Applied Vegetation Science
doi: 10.3170/2008-7-18451, published online 2 May 2008



# The natural regeneration of salt marsh on formerly reclaimed land

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**Abstract**
**Question:** Does the vegetation of restored salt marshes increasingly resemble natural reference communities over time?
**Location:** The Essex estuaries, southeast England.
**Methods:** Abandoned reclamations, where coastal defences had been breached in storm events, and current salt marsh recreation schemes were surveyed giving a chronosequence of salt marsh regeneration from 2 to 107 years. The presence, abundance and height of plant species were recorded and comparisons were made with adjacent reference salt marsh communities at equivalent elevations.
**Results:** Of the 18 paired sites surveyed, 13 regenerated marshes had fewer species than their adjacent reference marsh, three had an equal number and two had more. The plant communities of only two de-embankment sites matched that of the reference community. 0-50 year old sites and 51-100 year old sites had fewer species per quadrat than the 101+ year sites and the reference salt marshes. There was a weak relationship between differences in species richness for regenerated and reference marshes and the time since sites were first re-exposed to tidal inundation. Cover values for the invasive and recently evolved *Spartina anglica* were greater within regenerated than reference marshes.
**Conclusions:** Salt marsh plants will colonise formerly reclaimed land relatively quickly on resumption of tidal flooding. However, even after 100 years regenerated salt marshes differ in species richness, composition and structure from reference communities.

**Keywords:** Chronosequence; Managed realignment; Restoration success; *Spartina anglica*.

**Nomenclature:** Rodwell (2000) for plant communities, Stace (1997) for vascular plants and Hardy & Guiry (2003) for algae.

## Introduction

Centuries of over-exploitation, habitat modification and pollution have led to estuarine and coastal zone degradation, biodiversity loss and a decline in ecological resilience (Lotze et al. 2006). Replacing coastal habitats is important given the high level of ecosystem service they can provide (Costanza et al. 1997) and has become the focus of efforts to develop ecosystem-based management and restoration strategies. Particular attention has been given to the restoration of salt marshes to provide nursery habitats for fishes, nutrient and sediment sinks and coastline protection (Colclough et al. 2005; Moller & Spencer 2002; Shepherd et al. 2005). Since the early 1990s, restoring tidal inundation to formerly reclaimed land, either through a breach in current coastal defences or whole scale embankment removal (managed realignment) has been increasingly used throughout Europe as a cost effective and sustainable response to biodiversity loss and flood management (French 2006). Self-sustaining plant communities are often a primary goal of such restoration efforts as they perform many of the biological and economically desirable functions of wetland ecosystems and are the most common performance standard (Gopal & Mitsch 1995; Moller et al. 1999; Sullivan 2001; van Andel 1998; Zedler & Lindig-Cisneros 2000).

The successful restoration of plant communities depends on the availability of target species and suitable abiotic conditions (Bakker et al. 1996). Restoring hydrological functioning is often assumed to be sufficient for wetland communities to develop on previously reclaimed land (Mauchamp et al. 2002) where regular inundation provides the main dispersal agent for the delivery of diaspores to restoration sites. The availability and dispersal of target species may however, be a bottleneck for successful re-assembly and despite the potential for long-distance transport by tidal water there is a predominance for local dispersal in coastal settings (Huiskes et al. 1995; Middleton 1999; Sengupta et al. 2005; Wolters et al. 2005a). Re-colonisation may also be delayed by unsuitable hydrological and edaphic conditions that facilitate plant species establishment (Onaindia et al. 2001). Wetland communities are particularly susceptible to colonisation by invasive plant species as they act as 'landscape sinks' that accumulate materials from both terrestrial and wetland disturbances (Zedler & Kercher 2004). Invading alien species in wetlands often form mono-specific stands at the expense of native species and restoration sites that experience large scale disturbances on implementation are particularly vulnerable. Competition for space and the more complete use of resources in diverse communities is thought to make them more resistant to invasion than simple communities. By capturing more resources and using them more efficiently diverse communities leave lower nutrient levels available for invading species. Diverse communities also have a higher probability of containing species that are highly competitive for limited resources and can drive out invasive species (Symstad 2000). The ability of a restored community to resist invasion by alien species is an important measure of successful restoration (Cairns 1988; Ewel 1987) and achieving similar species richness to that of target communities an important goal.

The creation of coastal wetlands is a long-term process (Simenstad & Thom 1996) and it can take many years for restored salt marshes to develop plant communities similar to those in natural habitats (Garbutt et al. 2006; Wolters et al. 2005b). To date, timescales for ecosystem replacement have been based on spatial comparisons between restored coastal wetlands of differing ages, often less than 20 years old (Morgan & Short 2002). To overcome this, salt marshes that regenerated on abandoned land following storm breaches of coastal defences have been used as natural analogues for salt marsh development. Such abandoned reclamations have been used to assess sedimentary responses to the breaching of coastal defences (Cundy et al. 2002; French et al. 1999; French 1999) and to validate models on sedimentary processes in natural salt marshes (Allen 2000). They have been used to study the effect of time on natural regeneration of salt marshes in relation to edaphic factors (Onaindia et al. 2001) and to provide general information on the design and management of restoration schemes (Burd 1992). Wolters et al. (2005b) compared the success of salt marsh restoration schemes based on the richness of target species of several accidental and deliberate de-embankment sites across north-west Europe. However, length of time taken for a regenerated marsh to achieve equivalent plant community composition to that of natural marshes is largely unknown (Havens et al. 2002).

In this study we compare the vegetation structure and composition of salt marsh restoration sites and abandoned reclamations to that of adjacent natural communities. Our main objectives were to determine whether: (1) the plant community composition of naturally regenerated salt marshes resembles that of natural salt marshes and (2) over what timescale. These sites are used as analogues for modern day restoration efforts and provide a chronosequence of salt marsh development on formerly embanked agricultural land. The study compares species richness, abundance, sward height, fit of the regenerated marshes to British National Vegetation Communities (NVC) and similarity to reference conditions.

## Material and Methods

### *Study sites*

The Essex Estuaries European Marine Site comprises the major estuaries of the Colne, Blackwater, Crouch and Roach plus extensive areas of tidal flats in south-east England, UK. The area is a relatively undeveloped estuary complex with a wide range of typical estuarine and marine communities. Most of the salt marshes are backed by earth or concrete embankments. There has been significant erosion in the past as a result of coastal squeeze and coastal management (Cooper et al. 2001) and changes in climatic patterns (van der Wal & Pye 2004). The region is regularly used to demonstrate the effectiveness of managed realignment both in the implementation of realignment schemes and theoretical modelling (Anon. 2004; Pethick 1998; Shepherd et al. 2005).

We surveyed 14 abandoned reclamations and four managed realignment sites (all referred to hereafter as de-embankment sites) along the Essex coast during July 2004 (Fig. 1). The embankments of the oldest sites were breached during a storm in 1897 and the youngest (by managed realignment) in 2002, giving a chronosequence of salt marsh development on former agricultural land from 2 - 107 years (Table 1). Data on the time of breach and physical characteristics of the sites for the abandoned reclamations were comprehensively reviewed by Burd (1992). Data on breaching and physical characteristics of the managed realignment sites are described in Environment Agency (Anon. 1999, 2003); Dagely (1995) and Reading et al. (2002). There is no history of livestock grazing or management at any of the study sites.

### *Experimental design*

Successful restoration of plant communities depends on the availability of target species and the presence of favourable environmental conditions that allow the species to germinate and establish. Target species can

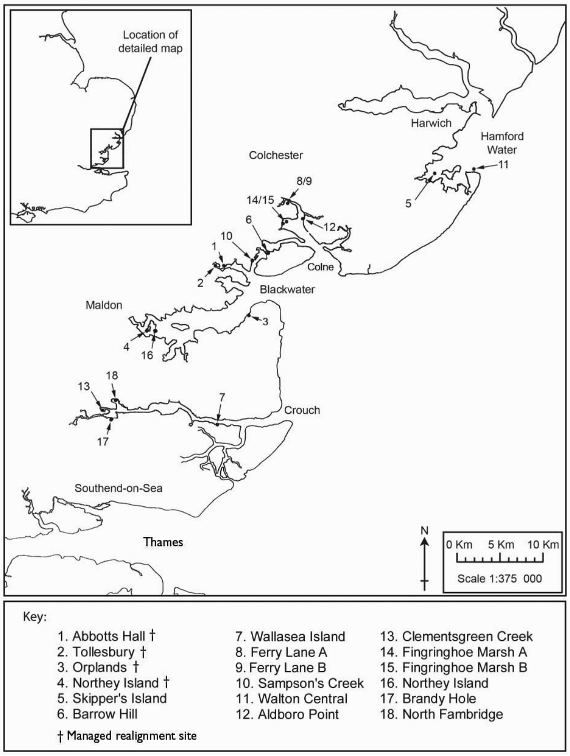


**Fig. 1.** Map showing location of study sites.

colonise a restoration site from several sources with dispersal from the local species pool being the most important (Wolters et al. 2005a). In this study the natural salt marshes adjacent to the de-embankment sites, only separated by the remains of the old embankment and connected by the same creek network, were used to identify the target species and plant communities. All 18 de-embankment sites surveyed had natural salt marsh directly adjacent allowing for a pair-wise comparison at each site.

The marshes of the study region occupy a range 0.25 - 0.65 m below mean high water tides dominated by the *Puccinellietum maritimae* and *Atriplex portulacoidis* salt marsh communities (Boorman 1992). In order to characterise the vegetation, five 2-m$^2$ quadrats were located along a 100-m transect placed at the same elevation (± 0.01 m) within the de-embankment site as that of the adjacent reference marsh using a laser theodolite. The elevation was selected by determining the range of the natural reference marsh by topographic survey, then selecting an elevation at random. Elevation differed between the 18 de-embankment sites. Transects were stratified into five 20-m lengths, with one quadrat placed at random within each 20-m length to avoid any periodicity that might be found in the vegetation (e.g. due to ridges and runnels that reflected old agricultural systems). Transects were placed parallel to the embankment and were centred on the original breach in the seawall. Where there were several breaches in the original embankment at a site, transects were centred on a breach identified at random. Elevation was used as a surrogate for tidal inundation to ensure that the plant communities within the de-embankment sites and reference marshes received equivalent submergence frequencies, and was checked by observing the depth and extent of the incoming tide for each site. No differences were observed.

*Vegetation monitoring*

Species presence and an estimate of percentage cover by eye were recorded for each quadrat. Additional species present along the 100-m transect but not recorded in the five quadrats were also recorded by direct searching and given an abundance score using a subjective five point scale from dominant to rare (DAFOR; Kent & Coker 1992).

The five quadrats sampling 10% of the total transect length were found to be an effective method of characterising the vegetation at a given elevation. None of the transects had more than one additional species recorded outside the quadrats and where additional species were present they were recorded as ‘rare’ (representing a single plant or tussock of vegetation). These data were not used in the analysis.

Five measurements of vegetation height were taken at each quadrat location by placing a hand lightly on the vegetation at the level below which ca. 80% of the vegetation is estimated by eye to be growing (thus ignoring occasional tall stalks) then reading this height with a ruler after Stewart et al. (2001).

*Statistical analysis*

Linear regression analysis was used to describe the relationship between changes in species richness over time in the chronosequence. Where there was a significant relationship between species richness over time, the time-scale for embanked salt marshes to have similar species richness to natural marshes (species richness equivalence) was estimated using the regression equation. In addition, the relationship between species richness, site area and the length of time the former marshes were reclaimed were also analysed. A paired *t*-test was used to test for significant differences in species richness and sward height between de-embankment sites and their adjacent reference marsh using the mean of the five quadrats in each transect.

The vegetation of the de-embankment sites and reference marshes were compared with all other British Plant Communities as described by the National

**Table 1.** Species richness (transect and quadrat), mean sward height, vegetation communities and percentage similarity between de-embankment sites and adjacent reference marshes in Essex. Salt marsh (SM) plant community codes (letters in sub-text denotes sub-communities of the main type as described by Rodwell 2000) and similarity between reference and de-embankment marshes (calculated by Tablefit and Sørensen's index). For differences between reference and de-embankment marsh for species richness per quadrat and sward height a paired *t*-test was used; levels of significant differences are indicated by asterisks (*$P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns = not significant). † indicates a managed realignment site.

| Site | Year of breach | Years since breach | Species richness per transect | | Species richness per quadrat (± SE) | | Sward height, cm (± SE) | | Plant communities | | % Similarity |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Years to 2004 | Reference marsh | De-embanked marsh | Reference marsh | De-embanked marsh | Reference marsh | De-embanked marsh | Reference marsh | De-embanked marsh | Sørenson's index |
| 1. Abbotts Hall† | 2002 | 2 | 10 | 4 | 8.4 (0.4) | 2.8 (0.4)*** | 11.7 (0.4) | 6.2 (0.4)*** | SM 14c | SM 8 | 8.2 |
| 2. Tollesbury† | 1995 | 9 | 11 | 10 | 8.6 (0.7) | 6.6 (0.7)$_{ns}$ | 9.2 (1.0) | 20.1 (1.5)*** | SM 13c | SM 13a | 35.1 |
| 3. Orplands† | 1995 | 9 | 11 | 8 | 7.2 (0.7) | 5.0 (1.0 )$_{ns}$ | 17.8 (2.3) | 20.2 (3.3)$_{ns}$ | SM 14c | SM 13 | 44.4 |
| 4. Northey Island† | 1991 | 13 | 12 | 4 | 9.8 (0.8) | 2.4 (0.2)** | 22.0 (1.0) | 44.1 (1.6)*** | SM 13 | SM 6 | 37.8 |
| 5. Skipper's Island | 1953 | 51 | 11 | 9 | 9.6 (0.2) | 7.2 (0.7)* | 17.0 (0.7) | 19.5 (1.7)*** | SM 13a | SM 13 | 66.1 |
| 6. Barrow Hill | 1953 | 51 | 12 | 7 | 7.6 (0.8) | 4.8 (0.2)* | 14.5 (1.2) | 23.8 (1.8)*** | SM 14c | SM 13a | 41.1 |
| 7. Wallasea Island | 1953 | 51 | 13 | 7 | 7.6 (0.8) | 6.0 (0.3)$_{ns}$ | 16.8 (0.5) | 29.9 (2.6)** | SM 14c | SM 13a | 53.8 |
| 8. Ferry Lane (A) | 1945 | 59 | 7 | 6 | 4.0 (0.7) | 4.6 (0.2)$_{ns}$ | 13.3 (0.7) | 13.1 (0.3)* | SM 14 | SM 13 | 73.4 |
| 9. Ferry Lane (B) | 1945 | 59 | 11 | 8 | 6.0 (0.7) | 5.4 (0.4)$_{ns}$ | 25.6 (1.8) | 32.4 (3.5)** | SM 14c | SM 13a | 92.1 |
| 10. Sampson's Creek | 1945 | 59 | 6 | 6 | 5.4 (0.2) | 4.0 (0.6)$_{ns}$ | 15.5 (1.3) | 20.6 (1.4)** | SM 8 | SM 8 | 80.0 |
| 11. Walton Central | 1938 | 66 | 14 | 7 | 8.4 (1.3) | 5.2 (0.6)$_{ns}$ | 19.8 (0.6) | 19.9 (1.6)$_{ns}$ | SM 14c | SM 14 | 68.6 |
| 12. Aldboro Point | 1921 | 83 | 7 | 7 | 4.2 (0.7) | 4.4 (0.2)$_{ns}$ | 14.6 (1.1) | 18.5 (0.7)$_{ns}$ | SM 14 | SM 13 | 88.4 |
| 13. Clementsgreen Creek | 1921 | 83 | 9 | 9 | 5.2 (0.6) | 6.4 (0.4)$_{ns}$ | 18.1 (0.9) | 19.4 (1.5)*** | SM 14c | SM 14c | 71.5 |
| 14. Fingringhoe Marsh A | 1897 | 107 | 8 | 9 | 5.8 (0.8) | 6.2 (0.7)$_{ns}$ | 22.0 (1.0) | 28.6 (0.9)* | SM 14c | SM 13a | 99.0 |
| 15. Fingringhoe Marsh B | 1897 | 107 | 8 | 10 | 5.8 (0.8) | 7.8 (0.6)** | 15.2 (0.5) | 15.0 (1.4)*** | SM14c | SM 13a | 40.5 |
| 16. Northey Island | 1897 | 107 | 12 | 7 | 9.8 (0.8) | 3.8 (0.8)** | 9.4 (0.8) | 16.7 (1.4)* | SM 13 | SM 6 | 52.6 |
| 17. Brandy Hole | 1897 | 107 | 12 | 9 | 8.6 (0.7) | 7.0 (0.4)** | 20.5 (2.4) | 11.1 (0.8)$_{ns}$ | SM 14c | SM 13a | 45.4 |
| 18. North Fambridge | 1897 | 107 | 11 | 10 | 8.4 (0.5) | 8.4 (0.2)$_{ns}$ | 20.5 (2.4) | 23.9 (1.5)*** | SM 13a | SM 12a | 51.9 |

Vegetation Classification (NVC; Rodwell 2000) using the Tablefit computer programme (Hill 1996). This provided a measure of the 'goodness-of-fit' of each de-embankment community to its adjacent reference marsh. In addition, the similarity between the vegetation of the de-embanked sites and reference marshes was quantified using Sørenson's Index (Kent & Coker 1992).

A mixed model with Wards test was used to test for differences in species richness, cover and vegetation height between the de-embankment and reference marshes with location as a random factor using the mean of the five quadrats. Species with very low cover values (< 0.5 %) were not included in the analysis. Means for percentage fit to the NVC and similarity using Sørenson's Index were compared using one-way ANOVA with F-test. Models were fitted using the method of residual maximum likelihood (REML) using the statistical package Genstat 6.

## Results

### *Plant species*

Of the 18 paired sites surveyed, 13 de-embankment sites had fewer species than their adjacent reference marsh, three had an equal number and two had more (Table 1). 17 halophytes were recorded during the survey (Table 2), all typical species of the region. Three species (*Armeria maritima*, *Plantago maritima* and *Spartina maritima)* were not recorded within the de-embankment sites and the annual halophyte *Spergularia marina* was not recorded in the reference marshes. The 0-50 year old sites and 51-100 year old sites had fewer species per quadrat than the 101+ year sites and the reference salt marshes (Table 3). There was a weak relationship in the difference in species richness between de-embankment sites and reference marshes and the time since the sites were first re-exposed to tidal inundation (Fig. 2). Using this relationship it was estimated that it would take 137

**Table 2.** Percentage cover (SE) of species in de-embankment and reference salt marshes. Means compared using a mixed model with locations as a random effect and angular transformed percentages with Wald test ($W$) for differences. Means which share a letter are not significantly different (5% level). NA – insufficient data for analysis. $^{*} = p < 0.05$; $^{**} = p < 0.01$; $^{***} = p < 0.001$.

| Species | Age class of de-embankment sites 0-50 | 51-100 | 101+ | Reference sites | *W* |
|---|---|---|---|---|---|
| **Vascular plants** | | | | | |
| *Armeria maritima* | 0 (0) | 0 (0) | 0 (0) | 0.05 (0.01) | NA |
| *Aster tripolium* | 1.1$_a$ (0.6) | 11.3a (4.7) | 5.2a (1.6) | 6.4a (2.8) | 2.41 |
| *Atriplex portulacoides* | 2.4$_a$ (2.1) | 28.5bc (9.0) | 9.0 (5.9)ac | 29.9b (4.5) | 15.96*** |
| *Atriplex prostrata* | 0 (0) | 0.1 (9.1) | 0.1 (0.1) | 0.0 (0.0) | NA |
| *Cochlearia anglica* | 0.1 (0.1) | 0.2 (0.2) | 0.0 (0.0) | 0.2 (0.1) | NA |
| *Limonium vulgare* | 0.2a (0.1) | 1.1 (0.4) | 23.1b (6.6) | 10.2b (3.2) | 21.76*** |
| *Plantago maritima* | 0 (0) | 0 (0) | 0 (0) | 0.1 (0.1) | NA |
| *Puccinellia maritima* | 46.5a (23.0) | 31.2a (6.4) | 30.4a (11.0) | 32.8a (3.9) | 1.27 |
| *Salicornia europaea* agg. | 13.4a (0) | 5.2a (0) | 11.4a (0) | 4.9a (0) | 4.68 |
| *Sarcocornia perennis* | 0.4a (0.2) | 0.4a (0.2) | 0.2a (0.3) | 0.9a (0.2) | 6.47 |
| *Spartina anglica* | 20.8a (19.8) | 13.4a (5.8) | 13.6a (7.9) | 3.2b (1.7) | 13.32** |
| *Spartina maritima* | 0 (0) | 0 (0) | 0 (0) | 0 (0) | NA |
| *Spergularia marina* | 0 (0) | 0 (0) | 0 (0) | 0 (0) | NA |
| *Spergularia media* | 0.7ab (0.7) | 0.2a (0.2) | 0.9b (0.5) | 1.1b (0.3) | 9.63* |
| *Suaeda maritima* | 5.8a (5.1) | 4.5a (1.7) | 1.1a (0.4) | 1.7a (0.5) | 7.76* |
| *Triglochin maritima* | 0a (0) | 0.2a (0.2) | 0.1a (0.1) | 6.5b (3.3) | 28.31*** |
| **Algae** | | | | | |
| *Bostrychia scorpioides* | 0a (0) | 1.6a (1.2) | 4.0a (4.0) | 2.0a (0.7) | 3.51 |

years for regenerated marshes to reach equivalent species richness with reference conditions, although not necessarily the same species. Species richness within the de-embankment sites was significantly reduced with increasing cover of *Spartina anglica* (Fig. 3). Difference in species cover between the de-embankment sites and reference marshes showed marked effects over time for three species; *Limonium vulgare* ($r$ = 0.75; $p$ < 0.001); *Suaeda maritima* ($r$ = – 0.58; $p$ = 0.023); and the algae *Bostrychia scorpioides* ($r$ = 0.52, $p$ = 0.026) with estimated return times to zero difference (species equivalence) of 79, 85 and 83 years respectively. There was no relationship between the length of time sites had been embanked prior to re-exposure to tidal inundation ($p$ = 0.82) or the area of the de-embankment sites ($p$ = 0.52) and species richness.

Several species showed significant differences in mean percentage cover between age classes and the reference marshes (Table 2). There was little evidence of a trend in cover values reaching equivalency with the reference marshes over time. The higher cover of *Atriplex portulacoides* in the 51-100 age class was mostly a result of values recorded at Walton Central (86.0%) and Clementsgreen Creek (42.0%). All age classes of de-embankment site had significantly higher mean percentage covers of *S. anglica* than the reference sites.

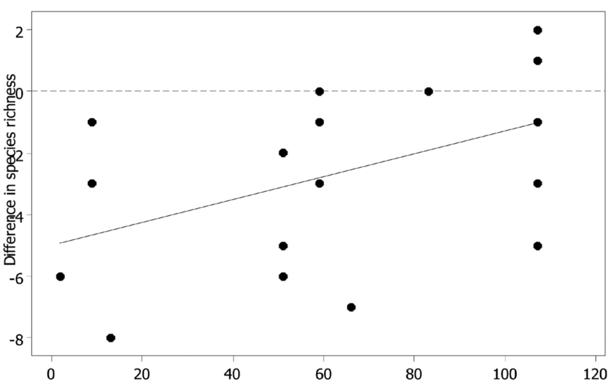


**Fig. 2.** Difference *ds* in species richness between de-embankment and reference marshes over time: $ds = -5.01 + 0.037a$, where $a$ = years since de-embankment. $R^2$ = 21.9%; $p$ = 0.05. Negative values indicate fewer species within a de-embankment site than adjacent reference marsh.

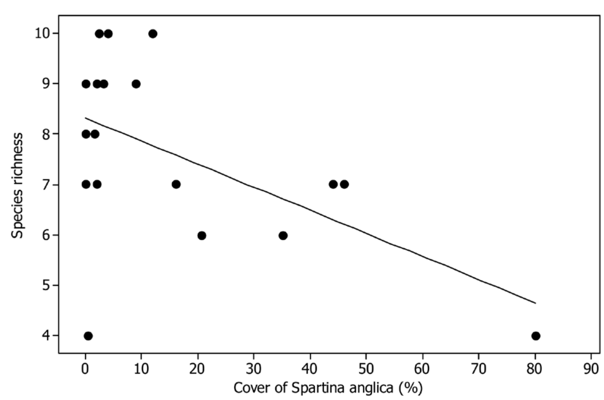


**Fig. 3.** Total species richness sr in relation to mean percentage cover of *Spartina anglica* within each de-embankment site: $sr = 8.3 - 0.04560a$, where $a$ = % *S. anglica*; $R^2$=30.3 %; $p$ = 0.018.

**Table 3.** Summary of the number of species, vegetation height, percentage fit of the vegetation communities to the National Vegetation Classification (NVC) and percentage similarity between de-embankment sites of different age classes and reference marshes (SEs in parentheses). Means for number of species and vegetation height compared using a mixed model with locations as a random effect and Wald test (*W*) for differences, Means for % fit and similarity compared using one-way ANOVA and *F*-test. Means which share a letter are not significantly different (5% level). * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

| Variable | Age class of de-embankment sites 0-50 | 51-100 | 101+ | Reference sites | *W/F* |
|---|---|---|---|---|---|
| Species per quadrat | $4.2_{a}$ (0.9) | $5.3_{ab}$ (0.4) | $6.4_{bc}$ (0.8) | $7.2_{c}$ (0.4) | 15.04 ** |
| Vegetation height | $22.7_{a}$ (7.9) | $21.9_{a}$ (2.0) | $19.0_{ab}$ (3.2) | $16.9_{b}$ (1.0) | 8.55 * |
| % fit to reference marsh communities (NVC) | 40.5 (4.7) | 84.2 (5.2) | 59.0 (4.3) | - | 16.9*** |
| % similarity to reference marshes (Sørensen's) | 31.4 (8.0) | 70.6 (5.3) | 57.9 (10.5) | - | 6.3* |

*Plant communities*

The plant communities of only two de-embankment sites (Sampson's Creek and Clementsgreen Creek) matched that of the reference community (Table 1). The plant communities of the reference marshes were dominated by communities, or sub-communities of *Atriplex portulacoides* salt marsh (SM14) and *Puccinellia maritima* salt marsh (SM13). The vegetation of Sampson's Creek was an annual *Salicornia* salt marsh (SM 8) community reflecting the sites' low elevation. The plant communities of 16 of the 18 de-embankment sites differed from their adjacent reference marshes. The de-embanked sites were mainly communities, or sub-communities of *Puccinellia maritima* salt marsh (SM 13), and communities found at lower elevations; *Aster tripolium* (SM 10), annual *Salicornia* and *Spartina anglica* (SM 6) salt marsh communities. The de-embankment sites in the 51-100 year age class had a significantly better fit and significantly higher similarity index to the reference marsh communities than the younger or older sites (Table 3), primarily as a result of the high cover value of *A. portulacoides*.

*Vegetation structure*

There were significant differences in mean sward height between the de-embankment sites and adjacent reference marshes. Taller vegetation was mainly recorded within the de-embankment sites (Table 1) as a result of a positive correlation between increasing sward height with the greater abundance of *Spartina anglica* ($R^2$ = 65.6%; $p < 0.001$).

## Discussion

While it is generally assumed that given enough time, salt marsh vegetation and other functional indicators will resemble those of natural marshes (Zedler & Callaway 1999), we found that after more than 100 years, regenerated salt marshes in Essex differed in plant community composition. The vegetation communities of the regenerated salt marshes within the de-embanked sites were, in general, representative of less diverse communities or those typical of a lower zone in the natural marshes with a higher tidal influence. Seeds of salt marsh plants are predominantly dispersed over short distances and colonisation of de-embankment sites probably occurs via stepping-stones (Wolters et al. 2005a) and the lack of continuous ecosystems along the coast can delay the re-colonisation process (Onaindia & Amezaga 1999). Seed limitation is unlikely to restrict colonisation in the present study however, where natural marshes occurred adjacent to every site with connecting creeks. It is perhaps surprising that, given the low levels of plant species diversity found in the salt marsh flora differences were detectable over such long timescales. This suggests that the vegetation communities may be relatively static or that severe disturbances are rare. Seedling recruitment in salt marsh communities is generally precluded in dense vegetation by competition from adults, but it is also relatively rare in disturbance generated space due to high soil salinities (Shumway & Bertness 1992). If the vegetation within the de-embankment sites is relatively static there may be little opportunities for new species to colonise.

The distribution of plant species on salt marshes is a balance between tolerance and competition (Gray 1985) and it appears that within the de-embankment sites this has not yet been achieved. This could be due to the greater abundance of *Spartina anglica* recorded within the salt marshes of the de-embankment sites. The successful establishment and spread of this *neoendemic* throughout the UK during the last century has been well documented and was largely due to the species' rapid dispersal by rhizomes, perennial life-history and the colonisation of mudflats formally unoccupied by salt marsh plants (Gray et al. 1990). *Spartina anglica* was first recorded in the study region in 1924 (Jermyn 1974) and the mudflats or developing salt marsh communities of the de-embankment sites would have been highly susceptible to invasion. *Spartina anglica* can drastically alter the sedimentary and drainage characteristics of its surroundings leading to the creation of waterlogged and anoxic soils (Doody 1984). In addition, soils undergo fundamental changes when reclaimed and subsequently re-exposed to tidal inundation by de-embankment (Hazelden & Boorman 2001) and re-colonisation may be delayed by unsuitable hydrological and edaphic conditions that facilitate plant species establishment (Onaindia et al. 2001). The water dynamics of the salt marsh sub-surface exerts a fundamental control on vegetation patterns, determining the potential for aerobic respiration and the ability of plant species to tolerate local conditions (Silvestri et al. 2005). This may account for the differences in species richness and abundance between the more moisture tolerant, species poor *Salicornia europaea*, *Spartina anglica*, *Aster tripolium* and *Puccinellia maritima* communities within the de-embankment sites and the dominance of the more moisture sensitive *A. portulacoides* communities in the reference marshes. Water dynamics or competition is likely to contribute to the exclusion of *Armeria maritima*, *Plantago maritima* and *Spartina maritima* from the de-embankment sites. Additional surveys of the abiotic characteristics of sites are required and experimental reciprocal transplants of 'rare' species should be undertaken to clarify this.

The greater abundance of *S. anglica* in the de-embankment sites, and in particularly the younger sites, reflects not only the species' invasive habit but questions the ability of the regenerated marshes to 'function' in a way that reflects a reference system. Restoration theory attempts to set criteria from which success can be measured, such as composition, sustainability, biotic interactions and nutrient retention (Zedler 2001). Globally, *Spartina* species are the most widespread invasive genera in salt marshes (Zedler & Adam 2002) and can fundamentally alter the composition and structure of invaded marshes (Callaway & Josselyn 1992; Spicher & Josselyn 1985). Differences in sward height and cover can also cause problems for wildlife habitat for native species such as breeding birds and insects (Middleton 1999; Zedler & Callaway 1999). The greater cover values and strong relationship between sward height and cover suggests *S. anglica* is responsible for the structural differences between the de-embanked and reference marshes.

Created salt marshes should ideally function within the normal variation found in natural marshes, thereby retaining key attributes (Atkinson et al. 2004), such as diversity, vegetation structure and ecological processes (Ruiz-Jaen & Aide 2005). Experience from current restoration efforts has shown that with relatively little management, intertidal mudflats will develop and if the elevation is suitable salt marsh plants will colonise (Garbutt et al. 2006). The present study provides further evidence that, contrary to recent claims (Hughes & Paramor 2004), it is possible for salt marshes to develop on reclaimed land and to persist as recognisable salt marsh communities. However, even after 100 years, salt marshes that regenerated within de-embankment sites differ in species richness, composition and structure from reference communities. This may be a result of differing abiotic conditions and higher cover of *S. anglica*. Additional research is required to identify the constraints to salt marsh re-assembly on formerly reclaimed land with particular attention to the abiotic conditions.

Whether the de-embankment sites are any less valuable for nature conservation or ecosystem function in their own right should be considered. The sites contain typical salt marsh communities and the most frequent vegetation community, the SM13 *Puccinellietum maritimae* is wide spread in the region. The *Puccinellietum maritimae* and *Atriplex portulacoidis* vegetation units of the natural reference marshes are adjacent in the zonation sequence within the regions salt marshes and both contained a similar cover of *Puccinellia maritima* (> 30%) through the survey. It may be that from a functional aspect they are not that different. Similarity (Sørensen's) between the de-embankment and reference marshes, especially through the middle age class, is relatively high. The similarity between de-embankment and reference marshes decreases towards the end of the chronosequence, possibly because of more stochastic processes that lead to the dominance of one or more species. Even so, typical salt marsh communities are still present. Because salt marshes and estuarine systems are subject to severe disturbance through storm events it may be unrealistic to expect a smooth successional trajectory over a specified time period to produce a typical end point. The results presented here should not be interpreted as the inevitable failure of salt marsh creation schemes in matching reference conditions, but as a cautionary note that in fact, restoration efforts may never fully replace natural wetland functions.

**Acknowledgements.** This study was funded by NERC under the Centre for Ecology and Hydrology's Sustainable Economies Programme; project number C02500. Thanks to Mick Yates, Lucy Goodman and Dave Dirks for assistance in the field and to Peter Rothery for advice on experimental design and analysis. We would also like to thank the land owners for access to their sites and Carol Reid and Michael Parken from English Nature for making this possible. Finally we would like to thank Helge Bruelheide, Miren Onaindia and an anonymous referee for helpful comments on the draft manuscript.

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Received 29 January 2007;
Accepted 10 December 2007;
Co-ordinating Editor: H. Bruelheide.