide, there is an average import of 0.5 g/m$^2$ per tide (Table 9), which would correspond to 0.4 kg m$^{-2}$ yr$^{-1}$, an annual accretion rate of 0.3 mm/yr. It may well be that sediment is picked up from the creek bed during the ebb at lower velocities than the 1.3 m/s mentioned above. The figures for the tide of the 23rd June 1994 show a much greater increase in ebb velocity than in flood velocity when compared with the next two smaller tides (which both show higher flood than ebb velocities). This could have resulted in an increased ebb sediment load from erosion of the creek bed on that date.

Assuming a sediment density of 1.2 g/cm$^3$, the net sediment input of 4.7 kg/m$^2$ at Tollesbury would suggest an annual accretion rate of 3.9 mm/yr. This figure compares well with the accretion rate measured directly. The import of sediment at Stiffkey was complicated by the large sediment exchanges occurring within the creek. The accretion estimated from sediment input at Stiffkey (0.3 mm/yr) is very much lower than the direct measurement (3.08 mm/yr). This would suggest that the exports of sediment within the creek itself, during very high tides, were even larger than inferred and concealed significant imports to the marsh surface. The measured rate of accretion would require a mean net import of sediment to the marsh of at least 5 g/m$^2$ per tide.

## CONCLUSIONS

The salt marshes at Tollesbury were classified as being over-mature (BOORMAN *et al.*, 1994a) and this assessment is supported by the observed rates of salt marsh retreat at this and other Essex salt marsh sites (BOORMAN, 1992). The latter studies also pointed out that predicted climate change and the consequent sea level rise were likely to accelerate the degenerative processes further.

The difference in soil $PO_4$-P concentrations between the lower and pioneer marsh at Tollesbury, and the contrast between these values and those recorded from nearby Northey Island and North Fambridge, suggest that sediment being deposited on the lower marsh at Tollesbury represents erosion elsewhere in the marsh. In addition, microbial activity is low, and nitrogen immobilization the dominant process in summer. Despite this, the primary productivity of the vegetation of both pioneer and lower marsh at Tollesbury is comparable with that determined for other marsh areas in this study and also with data from other workers over a range of sites (BOORMAN *et al.*, 1994a).

The marshes at Stiffkey were originally selected as providing a contrast to the Tollesbury marshes in terms of their relative levels. In terms of function, the marsh of the study site at Stiffkey must be regarded as mature, particularly in view of the lower rate of accretion. However, given that this marsh is contiguous with extensive areas of lower and pioneer marshes that are actively extending, the area as a whole can be regarded as being immature to mature. Although the rate of accretion at Stiffkey is low, the system is clearly a dynamic one with great variability in the exchange of particulate matter, although the height of the marsh means that the opportunities for these exchanges are restricted to the creeks except for the highest tides. This is in agreement with a previous study which showed that salt marsh accretion at Stiffkey was very much restricted to the margins of the creeks (PITMAN, 1995).

The productivity of the marsh vegetation at Stiffkey is similar to that at Tollesbury but rather lower than that determined from comparable marsh types in The Netherlands and France. The assessment of the greater dynamic activity of the Stiffkey marshes is supported by the higher rate of decomposition of dead plant material on the surface of the marsh and also by greater microbial activity recorded within the soil. It would appear that the rates of breakdown of organic matter both above and below the soil surface and the magnitude of physical processes within the creek system can be regarded as indicators of an active marsh system.

The importance for nature conservation of the functional aspects of salt marshes has long been recognized as a general principle (DAIBER, 1986). The importance of the present studies lies in their indication of ways of quantifying fluxes and exchanges within and between salt marshes, and in the provision of means of classifying marshes on a functional basis. The practical management of salt marshes needs to take into account both the internal functioning of a particular system and the direction and magnitude of the links with neighbouring ecosystems. Even if a particular marsh has an apparently satisfactory rate of accretion, the source of the sediment cannot be ignored; there are likely to be problems if the rate of accretion is largely dependent on internal erosion within other parts of the marsh. Our studies indicate the importance of the links between salt marshes and other coastal and marine ecosystems. It is tempting to think of marsh maturity in terms of the actual age of particular parts of the marsh. However, comparisons between Tollesbury and Stiffkey, particularly when viewed in the light of the other marsh areas that were studied, clearly indicate that the functional maturity of a marsh does not necessarily parallel its chronological age. It is also clear that a better understanding of functional maturity is the key to practical management of that marsh.

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