Restoration of salt marshes

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Aerial photo of the Blackwater estuary with the Tollesbury managed realignment site
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Restoration of salt-marsh vegetation in relation to site suitability, species pools and dispersal traits.

Mineke Wolters, Angus Garbutt, Renée M. Bekker, Jan P. Bakker & Peter D. Carey

The previous chapter has shown that seed dispersal may be a limiting factor in the restoration of salt-marsh vegetation. But could this be predicted from dispersal traits of the different species or their availability in the established vegetation of nearby source areas? And what is the role of elevation in the establishment of the species? These questions are addressed in the present chapter.

Introduction

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. For salt-marsh habitats, elevation in relation to tidal level is generally regarded as the most important environmental factor affecting the establishment of salt-marsh species, with soil salinity (Snow & Vince 1984), waterlogging (Cooper 1982), wave action (Wiehe 1935) or soil aeration (Armstrong *et al.* 1985) as the main determinants of the seaward limit of a species and interspecific competition for light (Ungar 1998) or nutrients (Levine *et al.* 1998) influencing the landward limit. Interspecific facilitation may extend the elevational ranges of some species, i.e. by shading to reduce hypersalinity in the soil as shown for salt marshes on the Atlantic coast of the US (Bertness & Hacker 1994; Pennings *et al.* 2003).

Traditionally, restoration management has focused mainly on restoring the abiotic environment, but recent studies have shown that availability and dispersal of the target species may be a bottleneck for successful restoration (Bakker & Berendse 1999; Bischoff 2002; Bissels *et al.* 2004; Wolters *et al.* 2005a, Chapter 6). Addition of seeds or plant material containing the target species greatly enhanced the establishment of those species in inland grassland communities (Pywell *et al.* 2002), floodplain grass-

lands (Hölzel & Otte 2003) and salt marshes (Rand 2002). Many restoration schemes, however, minimise human intervention and the target species have to come in spontaneously.

There are several sources from which the target species can colonize a restoration site. The fastest establishment is expected when the species are still present in the community species pool defined as the established vegetation and belowground seed bank of the target area (Zobel *et al.* 1998). In the case of managed-realignment sites, where seawalls are breached in order to restore tidal inundation to previously reclaimed land, the presence of salt-marsh species in the community species pool is highly unlikely as most sites have been embanked and exploited for decades to centuries, resulting in the disappearance of halophytic species from the established vegetation. Presence in the soil seed bank is also unlikely as the majority of salt-marsh species does not build up a long-term persistent seed bank (Wolters & Bakker 2002, Chapter 4; Tamis *et al.* 2004). Hence, the target species have to disperse into the restoration site from a local species pool (i.e. adjacent salt marsh) or regional species pool (i.e. all salt marshes within a biogeographically uniform region) (Zobel *et al.* 1998). A review of salt-marsh restoration at different de-embankment sites in northwest Europe showed that between 48 and 100% of the species present in the local species pool established in the restoration sites within 1 to 13 years after de-embankment. When compared to the regional species pool, only 26 to 64 % of the species established in the restoration sites (Wolters *et al.* 2005b).

Recently, restoration ecology has been linked to the search for assembly rules, which aim to identify the main factors that govern the development and changes in composition of plant communities (Keddy 1992; Young *et al.* 2001; Temperton *et al.* 2004). Attempts have been made to predict the sequence of species establishment and variation in species composition from environmental factors acting as filters on different sets of species (Weiher & Keddy 1995), plant functional traits (Díaz *et al.* 1999) and/or internal dynamics such as competition for resources (Belyea & Lancaster 1999). Advances in this area, however, are limited by scant data on initial development of the vegetation. Managed realignment presents an opportunity to study these initial processes when reclaimed land that has been cultivated for decades is transformed into intertidal habitat. It is expected that tidal water will act as an important agent for dispersing diaspores of salt-marsh species because the salt marshes are inundated up to twice a day and several halophyte seeds are able to float for some time in seawater (Koutstaal *et al.* 1987).

In the present chapter, we evaluate the process of salt-marsh restoration by (i) comparing the number of target species colonizing the site to the local and regional species pool, (ii) analysing spatial and temporal patterns in species abundance and (iii) determining whether an actual salt-marsh community has developed. In addition, we investigate how the sequence of species establishment is related to site suitability, availability of the target species in the local and regional species pool and dispersal traits of the target species.

Methods

Study area

The Tollesbury managed-realignment site is located in the Blackwater estuary, southeast England (51°46'N, 0°51'E) (Figure 7.1). The 21 ha site formed part of the Tollesbury and Old Hall salt marshes until it was embanked in the late 18th century and transformed into agricultural land (Boorman *et al.* 1997). In August 1995, a 50 m wide opening was made in the embankment with the aim of re-creating intertidal habitat. The breach connects the site to Tollesbury Creek, which is the main channel through which tidal water enters the site on a semi-diurnal cycle. A new seawall was built landward of the breached embankment in order to reduce the risk of seawater flooding the adjacent agricultural land. Surface elevation ranges from 0.9 m to 3.0 m above Ordnance datum (OD) corresponding to –1.15 m to 0.95 m + mean high tide (MHT). Mean high water neap (MHWN) and mean high water spring (MHWS) tide levels of the Blackwater estuary are 1.50 m and 2.60 m OD, respectively (Pye & French 1993).

Species pools

Natural plant colonization in the restoration site (i.e. community species pool) was monitored annually from 1997 (i.e. the second growing season after de-embankment) in three transects of 20 m wide and 125 m long, subdivided into 2500 contiguous quadrats of 1 m². Each transect was laid out perpendicular to the new seawall and
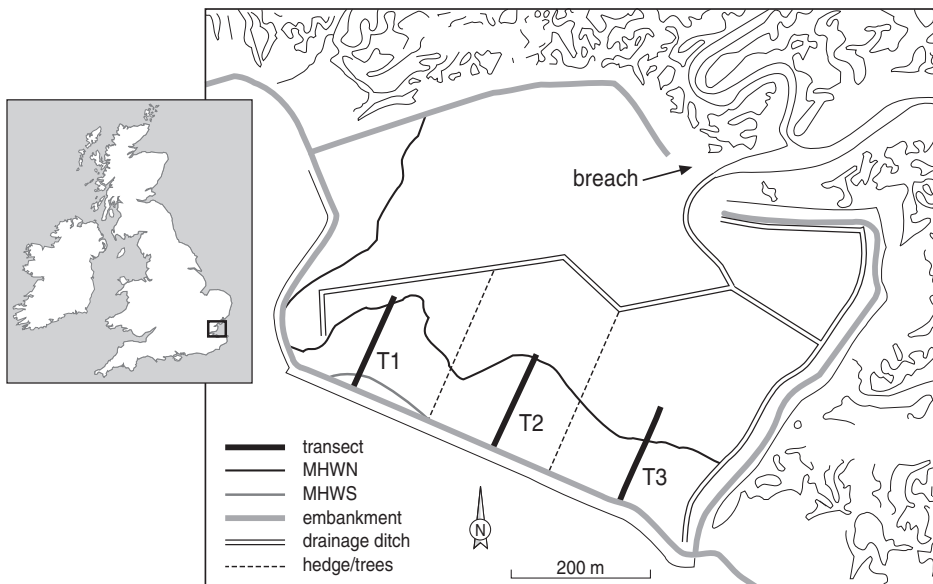

Figure 7.1. Study area with approximate location of transects and contour lines indicating mean high water spring (MHWS) and mean high water neap tide (MHWN).

extended for 125 m from high to low elevation towards the breach (Figure 7.1). In each quadrat the presence of a plant species was recorded and percentage cover estimated. Plant species nomenclature follows Stace (1997). No distinction has been made between different species of *Salicornia*.

North and east of the managed-realignment site are the Old Hall and Tollesbury marshes, which are regarded as the local species pool. Vegetation has been monitored annually since 1994 in 60 permanent plots of 1 m² by recording the frequency of occurrence in 100 cells of 10 cm x 10 cm.

The regional species pool is derived from Rodwell (2000) by selecting all saltmarsh species occurring with a frequency of more than 60 % in a particular salt-marsh community for south-east England (see Wolters *et al.* 2005b). Abundance in the regional species pool was calculated as the percentage frequency of a species in 212 10 km x 10 km squares in coastal south-east England as derived from Preston *et al.* (2002).

Site suitability

We used surface elevation in relation to tidal elevation as an indicator of site suitability. Surface elevation of the restoration site was measured with respect to Ordnance Datum at 5 m distance intervals along the north-west and south-east side of each transect with a theodolite in September 1998, June 2001 and December 2003. The boundaries of the zones did not change much over the study period and on the bases of MHWN and MHWS tide levels, three zones were distinguished: Zone 1: MHWS – MHWS + 0.40 m, Zone 2: MHT – MHWS, Zone 3: MHWN – MHT (Figure 7.2). Results are displayed in metres relative to MHT (2.05 m OD).

Surface elevation of the 60 permanent quadrats on the adjacent marsh was measured in 1994 and the 60 plots were divided into three elevational zones corresponding to the zones distinguished for the restoration site. Average accretion rates on the adjacent Old Hall and Tollesbury marsh were 3.2 and 4.5 mm per year respectively over the period 1994 to 2003 (Reading *et al.* 2004). Ellenberg's indicator values were used to describe a species' preference along a moisture and salinity gradient (Hill *et al.* 1999). Moisture values of the target species ranged from 5 to 10, indicating a distribution from moist, c.q. average dampness to shallow water. Salinity values ranged from 1 (slightly salt tolerant, but rare or occasionally on saline sites) to 9 (extreme saline conditions, where seawater evaporates).

Dispersal traits

We used seed weight and flotation time as the main dispersal traits to predict the sequence of species arrival in the restoration site. Data on seed weight were derived from the Leda Traitbase (Knevel *et al.* 2003). Flotation times of seeds and propagules were derived from Koutstaal *et al.* (1987) and supplemented with data from J. Geertsema (unpublished results) and the Leda Traitbase. Because of the sometimes large range of flotation times recorded within a species, we classified the data into six
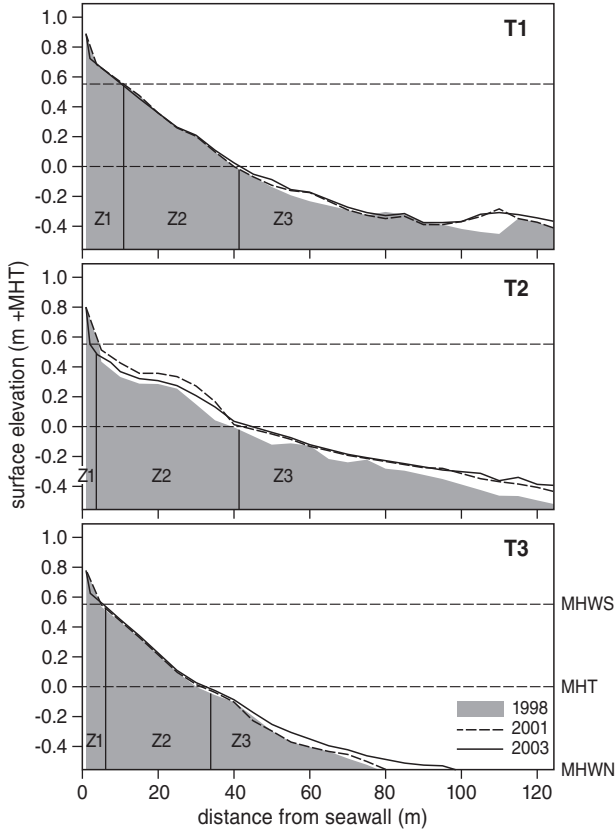
Figure 7.2. Surface elevation (in m + MHT) and elevation zones (Z1-3) of the three transects (T1-T3) in 1998, 2001 and 2003 with broken lines indicating mean high water spring (MHWS) and mean high tide (MHT) level.

categories based on the time after which 50 % of the seeds had sunk, i.e. 1: < 12h, 2: 12 - 24h, 3: 24 - 48h, 4: 48 -120h, 5: 120 - 240h and 6: > 240h.

Number of target species and species abundance

A saturation index (Wolters *et al.* 2005b) was calculated to compare the number of species in the restoration site to the local and regional species pool. Species response curves were fitted to display temporal trends in frequency of occurrence of the eight most abundant species. Four models described in Huisman *et al.* (1993) were fitted to species abundance data for each zone and each of the three transects and the simplest model giving the best fit (i.e. the highest R^2) was selected. The shapes of the possible response curves are: i) a sigmoid curve with an upper bound equal to the maximum value of the data (i.e. 100 in the case of percentages), ii) a sigmoid curve with a maximum below the upper bound, iii) a symmetric Gaussian curve and iv) an asymmetrical curve.

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Plant communities

Species composition of the restoration site was compared to existing plant community types defined by the British National Vegetation Classification (NVC) system (Rodwell 2000). At each of the three distinguished elevation zones, ten random non-adjacent plots of 1 m² were selected from each of the three transects and the mean abundance and percentage cover of each species entered into the program TableFit (Hill 1996). This resulted in a percentage fit to a specific plant community. NVC communities of the adjacent marsh were based on mean abundance data of all plots occurring in a particular elevation zone in 2003.

Sequence of species establishment in relation to site suitability, species pools and dispersal traits

A discriminant analysis (SPSS11.5) was performed to determine whether the order of species establishing in the restoration site could be predicted from variables measuring site suitability (salt and moisture tolerance defined by Ellenberg's values (Hill *et al.* 1999)), abundance in the regional and local species pools and seed dispersal traits (seed weight and flotation time). Four groups of species were distinguished, 1) early establishers, which arrived in year one or two, 2) intermediate establishers, arriving in year three, 3) late establishers, arriving in year four or five, and 4) still absent. A total of 23 species was included in the analysis. These species formed a subset of the regional target species pool defined by Wolters *et al.* (2005b), with 12 species being excluded because of a lack of data for one or more predictor variables.

Results

Number of target species and species abundance

The number of established target species in the restoration site was less than 10 % of the maximum regional species pool in the first year after de-embankment. After five years, this percentage had increased to 30 %, which fell within the range of the saturation index of the local species pool (Figure 7.3). The local species pool contained less than 40 % of the species of the regional target species pool.

Salicornia was by far the most abundant species in the transects during the entire study period followed by *Suaeda* in the third and fourth year after the breach (Figure 7.4). From the sixth year after the breach, *Puccinellia* became the dominant species of the upper part of the transects, and gradually extended seaward, whereas *Spartina* increased its abundance at lower elevations (Figure 7.4). The upper one metre strip of transect 1 was dominated by *Spergularia marina* in the fourth and fifth year after the breach (data not shown). All species except *Salicornia* and *Spartina* occurred in highest abundance at the upper zone of the transects.

The majority of species in the upper zone showed a sigmoidal increase in frequency of occurrence over time, either towards the maximum value of 100 % (*Aster,*
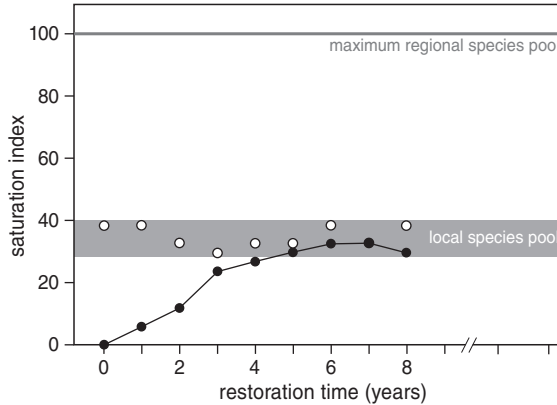
Figure 7.3. Saturation index, showing changes in number of target species in restoration site (black dots) and local species pool (open dots) over time as a percentage of the regional species pool (grey line).

Puccinellia, Salicornia, Spergularia media, Suaeda) or towards a lower value (*Atriplex portulacoides, Limonium)* (Figure 7.5). *Spergularia marina* showed an optimum in frequency of occurrence after seven, four and six years in transects 1, 2 and 3, respectively. In the intermediate zone, where five of the nine species occurred with a frequency of more than 10 % for three consecutive years, response curves were also sigmoidal towards the maximum value of 100 % except for *Suaeda* (Figure 7.5). This latter species showed a peak after two years of restoration after which the abundance rapidly declined, especially in transect 2. The goodness of fit (R^2) of the different curves ranged from 0.82 to 0.99, and the shape of the curves for a particular species was often similar for the different transects even though the actual data points were different, indicating that the trend was general for the restoration site.

Plant communities

Based on abundance and percentage cover data, three different National Vegetation Classification (NVC) communities could be distinguished in the restoration site by 2001 (TableFit, Hill (1996)). The upper part of the transects changed from annual *Salicornia* salt marsh (SM8, (Rodwell 2000)) in the first three years of restoration via *Suaeda maritima* (SM9) salt marsh in transects 1 and 3 to *Puccinellia* salt marsh (SM13a) after six or seven years of restoration (Figure 7.6). In the intermediate and lower zones of the transects, annual *Salicornia* salt marsh formed the only distinct plant community. The NVC communities of the adjacent marsh included annual *Salicornia* salt marsh (SM8) at the lowest zone and *Puccinellia* salt marsh (SM13) at the two higher zones. No non-expected non-target species have established so far, indicating the suitability of the site conditions for the species from the pre-defined species pool.

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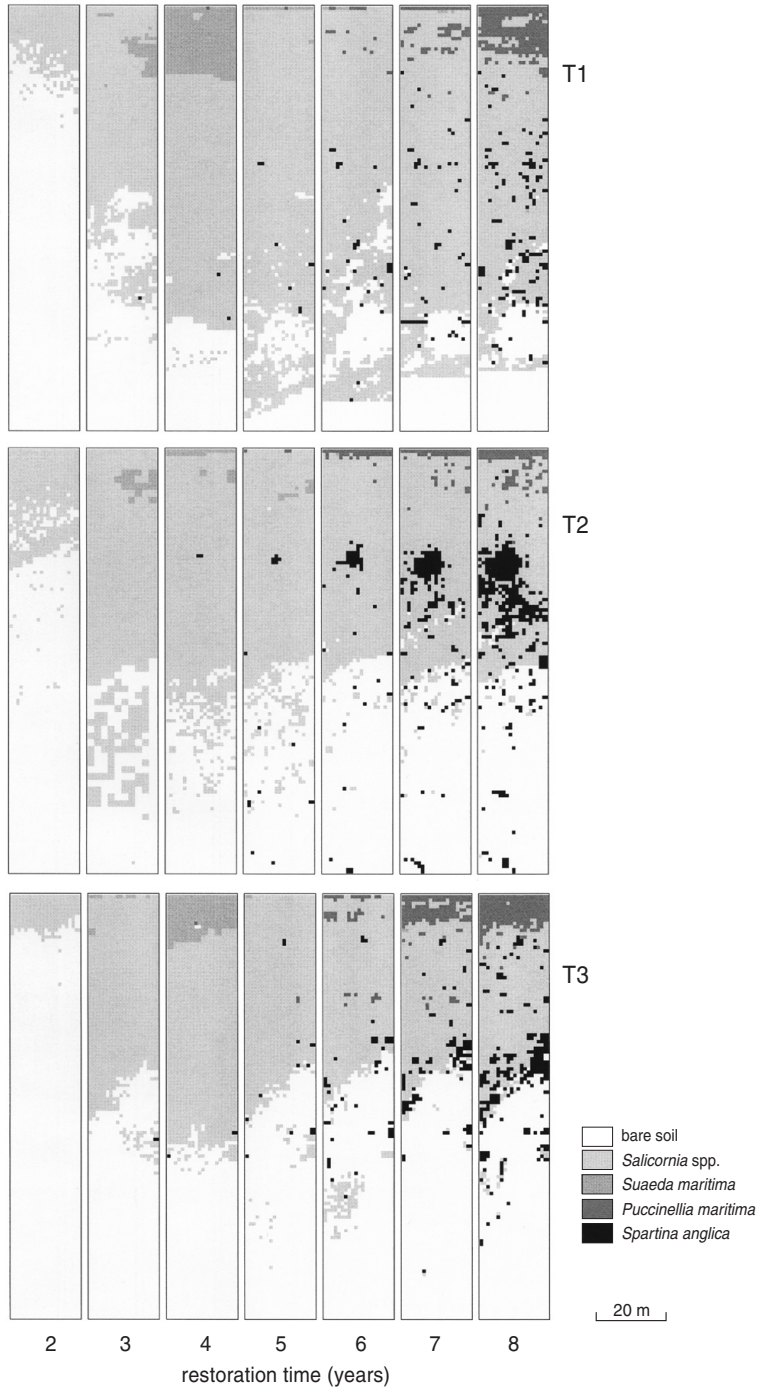**Figure 7.4.** Distribution of dominant species in three transects (T1-T3) for seven years.
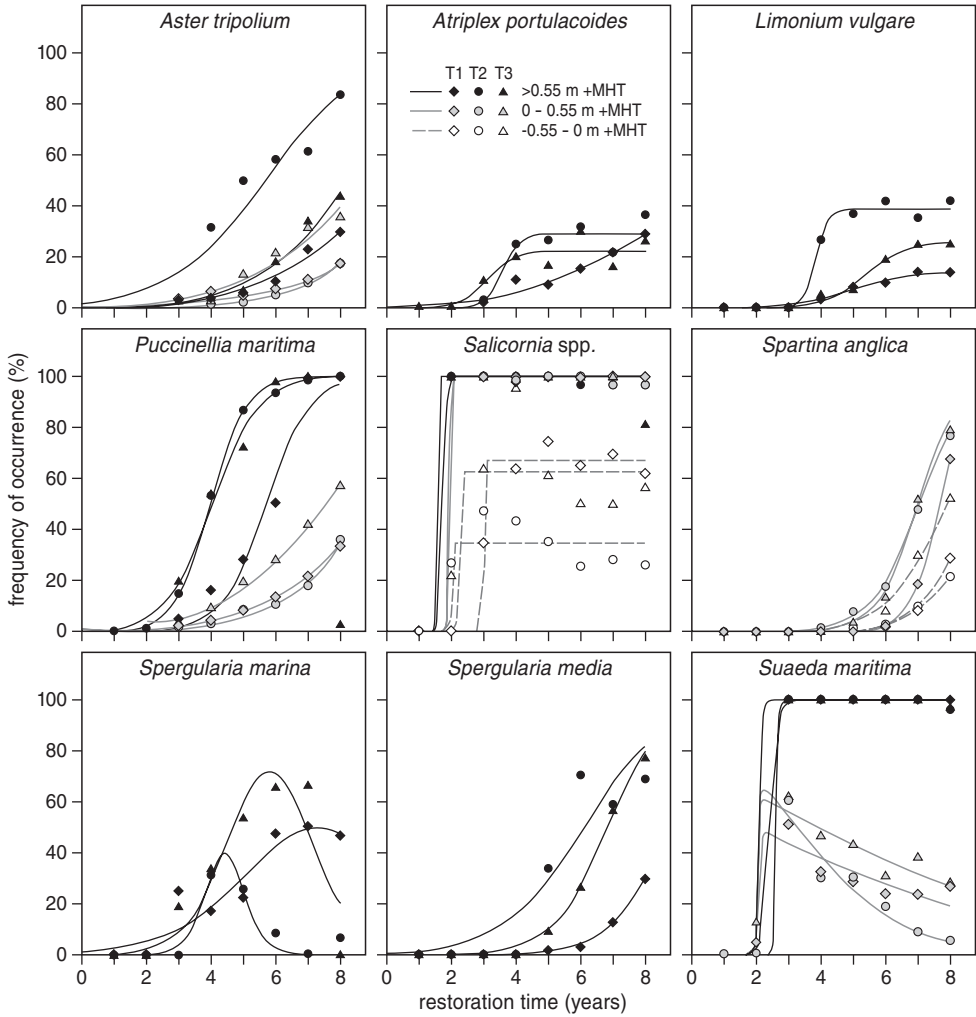
Figure 7.5. Response curves displaying temporal changes in frequency of occurrence for nine species with a minimum of 10 % occurrence for three consecutive years in three transects (T1, squares; T2, circles; T3, triangles) and 1- 3 elevational zones (> 0.55m + MHT, black; 0-0.55 + MHT, grey; -0.55-0 + MHT, white) .
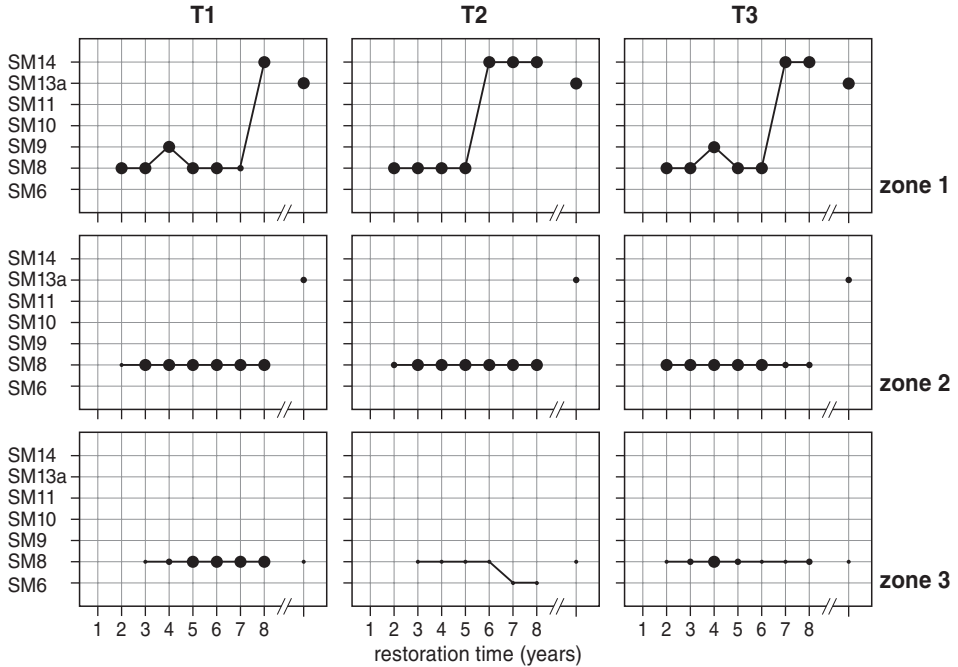
Figure 7.6. Goodness of fit to NVC communities in restoration site and adjacent marsh (after break in x-axis) for three different zones (zone 1: > 0.55 m + MHT, zone 2: 0 - 0.55 m + MHT, zone 3: - 0.55 - 0 m + MHT) and three transects (T1-3). Only the best fit to a community is given, with the size of the circle indicating the goodness of the fit, i.e. poor (< 50 %), intermediate (50-79 %) or good (80-100 %). Communities are ordered to represent zonation with *Spartina anglica* salt marsh (SM6), annual *Salicornia* salt marsh (SM8), *Suaeda maritima* salt marsh (SM9), transitional low marsh (SM10), *Puccinellia maritima* salt marsh (SM13 and SM13a) and *Halimione(Atriplex) portulacoides* salt marsh (SM14).

Sequence of species establishment in relation to site suitability, species pools and dispersal traits

Colonization of the transects started with the arrival of *Salicornia* spp., *Suaeda maritima, Sarcocornia perennis* and *Spartina anglica* (Table 7.1). In the third year of restoration (i.e. intermediate) the biggest increase in number of species occurred with *Aster tripolium, Atriplex portulacoides, Puccinellia maritima* and *Spergularia marina* establishing in the transects (Table 7.1). The late establishers included *Elytrigia atherica, Limonium vulgare* and *Spergularia media*, which established four or five years after de-embankment. The order of establishment of different groups of species was separated by two discriminant functions, accounting for 86.5 % ($P = 0.001$) and 10.0 % ($P = 0.307$) of the variation, respectively (Figure 7.7). Species' salt tolerance contributed most to the first discriminant function ($r = 0.664$), and mainly separated the early colonizers from the other groups by their higher Ellenberg value for salinity (Figure 7.7). The frequency of species in the local species pool ($r = 0.674$) and to a lesser

Table 7.1. Arrival order of target species (1: early; 2: intermediate; 3: late; 4: absent), percentage frequency in regional (R) and local (L) species pool, seed weight (mg), flotation time (T50, 1: < 12 h; 2: 12-24 h; 3: 24-48 h; 4: 48-120 h; 5: 120-240 h and 6: > 240 h) and Ellenberg indicator values for moisture (F) and salinity (S). Data on seed weight and T50 were derived from the Leda Traitbase (see references therein), unless otherwise stated. Species in bold were used in the analysis.

Target species	Abbreviations used	Arrival order	R (%)	L (%)	Seed weight (mg)	T50 (h)	F	S
Agrostis stolonifera	Agrsto	4	93.52	0	0.05	6	6	1
Armeria maritima		4	68.98	0.03	0.93		7	3
Aster tripolium	Asttri	2	66.67	13.71	1.21	4[1,2]	8	5
Atriplex portulacoides	Atrpor	2	59.26	50.08	3.69	6[1]	8	6
Atriplex prostrata	Atrpro	4	90.74	0	3.31	1[1,2]	7	2
Bolboschoenus maritimus	Bolmar	4	68.06	0	3.12	6	10	4
Elytrigia atherica	Elyath	3	71.30	0	4.20[3]	3[1,2]	6	4
Elytrigia repens	Elyrep	4	77.31	0	2.56	3	5	2
Festuca rubra	Fesrub	4	62.96	0	0.94	3[1]	5	2
Frankenia laevis		4	12.96	0	0.09[4]		8	5
Glaux maritima	Glamar	4	59.72	0	0.35	5[2]	7	4
Inula crithmoides		4	25.93	0	0.37		6	5
Juncus gerardii	Junger	4	65.74	0	0.03	1[2]	7	3
Juncus maritimus		4	43.06	0.02	0.03		8	5
Leontodon autumnalis		4	84.72	0	1.28		6	1
Limonium bellidifolium		4	0.46	0	0.73		8	5
Limonium binervosum agg.		4	24.07	0	0.56		8	5
Limonium vulgare	Limvul	3	44.44	15.63	0.84	1[1,2]	8	6
Oenanthe lachenalii	Oenlac	4	45.37	0	1.13	3	8	3
Plantago maritima	Plamar	4	72.69	1.38	0.95	1[1,2]	7	3
Potentilla anserina	Potans	4	86.57	0	0.89	1[2]	7	2
Puccinellia distans		4	46.30	0	0.27		8	4
Puccinellia maritima	Pucmar	2	53.70	61.23	0.72[5]	2[1]	8	5
Salicornia spp.	Salspp	1	53.24	42.25	0.42[6]	1[1]	8	9
Sarcocornia perennis		1	25.00	1.33			8	6
Schoenoplectus tabernaemontani	Schtab	4	48.15	0	1.33	3	10	3
Seriphidium maritimum	Sermar	4	39.81	0.02	0.75	1[1]	7	5
Spartina anglica	Spaang	1	41.20	1.53	12.10[3]	4	9	7
Spartina maritima		4	12.96	0			9	6
Spergularia marina	Spemar	2	68.98	0	0.08	5[2]	8	5
Spergularia media[7]	Spemed	3	59.26	3.49	0.13[6]	1[1,2]	8	5
Suaeda maritima	Suamar	1	58.33	33.39	0.73	1[1,2]	8	7
Suaeda vera		4	17.13	0			7	5
Trifolium repens		4	94.91	0	0.59		5	0
Triglochin maritimum	Trimar	4	59.26	12.2	0.50[8]	6[1]	7	4

[1] (Koutstaal et al. 1987)   [2] J. Geertsema, unpublished results
[3] Ecological flora of the British Isles at the University of York, www.york.ac.uk/res/ecoflora
[4] (Brightmore 1979)
[5] (Gray & Scott 1977)   [6] Personal observation
[7] Spergularia media was not regarded a target species in Wolters et al. (2005b)
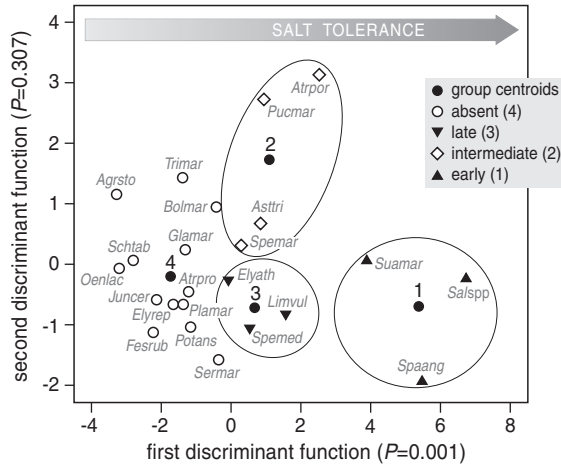[8] (Davy & Bishop 1991)

Figure 7.7. Discriminant analysis separating four groups of species differing in their sequence of establishment in the restoration site. Salt tolerance is highly correlated ($r = 0.664$) with the first discriminant function and abundance in the local species pool ($r = 0.674$) and flotation time ($r = 0.459$) are correlated with the second (non-significant) function.

extend seed flotation time ($r = 0.459$), were positively correlated with the second but non-significant discriminant function which separated the species of intermediate order of establishment from the other groups. The remaining variables (regional species pool, seed weight and moisture values) failed to explain the difference in arrival order. Group membership was predicted correctly for 91.3 % of the species, with 100 % of the species of early and late establishment being classified correctly. Of the intermediate establishers and species still absent, 25 % and 7.7 %, respectively, were wrongly classified as late establishers.

In order to check the robustness of the results, a stepwise discriminant analysis was performed (maximum significance of F to enter = 0.15), which also identified salt tolerance as the most important predictor ($r = 0.843$) explaining 89.1 % ($P = 0.000$) of the variance between the groups.

Discussion

Number of target species and species abundance
After eight years of restoration, 11 target species, or 32 % of the regional species pool, had established in the Tollesbury restoration site. This saturation index was low compared to other de-embankment sites of similar or younger age in north-west Europe where indices were generally above 45 % (Wolters *et al.* 2005b, Chapter 3). The number of species that colonized the restoration site at Tollesbury was also lower com-

pared to two other managed-realignment sites in the same estuary. The oldest of these sites, Northey Island, contained already 12 target species after three years of restoration, whereas at Orplands, 15 different species had established within seven years after the seawall was breached (Wolters *et al.* 2005b, Chapter 3). On the other hand, the rate of plant colonization at Tollesbury was similar to that of an estuarine restoration site in the USA, which was opened to tidal inundation after being embanked for 70 years (Thom *et al.* 2002). In this latter site, the largest increase in number of species occurred three years after de-embankment and after five years, species diversity was similar to a reference marsh containing 14 species (Thom *et al.* 2002).

Salicornia and *Suaeda* were the first species to reach 100 % abundance at the highest elevational zone (Figure 7.5). Both are annual species which can produce large transient seed banks, especially in early successional stages (Wolters & Bakker 2002, Chapter 4) and these seed banks become quickly depleted in spring due to germination (Tessier 2000; Davy *et al.* 2001). The large seed output (300 – 30,000 m^{-2}), high viability (Davy *et al.* 2001) and predominantly short-distance seed dispersal (Ellison 1987) may explain the rapid increase in abundance of *Salicornia* within the first two years after de-embankment. The response curve is similar to the colonization curve in Watkinson & Davy (1985), in which *Salicornia* reached the carrying capacity of the environment within three years. The peak in abundance of *Suaeda* at the intermediate elevation zone after two years is probably due to favourable climatic conditions. Seeds of this species have high viability, germinating well even in perennial vegetation (Tessier 2000). Seedling survival however, is negatively affected by dense *Puccinellia* and *Atriplex portulacoides* vegetation (Tessier *et al.* 2002), but this effect was not visible within our study period. *Spergularia marina* showed optimum abundance at different years for the three transects. This annual species is characteristic of disturbed soil conditions and typically occurs in dried up pans or along paths or tracks (Rodwell 2000). The presence of a motorbike track may explain the dominance of this species in the top row of transect 1 in the fourth and fifth year of restoration (data not shown).

Interestingly, the abundance of all perennial species increased sigmoidally, with *Puccinellia* being the first one to reach 100 % abundance. This species is tolerant of waterlogged soils (Gray & Scott 1977), which conditions are prevalent at the Tollesbury managed-realignment site (Watts *et al.* 2003; Garbutt *et al.* 2005). The distribution and abundance of *Aster* and *Puccinellia* may have been affected by a planting experiment performed by CEH Monks Wood. The two species were planted at different elevations in transect 1 and 3, but only the plants at the highest level (2 m OD) in transect 3 survived as isolated stands and expanded only after four years of restoration (Reading *et al.* 2002; Garbutt *et al.* 2005). Establishment of *Spartina* proceeded very slowly until after six years of restoration the abundance suddenly increased (Figure 7.5). Ranwell (1964) also reported very slow establishment of *Spartina* at new sites except near already existing clumps, which corresponds with the observation in our study, especially at transect 2 (Figure 7.4). *Spartina* successfully esta-

blished and spread throughout the UK after being deliberately introduced in the last century for stabilising mudflats, reducing coastal erosion and promoting accretion (Goodman *et al.* 1959; Adam 1990). Because of its perennial life history and its tolerance of tidal submergence *Spartina* is likely to extend its abundance in the sparsely vegetated lower elevations of the Tollesbury managed-realignment site and possibly invade the annual *Salicornia* spp. community.

Atriplex portulacoides* and *Limonium* were the only two species suggesting a maximum abundance of less than 100 % had been reached at the highest elevation zone within the study period. Although *Atriplex* has good reproductive ability, producing between 20 and several hundred seeds per plant and capable of spreading vegetatively at a rate of 1.3 cm per year, the species and especially its seedlings is intolerant to waterlogging (Chapman 1950). The prevalence of poorly drained soils may therefore explain its restricted abundance at Tollesbury. Generative reproduction in *Limonium* may be limited as the plants rarely flower until the third year (Boorman 1967) and viability of the seeds is very low compared to other salt-marsh species (Hutchings & Russell 1989). This species is a poor competitor for light (Boorman 1967) and its abundance may be limited by the presence of other perennial species. In general, the sigmoidal increase in abundance of perennials in our study suggests that their population dynamics are mainly determined by clonal growth, possibly as a result of limited germination and seedling establishment due to high soil salinities (Shumway & Bertness 1992).

Plant communities

The occurrence and abundance of the different species at the highest elevational zone of the restoration site became comparable to that of the *Puccinellia maritima* salt-marsh community of the adjacent marsh within six to eight years of restoration. However, the intermediate elevational zone of the restoration site was classified as annual *Salicornia* salt marsh, compared to a *Puccinellia maritima* salt-marsh community at similar elevation on the adjacent marsh (Figure 7.6), which implies that the restoration site is not yet fully developed along the entire elevation gradient. In a separate study, the lower elevational limits of the species in the restoration site were found to be above those of the adjacent marsh after six years of restoration (Garbutt *et al.* 2006). A similar timescale for salt-marsh development was observed for an estuarine marsh in the USA where low salt-marsh vegetation established within five years, but species composition continued to change for at least 11 years after a dike was breached (Thom *et al.* 2002). More time is needed to determine whether the *Puccinellia* community is the final stage of salt-marsh development at Tollesbury, because *Puccinellia* has been identified as a key species in trapping and stabilising sediment and an increase in *Puccinellia* cover led to the appearance of higher-marsh species and an increase in succession rate (Langlois *et al.* 2003).

Sequence of species establishment and relation to site suitability, species pools and dispersal traits

The most intriguing question arising from the present study is what determines the sequence of species establishment? Because all species were initially absent from the species pool of the target area, it was hypothesised that species abundance in the species pools and dispersal traits would be important. Nevertheless, the discriminant analysis indicated that salt tolerance was more important in determining the sequence of species establishment than abundance of the species in the local species pool or dispersal traits. For example, *Triglochin maritimum* was still absent from the restoration site after eight years, even though it was present in 12.2 % of the plots on the adjacent marsh. The Ellenberg value for salinity describes this species as being characteristic of salt meadows and upper marshes subject to occasional tidal inundation, or consistent brackish conditions (Hill *et al.* 1999). Other species present (though with a frequency of less than 2 %) on the adjacent marsh but absent from the restoration site include *Armeria maritima, Festuca rubra, Juncus maritimus, Plantago maritima* and *Seriphidium maritimum*. The Ellenberg values for salinity of these species are all below six, indicating that these species are slightly salt tolerant and generally occur on upper marsh sites not inundated by all tides. With less than 10 % of the restoration site at an elevation above the level of mean high water spring tide (Figure 7.2), these species have little chance to establish. Other salt-marsh restoration studies also suggest that differences in colonization rate are determined mainly by surface elevation, with higher sites becoming more rapidly colonized than lower sites (Williams & Orr 2002; Cornu & Sadro 2002). In mangrove systems, the ability of species to initiate roots or shoots in seawater appeared more important in explaining adult distribution patterns than seed buoyancy and seed weight (Clarke *et al.* 2001). The absence of a significant relationship between arrival order and seed weight is contrary to the competition/colonization trade-off hypothesis, which suggests that species investing in a few large seeds are mainly adapted to establishment in existing vegetation, whereas the production of many small seeds would favour colonization of new substrate (Turnbull *et al.* 1999).

Interestingly, the arrival of intermediate and late species at the highest elevation zone at Tollesbury was not governed by a change in surface elevation like general theory predicts (Chapman 1974) because accretion in the transects during the study period was negligible (Figure 7.2) and the species could have established from the start. Furthermore, these two groups of species were not separated by their salt tolerance (Figure 7.7). Abundance in the local species pool and flotation time appeared to be more important in predicting the sequence of establishment of these two groups of species, although overall this function was not significant (Figure 7.7). In a freshwater stream, occurrence of species in the local species pool and seed buoyancy were also good predictors of the number of diaspores trapped for terrestrial species but buoyancy was of little importance in explaining the composition of the diaspore pool of submergent species (Boedeltje *et al.* 2003). It was hypothesized that high flotation ability

in submerged species might be disadvantageous as their diaspores might be deposited on riverbanks where they are unable to germinate and grow (Boedeltje *et al.* 2003). The same may be true for salt-marsh species, because long flotation times can result in seeds being deposited in tidal driftline where the seedlings may desiccate before their roots reach the soil (Boorman 1967). Flotation times can also be misleading as not only single seeds, grains or fruits are dispersed but also entire spikelets (e.g. *Elytrigia atherica* (Koutstaal *et al.* 1987)), seedlings (e.g. *Salicornia dolichostachya* (Davy *et al.* 2001)) or whole plants (e.g. *Salicornia pusilla* (Dalby 1963)), which are likely to have different flotation times from seeds. Seeds of the pioneer species *Salicornia*, for example, will only float for a few hours (Koutstaal *et al.* 1987) but they are able to germinate in seawater after which the seedlings can stay afloat for up to three months, thus favouring long-distance dispersal (Davy *et al.* 2001).

In conclusion, our results show that the first species colonizing the Tollesbury restoration site are highly salt tolerant with two of the three species also being abundant in the local species pool. These species occupy the lowest elevation zones, which are inundated most often and which may increase the chance of a diaspore being transported from the source area into the restoration site. Species that are still absent are characteristic of higher marsh zones which are occasionally inundated. Their absence is mainly explained by the sparse availability of suitable space for establishment, possibly in combination with low abundance in the local species pool and reduced opportunity of dispersal by tidal water due to their occurrence at higher and less frequently flooded elevations. The difference between intermediate and late establishers appears to be related mainly to a combination of abundance in the local species pool and flotation time. Sowing or planting these species may help to increase their rate of establishment.

Summary

The practice of restoring salt marshes on previously reclaimed land provides an excellent opportunity to study plant colonization and subsequent development of salt-marsh vegetation. Insight into the process of salt-marsh development will be extremely important in guiding the design, implementation and evaluation of salt-marsh restoration schemes and for determining the appropriate management strategies. In the present paper, we evaluate the process of salt-marsh restoration at a species and plant-community level and investigate how the sequence of species establishment is related to site suitability, availability of the target species in the local and regional species pool and dispersal traits of the target species. Our results show that it took approximately five years for species diversity in the restoration site to become similar to a local reference marsh, which contained less than 40 % of the species of the regional target species pool. The annual species *Salicornia* spp. and *Suaeda maritima* were the first to colonize and to reach maximum abundance. Perennial species

(*Puccinellia maritima, Aster tripolium, Spartina anglica, Spergularia media, Atriplex portulacoides* and *Limonium vulgare*) only started to colonize or increase notably in abundance after three years of restoration. Plant composition at the highest elevation of the restoration site developed from annual *Salicornia* community into *Puccinellia maritima* salt marsh, which was similar to the local reference marsh. After eight years, the lower elevations were still covered by annual *Salicornia* salt marsh despite the potential for the development of a *Puccinellia* community. Salt tolerance appeared to be much more important in explaining the sequence of species establishment than the availability of the species in the local or regional species pool or dispersal traits of the target species. Proper surface elevation in relation to tidal inundation is therefore a prerequisite for successful salt-marsh development after managed realignment.

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