

Restoration of salt marshes

“Suddenly the boy looked around him in dismay. He had not noticed that the sun was setting. Now he saw that his long shadow on the grass had vanished. It was growing dark, he was still some distance from home, and in a lonely ravine, where even the blue flowers had turned to grey. He quickened his footsteps and, with a beating heart recalled many a nursery tale of children belated in dreary forests. Just as he was bracing himself for a run, he was startled by the sound of trickling water. Whence did it come? He looked up and saw a small hole in the dike through which a tiny stream was flowing. Any child in Holland will shudder at the thought of A LEAK IN THE DIKE! The boy understood the danger at a glance. That little hole, if the water were allowed to trickle through, would soon be a large one, and a terrible inundation would be the result.”



From: Hans Brinker or the silver skates, by Mary Mapes Dodge

Lay-out and figures: Dick Visser

Photo's cover: Mineke Wolters

Printed by: Van Denderen b.v., Groningen

ISBN: 90-367-2581-X

RIJKSUNIVERSITEIT GRONINGEN

Restoration of salt marshes

PROEFSCHRIFT

ter verkrijging van het doctoraat in de
Wiskunde en Natuurwetenschappen
aan de Rijksuniversiteit Groningen
op gezag van de
Rector Magnificus, dr. F. Zwarts,
in het openbaar te verdedigen op
maandag 1 mei 2006
om 13.15 uur

door

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geboren op 29 oktober 1975
te De Groeve

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Contents

Voorwoord		7
Chapter 1	Introduction	11
Chapter 2	Salt-marsh erosion and restoration in south-east England: squeezing the evidence requires realignment	23
Chapter 3	Salt-marsh restoration: evaluating the success of de-embankments in north-west Europe	39
Chapter 4	Soil seed bank and driftline composition along a successional gradient on a temperate salt marsh	69
Intermezzo 1	Composition of a soil seed bank before and after de-embankment	85
Chapter 5	Astroturf seed traps for studying hydrochory	93
Chapter 6	Plant colonization after managed realignment: the relative importance of diaspore dispersal	107
Chapter 7	Restoration of salt-marsh vegetation in relation to site suitability, species pools and dispersal traits.	123
Chapter 8	Restoration of salt marshes : a synthesis	143
Summary		155
Samenvatting		159
Curriculum vitae		167
List of publications		168



Excursion to the Karrendorfer Wiesen during the annual Coastal Ecology workshop in Greifswald

Voorwoord

De afgelopen ruim vier jaar promotieonderzoek waren als een ‘Tale of two cities’. Elke twee tot drie weken werden afwisselend in Engeland, danwel Nederland doorgebracht, om de ontwikkeling van verschillende verkwelderingsgebieden te onderzoeken. Zoveel overeenkomsten als er tussen de beide landen zijn, zoveel verschillen zijn er ook. Hierdoor ben ik nu een gevaar op de weg, heb ik weinig besef van zomer- en wintertijd en moet ik nog steeds naar het bedrag op muntjes kijken alvorens het juiste kleingeld te vinden. Maar als ik dan toch veilig op de goede tijd en met de juiste valuta op zak bij een kwelder in één van beide landen aankwam, stonden daar gewoon dezelfde plantjes als in het andere land.

Mijn eerste kennismaking met kwelders (de betekenis eerst in het woordenboek opgezocht) was tijdens een stage als van Hall student bij de afdeling plantenoecologie aan de RUG. Het onderwerp was zaadbankonderzoek op de kwelder van Schiermonnikoog, onder begeleiding van professor Jan Bakker. Samen met Geurt Verweij en Yzaak de Vries naar Schier, dat was leuk. Ik weet nog goed hoe ik de eerste ochtend vanuit de Herdershut de dijk op liep en daar tot mijn grote verbazing het land onder water zag staan. Een prachtig gezicht in de rode schijn van de opkomende zon. Maar wat minder praktisch voor het geplande veldwerk, want nu moesten we via het strand naar de Oosterkwelder. Door de korte november dagen werd de terugtocht nog een heel avontuur, maar onder leiding van Geurt en bijgestaan door de volle maan kwamen we weer veilig terug bij de Herdershut. Tijdens die ene veldwerkweek heb ik veel praktische vaardigheden en veldkennis opgedaan wat mij later nog vaak van pas is gekomen. Geurt en Yzaak, hartelijk bedankt hiervoor, ik kon geen beter veldwerkgezelschap wensen! Na het verzamelen van de bodemonsters brak een periode van kaswerk aan. Hier maakte ik voor het eerst kennis met Jacob Hogendorf, die mij met raad en daad, en vooral ook veel potgrond, zand en witte afwasteilen, bijstond. Jacob, ik heb de samenwerking met jou in de kas, eerst als stagaire en later ook als promovendus, altijd erg plezierig gevonden. Zelfs bij mijn ‘korte-termijn acties’, waarbij ik vaak de volgende ochtend het veld in moest, was je altijd bereid te helpen met het klaarleggen van het benodigde materiaal en in het laatste jaar heb je de organisatie voor het vangen van zaden in de Waddenzee op je genomen, wat ontelbare telefoontjes tot gevolg had. Daarnaast is het in de kas altijd prima voor elkaar en hoewel we dat graag als vanzelfsprekend aannemen, weet ik uit ervaring dat het elders wel anders kan zijn.

Tijdens het werk in de kas kwam de professor zelf regelmatig een kijkje nemen, benieuwd naar wat er zoal uit de monsters opkwam. Jan, jouw enthousiasme en interesse voor de plantenoecologie en het vertrouwen in en respect voor de mensen op de werkvloer, ongeacht hun functie, heb ik altijd zeer gewaardeerd. Je hebt dan ook een belangrijke rol gespeeld bij mijn beslissing om na het van Hall verder in de biologie te gaan. Hoewel de weg naar die vervolgstudie met omwegen en hindernissen gepaard ging, ben je altijd op de achtergrond betrokken geweest, wat tijdens moeilijke momenten erg motiverend was.

Na het afstuderen aan het van Hall en een jaartje Amerika werd het kwelderwerk vervolgd tijdens een tweejarige Master of Philosophy opleiding aan de Universiteit van London,

waar ik betrokken was bij onderzoek naar de erosie en het herstel van kwelders in zuidoost Engeland. Hierbij kwam ik al snel in contact met het Centre for Ecology and Hydrology, Monks Wood, die op hetzelfde studiegebied werkzaam was. Samenwerking met dit instituut leek een goede uitkomst voor het tot dan toe stagnerende onderzoek en de weinig adequate begeleiding vanuit London. Deze samenwerking is in stand gebleven toen ik in 2001 als AIO in de groep van Jan Bakker op het onderwerp kwelderherstel werd aangesteld. I am very grateful to Barry Wyatt, then head of CEH Monks Wood, and Mark Hill, former head of the EPMS section in which I came to work, for taking me on board as a student. I would also like to thank Pete Carey for supervising me throughout this period. Several other people at Monks Wood have helped me in some way or another for which I am very grateful. But most importantly, I would like to thank Angus Garbutt for the pleasant cooperation during my time in the UK. It was nice working together at Tollesbury and very stimulating to discuss salt-marsh issues on our way to fieldwork and in the office and I am pleased that you will be my paranimf during the PhD ceremony.

Aan de andere kant van de zee vond het veldwerk vooral plaats op het verkwelderingsgebied Noard Fryslân Bûtendyks in samenwerking met Peter Esselink (Koeman & Bijkerk) en Willem van Duin (Alterra, Texel). Beide wil ik bedanken voor het beschikbaar stellen van de data die gedurende vijf jaar jaarlijks is verzameld. Mijn eigen onderzoek in dit gebied was gericht op de dispersie van kwelderplanten via getijdenwater. Het gebied wordt beheerd door It Fryske Gea, en van deze instantie wil ik met name Henk de Vries en Albert Ferwerda van harte bedanken voor het toestaan van het veldwerk en het prettige contact. Gerrit van de Leest en Johannes Westerhof zijn daarnaast erg behulpzaam geweest toen ik bij windkracht 10 zonodig astroturf matjes uit het veld moest halen en ze mij met de tractor uit de modder hebben opgevisst. Julia Stahl wil ik van harte bedanken voor de logistieke ondersteuning (inclusief het meehelpen trekken van het karretje over het laatste eindje stukgereden dijk) bij het maandelijks vervangen van de astroturf matjes in mijn eerste jaar als AIO. Bij het veldwerk heb ik verder hulp gehad van twee doctoraalstudenten, Marjolein Willemsse en Marja Smith. Hoewel het onderzoek dat zij hebben uitgevoerd niet in dit proefschrift is opgenomen, hebben ze beide erg zelfstandig nuttig werk geleverd. Mijn dank hiervoor, ook richting Jacob en Yzaak die de begeleiding in het veld en in de kas van mij overnamen wanneer ik mij in Engeland bevond.

Op het lab in Haren heb ik mij altijd met veel plezier tussen de plantenoecologen en later coconners begeven. Met name de halfelfjes in de kantine konden voor welkome afleiding zorgen en je wist nooit wat er dit keer weer voor discussie, of vreemd of lachwekkend verhaal op tafel kwam. Die prettige sfeer, de collegialiteit en het enthousiasme van de groep zijn eigenschappen waar iedereen best wel een beetje trots op mag zijn. Ook op de kwelderkamer heb ik het altijd erg naar mijn zin gehad en mijn kamergenoten Roos Veeneklaas, Esther Chang en Dries Kuijper zorgden er altijd voor dat ik me na twee weken Engeland direct weer thuis voelde. Daarnaast brachten verschillende mensen, waaronder Roos, Julia, Irma Knevel en Renée Bekker mij meestal snel weer van alle nieuwtjes op de hoogte. Hartelijk dank hiervoor. De prettige sfeer was ook aanwezig tijdens de jaarlijkse Coastal Ecology Workshop en de tweejaarlijkse Coastal Expedition, waar studenten en onderzoekers van verschillende universiteiten en instanties bij elkaar komen. Het enthousiasme dat deze groep mensen voor hun vakgebied uitstraalt, werkt enorm motiverend en de gezamenlijke workshops, excursies en veldwerk vond ik altijd zeer plezierig.

Tijdens mijn aanstelling als promovendus heb ik veel vrijheid gekregen in het op elkaar afstemmen van werk en privéleven in twee landen, wat de situatie aanzienlijk makkelijker

heeft gemaakt. Helaas bleek de eindstreep van een vierjarig promotieonderzoek net een stapje te ver en heb ik het laatste traject op halve kracht af moeten maken. Tijdens die periode heb ik veel steun gehad van verschillenden mensen, via kaartjes, emails en telefoontjes naar Engeland, waar ik toen verbleef. Dit heb ik bijzonder gewaardeerd! Voor de laatste loodjes heb ik hulp gekregen van Dick Visser, die de lay-out van dit boekje op zich heeft genomen en daarbij een grote last van mijn schouders heeft gehaald. Bedankt Dick, ik had het zelf niet zo mooi voor elkaar gekregen.

I would like to thank professors Alan Gray (CEH Dorset, UK), Mark Bertness (Brown University, USA) and Jan van Groenendael (Radboud Universiteit Nijmegen) of the reading committee for enthusiastically accepting the task of reading the draft of this thesis. Mijn promotores professors Jan Bakker en Wim Wolff wil ik bedanken voor het altijd snel becommentariëren van manuscripten en hoofdstukken.

Voor de afleiding naast het werk was er het korfbalveld. In Nederland was dit het thuis-honk Ritola in Zuidlaren, waar verschillende mensen altijd erg belangstellend informeerden hoe het mijn vriend (tevens oud-Ritolist) Sijbren en mij in Engeland beviel en wanneer we nu eindelijk weer terug zouden komen. Helaas, dit duurt wat langer dan gepland zodat we inmiddels de veteranen leeftijd naderen. Jammer genoeg liet mijn gezondheid ook nog eens weinig sportieve activiteiten toe, maar het was altijd leuk om weer even een potje te tieren of een wedstrijd te kijken. Tot onze grote verassing bleken er in Cambridge maar liefst vijf senioren korfbal(l) clubs te zijn, zodat we daar onze hobby weer op konden pakken en we al gauw betrokken raakten bij de oprichting van Cambridge Knights Junior Korfbal. Door gebrek aan reguliere wedstrijden is deze club na een aantal jaren helaas als een nachtkaaersje uitgegaan, maar ik heb het altijd erg leuk en leerzaam gevonden om als assistent coach training te geven aan de onder 7's, onder 9's en onder 11's. Zo weet ik nu bijvoorbeeld dat 'Stuck in the Mud' ook gewoon een spelletje kan zijn.

In al die vier jaar heen en weer reizen werd ik in Nederland altijd trouw van station Assen, Haren of vliegveld Eelde gehaald door mijn ouders, bij wie ik zolang mocht logeren. Ik heb het altijd zeer gewaardeerd dat jullie telkens weer voor mij klaar stonden, niet alleen als taxi-service, maar ook met de warme maaltijd waar ik 's avonds moe en hongerig van de fietstocht uit Haren zo voor aan kon schuiven en zelfs een avond tellen van zaadjes die de volgende dag het veld in gebracht moesten worden. Daarnaast is mijn vader vaste hulp bij het vangen van zaden in de Waddenzee. Tijdens de jaarlijkse kerst en zomervakantie in Nederland logeerden we bij Sijbrens ouders, waar we als bleke stadskinderen al gauw weer bosjes kregen van de gezonde buitenlucht. We hebben het altijd gezellig gevonden om na wat klusjes in de tuin voor een knapperend openhaardvuur verwend te worden met zelfgemaakte appel- of kwarktaart. Bedankt voor al jullie goede zorgen.

De laatste persoon die ik hier wil bedanken is mijn vriend Sijbren met wie ik inmiddels vele jaren geheel of gedeeltelijk heb doorgebracht. Het was nooit leuk om elkaar weer voor een aantal weken te moeten missen maar des te leuker om dan weer even bij elkaar te zijn. Hartelijk dank voor de vele keren dat je mee het veld in ging om het fysiek zware werk te verlichten, maar ook voor je vertrouwen in mij en je acceptatie dat ik meestal maar weinig energie had. Ik hoop dat we in de nabije toekomst een plekje vinden waar we beide plezierig kunnen wonen en werken en waar we nog vele leuke dingen samen kunnen ondernemen.

Mineke



Mainland salt marsh at Noard Fryslân Bûtendyk with brushwood groynes and pioneer salt-marsh vegetation

Introduction

This chapter outlines the impetus and ideas behind salt-marsh restoration and introduces a conceptual framework to analyze the restoration of salt-marsh plant communities after de-embankment. This framework particularly emphasizes the role of species pools and dispersal in the establishment of salt-marsh vegetation. The specific aims of this thesis are presented at the end of this chapter.

Introduction

Salt marshes and their nature conservation interest

Coastal salt marshes are defined as vegetated areas that are subject to periodic flooding as a result of fluctuating water levels of adjacent saline water bodies (Adam 1990). Salt marshes in Europe generally occur in sheltered conditions, where wave action is low enough for fine sediment to settle and accumulate (Allen & Pye 1992). Once the sediment is above the level of mean high water neap tide (MHWN) and therefore not continuously submerged, terrestrial salt-marsh plants can colonize and establish (Beefink 1977). A characteristic feature of salt-marsh vegetation is the spatial distribution of different species or plant communities in parallel zones with elevation or distance from sea (i.e. zonation) (Chapman 1974; Beefink 1977; Adam 1990; Gray 1992). Factors associated with tidal inundation generally determine the seaward distribution of a species whereas interspecific competition for light or nutrients becomes increasingly important at higher elevation (Snow & Vince 1984; Greinier La Peyre *et al.* 2001). Because salt marshes are restricted to a narrow zone between land and sea, many salt-marsh plant species and their associated plant communities are considered rare (Doody *et al.* 1993) or vulnerable to extinction (Westhoff *et al.* 1993). The salt-marsh vegetation itself supports a wide variety of animals (Heydemann 1960; 1962; Adam 1990), many of which are restricted to saline habitats (Doody 1992; see also e.g. Pétillon *et al.* 2005). Salt marshes are considered particularly

important for migratory birds and waterfowl, which depend on these habitats for food, nesting and roosting sites (see e.g. Rowcliffe *et al.* 1995; Zedler & Callaway 1999; van der Wal *et al.* 2000; Dierschke & Bairlein 2004). This importance is reflected in the national and international policies on the conservation of salt marshes (Davidson *et al.* 1991; Doody *et al.* 1993; Janssen & Schaminée 2003; Ozinga & Schaminée 2005) .

Apart from their nature conservation interest, salt marshes are important as a natural flood control dissipating wave energy (Möller *et al.* 1999). It has been estimated that with a six metre wide salt marsh in front, a six metre high seawall would be sufficient to protect the hinterland, whereas in the absence of a salt marsh the seawall should be 12 metre high (King & Lester 1995). As building and maintaining seawalls is expensive there are obviously great economic advantages in having a salt marsh in front of coastal embankments.

Loss of salt marshes and the coastal squeeze hypothesis

Recently, large losses of salt marsh have been reported globally, including the US (Phillips 1986; Zedler 1996a; Schwimmer 2001), Spain (Castillo *et al.* 2000), south-east England (Burd 1992; Cooper *et al.* 2001) and the Netherlands (Dijkema 1987; Cox *et al.* 2003). These losses have been attributed to several factors associated with human development and climate change (Goodwin *et al.* 2001; Adam 2002). In south-east England, much attention has been given to the combined effect of historic land claim and current sea-level rise on salt-marsh erosion. In times of relative sea-level rise (i.e. a combination of land subsidence and eustatic sea-level rise) salt marshes must increase in elevation to avoid being ‘ecologically drowned’. This has generated the assumption that salt marshes have to move inland in order to adjust to the rising sea level. In situations where land claim has resulted in the construction of seawalls close to the mean high water level (a common feature in the UK), salt marshes will not be able to migrate further inland. This phenomenon is called ‘coastal squeeze’ (Doody 2004). The situation however, is much more complex because the vertical range of a salt marsh is not only controlled by sea level, but also by tidal range and sediment supply, whereas the horizontal extent is mainly affected by the local wind-wave climate (Allen 2000). Whether or not a salt marsh will be sustained in periods of relative sea-level rise depends on several, locally varying, factors. Nevertheless, in an attempt to halt any further losses and to promote salt-marsh development, the UK government has adopted a policy of managed realignment, which is the breaching or removal of coastal defence structures to allow salt marshes to develop on formerly reclaimed land (Anon. 1992).

The coastal squeeze hypothesis and the effectiveness of managed realignment in re-creating salt marshes in south-east England has been debated severely (Hughes & Paramor 2004; Morris *et al.* 2004) in particular with respect to the potential role of burrowing invertebrates (Paramor & Hughes 2004). The different issues raised in this debate form the subject of Chapter 2 of the present thesis.

Managed realignment and de-embankment of summerpolders

The concept of managed realignment to restore salt marshes is practiced in various countries, albeit under a different name and driven by different incentives. In the US for example, the 'no net loss of wetlands' policy serves as a major impetus for mitigation projects in which the area of wetland habitat being damaged or lost is re-created elsewhere (Zedler 1996b). The breaching of sea defences is only one option amongst several mitigation measures (Zedler 2001). Along the Dutch and German Wadden Sea coast, the option of de-embankment of summerpolders is currently pursued because of increased awareness of nature conservation issues together with the diminished value of reclaimed land for agricultural exploitation (Wolff 1992; Alhorn & Kunz 2002). The salt marshes in this area have mainly developed as a result of artificial reclamation works (Cools 1948; Dijkema *et al.* 1980), which involved the construction of sedimentation fields surrounded by brushwood groynes to enhance sediment accretion, followed by the excavation of ditches to improve drainage and accelerate plant establishment (Bakker *et al.* 2002). Once continuous vegetation had developed, these salt marshes were embanked by a low summerdike that would protect the newly claimed land from flooding in summer but not during storm surges or high tides in winter (Bakker *et al.* 2002; Alhorn & Kunz 2002). The so-called summerpolders were mainly used for cattle grazing and hay making.

In the United Kingdom, large areas of high salt marsh have been claimed successively in the past (Davidson *et al.* 1991) and mainly used as freshwater grazing marsh (Doody 1992). When techniques for protection against tidal flooding improved, several grazing marshes as well as newly enclosed land were transformed into arable fields (Williams & Hall 1987; Doody 1992) and seawalls were built further seaward. Nowadays, the diminishing value of arable land together with an increasing cost of seawall maintenance form the primary motives for managed realignment. In addition, the UK has a legal requirement to compensate for salt-marsh loss in order to comply with national and international policies on the conservation of wetland habitat (Pethick 2002).

The concept of managed realignment or de-embankment to re-create salt marshes is not new. In the past, accidental breaches in seawalls have occurred as a result of storm surges and, when left unrepaired, the newly inundated land often became transformed into salt marsh (Burd *et al.* 1994; van Duin *et al.* 1997). Chapter 3 provides an overview of accidental and deliberate de-embankments in north-west Europe. A total area of *c.* 2700 ha of embanked summerpolders can be found in the Wadden Sea, with 1000 ha in the Netherlands and 1700 ha in Niedersachsen, Germany. The total area of land claimed in the UK is 89,000 ha (Davidson *et al.* 1991), but here the embankment often functions as the main sea defence restricting the potential for de-embankment.

Salt-marsh restoration

The species pool concept

Successful restoration of plant communities depends on the availability of target species, the ability of the species to reach a target area and the presence of suitable environmental conditions that allow the species to germinate and establish. A useful starting point for unravelling the importance of these parameters is the concept of the species pool, first mentioned by Taylor *et al.* (1990) and later defined by Eriksson (1993) as a set of species that are potentially capable of co-existing in a certain community. Initially, the species-pool hypothesis related species diversity of a particular habitat to the commonness of that habitat (Taylor *et al.* 1990). This hypothesis evolved to include aspects of species migration between regions and dispersal between and within local populations, leading to the statement that species richness of a certain community on a smaller scale is mainly determined by the number of species at the next larger scale (Zobel 1997). The definition of the species pool was thus extended to distinguish different types of species pools related to the same target community but operating at different spatial scales (Zobel 1997; Zobel *et al.* 1998). At the largest spatial scale, the regional species pool is defined as the set of species occurring in a certain region and capable of co-existing in the target community. At the next smaller scale, the local species pool specifies the set of species occurring in the landscape type around a target community, which is capable of co-existing in that community. Finally, the community species pool is the set of species present in the target community, including the established vegetation and the diaspore bank (Zobel *et al.* 1998).

The importance of this species-pool concept for community restoration is that it assists in elucidating which species may potentially grow in a specified community and how they can arrive in a restoration site. A schematic representation of the species-pool concept and its use in the present thesis is given in Fig. 1.1. The first step in this figure is to select the species that are capable of co-existing in the target community from a regional flora. This step, which leads to the determination of the regional species pool, is addressed in Chapter 3. The actual arrival of species from the regional species pool in the local or community species pool will depend on different factors acting as filters or barriers between the different species pools (Fig. 1.1). These filters can be classified into two types: i) availability of the target species, and ii) presence of 'safe' sites (see also Zobel *et al.* 1998). The different factors associated with these filters and their contribution in this thesis are discussed below.

Availability of target species

Potential source areas of target species may be found at each of the three spatial scales distinguished in Fig. 1.1. In the case of salt-marsh restoration, the source area of the regional target species pool comprises all salt marshes within a biogeographically uniform region (see Chapter 3 for further details). Usually, the de-embankment sites are fronted by existing salt marshes, which then form the source area of the local

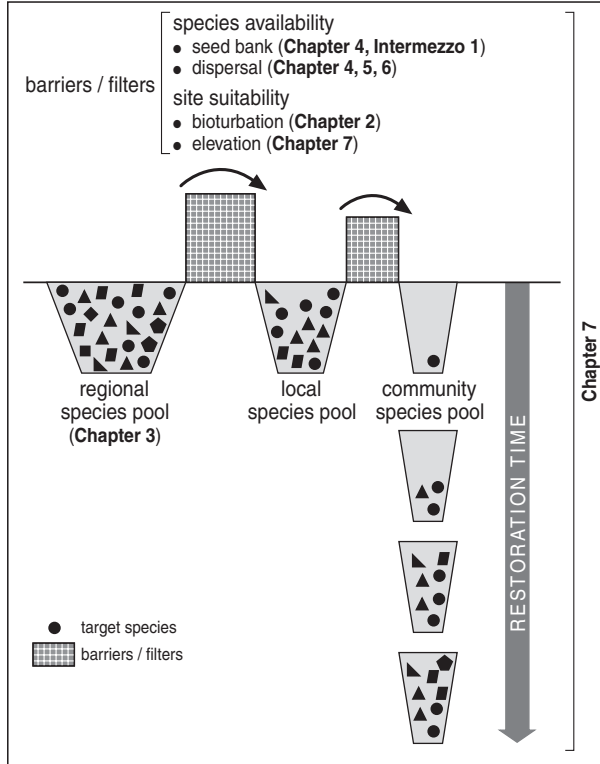


Figure 1.1. A framework for elucidating the mechanisms behind salt-marsh development after de-embankment. The probability of a target species becoming part of the community species pool of the target area depends on species availability in the regional and local species pool, dispersal constraints between the different species pools and the presence of suitable sites for their establishment. The selection of species for the regional species pool is the subject of Chapter 3; Chapter 4 and Intermezzo 1 describe the composition of the soil seed bank of a natural salt marsh and the soil seed bank prior to, and after de-embankment, respectively; dispersal by tidal water is studied in Chapters 4, 5 and 6; Chapter 2 surveys the potential role of bioturbating invertebrates on plant establishment; finally, salt-marsh development after de-embankment and the relative importance of species availability, dispersal traits and site suitability, with particular emphasis on elevation, are analyzed in Chapter 7.

species pool. Finally, the target species may be present in the community species pool of the restoration site. At each of these three spatial scales, the frequency and abundance of the target species in the established vegetation as well as their fecundity are important determinants of their availability. In addition, target species can be present in the diaspore bank of the community species pool, from which they may emerge when favourable conditions for their establishment appear. The potential role of the soil seed bank in the re-establishment of salt-marsh vegetation after de-embankment will largely be determined by the longevity of the seeds of the target species. The longer the seeds remain viable, the higher the chance that they survive the period of

embankment during which the original halophytic species will have been largely replaced by glycophytes in the established vegetation. A seed bank classification scheme has been developed to distinguish between transient, short-term persistent and long-term persistent seed banks (Thompson *et al.* 1997). Only long-term persistent seed banks are likely to contribute to the restoration of plant communities that have disappeared from the target area (Bakker *et al.* 1996). Chapter 4 explores the composition and longevity of the soil seed bank at different successional stages in a natural salt marsh, while Intermezzo 1 presents a case study of the soil seed bank prior to and after de-embankment.

If target species are absent from the established vegetation and long-term persistent seed bank of a restoration site they have to be dispersed into the site from a source area. Dispersal will be affected by the distance between the source area and the target area, a species' adaptation to dispersal, dispersal constraints and the presence of dispersal agents or vectors. Many salt-marsh species appear to be adapted to dispersal by water (i.e. hydrochory), as their diaspores such as seeds, fruits, spikes or entire plants are able to float for a few hours to several months in seawater (Dalby 1963; Koutstaal *et al.* 1987). Evidence of dispersal by seawater can be found in driftline material, which is often deposited at the upper salt marsh or foot of the seawall after storm and high tide in autumn or winter and usually contains a high concentration of seeds and vegetative material (Gerlach 1999; Persicke *et al.* 1999; Gettner 2003). It is often assumed that the action of seawater results in the homogeneous mixing of diaspores of salt-marsh species. However, Persicke *et al.* (1999) have shown that the composition of driftline material largely resembles the fronting salt-marsh vegetation. Chapter 4 investigates the composition of viable driftline material at different successional stages at a natural salt marsh.

Although large quantities of seeds can be dispersed into driftline material, the material is usually concentrated in a small area and species establishment may not be successful as the seedlings often desiccate in the thick litter before their roots reach the soil (Boorman 1968). Furthermore, the occurrence of driftline depends on weather and tidal conditions, making it hard to predict when and where the seeds will be deposited. For salt-marsh restoration after de-embankment, insight into the possibilities of seed dispersal by regular tidal inundation is important. Huiskes *et al.* (1995) investigated dispersal of halophytes by tidal water by trapping seeds in standing or floating nets during ebb and flood tides at different months. Their results show that there is considerable movement of propagules with tidal water within a salt marsh and net export of species growing at the lower marsh. It is not clear whether salt-marsh propagules are homogeneously distributed by tidal water and where the seeds will eventually land as they can move back and forth with the tide for some time. In order to investigate actual seed dispersal, seeds should be trapped at the surface of a salt marsh. Chapter 5 introduces the use of astroturf seed traps to study actual seed dispersal by tidal water, while in Chapter 6 this seed trapping method is applied to a restoration site.

Site suitability

When seeds of the target species have arrived in a restoration site, their germination and subsequent establishment will depend on abiotic and biotic conditions of the environment. For de-embankment sites, which are usually devoid of (halophytic) vegetation, successful germination and seedling establishment are mainly affected by factors associated with tidal inundation, such as high salinity (Alvarez Rogel *et al.* 2000), waterlogging (Armstrong *et al.* 1985) and wave action (Wiehe 1935). In addition, Hughes & Paramor (2004) and Paramor & Hughes (2004) postulated that pioneer plant species may fail to germinate and establish because of bioturbation and herbivory by the ragworm *Nereis diversicolor*. Chapter 2 provides a literature survey of the potential role of invertebrates in salt-marsh plant establishment. The relationship between elevation and salt-marsh development is described in Chapter 7, and this last chapter also brings together the role of species availability and site suitability in the development of salt-marsh vegetation after de-embankment.

Aims of the thesis

In the previous sections, the incentives for salt-marsh restoration, the evaluation of success and a framework summarizing the factors that are involved in salt-marsh restoration have been presented. The following questions will be addressed in this thesis:

1. What is the relative importance of physical and biological processes related to salt-marsh erosion, and what is the effect of bioturbation and herbivory by *Nereis diversicolor* on plant establishment? A literature survey is conducted in Chapter 2 to address these questions.
2. What are the target species for salt-marsh restoration, how can we evaluate and compare success of different de-embankment sites and what can we learn from historic breaches? An overview of de-embankment sites in north-west Europe and their plant species assemblages are presented in Chapter 3.
3. What is the composition and longevity of the soil seed bank at different successional stages in a natural salt marsh? What is the composition of driftline material and are seeds homogeneously distributed along different successional stages? These topics are discussed in Chapter 4.
4. Are target species present in the soil seed bank of the community species pool before de-embankment and, if not, how long will it take for salt-marsh species to form a seed bank and for non-target species to disappear from the seed bank after de-embankment? Intermezzo 1 answers these questions for a restoration site that had been embanked for only 30 years.
5. How can we assess actual dispersal (i.e. the deposition of seeds at the soil surface) of salt-marsh species by tidal water? Chapter 5 provides a technical account of the use of astroturf seed traps for studying hydrochory.

6. Which salt-marsh species are dispersed into a restoration site after de-embankment and what is the relationship with the established vegetation? (Chapter 6).
7. How does the vegetation develop after de-embankment and what is the importance of the species pools, dispersal traits and site suitability for salt-marsh restoration? These questions are analyzed in Chapter 7.

Finally, Chapter 8 will set out what the different chapters have contributed to our understanding of salt-marsh development and the evaluation of restoration success and what the implications for future restoration are.

The thesis focuses on salt marshes in north-west Europe with particular emphasis on the Tollesbury managed-realignment site in south-east England and the barrier island of Schiermonnikoog in the Dutch Wadden Sea.

References

- Adam, P. (1990) *Salt marsh ecology*. Cambridge University Press, Cambridge, UK.
- Adam, P. (2002) Salt marshes in a time of change. *Environmental Conservation*, **29**, 39-61.
- Alhorn, F. & Kunz, H. (2002) The future of historically developed summerdikes and polders: a salt marsh use conflict. *Littoral 2002, The Changing Coast*, 365-374.
- Allen, J. R. L. (2000) Morphodynamics of holocene salt marshes: a review sketch from the Atlantic and Southern North Sea coasts of Europe. *Quaternary Science Reviews*, **19**, 1155-1231.
- Allen, J. R. L. & Pye, K. (1992) Coastal salt marshes: their nature and importance. *Salt marshes, morphodynamics, conservation and engineering significance* (eds J. R. L. Allen & K. Pye), pp. 1-18. Cambridge University Press, Cambridge, UK.
- Alvarez Rogel, J., Ariza, F. A. & Silla, R. O. (2000) Soil salinity and moisture gradients and plant zonation in Mediterranean salt marshes of southeast Spain. *Wetlands*, **20**, 357-372.
- Anon. (1992) Coastal zone conservation. English Nature's rationale, objectives and practical recommendations. English Nature, Peterborough, UK.
- Armstrong, W., Wright, E. J., Lythe, S. & Gaynard, T. J. (1985) Plant zonation and the effects of the spring-neap tidal cycle on soil aeration in a Humber salt marsh. *Journal of Ecology*, **73**, 323-339.
- Bakker, J.P., Bunje, J., Dijkema, K.S., Frikke, J., Hecker, N., Kers, A.S., Körber, P., Kohlus, J. & Stock, M. (2005). Salt Marshes. *Wadden Sea Quality Status Report 2004*. (Eds K. Essink, C. Dettmann, H. Farke, G. Lüerssen, H. Marencic, & W. Wiersinga). Wadden Sea Ecosystem No 19, pp. 163-179. Trilateral Monitoring and Assessment Group. Common Wadden Sea Secretariat, Wilhelmshaven, Germany.
- Bakker, J. P., Esselink, P., Dijkema, K. S., van Duin, W. E. & de Jong, D. J. (2002) Restoration of salt marshes in the Netherlands. *Hydrobiologia*, **478**, 29-51.
- Bakker, J. P., Poschod, P., Strykstra, R. J., Bekker, R. M. & Thompson, K. (1996) Seed banks and seed dispersal: important topics in restoration ecology. *Acta Botanica Neerlandica*, **45**, 461-490.
- Beeftink, W. G. (1977) The coastal marshes of western and northern Europe: an ecological and phytosociological approach. *Wet coastal ecosystems* (ed V. J. Chapman), pp. 109-155. Elsevier, Amsterdam.
- Boorman, L. A. (1968) Some aspects of the reproductive biology of *Limonium vulgare* Mill., and *Limonium humile* Mill. *Annals of Botany*, **32**, 803-824.
- Burd, F. (1992) Erosion and vegetation change on the salt marshes of Essex and North Kent between 1973 and 1988. Report No. 42. Nature Conservancy Council, Peterborough, UK.
- Burd, F., Clifton, J. & Murphy, B. (1994) Sites of historical sea defence failure. Phase II study. Report to English nature, ZO38-94-F. Institute of Estuarine and Coastal Studies, Hull, UK.

- Castillo, J. M., Rubio-Casal, A. E., Luque, C. J., Nieva, F. J. & Figueroa, M. E. (2000) Wetlands loss by erosion in Odiel marshes (SW Spain). *Journal of Coastal Research*, **SI 36**, 134-138.
- Chapman, V.J. (1974) *Salt-marshes and salt-deserts of the world*. Cramer, Lehre.
- Cools, R.H.A. (1948) *Strijd om den grond in het lage Nederland*. Nijgh en van Ditmar, Rotterdam, the Netherlands.
- Cooper, N. J., Cooper, T. & Burd, F. (2001) 25 years of salt marsh erosion in Essex: Implications for coastal defence and nature conservation. *Journal of Coastal Conservation*, **9**, 31-40.
- Cox, R., Wadsworth, R. A. & Thomson, A. G. (2003) Long-term changes in salt marsh extent affected by channel deepening in a modified estuary. *Continental Shelf Research*, **23**, 1833-1846.
- Dalby, D. H. (1963) Seed dispersal in *Salicornia pusilla*. *Nature*, **199**, 197-198.
- Davidson, N. C., d'A Laffoley, D., Doody, J. P., Way, L. S., Gordon, J., Key, R., Pienkowski, M. W., Mitchell, R. & Duff, K. L. (1991) Nature conservation and estuaries in Great Britain. Nature Conservancy Council, Peterborough, UK.
- Dierschke, J. & Bairlein, F. (2004) Habitat selection of wintering passerines in salt marshes of the German Wadden Sea. *Journal of Ornithology*, **145**, 48-58.
- Dijkema, K.S., Reineck, H-E. & Wolff, W.J. (eds) (1980) *Geomorphology of the Wadden Sea area*. Report 1 of the Wadden Sea Working Group. Balkema, Rotterdam, the Netherlands.
- Dijkema, K. S. (1987) Changes in salt-marsh area in the Netherlands Wadden Sea after 1600. *Vegetation between land and sea* (eds A. H. L. Huiskes, C. W. P. M. Blom & J. Rozema), pp. 42-49. Dr. Junk Publishers, Dordrecht, the Netherlands.
- Doody, J. P. (1992) The conservation of British saltmarshes. Saltmarshes. Morphodynamics, conservation and engineering significance (eds J. R. L. Allen & K. Pye), pp. 80-114. Cambridge University Press, Cambridge.
- Doody, J. P. (2004) Coastal squeeze - an historical perspective. *Journal of Coastal Conservation*, **10**, 138.
- Doody, J. P., Johnston, C. & Smith, B. (1993) Directory of the North Sea coastal margin. Joint Nature Conservation Committee, Peterborough, UK.
- Eriksson, O. (1993) The species-pool hypothesis and plant community diversity. *Oikos*, **68**, 371-374.
- Gerlach, A. (1999) Winter driftline debris on the wadden island of Mellum, Germany; distribution, quantity and decomposition. *Abhandlungen Naturwissenschaftliches Verein Bremen*, **44**, 707-724.
- Gettner, S. (2003) Untersuchungen des Zusammenhangs zwischen Treibselmengen und Vorlandnutzung an der Westküste Schleswig-Holsteins. *Kieler Notizen Pflanzenkunde Schleswig Holstein Hamburg*, **31**, 57-71.
- Goodwin, P., Mehta, A. J. & Zedler, J. B. (2001) Tidal wetland restoration: An introduction. *Journal of Coastal Research*, **SI27**, 1-3.
- Gray, A. J. (1992) Saltmarsh plant ecology: zonation and succession revisited. *Saltmarshes; morphodynamics, conservation and engineering significance* (eds J. R. Allen & K. Pye), pp. 63-79. Cambridge University Press, Cambridge, UK.
- Greiner La Peyre, M. K., Grace, J. B., Hahn, E. & Mendelssohn, I. A. (2001) The importance of competition in regulating plant species abundance along a salinity gradient. *Ecology*, **82**, 62-69.
- Heydemann, B. (1960) Die biozönotische Entwicklung vom Vorland zum Koog. Vergleichend-ökologische Untersuchungen an der Nordseeküste. Teil 1. Spinnen (Aranea). Akademie der Wissenschaften und der Literatur. *Abhandlungen der Mathematisch-Naturwissenschaftlichen Klasse*. Jahrgang 1960, Nr. 11. Wiesbaden, Germany.
- Heydemann, B. (1962) Die biozönotische Entwicklung vom Vorland zum Koog. Vergleichend-ökologische Untersuchungen an der Nordseeküste. Teil 2. Käfer. Akademie der Wissenschaften und der Literatur. *Abhandlungen der Mathematisch-Naturwissenschaftlichen Klasse*. Jahrgang 1962, Nr. 11. Wiesbaden, Germany.
- Hughes, R. G. & Paramor, O. A. L. (2004) On the loss of saltmarshes in south-east England and methods for their restoration. *Journal of Applied Ecology*, **41**, 440-448.
- Huiskes, A. H. L., Koutstaal, B. P., Herman, P. M. J., Beefink, W. G., Markusse, M. M. & de Munck, W. (1995) Seed dispersal of halophytes in tidal salt marshes. *Journal of Ecology*, **83**, 559-567.
- Janssen, J.A.M. & Schaminée, J.H.J (2003) *Europese Natuur in Nederland – Habitattypen*. KNNV Uitgeverij, Utrecht, the Netherlands.
- King, S. E. & Lester, J. N. (1995) Pollution Economics. The value of salt marshes as a sea defence. *Marine Pollution Bulletin*, **30**, 180-189.

- Koutstaal, B. P., Markuse, M. M. & de Munck, W. (1987) Aspects of seed dispersal by tidal movements. *Vegetation between land and sea: Structure and processes* (eds A. H. L. Huiskes, C. W. P. M. Blom & J. Rozema), pp. 226-233. Dr. W. Junk publishers, Dordrecht, the Netherlands.
- Morris, R. K. A., Reach, I. S., Duffy, M. J., Collins, T. S. & Leafe, R. N. (2004) On the loss of saltmarshes in south-east England and the relationship with *Nereis diversicolor*. *Journal of Applied Ecology*, **41**, 787-791.
- Möller, I., Spencer, T., French, J. R., Leggett, D. J. & Dixon, A. M. (1999) Wave transformation over saltmarshes: a field and numerical modelling study from North Norfolk, England. *Estuarine, Coastal and Shelf Science*, **49**, 411-426.
- Ozinga, W.A. & Schaminée, J.H.J. (2005) *Target species – Species of European concern. A database driven selection of plant and animal species for the implementation of the PAN European Network*. Alterra report 1119. Alterra, Wageningen, the Netherlands.
- Paramor, O. A. L. & Hughes, R. G. (2004) The effects of bioturbation and herbivory by the polychaete *Nereis diversicolor* on the loss of saltmarsh in south-east England. *Journal of Applied Ecology*, **41**, 449-463.
- Persicke, U., Gerlach, A. & Heiber, W. (1999) Zur botanischen Zusammensetzung von Treibsel der niedersächsischen Deichvorländer und Deichabschnitte. *Drosera*, **1**, 23-34.
- Pethick, J. (2002) Estuarine and tidal wetland restoration in the United Kingdom: policy versus practice. *Restoration Ecology*, **10**, 431-437.
- Pétillon, J., Ysnel, F., Canard, A. & Lefeuvre, J.-C. (2005) Impact of an invasive plant (*Elymus athericus*) on the conservation value of tidal salt marshes in western France and implications for management: Responses of spider populations. *Biological Conservation*, **126**, 103-117.
- Phillips, J. D. (1986) Coastal submergence and marsh fringe erosion. *Journal of Coastal Research*, **2**, 427-436.
- Rowcliffe, J. M., Watkinson, A. R., Sutherland, W. J. & Vickery, J. A. (1995) Cyclic winter grazing patterns in Brent geese and the regrowth of salt-marsh grass. *Functional Ecology*, **9**, 931-941.
- Ruiz-Jaen, C. & Aide, T. M. (2005) Restoration success: how is it being measured? *Restoration Ecology*, **13**, 569-577.
- Schwimmer, R. A. (2001) Rates and processes of marsh shoreline erosion in Rehoboth Bay, Delaware, USA. *Journal of Coastal Research*, **17**, 672-683.
- Snow, A. A. & Vince, S. W. (1984) Plant zonation in an Alaskan salt marsh. II. An experimental study of the role of edaphic conditions. *Journal of Ecology*, **72**, 669-684.
- Taylor, D. R., Aarssen, L. W. & Loehle, C. (1990) On the relationship between r/K selection and environmental carrying capacity: a new habitat template for plant life history strategies. *Oikos*, **58**, 239-250.
- Thompson, K., Bakker, J. P. & Bekker, R. M. (1997) *Soil seed banks of North West Europe: methodology, density and longevity*. Cambridge University Press, Cambridge, UK.
- van der Wal, R., van Lieshout, S., Bos, D. & Drent, R. H. (2000) Are spring staging brent geese evicted by vegetation succession? *Ecography*, **23**, 60-69.
- van Duin, W. E., Dijkema, K. S. & Zegers, J. (1997) Veranderingen in bodemhoogte (opslibbing, erosie en inklink) in de Peazemerlanden. IBN raport 326, 1-104. Wageningen, the Netherlands.
- Westhoff, V., Hobohm, C. & Schaminée, J. H. J. (1993) Rote Liste der Pflanzengesellschaften des Naturraumes Wattenmeer unter Berücksichtigung der ungefärdeten Vegetationseinheiten. *Tuexenia*, **13**, 109-140.
- Wiehe, P. O. (1935) A quantitative study of the influence of tide upon the population of *Salicornia europaea*. *Journal of Ecology*, **23**, 323-333.
- Williams, G. & Hall, M. (1987) The loss of coastal grazing marshes in south and east England, with special reference to east Essex, England. *Biological Conservation*, **41**, 243-253.
- Wolff, W. J. (1992) The end of a tradition: 1000 years of embankment and reclamation of wetlands in the Netherlands. *Ambio*, **21**, 287-291.
- Zedler, J. B. (1996a) Coastal mitigation in southern California: The need for a regional restoration strategy. *Ecological Applications*, **6**, 84-90.
- Zedler, J. B. (1996b) Ecological issues in wetland mitigation: An introduction to the forum. *Ecological Applications*, **6**, 33-37.
- Zedler, J. B. & Callaway, J. C. (1999) Tracking wetland restoration: do mitigation sites follow desired trajectories? *Restoration Ecology*, **7**, 69-73.

- Zedler, J.B. (2001) *Handbook for restoring tidal wetlands*. CRC Press, New York, US.
- Zobel, M. (1997) The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? *Trends in Ecology and Evolution*, **12**, 266-269.
- Zobel, M., van der Maarel, E. & Dupré, C. (1998) Species pool: the concept, its determination and significance for community restoration. *Applied Vegetation Science*, **1**, 55-66.



Lateral erosion of the salt-marsh edge at Tollesbury

Salt-marsh erosion and restoration in south-east England: squeezing the evidence requires realignment

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Journal of Applied Ecology (2005) **42**, 844-851.

The previous chapter outlined the impetus for conserving and restoring salt marshes. In south-east England, severe erosion of salt marshes has been attributed to a combination of sea-level rise and the presence of fixed embankments that prevent salt marshes from migrating inland, a process termed coastal squeeze. Managed-realignment schemes have been implemented to compensate for salt-marsh loss by providing accommodation space for salt marshes through de-embankment of previously reclaimed land. However, the concept of coastal squeeze and the effectiveness of managed realignment have caused serious debate, especially with regard to the effect of burrowing invertebrates on erosion and plant establishment. In this chapter an overview of physical and biological processes relevant to the above three issues is presented, and the relative importance of these processes at different spatial and temporal scales discussed.

Introduction

Over the past century, 67% of the eastern coastline of the UK has exhibited landward retreat of the low-water mark (Taylor, Murdock & Pontee 2004). In south-east England (Fig. 2.1) large areas of salt marsh have been lost as a result of rapid lateral erosion of the seaward margin and internal dissection of marshes (Cooper, Cooper & Burd 2001). At present, these marshes occupy an area of 7261 ha, which is 33% of the total salt-marsh area on the North Sea coast of the UK (Barne *et al.* 1998). Half of the area of these marshes consists of the low and mid-marsh plant communities *Puccinellietum maritimae* [coded SM10 and SM13 in the National Vegetation Classification (NVC)] and *Halimionetum portulacoidis* (SM14) (Burd 1989; Rodwell 2000). Upper-marsh and driftline communities with *Juncus gerardi*, *Festuca rubra* and *Elytrigia atherica* or *E. repens* are rare, occupying less than 10% of the salt-marsh area in the region (Burd 1989).



Figure 2.1. Location of estuaries in south-east England (UK)

Salt marshes not only provide a habitat for nationally scarce plants, winter and migratory birds (Barne *et al.* 1998), but are also important natural dissipaters of tidal currents and waves (Möller & Spencer 2002), thus protecting landward sea defences from scour and wave erosion. Hence, increased rates of salt-marsh erosion have become a major conservation and coastal management concern on the UK south-east coast. Unfortunately, there is no general consensus regarding the causes of the increased rates of erosion, as a complex set of both natural and anthropogenic factors influence coastal hydrodynamics, salt-marsh development and sedimentation rates within the area. Nevertheless, in an attempt to restore and to promote salt-marsh development, the procedure of managed realignment was introduced in order to overcome loss of biodiversity and to maintain flood protection (English Nature 1992), and it is now widely adopted by different organizations and agencies in the UK and elsewhere (Hughes & Paramor 2004; Morris *et al.* 2004). Existing seawalls are breached to provide new intertidal habitat inland and new seawalls may be constructed some distance inland. Managed-realignment schemes have been carried out in response to the effects of coastal squeeze (c.f. Doody 2004), where the landward growth of an estuarine floodplain and the development of salt marsh are assumed to be constrained by land claim and the building of sea defences. In south-east England coastal squeeze is associated with marsh erosion at the seaward margin (lateral erosion)

and/or increased creek dissection (Burd 1992). These latter processes may be instigated or accelerated by a rise in sea level and an increase in hydrological flow in a restricted area.

The above statements imply that anthropogenic events promote hydrodynamic and other physical changes in these coastal systems that result in erosion. However, recently Hughes and Paramor (2004) and Paramor & Hughes (2004) have suggested that biological processes must be considered alongside physical processes in the promotion of salt-marsh erosion. Two recent studies from the Atlantic coast of Argentina (Iribarne *et al. subm.*) and the Pacific coast of North America (Talley, Crooks & Levin 2001) have shown convincingly that crabs and burrowing copepods, respectively, can erode and destroy existing marsh structures. Hughes & Paramor (2004) have proposed that in south-east England, bioturbation and herbivory from increased numbers of ragworm, *Nereis diversicolor* (O.F. Müller) on intertidal flats immediately seaward of salt marshes and in tidal marsh creeks may also cause the loss of pioneer zone species (e.g. *Salicornia* spp.), increased sediment instability and enhanced rates of erosion. These authors further suggest that new salt marshes will not develop in realignment sites because bioturbation will prevent the establishment of pioneer species, a suggestion strongly disputed by Morris *et al.* (2004).

The aim of the present Chapter was to bring together biological and physical studies addressing erosion in salt marshes. Focussing on salt marshes in south-east England, we present a brief overview of rates and physical causes of salt-marsh erosion, discuss the concept of coastal squeeze, examine the hypothesis that bioturbation and herbivory from *Nereis* restricts plant establishment and results in erosion of sediment, and discuss the implications for managed realignment.

Rates of salt-marsh erosion and accretion

Excellent overviews of erosion rates for different estuaries in south-east England (Fig. 2.1) have been presented by Burd (1992), Cooper, Cooper & Burd (2001) and by van der Wal & Pye (2004) for the Greater Thames region (i.e. Colne to Swale estuary). These studies show that salt marshes have experienced a net loss in area for most of the last century. Net salt-marsh loss from 1973 to 1998 was c. 1000 ha, or 33% of the total area present in 1973, but recent erosion rates (1988-98) have been slower compared to previous rates (1973-88) (Cooper, Cooper & Burd 2001). Erosion has manifested itself mainly in lateral retreat of the seaward edge of salt marshes, in some cases by several metres per year since the mid-20th century (Harmsworth & Long 1986). Areas particularly affected are the outer estuaries and wider parts of inner estuaries (van der Wal & Pye 2004). The less exposed sites have experienced internal dissection because of widening of creeks (Pethick 1993).

During the last three decades, average accretion rates on mature and immature marshes in the Greater Thames region were 2-3 mm yr⁻¹ and greater than 3 mm yr⁻¹

respectively, but locally much higher rates have occurred (van der Wal & Pye 2004). With an estimated sediment load of $1 \times 10^6 \text{ m}^3$, sediment availability is assumed to be sufficient to enable salt-marsh growth to occur in the region (van der Wal & Pye 2004). Newly developed salt marshes have been reported for the Medway and Swale estuaries (Fig. 2.1), but these recently accreted salt marshes may be particularly susceptible to increased rates of erosion associated with storminess, because of their low bulk density and low sheer strength (Pye 2000; van der Wal & Pye 2004).

The above studies imply that erosion and accretion rates are different processes, affecting different parts of the salt marsh. Accretion rates may be sufficient to raise the salt-marsh surface in response to sea-level rise, but at the same time lateral erosion of the seaward edge of salt marshes may lead to a net reduction of salt-marsh area.

Physical causes of salt-marsh erosion

A useful review of possible physical causes of salt-marsh erosion in south-east England is provided by Pye (2000) and, more recently, van der Wal & Pye (2004) and we will briefly discuss the main issues arising from these studies. Salt-marsh erosion has often been associated with sea-level rise (French & Spencer 2001), but the actual response of salt marshes to rising sea levels can vary from shrinkage to maintenance or even expansion of the salt-marsh area, depending on the available sediment (Phillips 1986). As shown above, vertical accretion rates on salt marshes in south-east England have been in the order of $2\text{-}3 \text{ mm yr}^{-1}$, which is sufficient to compensate for the estimated relative sea-level rise of between 1.22 mm yr^{-1} (Woodworth *et al.* 1999) and 3.4 mm yr^{-1} (Rossiter 1972). Any spatial variation in erosion could not be linked to regional differences in the relative rise in sea level (van der Wal & Pye 2004), although statistical testing was not performed. It should be noted, however, that sediment eroded from seaward marsh cliffs on the Dengie open coast has contributed significantly to vertical accretion on salt marshes in that area (Reed 1988), thus leading to a general steepening of the shore profile.

Sediment budgets are also important in determining the effects of land claim and dredging on salt-marsh erosion. Where sufficient sediment is available, land claim may be followed by increased accretion in front of the new embankment and silting up of the estuarine channels, decreasing the tidal prism and current velocities (Pye 2000). However, when the cross-sectional area of the entrance channel is not affected by land claim, tidal range and current velocities will increase, and the remaining salt marshes are likely to experience lateral erosion of the seaward edge and internal dissection as a result of extension and widening of the creeks (Pye 2000). The latter situation appears to account at least partly for the erosion of salt marshes in the inner Thames estuary (Pye 2000; van der Wal & Pye 2004), where tidal range has increased since the 1950s (Rossiter 1972). Dredging may have a similar effect as land claim and

it has been shown to be the main cause of lateral erosion of salt marshes in the Westerschelde estuary, the Netherlands (Cox, Wadsworth & Thomson 2003). However, for the Greater Thames region, the effect of dredging appears to be relatively small and localized (Pye 2000; van der Wal & Pye 2004).

Superimposed on sea-level rise and land claim is the effect of increased wind/wave energy. Since the 1960s there has been a higher incidence of strong south and south-westerly winds in southern UK (Pye 2000) and the frequency and intensity of easterly winds increased between 1973 and 1997 (van der Wal & Pye 2004). Simultaneously, mean wave heights in the North Sea increased and peaked in 1980 (Rye 1976; Bacon & Carter 1991), which coincided with the period of increased rates of erosion reported for the marshes in south-east England (Pye 2000; van der Wal & Pye 2004). In the last decade, rates of retreat of the seaward edge of marshes have decreased concurrent with a decrease in the frequency and intensity of strong winds (van der Wal & Pye 2004). The combination of wind action, high tides, and increased wave height appears to be largely responsible for the increased rate of marsh erosion and creek dissection in the 1970s (Pye 2000; van der Wal & Pye 2004).

The role of *Nereis* in salt-marsh erosion

Part of the debate regarding the coastal squeeze hypothesis centres on the potential role of *Nereis* and other invertebrates in salt-marsh erosion. Hughes & Paramor (2004) postulated that the increase in the rate of salt-marsh erosion in recent decades was related, at least in part, to an increase in the abundance of *N. diversicolor*. Bioturbation and herbivory by this species are thought to be responsible for a loss of pioneer plants, increased sediment instability and erosion of salt-marsh creeks. In the Dutch and Danish Wadden Sea, there are indeed indications that the abundance of *Nereis* has increased over the last decade (Beukema 1989; Jensen 1992), possibly as a result of the indirect effects of eutrophication promoting algal growth on sediments (Beardall, Gooch & Pilcher 1990). Nutrient loads have increased in many rivers in south-east England, especially during the period from 1980 to 1986 (Parr & Mason 2003). But in the absence of published results on increased *Nereis* abundance in south-east England over the last decades, the evidence that *Nereis* causes marsh erosion is equivocal. Nevertheless, there is strong evidence from other marsh systems that biological processes can cause marsh erosion (Talley, Crooks & Levin 2001; Iribarne *et al. subm.*).

Nereis is an omnivore, feeding on epipellic diatoms (Smith, Hughes & Cox 1996), algae and marine vascular plants (Olivier *et al.* 1996), as well as small invertebrates such as *Corophium volutator* (Scaps 2002). The polychaete obtains food by filter feeding, surface-deposit feeding or active predation (Goerke 1966, 1971; Muus 1967). The food is either ingested immediately or transported into the burrow, where it frequently decomposes before ingestion (Scaps 2002). *Nereis* may have both a positive

and negative effect on sediment stability (Jumars & Nowell 1984). In a laboratory experiment, secretions produced by *Nereis* while making burrows increased the shear strength of sediments (Meadows, Tait & Hussain 1990), and high densities of burrows enhanced surface roughness of sediments and reduced erosion by dissipating wave energy, similar to the effect of vegetation (Murray 2002). However, when sediment was sprayed with insecticide to reduce *Nereis* abundance in a field experiment, it resulted in increased sediment stability because of a reduction in bioturbation and grazing pressure and a decrease in the water content of the sediment (de Deckere, Tolhurst & de Brouwer 2001). A decrease in water content also occurred when the abundances of other invertebrates were reduced (e.g. *Macoma baltica*, Widdows *et al.* 2004; *C. volutator*, Daborn *et al.* 1993; Gerdol & Hughes 1994; *Hydrobia ulvae*, Austen, Andersen & Edelvang 1999).

It is possible that herbivory and bioturbation by *Nereis* may account for the loss of salt-marsh vegetation from the pioneer zone (foraging, burial of seeds and seedlings) and the high marsh (creek erosion and failure of seedling establishment). In laboratory experiments, *Nereis* consumed and buried seeds and seedlings of *Salicornia* spp. (Paramor & Hughes 2004), *Zostera noltii* (Hughes *et al.* 2000) and *Spartina anglica* (Emmerson 2000). These laboratory experiments, however, were highly artificial (i.e. unnatural densities of *Salicornia* seeds and seedlings, 4540 m⁻² compared with 506 m⁻² adult plants in the field, and of *Nereis*, 681 m⁻² compared with 452 m⁻² in the field, and presumably no alternative food source) and the applicability of the results to the field situation is questionable. Moreover, a direct link between the removal of *Nereis* and the establishment of *Salicornia* seedlings could not be made in a field experiment. *Nereis* was excluded from the sediment by placing fine-mesh mats in creeks and on creek banks but *Salicornia* failed to establish on the mats (Paramor & Hughes 2004). These field experiments were flawed because they did not include a procedural control. This is particularly troubling because the mats stabilize substrate and thereby influence a key factor affecting seedling establishment. Proper controls are absolutely essential and cannot be ignored. When the sediment was sprayed with insecticide to remove the amphipod, *C. volutator*, it resulted in establishment of *Salicornia* plants at a lower elevational level than where the species naturally occurred (Gerdol & Hughes 1993). A comparable result was observed for the seagrass *Z. noltii*, which was transplanted to areas of the intertidal flat that were devoid of the seagrass and where the lugworm *Arenicola marina* occurred in mean densities of 68 individuals m⁻². Exclusion of the lugworm by fine-mesh mats inserted 5 cm deep into the sediment resulted in increased biomass and density of the *Zostera* transplants compared with areas where the lugworm was not excluded (Philippart 1994). However, in areas where seagrasses had established naturally, bioturbation by *Arenicola* was restricted, although this was largely attributed to the presence of a compact clay layer inhibiting burrowing by the worm, rather than the actual presence of the seagrasses (Philippart 1994). While seedling establishment at the boundary of the intertidal mudflat and the salt marsh and in creeks may be affected adversely by the

presence of invertebrates, this effect has to be seen in relation to the influence of physical factors. Nearly 100% of the seeds of *Spartina anglica* and *Salicornia dolichostachya*, for example, were lost from the intertidal flat during winter because of mobility of the top layer of sediment (van Eerd 1985; Houwing 2000). This result was mainly attributed to the mud-sand ratio of the sediment with the sand fraction being more susceptible to wind-induced wave erosion (Houwing *et al.* 1999; Houwing 2000). In early spring, large numbers of *Salicornia* seedlings were caught in nets used for studying seed dispersal (Huiskes *et al.* 1995), and Wiehe (1935) observed that a 2-3 day period of relatively weak tidal currents greatly enhanced establishment of *Salicornia* seedlings below the high water mark of neap tides. Hence, the effect of invertebrate activity has to be seen in the context of, and relative to, the frequency and intensity of a suite of physical processes that are spatially and temporally variable. Critical experimental field studies are lacking at this time to assess the relative contributions of physical and biological processes to the initiation and maintenance of creek and lateral erosion in salt marshes.

Salt-marsh erosion and coastal squeeze

It is evident that a number of factors have contributed to the changes to the coastal and estuarine marshes in south-east England. Van der Wal & Pye (2004) indicate that the development of cliff edges at the seaward margins of marshes began in the 19th century and that the timing and intensity of lateral erosion has varied throughout the region. At most sites since 1960, rates of erosion were greater from 1973 to 1988 than between 1988 and 1998 (van der Wal & Pye 2004). However, during these decades intact marshes accreted sediment and maintained their height relative to the tidal range (French 1993; Cahoon *et al.* 2000; van der Wal & Pye 2004), in spite of modest increases in relative mean sea level at the different sites ($1.22\text{--}2.14\text{ mm yr}^{-1}$) (Woodworth *et al.* 1999). At some sites there has been an increase in marsh elevation relative to mean sea level (Allen & Duffy 1998; Allen 2000; French & Reed 2001). Nevertheless, embankment constructions and land claims over the centuries have reduced the width of the intertidal zone forcing water upstream and increasing tidal ranges and current velocities (Pye 2000; van der Wal & Pye 2004). This process has resulted in a narrowing and/or steepening of the shore profile (Davidson *et al.* 1991). The changes can occur naturally, as a result of the accretionary processes on salt-marsh surfaces leading to an increase in surface elevation of salt marshes with respect to the adjacent intertidal mudflats (van de Koppel *et al.* 2005).

The increase in extreme water levels and storminess since the 1960s, but especially between 1987 and 1990 (Pye 2000), accelerated lateral erosion and vertical marsh accretion where marshes were exposed. This phenomenon has also been observed for salt marshes along the North Atlantic and Pacific coasts of the USA (Stumpf 1983; Roman *et al.* 1997). Hughes and Paramor (2004) indicated that the loss of pioneer-

plant communities at the seaward edge has not been accompanied by a loss of upper-marsh plants, as predicted by the coastal squeeze hypothesis, except where increased creek dissection has led to local erosion as a result of back flooding of the upper marsh. These upper-marsh plants mainly consist of perennial species (predominantly *Atriplex (Halimione) portulacoides* and *Puccinellia maritima*), which can survive as adult plants during the winter and are less vulnerable to environmental changes than pioneer species such as *Salicornia* spp. that establish from seed each spring and typically dominate the interface between the intertidal flat and the salt marsh. Moreover, these perennial species are well known for their ability to attenuate wave and current energy (Möller & Spencer 2002). *Puccinellia* traps sediment efficiently (Andresen *et al.* 1990; Langlois, Bonis, Bouzille 2003) at a rate that is sufficient to compensate for prevailing sea-level rise (French & Reed 2001). Field studies of the process of wave-height attenuation over surfaces of tidal salt marshes, intertidal sandflats, and intertidal mudflats confirm that waves incident upon the salt-marsh edge are efficiently attenuated within the first 20 m of permanent vegetation cover (Möller, French & Spencer 1996; Möller *et al.* 1999; Möller & Spencer 2002). Hence, as long as sufficient sediment is available, salt marshes beyond the immediate seaward margin appear able to maintain their vegetation cover in spite of modest rises in sea level and increases in incident wave energy.

A high degree of spatial variability characterizes intertidal surfaces (Dijkema 1987; Pethick 1992; French & Reed 2001). The composition of the intertidal plant community, creek morphology, and marsh-edge morphology all vary at a range of spatial scales and account for differences in surface 'roughness' from smooth exposed mud to algae-covered surfaces and surfaces colonized by macrophytes and incised by drainage channels and salt pans. It is likely, therefore, that patterns of wave transformation and thus the degree to which wave energy may be responsible for marsh-surface erosion, are dependent on marsh-edge configuration and the presence, density, orientation and size of creeks and salt pans. Little information is available, however, on the sustainability of marsh surfaces and vegetation cover under increased water depths and current flows (French & Reed 2001; Möller & Spencer 2002). In addition, seasonal variability in vegetative cover may lead to temporally varying patterns of wave dissipation at the transition from unvegetated intertidal flats to vegetated salt marshes (Möller & Spencer 2002). An extreme episodic tidal event may destroy the vegetation growing at the marsh edge followed by the formation of a cliff (van de Koppel *et al.* 2005). Subsequently, the wave energy on the cliff face may lead to further lateral erosion, even when sea-level rise is minimal and there is no overall change in the wave climate (van de Koppel *et al.* 2005). Further investigations on the frequency of occurrence of extreme events that pass a threshold and trigger cliff formation and creek erosion are sorely needed to resolve the debate on the processes that initiate lateral erosion that can result in a narrowing of salt marshes.

Plant establishment after managed realignment

Managed realignment is when the coastal defence line is moved further inland in order to allow intertidal habitat to develop on previously reclaimed land. A major incentive for this practice is coastal defence, as a well-developed salt marsh in front of a seawall efficiently dissipates wave energy (Brampton 1992; Möller & Spencer 2002), thereby reducing sediment erosion and maintenance costs of the seawall. Other objectives of managed realignment include specific nature conservation targets, meeting economic and social demands, and achieving environmental sustainability at the landscape level (DEFRA/EA, 2002). Managed-realignment schemes have been implemented in at least 17 sites in the UK since 1991 (Wolters, Garbutt & Bakker 2005b). Recently, Hughes & Paramor (2004) have raised concern about the effectiveness of managed realignment in creating salt-marsh habitat, as many sites have subsided considerably during their period of embankment and require high rates of sediment accretion, in order to raise the elevation to levels at which salt-marsh vegetation can establish. The authors believe that this newly accreted sediment will first be colonized by invertebrates that will prevent plant establishment because of the effects of bioturbation and herbivory. Although we do not dispute this possibility, there appears to be little evidence to support the concerns raised by Hughes & Paramor (2004). In a review of 37 accidental and deliberate changes to the position of embankments where the developing salt marshes were monitored for plant species assemblages, a minimum of six salt-marsh species had established at the different sites over periods ranging from 1 to 193 years (Wolters, Garbutt & Bakker 2005b). Pioneer species were most commonly recorded and 65% and 95% of the sites contained plants of *Spartina anglica* and *Salicornia* spp. respectively. Plants of *Salicornia* often occurred at high frequencies within sites where these annual species were recorded. Results from other studies describing vegetational development during salt-marsh restoration following managed realignment, dredging and excavating, also indicate rapid plant establishment (Alphin & Posey 2000; Edwards & Proffitt 2003). Nevertheless, authors of several studies point out that the resultant species abundances do not resemble those in established marshes and that rates of establishment of the different species largely depend on initial site elevation (Cornu & Sadro 2002; Williams & Orr 2002; Thom, Zeigler & Borde 2002). Sites with surface elevation levels that are too low for pioneer salt-marsh species to establish (because of dewatering and compaction of sediments and limited sediment supply during the period of embankment), may revert to intertidal flats or standing water after managed realignment (Pye 2000), unless positive sediment budgets can significantly raise the elevation (Morris *et al.* 2004). At the transition from intertidal flat to pioneer zone, the success or failure of salt-marsh plant establishment is likely to be determined by stochastic events superimposed on a combination of physical factors (Wiehe 1935; Houwing *et al.* 1999; Houwing 2000), seed availability (Wolters, Garbutt & Bakker 2005a) and foraging by invertebrates (Hughes & Paramor 2004).

Conclusions

The physical and biological processes discussed above operate at different spatial and temporal scales, and the erosional processes do not necessarily occur concurrently or at a similar rate within the different estuaries and coastlines. In addition, feedbacks between physical and biological processes that operate at different scales are poorly studied. If interactions between biotic and abiotic events in regulating erosional processes are to be better understood, more attention has to be given to long-term field experimental studies within the region. In addition, modelling studies of the coastal dynamics need to accompany the experimental studies.

Hughes & Paramor (2004) have suggested that seasonal biological processes that operate at spatial scales of centimetres to metres may restrict plant colonization of exposed intertidal mudflats and creek banks that are in fact the outcome of erosional processes operating at much larger spatial and temporal scales. Their experimental studies are incomplete, at least at the field level, but there is sufficient evidence to warrant further investigations, including an attempt to scale-up the effects of biological processes on salt-marsh erosion from a scale of metres to an entire estuary or coastline ecosystem. Where survey studies of plant colonization of exposed sediment at managed-realignment sites have been conducted it appears that, at the larger spatial scale, as distinct from the local scale (metres), there is very strong evidence that vegetative cover rapidly develops following sedimentation (Morris *et al.* 2004; Wolters, Garbutt & Bakker 2005b). The observations highlight the inherent difficulties of extrapolating results at one spatial scale to another in determining the causes of erosion.

There is no dispute that there has been a substantial loss of salt marsh within south-east England in recent decades and earlier since estuarine and coastal floodplains were embanked. Whether the term coastal squeeze is appropriate to describe the loss is likely to remain contentious until the quantitative contributions of the different erosional processes are evaluated. We agree with Hughes & Paramor (2004) that salt marshes in the region are able to accrete vertically in spite of small rises in sea level, that in recent decades the rise in sea level has been no higher than in the past when the salt marshes developed, and that pioneer-zone species, as opposed to the predicted loss of higher-marsh species, have disappeared as a result of lateral erosion and creek widening. Overall, the latter two processes largely account for the loss of salt marshes and the extent to which biological processes sustain sediment instability remains to be determined. If coastal squeeze is interpreted within this context, there appears to be no difficulty. However, to call into question the effectiveness of managed realignment in re-creating salt marshes (Hughes & Paramor 2004) on the basis of results from laboratory studies and field experiments (Paramor & Hughes 2004) that are open to criticism and have been conducted at a different spatial scale, is not justified. The challenge now is to design suitable experiments at different scales and using the appropriate controls to determine the relative impacts of abiotic and biotic factors in the erosion and restoration of salt marshes.

Summary

Salt marshes in south-east England have been eroding rapidly since 1960. Recently, Hughes & Paramor (2004) and Morris *et al.* (2004) have presented contrasting views on the extent to which physical and biological processes might contribute to the erosion. There are three contentious issues: (i) salt-marsh erosion is the result of coastal squeeze, where seawalls prevent a landward migration of a salt marsh in response to a sea-level rise; (ii) salt-marsh erosion is linked to bioturbation and herbivory of seedlings by the ragworm, *Nereis diversicolor*; (iii) new salt marshes will not develop on managed-realignment sites where existing seawalls have been removed because of the effects of ragworms.

In this Chapter, we provide a literature review of physical and biological processes relevant to the above three issues, and discuss the relative importance of these processes at different spatial and temporal scales. Our synthesis shows that, at a regional scale, the combination of strong winds, high tides, and increased wave height appears to be responsible for the increased rate of marsh erosion and creek dissection recorded in the 1970s. There is also some laboratory evidence that bioturbation and herbivory from populations of *Nereis* can lead to sediment instability and loss of pioneer plant species, such as *Salicornia* spp. However, the field evidence is more equivocal and has been conducted at small spatial scales. At a large number of different managed-realignment sites there is strong evidence that even if bioturbation and herbivory by *Nereis* have occurred, overall the effects have been insufficient to restrict plant succession of exposed sediment.

There is an urgent need for long-term field studies that integrate and quantify physical and biological processes and the related feedbacks at the different spatial and temporal scales. Until this is completed, terms such as coastal squeeze will remain contentious and management decisions will invite criticism.

Acknowledgements

We wish to thank Prof. W.J. Wolff, Dr. P. Atkinson and an anonymous referee for constructive criticism of an early version of this MS. R.L. Jefferies thanks the Natural Sciences and Engineering Council for financial support.

References

- Allen, J. R. L. (2000) Morphodynamics of holocene salt marshes: a review sketch from the Atlantic and Southern North Sea coasts of Europe. *Quaternary Science Reviews*, **19**, 1155-1231.
- Allen, J. R. L. & Duffly, M. J. (1998) Medium-term sedimentation on high intertidal mudflats and salt marshes in the Severn Estuary, SW Britain: the role of wind and tide. *Marine Geology*, **150**, 1-27.

- Alphin, T. D. & Posey, M. H. (2000) Long-term trends in vegetation dominance and infaunal community composition in created marshes. *Wetlands Ecology and Management*, **8**, 317-325.
- Andresen, H., Bakker, J. P., Brongers, M., Heydeman, B. & Irmiler, U. (1990) Long-term changes of salt marsh communities by cattle grazing. *Vegetatio*, **89**, 137-148.
- Austen, I., Andersen, T. J. & Edelvang, K. (1999) The influence of benthic diatoms and invertebrates on the erodibility of an intertidal mudflat, the Danish Wadden sea. *Estuarine, Coastal and Shelf Science*, **49**, 99-111.
- Bacon, S. & Carter, D. J. T. (1991) Wave climate changes in the North Atlantic and North Sea. *International Journal of Climatology*, **11**, 545-558.
- Barne, J. H., Robson, C. F., Kaznowska, S. S., Doody, J. P., Davidson, N. C. & Buck, A. L. (1998) *Coasts and seas of the United Kingdom. Region 7 South-east England: Lowestoft to Dungeness*. Joint Nature Conservation Committee, Peterborough, UK.
- Beardall, C. H., Gooch, S. M. & Pilcher, R. (1990) The intertidal invertebrate fauna of the Orwell estuary. *Transactions of the Suffolk National Society*, **26**, 33-45.
- Beukema, J. J. (1989) Long-term changes in macrozoobenthic abundance on the tidal flats of the western part of the Dutch Wadden sea. *Helgolander Meeresuntersuchungen*, **43**, 405-415.
- Brampton, A. H. (1992) Engineering significance of British saltmarshes. *Saltmarshes: Morphodynamics, Conservation and engineering significance* (eds J. R. L. Allen & K. Pye), pp. 115-122. Cambridge University Press, Cambridge, UK.
- Burd, F. (1989) *The saltmarsh survey of Great Britain. An inventory of British saltmarshes*. Nature Conservancy Council, Peterborough, UK.
- Burd, F. (1992) *Erosion and vegetation change on the salt marshes of Essex and North Kent between 1973 and 1988*. Nature conservancy council, Peterborough, UK.
- Cahoon, D. R., French, J. R., Spencer, T., Reed, D. & Möller, I. (2000) Vertical accretion versus elevational adjustment in UK saltmarshes: an evaluation of alternative methodologies. *Coastal and Estuarine Environments: sedimentology, geomorphology and geoarchaeology*. (eds K. Pye and J. R. L. Allen). Special publication of the Geological Society London, **175**, 223-238.
- Cooper, N. J., Cooper, T. & Burd, F. (2001) 25 years of salt marsh erosion in Essex: Implications for coastal defence and nature conservation. *Journal of Coastal Conservation*, **9**, 31-40.
- Cornu, C. E. & Sadro, S. (2002) Physical and functional responses to experimental marsh surface elevation manipulation in Coos Bay's south Slough. *Restoration Ecology*, **10**, 474-486.
- Cox, R., Wadsworth, R. A. & Thomson, A. G. (2003) Long-term changes in salt marsh extent affected by channel deepening in a modified estuary. *Continental Shelf Research*, **23**, 1833-1846.
- Daborn, G. R., Amos, C. L., Brylinsky, M., Cristian, H., Drapeau, G., Faas, R. W., Grant, J., Long, B., Paterson, D. M., Perillo, G. M. E. & Piccolo, M. C. (1993) An ecological cascade effect: Migratory birds affect stability of intertidal sediments. *Limnology and Oceanography*, **38**, 225-231.
- Davidson, N. C., d'A Laffoley, D., Doody, J. P., Way, L. S., Gordon, J., Key, R., Pienkowski, M. W., Mitchell, R. & Duff, K. L. (1991) *Nature conservation and estuaries in Great Britain*. Nature Conservancy Council, Peterborough, UK.
- de Deckere, E. M. G. T., Tolhurst, T. J. & de Brouwer, J. F. C. (2001) Destabilization of cohesive intertidal sediments by infauna. *Estuarine, Coastal and Shelf Science*, **53**, 665-669.
- DEFRA/EA (2002) Managed Realignment Review. Project FD2008, http://www.defra.gov.uk/science/projectdata/DocumentLibrary/FD2008/FD2008_537_TRP.pdf, DEFRA/Environment Agency Policy Research.
- Dijkema, K. S. (1987) Geography of salt marshes in Europe. *Zeitschrift für Geomorphologie*, **31**, 489-499.
- Doody, J. P. (2004) Coastal squeeze - a historical perspective. *Journal of Coastal Conservation*, **10**, 138.
- Edwards, K. R. & Proffitt, C. E. (2003) Comparison of wetland structural characteristics between created and natural salt marshes in southwest Louisiana, USA. *Wetlands*, **23**, 344-356.
- Emmerson, M. (2000) Remedial habitat creation: does *Nereis diversicolor* play a confounding role in the colonisation and establishment of the pioneering saltmarsh plant *Spartina anglica*? *Helgolander Meeresuntersuchungen*, **54**, 110-116.
- English Nature (1992) *Coastal zone conservation. English Nature's rationale, objectives and practical recommendations*. English Nature, Peterborough, UK.

- French, J. R. (1993) Numerical simulation of vertical marsh growth and adjustment to accelerated sea-level rise, North Norfolk, UK. *Earth Surface Processes & Landforms*, **18**, 63-81.
- French, J. R. & Reed, D. J. (2001) Physical contexts for saltmarsh conservation. *Habitat conservation: managing the physical environment* (eds A. Warren & J. R. French), pp. 179-228. John Wiley & Sons Ltd., London, UK.
- French, J. R. & Spencer, T. (2001) Sea-level rise. *Habitat conservation: managing the physical environment* (eds A. Warren & J. R. French), pp. 305-347. John Wiley & Sons Ltd., London, UK.
- Gerdol, V. & Hughes, R. G. (1993) Effect of the amphipod *Corophium volutator* on the colonisation of mud by the halophyte *Salicornia europaea*. *Marine Ecology Progress Series*, **97**, 61-69.
- Gerdol, V. & Hughes, R. G. (1994) Effect of *Corophium volutator* on the abundance of benthic diatoms, bacteria and sediment stability in two estuaries in southeastern England. *Marine Ecology Progress Series*, **114**, 109-115.
- Goerke, H. (1966) Nahrungsfiltration von *Nereis diversicolor* O.F. Müller (Nereidae, Polychaeta). *Veröffentlichungen Institut für Meeresforschung Bremerhaven*, **10**, 49-58.
- Goerke, H. (1971) Die Ernährungsweise der *Nereis*-Arten (Polychaeta, Nereidae) der deutschen Küsten. *Veröffentlichungen Institut für Meeresforschung Bremerhaven*, **13**, 1-50.
- Harmsworth, G. C. & Long, S. P. (1986) An assesment of saltmarsh erosion in Essex, England with reference to the Dengie Peninsula. *Biological Conservation*, **35**, 377-387.
- Houwing, E.-J. (2000) Morphodynamic development of intertidal mudflats: consequences for the extension of the pioneer zone. *Continental Shelf Research*, **20**, 1735-1748.
- Houwing, E.-J., van Duin, W. E., Smit-van der Waaij, Y., Dijkema, K. S. & Terwindt, J. H. J. (1999) Biological and abiotic factors influencing the settlement and survival of *Salicornia dolichostachya* in the intertidal pioneer zone. *Mangroves and Saltmarshes*, **3**, 197-206.
- Hughes, R. G., Lloyd, D., Ball, L. & Emson, D. (2000) The effects of the polychaete *Nereis diversicolor* on the distribution and transplanting succes of *Zostera noltii*. *Helgolander Meeresuntersuchungen*, **54**, 129-136.
- Hughes, R. G. & Paramor, O. A. L. (2004) On the loss of saltmarshes in south-east England and methods for their restoration. *Journal of Applied Ecology*, **41**, 440-448.
- Huiskes, A. H. L., Koutstaal, B. P., Herman, P. M. J., Beefink, W. G., Markusse, M. M. & de Munck, W. (1995) Seed dispersal of halophytes in tidal salt marshes. *Journal of Ecology*, **83**, 559-567.
- Iribarne, O., Gutiérrez, G., Botto, F., Palomo, G., Ribeiro, P. & Perillo, G. Shoreline ecosystem engineering: Crab-halophytic plant interactions facilitate creek growth. *Submitted to Estuarine, Coastal and Shelf Science*.
- Jensen, K. T. (1992) Macrozoobenthos on an intertidal mudflat in the Danish Waddensea: comparisons of surveys made in the 1930's, 1940's and 1980's. *Helgolander Meeresuntersuchungen*, **46**, 363-376.
- Jumars, P. A. & Nowell, A. R. M. (1984) Effects of benthos on sediment transport: difficulties with functional grouping. *Continental Shelf Research*, **3**, 115-130.
- Langlois, E., Bonis, A. & Bouzille, J. B. (2003) Sediment plant dynamics in saltmarshes pioneer zone: *Pucinellia maritima* as a key species? *Estuarine, Coastal and Shelf Science*, **56**, 239-249.
- Meadows, P. S., Tait, J. & Hussain, S. A. (1990) Effects of estuarine infauna on sediment stability and particle sedimentation. *Hydrobiologia*, **190**, 263-266.
- Morris, R. K. A., Reach, I. S., Duffy, M. J., Collins, T. S. & Leafe, R. N. (2004) On the loss of saltmarshes in south-east England and the relationship with *Nereis diversicolor*. *Journal of Applied Ecology*, **41**, 787-791.
- Möller, I. & Spencer, T. (2002) Wave dissipation over macro-tidal saltmarshes: Effects of marsh edge typology and vegetation change. *Journal of Coastal Research*, **SI 36**, 506-521.
- Möller, I., Spencer, T. & French, J. (1996) Wind wave attenuation over saltmarsh surfaces: preliminary results from Norfolk, England. *Journal of Coastal Research*, **12**, 1009-1016.
- Möller, I., Spencer, T., French, J. R., Leggett, D. J. & Dixon, A. M. (1999) Wave transformation over saltmarshes: a field and numerical modelling study from North Norfolk, England. *Estuarine, Coastal and Shelf Science*, **49**, 411-426.
- Murray, J. M. H. (2002) Biogeomorphological implications of microscale interactions between sediment geotechnics and marine benthos: a review. *Geomorphology*, **47**, 15-30.

- Muus, B.J. (1967) The fauna of Danish estuaries and lagoons. Distribution and ecology of dominating species in the shallow reaches of the mesohaline zone. *Meddedelser Danmarks Fiskeri og Havundersøgelser* (NS), **5**, 1-316.
- Olivier, M., Desrosiers, G., Caron, A., Retiere, C. & Cailou, A. (1996) Juvenile growth of *Nereis diversicolor* (O.F. Muller) feeding on a range of marine vascular and macroalgal plant sources under experimental conditions. *Journal of Experimental Marine Biology and Ecology*, **208**, 1-12.
- Paramor, O. A. L. & Hughes, R. G. (2004) The effects of bioturbation and herbivory by the polychaete *Nereis diversicolor* on the loss of saltmarsh in south-east England. *Journal of Applied Ecology*, **41**, 449-463.
- Parr, I. B. & Mason, C. F. (2003) Long-term trends in water quality and their impact on macroinvertebrate assemblages in eutrophic lowland rivers. *Water Research*, **37**, 2969-2979.
- Pethick, J. (1993) Shoreline adjustments and coastal management: physical and biological processes under accelerated sea-level rise. *Geographical Journal*, **159**, 162-168.
- Pethick, J. S. (1992) Saltmarsh geomorphology. *Saltmarshes: Morphodynamics, conservation and engineering significance* (eds J. R. L. Allen & K. Pye), pp. 41-62. Cambridge University Press, Cambridge, UK.
- Philippart, K. J. M. (1994) Interactions between *Arenicola marina* and *Zostera noltii* on a tidal flat in the Wadden Sea. *Marine Ecology Progress Series*, **111**, 257.
- Phillips, J. D. (1986) Coastal submergence and marsh fringe erosion. *Journal of Coastal Research*, **2**, 427-436.
- Pye, K. (2000) Saltmarsh erosion in southeast England: mechanisms, causes and implications. *British saltmarshes* (Eds B.R. Sherwood, B.G. Gardiner & T. Harris), pp. 360-396. The Linnean Society of London, London, UK.
- Reed, D. J. (1988) Sediment dynamics and deposition on a retreating coastal salt marsh. *Estuarine, Coastal and Shelf Science*, **26**, 67-79.
- Rodwell, J. S. (2000) *British plant communities. Maritime communities and vegetation of open habitats*. Cambridge University Press, Cambridge, UK.
- Roman, C. T., Peck, J. A., Allen, J. R., King, J. W. & Appleby, P. G. (1997) Accretion of a New England (USA) saltmarsh in response to inlet migration, storms and sealevel rise. *Estuarine, Coastal and Shelf Science*, **45**, 717-727.
- Rossiter, J. R. (1972) Sea-level observations and their secular variation. *Philosophical Transactions of the Royal Society London A*, **272**, 131-139.
- Rye, H. (1976) Long term changes in the north sea wave climate and their importance for the extreme wave predictions. *Marine Science Communications*, **2**, 419-448.
- Scaps, P. (2002) A review of the biology, ecology and potential use of the common ragworm *Hediste diversicolor* (O.F. Muller) (Annelida: Polychaeta). *Hydrobiologia*, **470**, 203-218.
- Smith, D., Hughes, R. G. & Cox, E. J. (1996) Predation of epipellic diatoms by the amphipod *Corophium volutator* and the polychaete *Nereis diversicolor*. *Marine Ecology Progress Series*, **145**, 53-61.
- Stumpf, R. P. (1983) The process of sedimentation on the surface of a salt marsh. *Estuarine, Coastal and Shelf Science*, **17**, 495-508.
- Talley, T. S., Crooks, J. A. & Levin, L. A. (2001) Habitat utilization and alteration by the invasive burrowing isopod, *Sphaeroma quoyanum*, in California salt marshes. *Marine Biology*, **138**, 561-573.
- Taylor, J. A., Murdock, A. P. & Pontee, N. I. (2004) A macroscale analysis of coastal steepening around the coast of England and Wales. *The Geographical Journal*, **170**, 197-188.
- Thom, R. M., Zeigler, R. & Borde, A. B. (2002) Floristic development patterns in a restored Elk River Estuarine marsh, Grays Harbor, Washington. *Restoration Ecology*, **10**, 487-496.
- van de Koppel, J., van der Wal, D., Bakker, J. P. & Herman, P. M. J. (2005) Self-organization and vegetation collapse in salt marsh ecosystems. *The American Naturalist*, **165**, E1-E12.
- van der Wal, D. & Pye, K. (2004) Patterns, rates and possible causes of saltmarsh erosion in the Greater Thames area (UK). *Geomorphology*, **61**, 373-391.
- van Eerd, M. M. (1985) The influence of vegetation on erosion and accretion in saltmarshes of the Oosterschelde, The Netherlands. *Vegetatio*, **62**, 367-373.

- Widdows, J., Blauw, A., Heip, C. H. R., Herman, P. M. J., Lucas, C. H., Middelburg, J. J., Schmidt, S., Brinsley, M. D., Twisk, F. & Verbeek, H. (2004) Role of physical and biological processes in sediment dynamics of a tidal flat in Westerschelde Estuary, SW Netherlands. *Marine Ecology Progress Series*, **274**, 41-56.
- Wiehe, P. O. (1935) A quantitative study of the influence of tide upon the population of *Salicornia europaea*. *Journal of Ecology*, **23**, 323-333.
- Williams, P. B. & Orr, M. K. (2002) Physical evolution of restored breached levee salt marshes in the San Francisco Bay estuary. *Restoration Ecology*, **10**, 527-542.
- Wolters, M., Garbutt, R. A. & Bakker, J. P. (2005a) Plant colonisation after managed realignment: the relative importance of diaspore dispersal. *Journal of Applied Ecology* **42**, 770-777.
- Wolters, M., Garbutt, R. A. & Bakker, J. P. (2005b) Salt-marsh restoration: evaluating the success of de-embankments in north-west Europe. *Biological Conservation*, **123**, 249-268.
- Woodworth, P. L., Tsimplis, M. N., Flather, R. A. & Shennan, I. (1999) A review of the trends observed in British Isles mean sea level data measured by tide gauges. *Journal of International Geophysics*, **136**, 651-670.



De-embankment at Tollesbury

CHAPTER 3

Salt-marsh restoration: evaluating the success of de-embankments in north-west Europe

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Biological Conservation (2005) **123**, 249-268.

It has become clear from the previous chapter that the effectiveness of managed realignment (or de-embankment) in recreating salt-marsh vegetation has caused some controversy. The present chapter presents an overview of different de-embankment sites in north-west Europe and their plant species assemblages. Factors affecting plant establishment and management options to increase the number of regional target plant species in the restoration sites are discussed.

Introduction

Over the past centuries, large areas of salt marsh have been reclaimed from the sea by the construction of embankments (Dijkema 1987; Pethick 2002). These embankments would either function as the main sea defence, protecting the hinterland from all tidal flooding, or as low summerdikes in front of an existing seawall, protecting the reclaimed land (polder) from normal tidal inundations, but not during winter storms (Bakker *et al.* 2002). The polder was usually used for intensive agricultural exploitation, which often involved the construction and/or maintenance of drainage structures and the application of fertiliser. As a result, the characteristic halophytic communities have largely disappeared. Continuing sediment accumulation in front of the embankments resulted in the development of new salt marshes and, after sufficient vertical accretion, these could in turn be reclaimed.

This process of successive reclamations has now become less acceptable for various reasons. Firstly, the need for extension of agricultural areas has diminished

(Bakker *et al.* 1997). At the same time, it has been realised that salt-marsh communities are important habitats that need to be preserved. Apart from their nature conservation interest, salt marshes are important for coastal defence, as they act as a natural buffer for dissipating wave energy (Möller *et al.* 1996). Moreover, regular tidal inundation on salt marshes ensures the input of fresh sediment, the rate of which may be high enough to compensate for current and future sea-level rise. In contrast, most embanked polders are characterised by a sediment deficit and may subside to below mean sea level. The presence of a salt marsh in front of a seawall will thus improve safety of the hinterland and reduce the cost involved in seawall maintenance (King & Lester 1995). Especially in the United Kingdom, where a combination of the sinking of the land and rising sea level has caused extensive erosion of salt marshes (Cooper *et al.* 2001), coastal defence is the main incentive for de-embankment (Pethick 2002).

The idea for using de-embankment to re-create salt marshes is developed from evidence of spontaneous salt-marsh formation after accidental breaching of seawalls due to storm tides (French 1999). However, not all natural breaches have resulted in successful salt-marsh development, hence it will be important to evaluate the success of different sites in order to provide insight into possible outcomes for deliberate de-embankments. In this Chapter the results of several natural and deliberate de-embankment cases will be discussed. Under deliberate de-embankment we include complete or partial removal of a seawall or summerdike as well as regulated tidal exchange where sluices or one-way valves have been inserted in the embankment to allow specified tidal amplitude (Lamberth & Haycock 2001). The aims of the Chapter are: (i) to present an overview of sites subjected to natural or deliberate breaching of seawalls or summerdikes or regulated tidal exchange, (ii) to introduce a method for evaluating restoration success, (iii) to compare restoration success of different sites, (iv) to determine which factors are likely to affect restoration success, and (v) to provide recommendations for future restoration schemes.

Selection and general description of study sites

A literature survey was conducted to identify restoration sites across north-west Europe. This resulted in a total of 89 sites (App. 3.1). Sites that had no information on location, type of scheme, size or year of restoration, or sites for which the scheduled restoration had not been implemented, were not included in the analysis. This reduced their number to 70. The majority of the restoration sites (48) is located in the United Kingdom, in particular on the south-east coast (Fig. 3.1). However, they rarely exceed 100 ha in size and the total restoration area of these 48 sites (2007 ha) is lower than that of the ten German sites (2590 ha) (Fig. 3.2). For fifty percent of the sites, embankments were accidentally breached during storm surges, in particular in 1897 and 1953. The oldest accidentally breached embankment reported in the literature dates back to 1802. The first deliberate de-embankment was executed in 1991



Figure 3.1. Location of salt-marsh restoration sites for which information on year of breach, type of scheme and area was available ($n = 70$). Different symbols are used for different countries. For sites names and detailed information see Appendix 3.1. Lettering to indicate multiple sites at one location are omitted on the map for clarity.

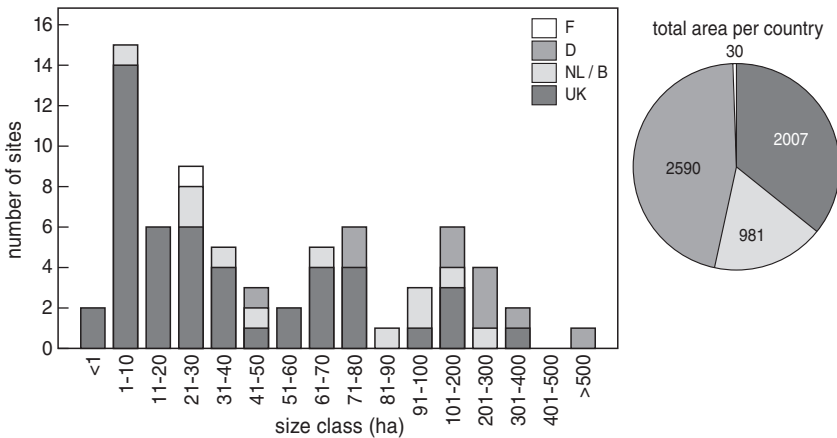


Figure 3.2. Frequency distribution of sizes of sites ($n = 70$) and total area per country (UK: $n = 48$; NL/B: $n = 11$; D: $n = 10$; F: $n = 1$).

(Northey Island, site Nr. 30b), after which between one and seven new de-embankments were initiated in north-west Europe each year (Fig. 3.3). Habitat creation/restoration is the most common reason for de-embankment, especially in the Netherlands, Belgium and Germany (Fig. 3.3). In many cases this habitat creation is driven by European legislation e.g. the Habitats Directive, which requires member states to designate special areas of conservation (Pethick 2002). Flood defence is another major reason for de-embankment, as the re-creation of a salt-marsh in front of a sea defence is considered a cost-effective way of improving safety to the hinterland.

How to evaluate success?

Definition of success

There is much recent debate on the question of how to define restoration success. One approach is to determine whether or not the terms set in an agreement, contract or permit have been met (Kentula 2000). Use of compliance success is appropriate whenever restoration targets are set beforehand. However, in many cases there are no clearly specified targets. In the present overview, for example, many sites had no clear pre-defined targets.

Other possibilities for assessing success are to compare the ecological structure or functioning of a restored site with one or more reference sites (Thom *et al.* 2002; Edwards & Proffitt 2003). However, the choice of the reference sites strongly affects the outcome of such a comparison (Kentula 2000; Morgan & Short 2002). Besides, comparing conditions with a natural reference system may not be realistic or appropriate because restoration may start on different substrate or different elevation (Thom 2000), or because the reference site itself may be degraded. Historical reference has also been used for assessing success, in which case success criteria have often been based on the situation before the industrial revolution and before the application of artificial fertiliser (De Jonge & De Jong 2002). However, when taking into account the increased human population with the accompanying levels of pollution, landscape fragmentation and species extinctions, a return to pre-industrial revolution ecosystems is hardly achievable.

Part of the debate on how to define success focuses on the question of whether the aim should be the restoration of the structure of an ecosystem or its functioning. Zedler & Lindig-Cisneros (2000) defined structure as a condition at one point in time (e.g. species diversity) and function as a process that occurs over time (e.g. primary production), and concluded that structural measures are often (wrongly) used as substitutes for functioning. Zedler & Callaway (1999) further point out that the restoration of functionality often takes longer than the restoration of the plant communities themselves. Although we do not dispute the fact that successful restoration should include proper structure and functioning of the system, we focus on restoration of the structural component as the first and most important stage in salt-marsh restoration.

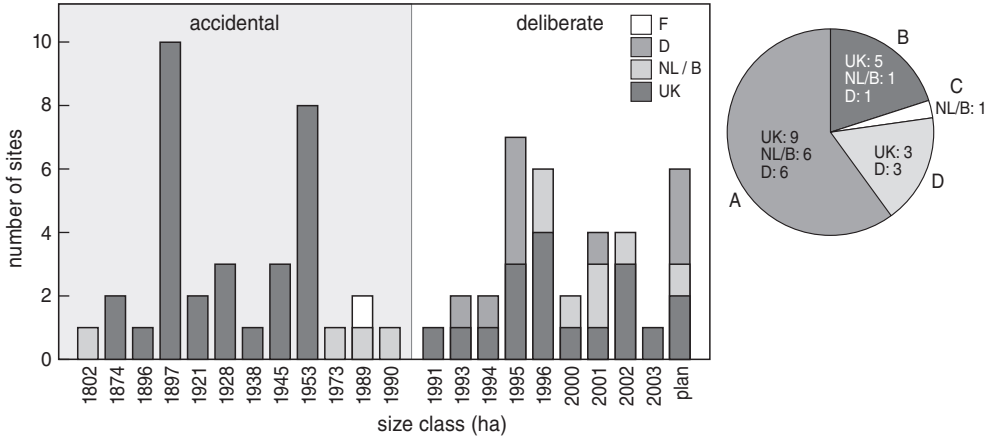


Figure 3.3. Year of de-embankment and main reasons for deliberate de-embankment with the number of sites per country for each category (A: habitat creation or restoration; B: flood defence; C: gaining experience; D: unknown).

By definition, coastal salt marshes are referred to as the vegetated part between land and sea, receiving frequent tidal inundation (Adam 1990). Once the vegetation has established it can serve different functions, e.g. sediment trapping, nutrient cycling, dissipation of wave energy, spawning area for fish, feeding, breeding and resting area for birds etc. If these functions do not follow upon the restoration of the vegetation, it can be because the site is not accessible or because the habitat structure is not suitable (e.g. geese will not use a site if it is dominated by tall plants) (van der Wal *et al.* 2000). In the latter case, management strategies may be incorporated to improve the structure of the site (e.g.. grazing or mowing of tall vegetation). It should be noted however, that different functions may require different structural components. Hence, in order for a restoration site to serve as many different functions as possible, high structural diversity should be created. In the present Chapter we will focus on plant species diversity based on a well-defined target species list as a first step for measuring structural success in restoration sites.

Applying the species pool concept for measuring success

For community restoration it is important to know which species are part of the target community and how they can arrive in the target community. These questions can be addressed through the species pool concept, reviewed by Zobel *et al.* (1998). In their review, three species pools are distinguished, each at a different spatial scale: (i) the regional species pool: a set of species occurring in the region and capable of co-existing in the target community, (ii) the local species pool: a set of species occurring in the landscape surrounding a target community, (iii) the community species pool: a set of species present in the target community. Various abiotic and biotic processes will act as filters between the different pools and determine whether a species from the region-

al or local pool will actually arrive and establish in the target area. The actual determination of the species pools is still in its infancy, but a promising approach is to select species from the local or regional flora based on phytosociological similarity (Zobel *et al.* 1998). We have applied this approach to define a regional target species list for north-west European salt-marsh and brackish-water plant communities. This regional species pool should include all species that have the potential to establish in a salt-marsh restoration site of the region concerned if the site were suitable and accessible.

Determining the regional species pool for north-west European salt marshes

On the basis of a differential influence of climate and sea currents on the distribution of salt-marsh plants in north-west Europe, we have classified our study sites into two distinct biogeographical regions, following Dijkema *et al.* (1984). The two regions are i) the Central North-Atlantic, extending from Scotland and south Scandinavia to North France, and ii) the Southern North-Atlantic, covering south and south-east England, Brittany, south-west France and north-west Spain (Fig. 3.4). In addition, the German Baltic shore is treated as a separate region because the salinity of the submerging water, tidal range and geomorphology are very different from the North-Atlantic region (Dijkema 1990).

For each region, typical salt-marsh communities were identified from the extensive work on National Vegetation Classification surveys by Schaminée *et al.* (1998) for the Central North-Atlantic and Rodwell (2000) for the Southern North-Atlantic, and a paper by Krisch (1990) for the German Baltic region (App. 3.2). Species were included in the target species list if they occurred in 61% or more of the phytosociological relevés of each salt-marsh community. This minimum percentage of occurrence ensured that all species characteristic of salt-marsh communities were included whereas non-typical species were excluded. No distinction has been made between different *Salicornia* species, because of difficulties in correctly identifying these species in the field. The procedure for selecting target species for the regional species pool resulted in a total of 39 species for the Central North-Atlantic, 34 for the Southern North-Atlantic and 27 for the German Baltic region. The names of these species and a number indicating for which region the species is considered a target species are shown in the first two columns of Table 3.1.

Evaluating restoration success

For the evaluation and comparison of the success of different salt-marsh restoration projects we have used a saturation index, where the presence of all target plant species in a restoration site is expressed as a percentage of the total regional target species pool of the region concerned (i.e. 39 species for the Central North-Atlantic, 34 for the Southern North-Atlantic and 27 for the German Baltic region). We realise that this index does not take into account important drivers of diversity, such as size of the

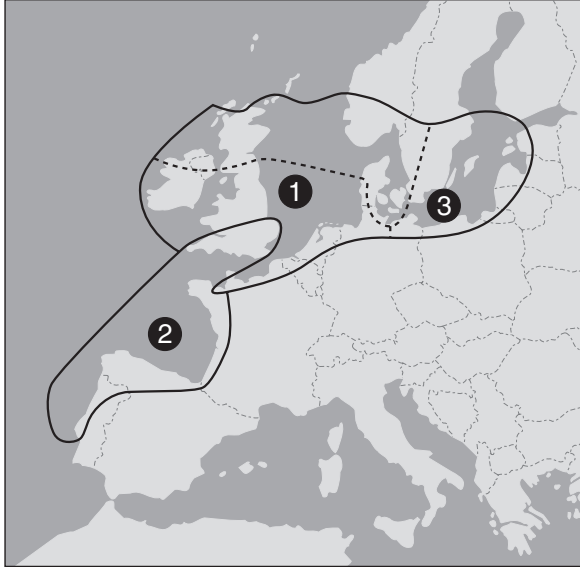


Figure 3.4. Biogeographical regions of salt-marsh vegetation. 1 = Central North-Atlantic; 2 = Southern North-Atlantic; 3 = German Baltic (adapted from Dijkema *et al.* (1984)).

site, age and elevation range, which would have resulted in a more realistic, but also site specific evaluation. Instead, our intention is to evaluate and compare success of all the sites identified in this review on an idealistic concept where all regional target species have the potential to establish in a site, but may not actually do so because the site is unsuitable or inaccessible. Factors affecting the presence or absence of certain species are discussed later and this information can be used by site managers to determine which management options may be required to increase the chance of certain plant species establishing in the site.

Species lists were available for only 37 out of the 70 study sites (Table 3.1). The saturation index for the different sites ranged from 18% to 64% (Table 3.1). In comparison, the saturation index of 40 established marshes in the Wadden Sea region, ranged from 56% to 92% (Dijkema & Wolff 1983). Restoration sites in the United Kingdom were the least diverse, with the majority of the sites having saturation indices below 30% (Fig. 3.5). Species that were absent from all restoration sites included *Spartina maritima*, *Poa subcoerulea*, *Puccinellia fasciculata*, *Carex serotina*, *Blasmus rufus*, *Oenanthe lachenalii*, *Ononis repens spinosa*, *Limonium binervosum*, *Frankenia laevis* and *Limonium bellidifolium*. Many of these species are characteristic of high-marsh and transition state communities. More research is needed to establish whether these species are nationally or regionally rare and missed as a result of insufficient sampling effort, or whether their absence is due to limited dispersal capabilities, abiotic or biotic constraints within the restoration sites. The most common species were *Salicornia* spp., *Suaeda maritima*, *Aster tripolium* and *Puccinellia mariti-*

Table 3.1. Target species of the regional species pool and frequency abundance (I = 1-20%, II = 21-40%, III = 41-60%, IV = 61-80%, V = 81-100%, P = present) of target species in 37 restoration sites with saturation index per site. Sites are listed in order of decreasing restoration time. The first column after the species list shows the regional species pool (1 = Central North-Atlantic, 2 = Southern North-Atlantic, 3 = German Baltic).

Site number	Region	62	40	13	20a	20b	8a	8b	16	29a	29b	21b	2	47	19	37	25	48	39	5
Years after breach		193	119	119	96	96	96	96	96	96	96	72	72	55	48	48	40	40	40	40
Number of quadrats		107	5	4	7	5	9	10	6	11	12	6	7	8	10	6	11	8	12	5
Quadrat size (m ²)																				
<i>Spartina maritima</i>	1,2																			
<i>Spartina anglica</i>	1,2	I	I	I	II	I		I		I		I			I		II	I	II	I
<i>Salicornia</i> spp.	1,2,3	I	II	III	II	IV	III	III	IV	III	III	I	II	II	I	IV	II	III	III	I
<i>Suaeda maritima</i>	1,2,3	II	II	III	II	I	II	III	II	III	III	III	III	II	III	III	II	II	II	III
<i>Aster tripolium</i>	1,2,3		II	III	II	I	II	III	II	III	III	II	II	I	II	III	II	I	II	I
<i>Plantago maritima</i>	1,2,3	I					I		I		I						I	I		
<i>Triglochin maritima</i>	1,2,3				I		I	I										I		
<i>Spergularia media</i>	1	I																		
<i>Limonium vulgare</i>	1,2	I	III		II	II	II	I	II	I	I	I	I	III		I	III		I	
<i>Atriplex portulacoides</i>	1,2	I	II	II	I	I	III	III	III	II	III	IV	II	III	I	I	II		I	III
<i>Glaux maritima</i>	1,2,3	I															I	I		
<i>Poa subcoerulea</i>	3																			
<i>Puccinellia maritima</i>	1,2,3	I	IV	II	IV	V	III	IV	III	I	I	III	III	IV	IV	III	I	II	III	III
<i>Atriplex prostrata</i>	1,2	II																I		
<i>Spergularia marina</i>	1,2,3	I				I			I					I		I				
<i>Puccinellia distans</i>	1,2,3																			
<i>Puccinellia fasciculata</i>	1																			
<i>Hordeum marinum</i>	1																			
<i>Juncus gerardi</i>	1,2,3	II																		
<i>Festuca rubra</i>	1,2	I															I	II		
<i>Armeria maritima</i>	2																			
<i>Carex extensa</i>	1																			
<i>Carex serotina</i>	3																			
<i>Centaureum pulchellum</i>	1																			
<i>Blysmus rufus</i>	1,3																			
<i>Seriphidium maritimum</i>	1,2													I						
<i>Elytrigia atherica</i>	1,2	III					I										I			
<i>Juncus maritimus</i>	1,2,3	I																		
<i>Oenanthe lachenalii</i>	1,2,3																			
<i>Samolus valerandi</i>	3																			
<i>Potentilla anserina</i>	1,2,3	I																		
<i>Agrostis stolonifera</i>	1,2,3	II																		
<i>Elytrigia repens</i>	2,3																			
<i>Leontodon autumnalis</i>	2																			
<i>Trifolium fragiferum</i>	1,3	I																		
<i>Carex distans</i>	1,3	I																		
<i>Ononis repens spinosa</i>	1																			
<i>Lotus corniculatus</i>	1	I																		
<i>Trifolium repens</i>	1,2	I																		
<i>Sagina maritima</i>	1	I																		
<i>Plantago coronopus</i>	1	I																		
<i>Cochlearia danica</i>	1	I																		
<i>Festuca arundinacea</i>	1	I																		
<i>Bulboschoenus maritimus</i>	1,2,3																			
<i>Schoenoplectus tabernaemonti</i>	1,2,3																			
<i>Phragmites australis</i>	3																			
<i>Triglochin palustris</i>	3																			
<i>Eleocharis uniglumis</i>	3																			
<i>Juncus articulatus</i>	3																			
<i>Sarcocornia perennis</i>	2																			
<i>Inula crithmoides</i>	2		I									I		I						
<i>Suaeda vera</i>	2																			
<i>Limonium binervosum</i>	2																			
<i>Frankenia laevis</i>	2																			
<i>Limonium bellidifolium</i>	2																			
Total	39,34,27	25	8	6	8	8	9	8	8	7	7	8	6	9	6	7	11	10	7	6
Saturation index	100	64	24	18	24	24	26	24	24	21	21	24	18	26	18	21	32	29	21	18
Reference:		1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2

Table 3.1. Continued.

1. van Dort & Leusink (1998); 2. Burd *et al.* (1994); 3. van Duin *et al.* (1997); 4. Koppejan (2000); 5. Arnel Dausse, pers. comm.; 6. Sabine Arens, pers. comm.; 7. Zander (2002); 8. Pers. obs.; 9. Bernhardt & Koch (2003); 10. Reading *et al.* (2002); 11. Dagley (1995); 12. van Gennip & Knotters (2002); 13. Främbs *et al.* (2000); 14. Diack (1998); 15. van Duin *et al.* (2003); 16. Angus Garbutt, pers. comm.; 17. www.

Site number	Region	46a	46b	59	77a	61	66	76	32	44	67	36	30b	57	65	1a	58	22	50
Years after breach		40	40	23	13	8	8	7	7	6	5	4	3	3	3	2	1	1	1
Number of quadrats		6	4	26	10	48	12	?	620	7500		48	50	221		144	820	160	7
Quadrat size (m ²)									1	1		1	1			1	100	1	
<i>Spartina maritima</i>	1,2								I	I			I	I			I	II	
<i>Spartina anglica</i>	1,2	I	I	I	I	I			I	I			I	I			I	II	
<i>Salicornia</i> spp.	1,2,3	II	IV	III		I	I	P	IV	III	I	II	V	II	P	I	V	IV	
<i>Suaeda maritima</i>	1,2,3	II	I	V			II		II	I			IV	I	P	I	V	I	
<i>Aster tripolium</i>	1,2,3	I	III	V	I	IV	V	P	I	I	I	II	I	II	P	I	V	II	
<i>Plantago maritima</i>	1,2,3				I	I	I				II			I	P		II		
<i>Triglochin maritima</i>	1,2,3				II	I		P			II				P		I		
<i>Spergularia media</i>	1			I	I	I								I	P		II		
<i>Limonium vulgare</i>	1,2	I	I			I			I	I			I	I					
<i>Atriplex portulacoides</i>	1,2	II	I	III					II	I			I	I		I	I	II	
<i>Glaux maritima</i>	1,2,3			I	II	II	III	P						I	P		I		I
<i>Poa subcoerulea</i>	3																		
<i>Puccinellia maritima</i>	1,2,3	III	IV	V	I	IV	II	P	III	I		I	II	I	P	I	V	III	
<i>Atriplex prostrata</i>	1,2			IV	I	III	V		I	I		I	I	I	P	I	V		
<i>Spergularia marina</i>	1,2,3				I	I		P	I	I	I	I	I	I	P	I	V		II
<i>Puccinellia distans</i>	1,2,3							P							P		I		II
<i>Puccinellia fasciculata</i>	1																		
<i>Hordeum marinum</i>	1																		
<i>Juncus gerardi</i>	1,2,3				IV	I	I	P			III			II	P		I		III
<i>Festuca rubra</i>	1,2				I	I	V		I			I	I	I	P		I		III
<i>Armeria maritima</i>	2																		
<i>Carex extensa</i>	1													I	P				
<i>Carex serotina</i>	3																		
<i>Centaurium pulchellum</i>	1													I	P				
<i>Blysmus rufus</i>	1,3																		
<i>Seriphidium maritimum</i>	1,2						II									I	I		
<i>Elytrigia atherica</i>	1,2			I		II	V		I	I		I	I	I		I			
<i>Juncus maritimus</i>	1,2,3																		
<i>Oenanthe lachenalii</i>	1,2,3																		
<i>Samolus valerandi</i>	3							P											
<i>Potentilla anserina</i>	1,2,3					I	II				I	I		II	P		V		III
<i>Agrostis stolonifera</i>	1,2,3				V	IV	III		I	IV	III		II	P	I	V		V	
<i>Elytrigia repens</i>	2,3				I				I		II	I				I			
<i>Leontodon autumnalis</i>	2																		
<i>Trifolium fragiferum</i>	1,3					I		P			III			I	P		I		II
<i>Carex distans</i>	1,3													I	P				
<i>Ononis repens spinosa</i>	1																		
<i>Lotus corniculatus</i>	1															I			
<i>Trifolium repens</i>	1,2				I	I						I		I	P		I		IV
<i>Sagina maritima</i>	1																		
<i>Plantago coronopus</i>	1													I					
<i>Cochlearia danica</i>	1																		
<i>Festuca arundinacea</i>	1					II									P				I
<i>Bulboschoenus maritimus</i>	1,2,3				III	IV		P			I			I	P		I		
<i>Schoenoplectus tabernaemonti</i>	1,2,3							P						I	P				
<i>Phragmites australis</i>	3										II								
<i>Triglochin palustris</i>	3							P											
<i>Eleocharis uniglumis</i>	3							P											
<i>Juncus articulatus</i>	3										III								
<i>Sarcocornia perennis</i>	2								I	I			I						
<i>Inula crithmoides</i>	2																		
<i>Suaeda vera</i>	2							I											
<i>Limonium binervosum</i>	2																		
<i>Frankenia laevis</i>	2																		
<i>Limonium bellidifolium</i>	2																		
Total	39,34,27	7	7	10	15	19	14	14	15	11	13	11	12	25	23	11	21	6	10
Saturation index	100	21	21	26	44	49	36	52	44	32	48	32	35	64	59	32	54	18	26
Reference:		2	2	3	5	4	6	7	8	10	9	16	11	12	13	14	15	16	17

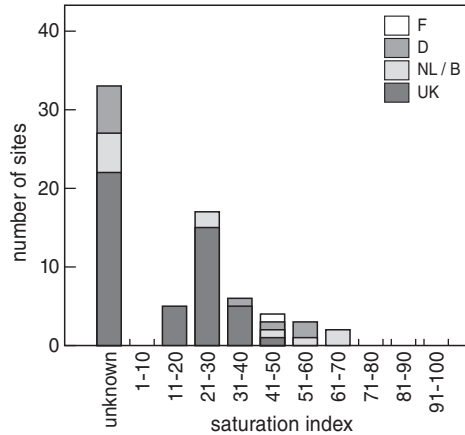


Figure 3.5. Frequency distribution of saturation indices for 70 de-embankment sites.

ma, which were encountered in more than 80% of the sites (Fig. 3.6). These species often occurred in more than 61% of the plots in a particular restoration site and are characteristic of pioneer and low-marsh communities.

Factors affecting restoration success

Surface elevation

In salt-marsh systems, elevation in relation to tidal inundation is generally accepted as the major abiotic factor governing the establishment and survival of halophytes at different zones within the range from mean high water neap (MHWN) to mean high water spring (MHWS) tide levels. In the present study we have examined the relationship between elevational range and restoration success by expressing the difference between maximum and minimum elevation recorded within a site as a percentage within the range from MHWN to MHWS. The results show that the elevational range is positively related to the saturation index ($R^2 = 0.37$, $P < 0.01$) (Fig. 3.7, UK sites only, MHWN and MHWS tide levels from Pye & French (1993)). Remarkably, many sites occupy less than 50% of the elevational range from MHWN to MHWS tide levels, hence these sites do not have the full restoration potential. Elevation has also been identified as the primary factor controlling species composition in restored salt marshes in the USA. Thom *et al.* (2002) for example, observed that their study site had subsided approximately one metre during the 70 years of embankment. As a result, restoration resulted in a different species composition than was anticipated from historical and nearby references. Other studies reveal that the rate at which vegetation develops in de-embanked sites is determined by the initial elevation (Cornu & Sadru 2002; Williams & Orr 2002) or that sites lower than 1.5 m below high water spring

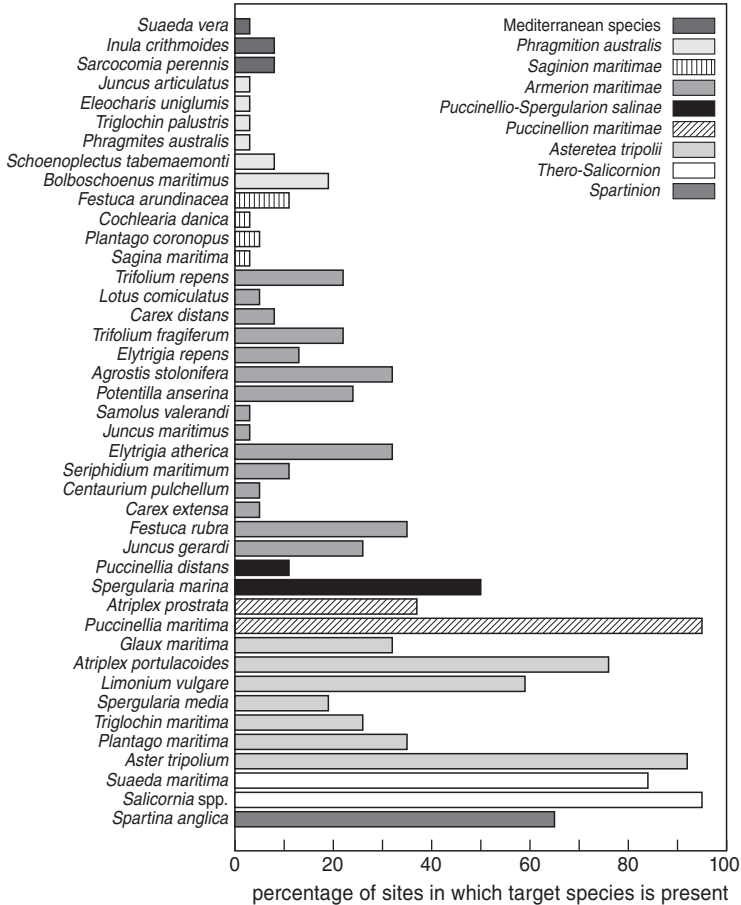


Figure 3.6. Percentage of sites in which a target species occurs ($n = 37$). Species are arranged by their syntaxonomical class (Schaminée *et al.* 1998).

tides will fail to colonise with salt-marsh vegetation (Pethick 2002). However, initially low elevation in itself may not be a problem if sedimentation rates are high enough. Data on sedimentation rates were available for 26 sites in our review. Because the techniques used for measuring sedimentation in these sites do not differentiate between net accretion and the effect of soil shrinkage and compaction, it is more appropriate to speak of surface elevation change, defined as the change in elevation relative to a sub-surface datum (Cahoon *et al.* 1995). Surface elevation change decreases linearly with the age of the restoration sites ($R^2 = 0.55$, $P < 0.0001$) (Fig. 3.8). Sites for which the technique used to measure surface elevation change could not be determined (Hauener Hooge, Nr. 66 and Sieperdachor, Nr. 61) were not included in the analysis. Blackshore Mill (Nr. 6) and Bulcamp Marsh (Nr. 11) were also excluded from the analysis as sedimentation-erosion measurements were taken

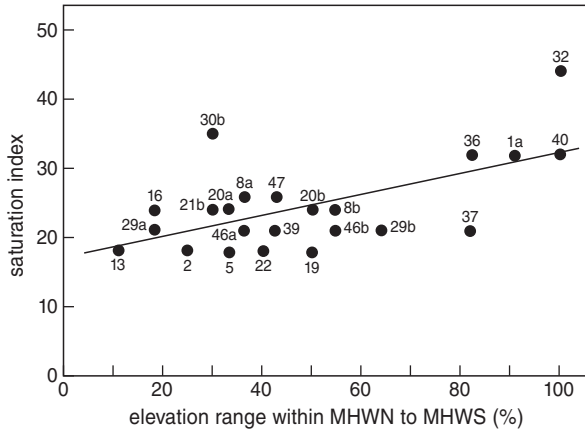


Figure 3.7. Relationship between saturation index and percentage elevational range falling within mean high water neap (MHWN) to mean high water spring (MHWS) tide levels ($n = 24$, $P < 0.01$, $R^2 = 0.37$).

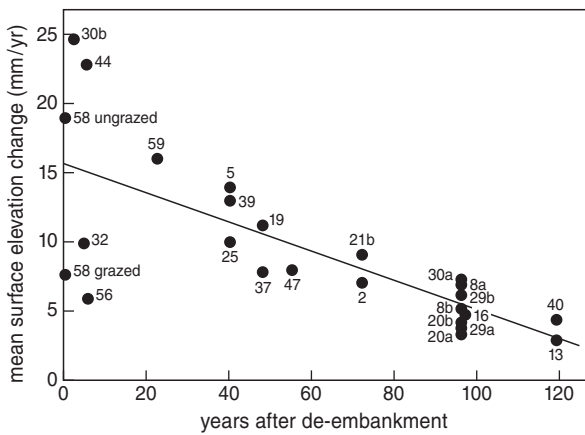


Figure 3.8. Relationship between surface elevation change and restoration time ($n = 26$, $P < 0.0001$, $R^2 = 0.55$).

recently, whereas the sites were 53 and 45 years old respectively. The results suggest that the elevation of the sites, which are likely to have subsided considerably during the period of embankment due to soil shrinkage and a lack of fresh sediment input, can increase rapidly during the first years after de-embankment. Over time, when pre-reclamation levels or levels similar to existing marshes and suitable for vegetation establishment are gained, the rate of surface elevation change is likely to decrease. Morgan & Short (2002) also observed a higher amount of deposited sediment in the younger sites compared to older ones, in a comparison of six salt-marsh restoration

sites in New Hampshire, and the same observation at 15 re-flooded sites in San Francisco Bay formed the bases for a conceptual model of salt-marsh plain evolution with time since breaching (Williams & Orr 2002). The decrease in sedimentation rates over time after de-embankment may be explained by the fact that once the substrate has become high enough for vegetation to colonise, accretion rates will decline due to less frequent flooding (Brown *et al.* 1999; Bakker *et al.* 2002) and because much sediment is trapped by vegetation and is therefore unavailable for the interior marsh (Adam 1990; Schröder *et al.* 2002). *Puccinellia maritima*, has been identified as a key species in the process of trapping and stabilising sediment on European marshes (Andresen *et al.* 1990; Langlois *et al.* 2003).

For the sustainability of re-created and established salt marshes it is required that rates of surface elevation change are at least equal to local rates of relative sea-level rise (Reed *et al.* 1999). For 25 sites in the present study, surface elevation change is higher than relative sea-level rise, which is in the order of 1.0 to 3.0 mm yr⁻¹ (Pye & French 1993; van Duin *et al.* 1997). At Canvey point, (Nr. 13), rates of surface elevation change are lower than the rate of relative sea-level rise.

Size of restoration sites

It has been established that, for a variety of organisms and habitats, a linear relationship exists between the number of species and the size of the area (plotted on a log scale) (Begon *et al.* 1996). Therefore, the size of restoration sites may be an important determinant of success in restoration sites. Indeed, a significant relationship ($P < 0.01$) between the percentage of regional target species and size of the restoration area is observed for our study sites (Fig. 3.9), although the regression coefficient is low ($R^2 = 0.25$). The data in Fig. 3.9 suggest that restoration sites should be at least 30 ha in order to be able to harbour 50% or more of the target species. The best results are found for sites larger than 100 ha. It should be noted however, that the width of a site (i.e. the line perpendicular to the coastline) is likely to be more important than the length (i.e. the line parallel to the coastline), due to zonal processes leading to higher species diversity.

Soil salinity

Soil salinity is an important factor affecting the composition of salt-marsh vegetation. High salinities for example may prevent germination and seedling establishment (De Jonge & De Jong 2002), whereas low salinities allow glycophytes to outcompete halophytes (Adam 1990; Zedler & Callaway 2001). Monitoring of soil salinity during salt-marsh restoration will thus be helpful for the evaluation of success. However, in this review only three sites were found to have measurements on soil salinity. At one of these sites (Noord Friesland Buitendijk Nr. 58), soil salinity of the de-embanked polder was compared to that of the fronting upper marsh. Results show that prior to breaching the summerdike, salinity levels in the summerpolder were at most 20% of those of the established marsh, whereas one year after the breach they had risen to

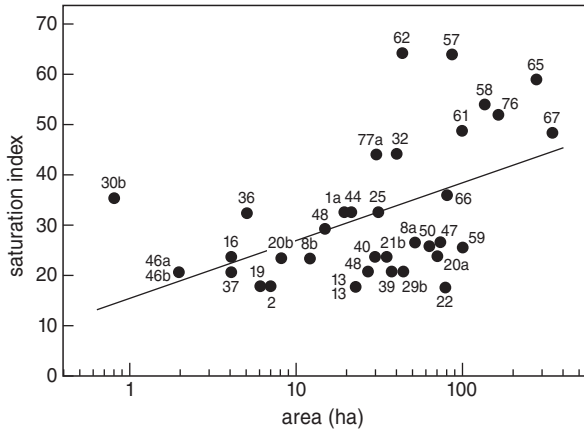


Figure 3.9. Relationship between saturation index and size of restoration sites ($n = 37$, $P < 0.01$, $R^2 = 0.25$).

70%. Much lower levels were found at Berensch (Nr. 65) where soils had a 6-15‰ salinity, which was ascribed to restricted tidal flooding (Främbs *et al.* 2000). Together with temperature and rainfall, salinity of the incoming water will be a major determinant of soil salinity in de-embanked sites. In the Baltic sea for example, salinities of open water are between 5 and 10‰ (Dijkema 1990). In this region, a 5-13‰ soil salinity was reported for the restoration site Ziesetal (Nr. 76).

Accessibility

A prerequisite for the successful restoration of salt-marsh communities is the availability of a target species source and the ability of the species to reach the target area. The best results may be expected when the target species are still present in the community species pool of the target area, which consists of the established vegetation and the soil seed bank (Zobel 1997; Zobel *et al.* 1998). The contribution of the latter however, quickly declines with time after embankment, as many salt-marsh species do not build up a long-term persistent seed bank (Thompson *et al.* 1997; Wolters & Bakker 2002; **Chapter 4**). Unfortunately, the community species pool before de-embankment has rarely been assessed. In fact, only one site (Noord Friesland Buitendijks, site Nr. 58) in this review has quantitative information on both the established vegetation and the soil seed bank before de-embankment (Bakker *et al.* 2001; van Duin *et al.* 2003). This study shows that 49% of the species of the regional pool were already present in the community species pool before de-embankment, mainly as a result of high tides flooding over the low summerdike during storms in winter. Not surprisingly therefore, restoration of this site is proceeding rapidly with 54% of the target species establishing in the vegetation within one year after de-embankment (Table 3.2). However, in cases where embankments have functioned as the main sea defence fronting the restoration site, it is reasonable to assume that target species will

be absent from the community species pool. Their natural establishment will therefore depend on dispersal from other areas, i.e. the local or regional species pool. It is generally assumed that the distance between the target area and a target species source will largely determine the chance of a species arriving in the target area. Thus, better results may be expected when an established salt marsh (i.e. local species pool) is directly adjacent to a de-embanked site. Indeed, a comparison between the presence of target species in the target area with the local pool, taking into account only species of the regional target list, shows that the composition of restoration sites and adjacent marshes closely resemble each other even within a short period of time (< 5 years) (Table 3.2). An exception is polder Breebaart, (Site Nr. 50) where only 48% of the target species present in the local pool have established in the site within one year. This might be explained by the fact that the only opening through which tidal water can enter the site is a 1 m by 2 m wide sluice, which may form a barrier to successful seed dispersal. In some situations, the presence or absence of a local source of target species does not seem to be the main factor governing the establishment of a species in the target area. A comparison between Tollesbury (adjacent to established marsh) and Saltram (nearest marsh > 16 kilometres away) for example, shows that 26 and 32% of the target species have established in the site four years after de-embankment, respectively (Reading *et al.* 2002). On the other hand, Onaindia *et al.* (2001) concluded that 20 and 35 years after the collapse of a seawall, species diversity of two restoration sites was still low compared to a reference marsh (17 and 16 species versus 36 respectively), and suggested this may be due to the large distance (80 km) between the nearest established marsh and the restoration sites. Nevertheless, a few restoration sites harbour more target species than the local source, hence these species will have travelled over longer distances.

Table 3.2. Number of target species in regional (R), local (L) and community (C) species pool, number of species shared between local and community species pool and percentage of target species (community vs regional, local vs regional and community vs local) for six sites in different regions.

Site number & name	t (yrs)	R	L	C	Shared C,L	C/R (%)	L/R (%)	C/L (%)	Ref.
61. Sieperdaschor	13	39	21	19	18	49	54	90	1
44. Tollesbury	6	34	10	11	8	32	29	110	2
67. Karrendorfer Wiesen	5	27	18	13	13	48	67	72	3; 4
57. Kroons polders	3	39	26	25	20	64	67	96	5
58. Noord Friesland Buitendijks	1	39	20	21	18	54	51	105	6; 7
50. Breebaart	1	39	21	10	8	26	54	48	8; 9

R = regional pool, L = local pool, C = community pool

References: 1. Koppejan (2000); 2. Reading *et al.* (2002); 3. Bernhardt and Koch (2003); 4. Zimmermann (2001); 5. van Gennip & Knotters (2002); 6. van Duin *et al.* (2003); 7. Hommel & Horsthuis (2002); 8. www.Groningerlandschap.nl/dollard/breebaartprojectvegetatie.htm; 9. Vreeken-Buijs (2002).

Management options

The management policy for most restoration sites is to abandon all human intervention after de-embankment and leave the site to develop naturally. However, it is questionable whether this policy would result in the most successful restoration, i.e. in this case highest number of target species.

Construction and maintenance of drainage structures

At the start of the restoration, artificial creeks may be required to improve drainage and increase colonisation rates (Eertman *et al.* 2002). Creeks will be especially important in sites where embankment has resulted in an over-consolidated soil surface acting as an aquaclude that impedes subsurface drainage (Crooks *et al.* 2002). Moreover, creeks may assist in supplying sediment to the salt-marsh surface (Reed *et al.* 1999) and differential sediment deposition patterns related to distance from creeks may positively influence (plant) species richness and distribution (Zedler & Callaway, 2001). In artificially drained sedimentation fields for example, plant growth may start 20 cm lower in elevation than on natural island marshes (Bakker *et al.* 2002). In some restoration sites therefore, meandering creeks are dug deliberately to enhance colonisation rates. In the Sieperdaschor (Nr. 61), a new creek, which was dug five years after de-embankment, resulted in enhanced tidal intrusion to the site's interior, coupled with higher sedimentation rates and more rapid colonisation of bare mud (Eertman *et al.* 2002). In order to accommodate the high tidal amplitude, this creek started to meander spontaneously. In most de-embanked sites, however, drainage occurs predominantly through existing ditches (Appendix 3.2) and a dendritic creek network as found on many natural marshes may never develop (Verbeek & Storm, 2001), especially when the initial elevation of the site is high. Williams & Orr (2002), for example, concluded that on sites that were raised to mature marsh level prior to de-embankment, tidal drainage channels had not developed after 24-29 years. In contrast, dendritic channel systems developed spontaneously on subsided sites during the build up of intertidal mudflat (Williams & Orr, 2002). Another factor affecting creek development is the composition of the soil subsurface. In south-east England for example, low quantities of calcium carbonate in the soil in combination with the transition from marine to fresh water hydrology, have resulted in the formation of an aquaclude (i.e. a layer of over-consolidated material acting as a barrier to water movement) (Crooks *et al.* 2002). In such cases, the construction of artificial creeks may be required to enhance restoration success. Apart from the role of creeks, drainage is also affected by the size of the opening in the embankment. Boumans *et al.* (2002) for example reported enhanced salt-marsh vegetation development when culverts were enlarged by c.a. one metre in diameter. Lowering of the elevation at which the culverts were placed did not increase success.

Grazing or mowing regimes

Management may also be required to prevent successional processes from reducing species diversity over time. A comparison between restoration time and saturation index for 37 study sites showed that with the exception of a 197 year old site, the highest saturation index was observed for the youngest sites, with a rapid decrease setting in after 15 years of restoration (Fig. 3.10). Highest species richness also occurred at around 15 years of restoration time in a comparison of six constructed restoration sites in New Hampshire (USA) (Morgan & Short, 2002). On the basis of their trajectory model, these authors suggest that the level of species diversity will be maintained over time. However, long-term experiments on barrier island and mainland marshes in Germany and the Netherlands, show that successional processes are likely to result in the dominance of a single or few tall growing species, such as *Atriplex portulacoides* at the low marsh and *Elytrigia atherica* at the high marsh (Andresen *et al.* 1990; Bos *et al.* 2002; Schröder *et al.* 2002; Bakker *et al.* 2003). Under brackish conditions, *Elytrigia repens* and *Phragmites australis* will expand if successional processes are not restrained (Dijkema 1990; Esselink *et al.* 2000; Esselink *et al.* 2002). The dominance of these tall species results in the suppression or disappearance of species of shorter stature and loss of diversity. Species diversity may be maintained over time by the implementation of a grazing or mowing regime. In nine restoration sites grazing or mowing regimes have been implemented (seven of which have data on plant species abundances), and the effect of grazing has been studied in two of these. Results of one of these studies (Sieperdaschor, Nr. 61) show that nine years after de-embankment, the number of target species in lightly grazed plots is higher than in ungrazed plots (Bakker *et al.* 2002). At the cessation of grazing, the percentage cover of *Elytrigia atherica* and *Bolboschoenus maritimus* rapidly increased

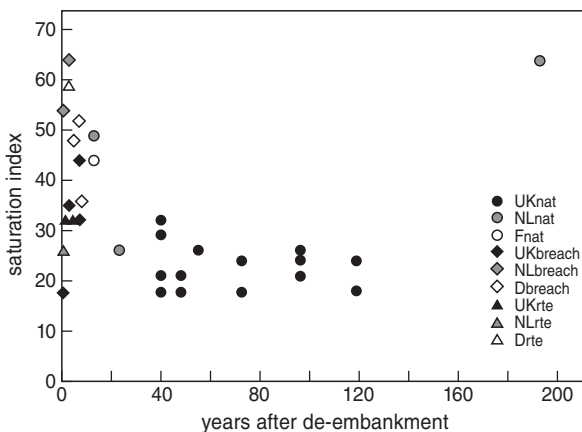


Figure 3.10. Relationship between saturation index and restoration time. Nat, natural de-embankments; Breach, deliberate partial or complete removal of seawall; RTE, regulated tidal exchange by means of sluices or pipes.

(Bakker *et al.* 2002) and in recent years, *Phragmites australis* has expanded rapidly in the ungrazed areas of this site (Eertman *et al.* 2002). *Elytrigia atherica* was also the dominant species in the ungrazed site Peazemerlannen (Nr. 59), 25 years after de-embankment (Bakker *et al.* 2002). According to Scherfose (1993), salt-marsh species that are likely to benefit from grazing are those with short-time strategies (i.e. annuals or biennials, low growing, early flowering, without storage organs and with stolons, rosettes or creeping shoots). This might then explain why some target species are rarely present in the restoration sites (Fig. 3.6), as the majority of sites are ungrazed. In fact, the only seven sites that have a grazing or mowing regime are also the top seven most successful sites on the bases of the saturation index.

Apart from the effect on the vegetation, grazing may also affect soil salinity and surface elevation change. This has been studied in one of the restoration sites (Noord Friesland Buitendijks, Nr. 58), where grazing resulted in up to two times higher soil salinity and a 40% lower rate of surface elevation change (van Duin *et al.* 2003). A negative influence of grazing on sedimentation rates was also reported by Andresen *et al.* (1990) and is most likely the result of reduced sward height and density of tillers (Esselink *et al.* 1998). Short turf with relatively high evapotranspiration was also suggested as the main cause for increased soil salinities in grazed plots (Bakker 1985).

Recommendations for future restoration schemes

A major challenge in the restoration of salt marshes is to identify which factors are important in salt-marsh development. Past and future de-embankment schemes can contribute to this understanding, provided that key parameters and processes are being monitored. Paramount in future restoration cases is the need for clear targets in order to be able to evaluate restoration success. A possibility presented in this review is to identify target plant species from a regional species pool and to use species diversity within this restricted set of species to assess success. It should be realised however, that the presence of a species does provide information as to whether a salt-marsh community has formed. Therefore, collecting data on plant species abundance, preferably recorded in standard 2 m × 2 m permanent quadrats will be the next important step. In addition, species abundance should be recorded in transects covering the entire range from high to low elevation to allow the mapping of vegetation communities and their spatial distribution. Monitoring will not only allow the evaluation of success but also provide important feedback based on which management of the site can be adapted if necessary. A management option that most likely influences success is the construction of creeks to enhance tidal flooding of interior parts, increase sedimentation rates, improve drainage and enhance plant colonisation rates, species diversity and distribution ranges. Another option is the implementation of a grazing or mowing regime in order to create heterogeneity in the soil and vegetation and prevent dominance of a single species. A prerequisite for this type of management

is that the sites are high enough for the establishment of vegetation communities suitable for grazing or mowing regimes. Experiments can be designed to test the effect of different management strategies or to study specific factors involved in salt-marsh development (e.g. seed dispersal, algae/invertebrate/plant relationships, nutrient availability etc.).

Summary

De-embankment of historically reclaimed salt marshes has become a widespread option for re-creating salt marshes, but to date little information exists on the success of de-embankments. One reason is the absence of pre-defined targets, impeding the measurement of success. In this Chapter, success has been measured as a saturation index, where the presence of target plant species in a restoration site is expressed as a percentage of a regional target species pool. This study is intended to evaluate and compare success of many different sites on an idealistic concept where all regional target species have the potential to establish in a site, but may not actually do so because the site is unsuitable or inaccessible. Factors affecting suitability and accessibility and management options to increase regional species diversity are discussed. The results show that many sites contain less than 50% of the regional target species, especially when sites are smaller than 30 ha. Higher species diversity is observed for sites exceeding 100 ha and for sites with the largest elevational range within mean high water neap to mean high water spring tide. Most sites younger than 20 years contain more target species than older sites. For future de-embankments it is recommended that clear targets are set from the start. This brings along the need for monitoring. Only 37 out of 70 sites with de-embankment were monitored for plant species assemblages. Setting targets will also allow adaptive management of the site. Management options that are likely to result in higher species diversity are the construction and maintenance of drainage structures and the implementation of a grazing or mowing regime.

Acknowledgements

We are sincerely grateful to everyone who provided us with information on the restoration sites. In particular: Erwin Adema, Sabine Arens, Armel Dausse, Jaap Graveland, Willem van Duin, Peter Esselink, Anja van Hetinga, Dick de Jong, Cora de Leeuw, Aante Nicolai, Hanz Niemeyer and Stefan Seiberling. In addition we thank the participants and organisers of the Coastal Ecology workshops 2002 and 2004 and the Coastal Ecology Expedition 2003 for useful discussions, field visits and assistance with composing species lists of the vegetation.

References

- Adam, P. (1990) *Salt marsh ecology*. Cambridge University Press, Cambridge.
- Andresen, H., Bakker, J. P., Brongers, M., Heydeman, B. & Irmiler, U. (1990) Long-term changes of salt marsh communities by cattle grazing. *Vegetatio*, **89**, 137-148.
- Bakker, J. P. (1985) The impact of grazing on plant communities, plant populations and soil conditions on salt marshes. *Vegetatio*, **62**, 391-398.
- Bakker, J. P., Bos, D. & de Vries, Y. (2003) To graze or not to graze: that is the question. *Challenges to the Wadden Sea, Proceedings of the 10th international scientific Wadden Sea symposium* (eds. W.J. Wolff, K. Essink, A. Kellerman & M.A. van Leeuwen), pp. 67-88. Groningen.
- Bakker, J. P., Esselink, P., Dijkema, K. S., van Duin, W. E. & De Jong, D. J. (2002) Restoration of salt marshes in the Netherlands. *Hydrobiologia*, **478**, 29-51.
- Bakker, J. P., Esselink, P., van der Wal, R. & Dijkema, K. S. (1997) *Options for restoration and management of coastal salt marshes in Europe. Restoration Ecology and Sustainable development* (eds. K. M. Urbanska, N. R. Webb & P. J. Edwards), pp. 286-322. Cambridge University Press, Cambridge.
- Bakker, J. P., van den Brink, G., Verwey, G. L. & Esselink, P. (2001) Zaadvoorraad en dispersie bij een proefverkweldering in Noard-Fryslân Bûtendyks. *De Levende Natuur*, **102**, 19-23.
- Begon, M., Harper, J. L. & Townsend, C. R. (1996) *Ecology*, 3rd edn. Blackwell Science, Oxford.
- Bernhardt, K.-G. & Koch, M. (2003) Restoration of a salt marsh system: temporal change of plant species diversity and composition. *Basic and Applied Ecology*, **4**, 441-451.
- Bos, D., Bakker, J. P., de Vries, Y. & van Lieshout, S. (2002) Long-term vegetation changes in experimentally grazed and ungrazed back-barrier marshes in the Wadden Sea. *Applied Vegetation Science*, **5**, 45-54.
- Boumans, R. M. J., Burdick, D. M. & Dionne M. (2002) Modelling habitat change in salt marshes after tidal restoration. *Restoration Ecology*, **10**, 543-555.
- Brown, S. L., Warman, E. A., McGrorty, S., Yates, M., Pakeman, R. J., Boorman, L. A., Goss-Custard, D. & Gray, A. J. (1999) Sediment fluxes in intertidal biotopes:BIOTA II. *Marine Pollution Bulletin*, **37**, 173-181.
- Burd, F., Clifton, J. & Murphy, B. (1994) *Sites of historical sea defence failure*. Phase II study. Report nr. ZO38-94-F. Institute of Estuarine and Coastal Studies, Hull.
- Cahoon, D. R., Reed, D. J. & Day, J. W. Jr. (1995) Estimating shallow subsidence in microtidal salt marshes of the southeastern United States: Kaye and Barghoorn revisited. *Marine Geology*, **128**, 1-9.
- Cooper, N.J., Cooper, T. & Burd, F. (2001) 25 years of salt marsh erosion in Essex: Implications for coastal defence and nature conservation. *Journal of Coastal Conservation*, **9**, 31-40.
- Cornu, C.E. & Sadro, S. (2002) Physical and functional responses to experimental marsh surface elevation manipulation in Coos Bay's South Slough. *Restoration Ecology*, **10**, 474-486.
- Crooks, S., Schutten, J., Sheern, G. D., Pye, K. & Davy, A. J. (2002) Drainage and elevation as factors in the restoration of salt marsh in Britain. *Restoration Ecology*, **10**, 591-602.
- Dagley, J. R. (1995) *Northey Island: managed retreat scheme. Results of botanical monitoring 1991 to 1994*. Report nr. 128, English Nature, Colchester.
- De Jonge, V. N. & De Jong, D. J. (2002) Ecological restoration in coastal areas in the Netherlands: concepts, dilemmas and some examples. *Hydrobiologia*, **478**, 7-28.
- Diack, I. (1998) *Botanical monitoring of the salt marsh option of the habitat scheme 1995-1997*. ADAS, Oxford.
- Dijkema, K. S. (1987) Changes in salt-marsh area in the Netherlands Wadden Sea after 1600. *Vegetation between land and sea* (eds. A. H. L. Huiskes, C. W. P. M. Blom & J. Rozema), pp. 42-49. Dr. Junk Publishers, Dordrecht.
- Dijkema, K. S. (1990) Salt and brackish marshes around the Baltic sea and adjacent parts of the North sea: their vegetation and management. *Biological Conservation*, **51**, 191-209.
- Dijkema, K. S., Beefink, W. G., Doody, J. P., Gehu, J. M., Heydeman, B. & Rivas Martinez, S. (1984) *Salt marshes in Europe*, Council of Europe, Strasbourg.
- Dijkema, K. S. & Wolff, W. J. (1983) *Flora and vegetation of the Wadden Sea islands and coastal areas*. Wadden Sea Working Group, Leiden.

- Edwards, K.R. & Proffitt, C.E. (2003) Comparison of wetland structural characteristics between created and natural salt marshes in southwest Louisiana, USA. *Wetlands*, **23**, 344-356.
- Eertman, R. H. M., Kornman, B. A., Stikvoort, E. & Verbeek, H. (2002) Restoration of the Sieperda tidal marsh in the Scheldt estuary, the Netherlands. *Restoration Ecology*, **10**, 438-449.
- Esselink, P., Dijkema, K. S., Reents, S. & Hageman, G. (1998) Vertical accretion and profile change in abandoned man-made tidal marshes in the Dollard estuary, The Netherlands. *Journal of Coastal Research*, **14**, 570-582.
- Esselink, P., Fresco, L. F. M. & Dijkema, K. S. (2002a) Vegetation change in a man-made salt marsh affected by a reduction in both grazing and drainage. *Applied Vegetation Science*, **5**, 17-32.
- Esselink, P., Zijlstra, W., Dijkema, K. S. & van Diggelen, R. (2000) The effects of decreased management on plant-species distribution patterns in a salt marsh nature reserve in the Wadden Sea. *Biological Conservation*, **93**, 61-76.
- Främbs, H., Kinder, M., Hielen, B., Böhme, B., Günther, C.-P., Rachor, E., Cordes, H. & Mossa-kowski, D. (2000) Renaturierung salzbeeinflusster Lebensräume der Nordseeküste. *Abschlussbericht zum Salzwiesenprojekt "Wuster Küste" (1991-1999)*. Universität Bremen, Bremen.
- French, P. W. (1999) Managed retreat: a natural analogue from the Medway estuary, UK. *Ocean & Coastal Management*, **42**, 49-62.
- Hommel, P. W. F. M. & Horsthuis, M. A. P. (2002) *Excursieverslagen 1999. Het Noorderleech*. Plantensociologische kring Nederland.
- Kentula, M. E. (2000) Perspectives on setting success criteria for wetland restoration. *Ecological Engineering*, **15**, 199-209.
- King, S. E. & Lester, J. N. (1995). Pollution Economics. The value of salt marshes as a sea defence. *Marine Pollution Bulletin*, **30**, 180-189.
- Koppejan, H. (2000) *Toelichting bij de vegetatiekartering Westerschelde 1998. Op basis van false colour-luchtfoto's 1:5000/10000*. Report nr. MDGAE-2000.11., RIKZ, Den Haag.
- Krisch, H. (1990) Ökologisch-soziologische Artengruppen und Pflanzengesellschaften im Geolitoral der Boddenküste (Ostsee). *Phytocoenologia*, **19**, 1-28.
- Lamberth, C. & Haycock, N. (2001) *Regulated tidal exchange. Phase II report. Case studies and guidelines for the assessment of sites capable of supporting a saline wetland creation project using regulated tidal exchange techniques*, Haycock associates Ltd., St. Albans.
- Langlois, E., Bonis, A. & Bouzille, J. B. (2003) Sediment plant dynamics in the salt marsh pioneer zone: *Puccinellia maritima* as a key species? *Estuarine, Coastal and Shelf Science*, **56**, 239-249.
- Morgan, P. A. & Short, F. T. (2002) Using functional trajectories to track constructed salt marsh development in the Great Bay Estuary, Maine/New Hampshire, USA. *Restoration Ecology*, **10**, 461-473.
- Möller, I., Spencer, T. & French, J. (1996) Wind wave attenuation over saltmarsh surfaces: preliminary results from Norfolk, England. *Journal of Coastal Research*, **12**, 1009-1016.
- Onaindia, M., Albizu, I. & Amezcaga, I. (2001) Effect of time on the natural regeneration of salt marsh. *Applied Vegetation Science*, **4**, 247-256.
- Pethick, J. 2002. Estuarine and tidal wetland restoration in the United Kingdom: policy versus practice. *Restoration Ecology*, **10**, 431-437.
- Pye, K. & French, P. W. (1993) Erosion and accretion on British salt marshes. *Database of British saltmarshes*. Report nr. ES19B(2), Cambridge Environmental Research Consultants Ltd., London.
- Reading, C. J., Gray, A. J., Paramor, O. A. L., Garbutt, R. A., Watts, C. W., Spearman, J. R., Barratt, D. R., Chesher, T., Cox, R., Hughes, R. G., Mann, J. L., Myhill, D. G., Rothery, P., Semmence, J. & Wolters, M. (2002) *Managed realignment at Tollesbury and Saltram*. Final report. Report nr. CSA2313. Centre for Ecology and Hydrology, Dorchester.
- Reed, D. J., Spencer, T., Murray, A. L., French, J. R. & Lynn, L. (1999) Marsh surface sediment deposition and the role of tidal creeks: Implications for created and managed coastal marshes. *Journal of Coastal Conservation*, **5**, 81-90.
- Rodwell, J. S. (2000) *British plant communities. Maritime communities and vegetation of open habitats*, Cambridge University Press, Cambridge.
- Schaminée, J. H. J., Weeda, E. J. & Westhoff, V. (1998) *De vegetatie van Nederland. Deel 4. Plantengemeenschappen van de kust en binnenlandse pioniermilieus*. Opulus Press, Uppsala.

- Scherfose, V. (1993) Zum Einfluß der Beweidung auf das Gefäßpflanzen-Artengefüge von Salz- und Brackmarschen. *Zeitschrift für Ökologie und Naturschutz*, **2**, 201-211.
- Schröder, H. K., Kiehl, K. & Stock, M. (2002) Directional and non-directional vegetation changes in a temperate salt marsh in relation to biotic and abiotic factors. *Applied Vegetation Science*, **5**, 33-44.
- Thom, R. M. (2000) Adaptive management of coastal ecosystem restoration projects. *Ecological Engineering*, **15**, 365-372.
- Thom, R. M., Zeigler, R. & Borde, A. B. (2002) Floristic development patterns in a restored Elk River Estuarine marsh, Grays Harbor, Washington. *Restoration Ecology*, **10**, 487-496.
- Thompson, K., Bakker, J. P. & Bekker, R. M. (1997). *Soil seed banks of North West Europe: methodology, density and longevity*. Cambridge University Press, Cambridge.
- van der Wal, R., van Lieshout, S. Bos, D. & Drent, R.H. (2000) Are spring staging Brent geese evicted by vegetation succession? *Ecography*, **23**, 60-69.
- van Dort, K. W. & Leusink, L. (1998) *Toelichting bij de vegetatiekartering Het Zwin en de Verdrongen Zwarte Polder 1995 op basis van false-colour luchtfoto's 1:5000*. Report nr. MDGAE-9861. RIKZ Meetkundige Dienst, Delft.
- van Duin, W. E., Dijkema, K. S. & Zegers, J. (1997) *Veranderingen in bodemhoogte (opslibbing, erosie en inklink) in de Peazemerlanden*. IBN Report nr. 326, Wageningen.
- van Duin, W. E., Esselink, P., Verweij, G. & Engelmoer, M. (2003) *Monitoringsonderzoek proefverkweldering Noard Fryslân Bûtendyks. Tussenrapportage 2001-2002*. Alterra, Den Burg.
- van Gennip, B. & Knotters, A. G. (2002) *Toelichting bij de vegetatiekartering Kroon's Polders en Westerveld 1999. Op basis van false colour-luchtfoto's 1:5000*. Report nr. MDGAE-2002.35. RIKZ, Den Haag.
- Verbeek, H. & Storm, H. (2001) Tidal wetland restoration in the Netherlands. *Journal of Coastal Research*, **SI 27**, 192-202.
- Vreeken-Buijs, M. J. (2002) *Toelichting bij de vegetatiekartering Dollard en Punt van Reide 1999. Op basis van false colour-luchtfoto's 1:10000*. Report nr. MD-GAE-2002.9. RIKZ, Den Haag.
- Williams, P. B. & Orr, M. K. (2002) Physical evolution of restored breached levee salt marshes in the San Francisco Bay estuary. *Restoration Ecology*, **10**, 527-542.
- Wolters, M. & Bakker, J. P. (2002). Soil seed bank and driftline composition along a successional gradient on a temperate salt marsh. *Applied Vegetation Science*, **5**, 55-62.
- Zander, B. (2002) Vegetation dynamics in coastal grasslands at the 'Greifswalder Bodden' (Baltic Sea) after removing the dyke and reintroduction of flooding. *Salt grasslands and coastal meadows in the Baltic region, Conference proceedings* (eds. T. Frock, K. Hergarden & D. Repasi) pp. 155-166. Neubrandenburg.
- Zedler, J.B. & Callaway, J.C. (1999) Tracking wetland restoration: do mitigation sites follow desired trajectories? *Restoration Ecology*, **7**, 69-73.
- Zedler, J. B. & Callaway, J. C. (2001) Tidal wetland functioning. *Journal of Coastal Research*, **SI27**, 38-64.
- Zedler, J. B. & Lindig-Cisneros, R. (2000) Functional equivalency of restored and natural salt marshes. *Concepts and controversies in tidal marsh ecology* (eds. M.P. Weisnstein & D.A. Kreeger) pp. 565-582. Kluwer, Dordrecht.
- Zimmermann, R. (2001) *Landschaftsökologisches Untersuchungen der Küsten-Überflutungsmooses Kooser Wiesen*. PhD thesis, Botanisches Institut, Ernst-Möritz-Arndt-Universität, Greifswald.
- Zobel, M. (1997) The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? *Trends in Ecology and Evolution*, **12**, 266-269.
- Zobel, M., van der Maarel, E. & Dupré, C. (1998) Species pool: the concept, its determination and significance for community restoration. *Applied Vegetation Science*, **1**, 55-66.

Appendix 3.1. Site number, name, location and sources of references. Bold sites have information on target species in vegetation ($n = 37$).

Site Nr	Site name	Location	Country	Type ⁱ	Area (ha)	Breach ⁱⁱ	Years embanked	Land use ⁱⁱⁱ	Main reason ^{iv}	Number, type and dimension (m) of breach (B), sluice (S) or pipe (P)	Drainage ^v	Elevation (m + sea level or ordnance datum) ^{vi}	Tidal range (m)	SFC (mm/yr) ^{vii}	Soil salinity	Management ^{viii}	References
1a	Abbots Hall A	Blackwater estuary	UK	R	20	1996		A	2	2 P; 0.46 & 0.30 dia	III	-0.5-1.0 MHWN	4.7				1; 2; 3; 4; 5; 6
1b	Abbots Hall B	Blackwater estuary	UK	B	115	2002		A	2	5 B			4.7				6
2	Aldboro Point	Colne estuary	UK	N	7	1921	25		1	6 B; 50	II	0.7-1.0 MHWN	4.5	7.22a			7; 8
3	Alkborough	Humber estuary	UK	B	400	2004			2	B			6.4				6
4	Barshore	Medway estuary	UK	N		1897	78		1	B							9
5	Barrow Hill	Colne estuary	UK	N	23	1953	154	P	1	3 B; 95	II,IV	0.8-1.4 MHWN	4.5	14 a			7; 8
6	Blackshore Mill	Blyth estuary	UK	N	<1	1953		A	1	B		-0.8 OD	2	13-16e			10
7	Brancaster West	North Norfolk	UK	B	7.5	1996		F	3	B			6.5				6; 11
8a	Brandy Hole A	Crouch estuary	UK	N	51	1897	123	A	1	2 B; 135	II	0.4-0.8 MHWN	5	6.88a			7; 8
8b	Brandy Hole B	Crouch estuary	UK	N	12	1897	123	A	1	2 B; 25	II	0.2-0.8 MHWN	5	5.21a			7; 8
9a	Bridgemarsh Island A	Crouch estuary	UK	N	29	1928	114		1	1 B; 45			5				7; 8
9b	Bridgemarsh Island B	Crouch estuary	UK	N	69	1928	114		1	3 B; 105			5				7; 8
9c	Bridgemarsh Island C	Crouch estuary	UK	N	51	1928	114		2	2 B; 155			5				7; 8
10	Brue Pill	Weston Bay, Somerset	UK	B		1990			2	B			11.6				6
11	Bulcamp Marsh	Blyth estuary	UK	N	100	1945	141	A	1	B	II	-0.6 OD	2	-10-6.5e			12
12	Burntwick	Medway estuary	UK	N	71.3	1897	27		1	B							9
13	Canvey Point	Thames estuary	UK	N	23	1874	34		1	entire; 1330	I	-0.5-0.1 MHWN	5.2	2.86a			7; 8
14	Canforth Marsh	Morecambe Bay	UK	R	51.2					5 S; 2 P			8.4				5
15	Chaldock Point	Chichester Harbour	UK	B		2000				B			4.4				4
16	Clementisgreen Creek	Crouch estuary	UK	N	4	1897	123	A	1	2 B; 45	II	0.4-0.6 MHWN	5	5.21a			7; 8
17	Copperhouse	Medway estuary	UK	N	1.9	1897	34		1	2 B							9
18	Cotehele	River Tamar, Cornwall	UK	B	15	2002	152	A	2	B			4.2				6
19	Ferry Lane	Colne estuary	UK	N	6	1945	105	A,P	1	3 B; 50	IV	0.8-1.4 MHWN	4.5	11.25a			7; 8
20a	Fingringhoe Marsh A	Colne estuary	UK	N	70	1897	57	P	1	4 B; 220	IV	0.8-1.2 MHWN	4.5	3.75a			7; 8
20b	Fingringhoe Marsh B	Colne estuary	UK	N	8	1897	98	A	1	3 B; 35	IV	0.6-1.3 MHWN	4.5	4.58a			7; 8
21a	Foulton Hall A	Hamford water	UK	N	66	1896	122	P	1	3 B; 125	II,III	0.6-0.8 MHWN	3.8	4.74a			7; 8
21b	Foulton Hall B	Hamford water	UK	N	34	1921	147	P	1	1 B; 15	II,III	0.6-1.0 MHWN	3.8	9.17a			7; 8
22	Freiston	The Wash	UK	B	78	2002	19	A	2	3 B	II,III	0.8-1.6 MHWN	6.4	47; 13			5
23	Gwent Levels	Bristol Channel N	UK	R	10.8					2 S; 1.05*1.05							5
24	Havergate Island	Deben estuary	UK	R	12	2000				1 S; 0.23			3.6				5; 4
25	Hemley	Deben estuary	UK	N	31	1953	155	P	1	1 B; 45			3.6	10a			3; 6
26a	Horsely Island A	Hamford water	UK	N	5	1953	179	F	1	entire; 605	I	-0.2-0.7 MHWN	3.8				7; 8
26b	Horsely Island B	Hamford water	UK	R				A	2,3	1 S/P			3.8				14; 3
27	Humber	Humber estuary	UK	B	1000	Plan		A ₁	2,3	various							48
28	Millfordhope	Medway estuary	UK	N		1908	10	A ₁	1	B							9

Appendix 3.1. Continued

Site Nr	Site name	Location	Country	Type ⁱ	Area (ha)	Breach ⁱⁱ	Years embanked	Land use ⁱⁱⁱ	Main reason ^{iv}	Number, type and dimension (m) of breach (B), sluice (S) or pipe (P)	Drainage ^v	Elevation (m + sea level or ordnance datum) ^{vi}	Tidal range (m)	SEC (mm/yr) ^{vii}	Soil salinity	Management ^{viii}	References
29a	North Farnbridge A	Crouch estuary	UK	N	27	1897	123	A	1	4 B; 155	II	0.4-0.6 MHWN	5	4.17 a			7; 8
29b	North Farnbridge B	Crouch estuary	UK	N	43	1897	123	A	1	2 B; 105	II	0.2-0.9 MHWN	5	6.25 a			7; 8
30a	Northey Island A	Blackwater estuary	UK	N	79	1897	123	A,P	1	6 B; 870	II,IV	-0.1-0.4 MHWN	4.8	7.08 a			7; 8
30b	Northey Island B	Blackwater estuary	UK	N	0.8	1991	118	A,F	3	1 B; 20	I	0.7-1.6 MHWN	4.8	24.8 b			15; 3; 14
31	Oakham	Medway estuary	UK	N	1897	78			1	B							9
32	Orplands	Blackwater estuary	UK	B	40	1995	175	A,F	2	2 B; 50 & 40	III	0.2-5 MHWN	4.7	10 e			16; 1; 2; 3; 14
33	Pawlett Hams	River Parret, Somerset	UK	B	4.8	1994			3	B		2.7-3.7 MHWN	11.1				14
34	Porlock Marsh	Somerset	UK	N	101	1996		A,P	1	B			11.1				17; 4
35	Ryans Field	Hayle, Cornwall	UK	R	6					S			5.8				5
36	Saltram	Hayle, Cornwall River Plym, Devon	UK	R	5	1995	145	P	2	1 B (to 2.4m); 13m, 5 P; 0.6m	I	-0.1-0.9 MHWN	4.7				18; 19; 1; 3
37	Sampson's Creek	Blackwater estuary	UK	N	4	1945	105		1	1 B; 20	IV	0.2-1.2 MHWN	4.7	7.92 a			7; 8
38	Seal Sands	Tees estuary	UK	R	9	1993	19	Po	2	1 P; 1.05	III		4.6				20; 4; 5
39	Skipper's Island	Hamford water	UK	N	37	1953	113	P	1	2 B; 70	I	0.5-1.5 MHWN	3.8	13 a			7; 8
40	Stone Marsh	Hamford water	UK	N	30	1874	34	P	1	1 B; 20	IV	0.2-0.6 MHWN	3.8	4.37 a			7; 8
41	Thorngumbald / Paul's Strays	Humber estuary	UK	B	70	2003		A,P	2,3	2 B			6.4				6
42	Thornham Bay	Chichester Harbour	UK	B	6.9	1996		W		B	III		4.4				14; 4
43	Titchwell	North Norfolk	UK	R	36					? P; 0.6			6.5				5
44	Tollesbury	Blackwater estuary	UK	B	21	1995	150	A	3	1 B; 50	I	-0.6-1.5 MHWN	4.7	23 c			21; 19; 4; 3; 14; 8; 6
45	Trimley	Orwell estuary	UK	B	16	2001				B			3.6				4
46a	Wallasea A	Crouch estuary	UK	N	2	1953	179	A	1	3 B; 160	I	-0.2-0.4 MHWN	5				7; 8
46b	Wallasea B	Crouch estuary	UK	N	2	1953	179	A	1	2 B; 90	I	-1.0-0.6 MHWN	5				7; 8
46c	Wallasea C	Crouch estuary	UK	B	110	2005		A	2	B							49
47	Walton Central	Hamford water	UK	N	73	1938	64		1	1 B; 130	IV	0.5-0.9 MHWN	3.8	8 a			7; 8
48	Woodbridge	Deben estuary	UK	N	15	1953	155	A	1	1 B; 35			3.6				7; 8
49	Boonepolder/ O Zwaakpolder	Westerschelde	NL	B	80	*1995			2	NA							22
50	Breebaart	Doiland estuary	NL	R	63	2000	21	A,P	2	1 S; 1*2	II,III		3				23
51	Dordise Biesbosch	Haringvliet	NL	B	235	*1995			2	B							22
52	Everingepolder	Westerschelde	NL	B	23	1996		D	2	S							23
53	Groene Strand	Terschelling	NL	B	320	*1995			2	NA							23; 24
54	Hedwigepolder	Westerschelde	NL	B	320	*1995			2	NA							22
55	Hellegatpolder	Westerschelde	NL	B	125	*1995			2	NA							22

Appendix 3.1. Continued

Site Nr	Site name	Location	Country	Type ⁱ	Area (ha)	Breach ⁱⁱⁱ	Years embanked	Land use ^{iv}	Main reason ^v	Number, type and dimension (m) of breach (B), sluice (S) or pipe (P)	Drainage ^v	Elevation (m +sea level or ordnance datum) ^{vi}	Tidal range (m)	SEC (mm/yr) ^{vii}	Soil salinity	Management ^{viii}	References	
56	Holwerder summerpolder	Friesland	NL	R/B	37	1989/95	33	P	2	3 S; 1*2 / 1 B; 12	II,III	1.1 MSL	2	6 e			8; 24	
57	Kroons polders	Vlieland	NL	B	85	1996	76	D	2	1 B; 10		0.82-1.26 OD		6.2-12.6c		M	23; 25; 52; 53	
58	Noard Fryslân	Friesland	NL	B	135	2001	91	P	2	3 B; 60	II,III	0.4-0.9 MHT	2	7.78- 19.1c	10-70% of ref	G	26; 27; 23; 28	
59	Bûtenryk	Friesland	NL	N	100	1973/79	40	P	1	2 B; 500	II,IV	1.4 MSL	2.2	16.1d			29; 8; 23; 30	
60	Schelde	Schelde estuary	NL	R	10	2001		A,P	4	S							31	
61	Sieperdaschor	Westerschelde	NL	N	100	1990	24	A,P	1	1 B; 15; 1 S; 1.5*1.2	II,III	2.6 MSL	5	5-30e		G	32; 33; 8; 34;	
62	Verdronken Zwaarte polder	Zeeuws Vlaanderen	NL	N	43	1802	2	D	1	B						G/M	30 35; 36	
63	Zwaarte polder	Westerschelde	NL	B	65	*1995			2	NA							22	
78	Kerenisse polder	Schelde estuary	B	R	30	2002		P	2	entire	I						37	
64	Zeeschelde	Schelde estuary	B	R	300	plan		P	2,3	S							31	
65	Berensch (Spieka-Neufeld)	Niedersachsen	D	R	280	1995	125	P	2	1 S; 1.3	II,III	0-1.0 MHT	3.2		6-15%	G	38; 39	
66	Hauener Hooge	Leybucht	D	B	80	1994	60	P	2,3	1 B; 100	II,III	0.1-0.6 MHT	2.8	20-87e			40; 50	
67	Karendorfer Wiesen	Mecklenburg- Vorpommern	D	B	350	1993	83	A,P	2	entire; 5000	I	-0.7-3.0 MSL	0.02				41; 42	
68	Langeoog	Niedersachsen	D	B	240	Plan	156	P	2	entire; 5500	II,III	0.2-0.5 MHWN	2.6				40	
69	Luereisburg	Niedersachsen	D	B	50	Plan	48	B	2	B		1.5-2.2 OD					43; 39	
70	Munster polder	Niedersachsen	D	B	92	plan		A,1	2	undecided		1.4-2.1 OD					40	
71	Neuensien polder	Rügen	D	B	80	2001		B		B							41	
72	Preetz polder	Rügen	D	B	180	1995		B		B							41	
74	Sundische Wiese	Mecklenburg- Vorpommern	D	B	943	2009	49	P	2	? B			0.02				44	
75	Zickemiss-Niederung	Rügen	D	B	225	1995		B		B							41	
76	Ziesetal	Mecklenburg- Vorpommern	D	B	162	1995/99	110	P	2	B / entire	II		0.02		5-13%	G	45; 46	
77a	Baie des Veys A	Normandie	F	N/R	30.2	1989	119	P	1,2	1 S; 1*1	II,III	1.9-2.5 OD	6				51	
77b	Baie des Veys B	Normandie	F	R	900	*1995			2	NA							8	
	Sites not known from start:																	
	Pillmouth	River Torridge, Devon	UK	B		2000	>200	A	3	3 B	II		7		25150 µS		54	

Appendix 3.1. Continued.

ⁱ N = natural breach; B = deliberate breach; R = regulated tidal exchange

ⁱⁱ * = plan for breach not carried out

ⁱⁱⁱ A = arable; P = pasture; F = freshwater grazing marsh; D = dune valley or beach plain; I = industry or commerce; W = waste ground; Po = pool

^{iv} 1 = accidental; 2 = habitat creation/compensation; 3 = flood defence; 4 = gaining experience

^v I = superficial; II = drainage ditches; III = artificial creeks; IV = natural creeks

^{vi} MHWN = mean high water neap tide; MHW = mean high water; MSL = mean sea level; OD = ordnance datum

^{vii} SEC = surface elevation change. Methods use: a = depth to agricultural layer; b = sedimentation plate;

c = sedimentation-erosion bar; d = repeated leveling; e = unknown

^{viii} G = grazed; M = mown

Appendix 3.1. References

1. Diack, I. (1998) Botanical monitoring of the salt marsh option of the habitat scheme 1995-1997, pp 1-38. ADAS, Oxford.
2. Dixon, A.M., Leggett, D.J. & Weight, R.C. (1998) Habitat creation opportunities for landward coastal realignment: Essex case studies. *Journal of the Chartered Institute of Water and Environmental Management* 12, 107-112.
3. Anon. (1998) Review of coastal habitat creation, restoration and recharge schemes. R.909, pp. 1-190. ABP Research & Consultancy Ltd, Southampton.
4. Atkinson, P.W., Crooks, S., Grant, A. & Rehfish, M.M. (2001) The success of creation and restoration schemes in producing intertidal habitat suitable for waterbirds. No425, pp.1-167. English Nature, Peterborough.
5. Lamberth, C. & Haycock, N. (2001) Regulated tidal exchange. Phase II report. Case studies and guidelines for the assessment of sites capable of supporting a saline wetland creation project using regulated tidal exchange techniques. Haycock associates Ltd., St. Albans.
6. Halcrow group Ltd. (2002) Managed realignment review. Flood and Coastal Defence R&D programme FD2008. Defra, London.
7. Burd, F., Clifton, J. & Murphy, B. (1994) Sites of historical sea defense failure. Phase II study. Report to English nature. ZO38-94-F. Institute of Estuarine and Coastal Studies, Hull.
8. van Oevelen, D., van den Bergh, E., Ysebaert, T. & Meire, P. (2000) Literatuuronderzoek naar ontpolderingen. IN.R.2000.7. Instituut voor Natuurbehoud, Brussel.
9. French, P.W. (1999) Managed retreat: a natural analogue from the Medway estuary, UK. *Ocean & Coastal Management* 42, 49-62.
10. Cahoon, D.R., French, J.R., Spencer, T., Reed, D. & Möller, I. (2000) Vertical accretion versus elevational adjustment in UK saltmarshes: an evaluation of alternative methodologies. *Coastal and Estuarine Environments: sedimentology, geomorphology and geoarchaeology*. (Eds. K. Pye & J.R.L. Allen), pp. 223-238. Geological Society, London.
11. Myatt, L.B., Scrimshaw, M.D. & Lester, J.N. (2003) Public perceptions and attitudes towards a current managed realignment scheme: Brancaster West marsh, North Norfolk, U.K. *Journal of Coastal Research* 19, 278-286.
12. French, C.E., French, J.R., Clifford, N.J. & Watson, C.J. (2000). Sedimentation-erosion dynamics of abandoned reclamations: the role of waves and tides. *Continental Shelf Research* 20, 1711-1733.
13. Myatt, L.B., Scrimshaw, M.D. & Lester, J.N. (2003) Public perceptions and attitudes towards a forthcoming managed realignment scheme: Freiston Shore, Lincolnshire, UK. *Ocean & Coastal Management* 46, 565-582.
14. Brooke, J., Landin, M., Meakins, N. & Adnitt, C. (1999). The restoration of vegetation on salt marshes. R&D W208, pp. 1-85. Environment Agency, Swindon.
15. Dagley, J.R. (1995) Northey Island: managed retreat scheme. Results of botanical monitoring 1991 to 1994. No128 English Nature, Colchester.
16. Dixon, A.M. & Weight, R.S. (1996) Managing coastal realignment. Case study at Orplands Sea wall, Blackwater estuary, Essex. *Saltmarsh management for flood defence. Research seminar proceedings, November 1995* (Eds. sir William Halcrow & partners Ltd.), 480/1/SW, pp.1-22. National Rivers Authority.
17. Tinkler, B. (1993) Let's go for managed retreat - what is it? London Zoo conference. Seminar on managed retreat.
18. Boorman, L.A., Garbutt, A., Barratt, D. & Rothery, P. (1997) Large scale managed realignment. Volume 2 Saltram, Final report to MAFF, ITE, Monks Wood, Devon.
19. Reading, C. J., Gray, A. J., Paramor, O. A. L., Garbutt, R. A., Watts, C. W., Spearman, J. R., Barratt, D. R., Chesher, T., Cox, R., Hughes, R. G., Mann, J. L., Myhill, D. G., Rothery, P., Semmence, J. & Wolters, M. (2002) Managed realignment at Tollesbury and Saltram. Final report. Report No. CSA2313. Centre for Ecology and Hydrology, Dorchester.
20. Evans, P.R., Ward, R.M., Bone, M. & Leakey, M. (1998) Creation of temperate-climate intertidal mudflats: factors affecting colonization by benthic invertebrates and their bird predators. *Marine Pollution Bulletin* 37, 535-545.
21. Boorman, L.A. & Ashton, C. (1997) The productivity of salt marsh vegetation at Tollesbury, Essex and Stiffkey, Norfolk, England. *Mangroves and Saltmarshes* 1, 113-126.
22. Lenselink, G. & Gerits, R. (2000) Kansen voor herstel van zoet-zout overgangen in Nederland. 2000.032. RIZA, Lelystad.
23. De Leeuw, C. & Meijer, M.L. (2002) Proefgebieden herstel zoet-zout overgangen in Noord Nederland. werkdokument concept. RIKZ, Haren.

24. Esselink, P., De Leeuw, C., Berg, G. & Graveland, J. (2002) Evaluatie van 25 ecologische herstelmaatregelen in de zoute rijkswateren. RIKZ, Ministerie van Verkeer en Waterstaat, Haren.
25. van Gennip, B. & Knotters, A.G. (2002) Toelichting bij de vegetatiekartering Kroon's Polders en Westerveld 1999. Op basis van false colour-luchtfoto's 1:5000. MDGAE-2002.35. RIKZ, Den Haag.
26. van Duin, W.E., Esselink, P., Verweij, G. & Zegers, K. (2002) Monitoringsonderzoek proefverkweldering Noard Fryslân Bûtendyks. Uitgangssituatie. Alterra, Den Burg.
27. van Duin, W.E., Esselink, P., Verweij, G. & Engelmoer, M. (2003) Monitoringsonderzoek proefverkweldering Noard Fryslân Bûtendyks. Tussenrapportage 2001-2002. Alterra, Den Burg.
28. Hommel, P.W.F.M. & Horsthuis, M.A.P. (2002) Excursieverslagen 1999. Het Noorderleech. Plantensociologische kring Nederland.
29. van Duin, W.E., Dijkema, K.S. & Zegers, J. (1997) Veranderingen in bodemhoogte (opslibbing, erosie en inklink) in de Peazemerlanden. IBN rapport 326, Wageningen.
30. Bakker, J.P., Esselink, P., Dijkema, K.S., van Duin, W.E. & De Jong, D.J. (2002). Restoration of salt marshes in the Netherlands. *Hydrobiologia* 478, 29-51.
31. van Oevelen, D., van den Bergh, E., Ysebaert, T. & Meire, P. (2000) Literatuuronderzoek naar estuarine herstel maatregelen. IN.R.2000.4. Instituut voor Natuurbehoud, Brussel.
32. Verbeek, H. & Storm, H. (2001) Tidal wetland restoration in the Netherlands. *Journal of Coastal Research* SI 27, 192-202.
33. Eertman, R.H.M., Kornman, B.A., Stikvoort, E. & Verbeek, H. (2002) Restoration of the Sieperda tidal marsh in the Scheldt estuary, The Netherlands. *Restoration Ecology* 10, 438-449.
34. Koppejan, H. (2000) Toelichting bij de vegetatiekartering Westerschelde 1998. Op basis van false colour-luchtfoto's 1:5000/10000. MDGAE-2000.11. RIKZ, Den Haag.
35. van Dort, K.W. & Leusink, L. (1998) Toelichting bij de vegetatiekartering Het Zwin en de Verdrongen Zwarte Polder 1995 op basis van false-colour luchtfoto's 1:5000. MDGAE-9861. RIKZ Meetkundige Dienst, Delft.
36. Hommel, P.W.F.M., Horsthuis, M.A.P. & Westhoff, V. (2000) Excursieverslagen 1998. Het Zwin en de Verdrongen Zwarte Polder. Plantensociologische Kring Nederland.
37. Vandevoorde, B. van den Bergh, E., Verbessem, I., Spanoghe, G., de Regge, N., Soors, J., de Belder, W., Muylaert, K., Nijssen, D. & Piesschaert, F. (2004) Ketenissepolder: herstel van een brakwaterschor. (Wintersymposium 14-15 January, 2004). Nederlands-Vlaamse Vereniging voor Ecologie, Gent, Belgium.
38. Kinder, M., Främbs, H., Hielen, B. & Mossakowski, D. (2003) Regeneration von Salzwiesen in einem Sommergroden an der Nordseeküste: E + E-Vorhaben "Salzwiesenprojekt Wurster Küste". *Natur und Landschaft* 78, 343-353.
39. Alhorn, F. & Kunz, H. (2002) Literaturstudie zur Entwicklung und Bedeutung von Sommerdeichen. Arbeiten aus der Forschungsstelle Küste, Niedersächsisches Landesamt für Ökologie, Niedersachsen, 14.
40. Alhorn, F. & Kunz, H. (2002) The future of historically developed summerdikes and polders: a salt marsh use conflict. *Littoral 2002, The Changing Coast*, pp. 365-374.
41. Seiberling, S. (2003) Auswirkungen veränderte Überflutungsdynamik auf Polder- und Salzgraslandvegetation der Vorpommerschen Boddenlandschaft. PhD thesis Ernst-Moritz-Arndt-Universität, Greifswald.
42. Bernhardt, K.-G. & Koch, M. (2003) Restoration of a salt marsh system: temporal change of plant species diversity and composition. *Basic and Applied Ecology* 4, 441-451
43. Mai, S. & Zimmerman, C. (2002) Diked forelands and their importance in coastal zone management. *Hydro 2002, Tools for coastal zone management in the future*.
44. Beil, T. (2002) Economic valuation of biodiversity restoration and conservation of salt meadows - costs and benefits. *Salt grasslands and coastal meadows in the Baltic region*. (Eds. T. Frock, K. Hergarden & D. Repasi), pp. 199-204. Conference proceedings, Neubrandenburg.
45. Grünwald, M. (2002) Carabid Beetles as indicators for restoration of salt grassland: the example of polder Ziesetal. *Salt grasslands and coastal meadows in the Baltic region*. (Eds. T. Frock, K. Hergarden & D. Repasi), pp. 101-113. Conference proceedings, Neubrandenburg.
46. Zander, B. (2002) Vegetation dynamics in coastal grasslands at the 'Greifswalder Bodden' (Baltic Sea) after removing the dyke and reintroduction of flooding. *Salt grasslands and coastal meadows in the Baltic region*. (Eds. T. Frock, K. Hergarden & D. Repasi), pp. 155-166. Conference proceedings, Neubrandenburg.
47. Personal communication A. Garbutt and RSPB
48. Coastnet cd rom 2002
49. Defra public consultation leaflet, September 2003
50. Personal communication S. Arens
51. Personal communication A. Dausse
52. Adema, E.B. & Grootjans, A.P. (2002) Vegetatie en abiotiek in de derde en vierde Kroon's Polders van Vlieland: Effectmonitoring van frequentere in- en uitstroming van zout water. Laboratorium voor Plantenecologie, Rijksuniversiteit Groningen, Haren.
53. Esselink, P.E. (2004) Sedimentatie en hoogte-ontwikkeling in de Kroon's Polders (Vlieland). Monitoring door middel van sedimentatie-erosie-balk metingen meetjaar 2003. Koeman en Bijkerk bv, Haren.
54. Blackwell, M.S.A., Hogan, D.V. & Maltby, E. (2004) The short-term impact of managed realignment on soil environmental variables and hydrology. *Estuarine, Coastal and Shelf Science*, 59, 687-701.

Appendix 3.2. Salt-marsh communities used for selecting regional target species for 1) the Central North-Atlantic (Schaminée *et al.* 1998) 2) the Southern North-Atlantic (Rodwell 2000) and 3) the German Baltic (Krisch 1990) regions.

	1	2	3
Syntaxon			
Spartinion			
<i>Spartinetum maritimae</i>	24Aa1		
<i>Spartinetum townsendii</i>	24Aa2	SM6	
Thero-Salicornion			
<i>Salicornietum dolychostachya</i>	25Aa1		
<i>Salicornietum brachystachya</i>	25Aa2	SM8	<i>Salicornia europaea</i> group
<i>Suaedetum maritimae</i>	25Aa3	SM9	
Puccinellion maritimae			
<i>Puccinellietum maritimae</i>	26Aa1	SM10,11,13*	<i>Puccinellia maritima</i> group
<i>Plantagini Limonietum</i>	26Aa2		
<i>Halimionetum portulacoidis</i>	26Aa3	SM8,14,26	
Puccinellio-Spergularion salinae			
<i>Puccinellietum distans</i>	26Ab1	SM23	<i>Spergularia salina</i> group
<i>Puccinellietum fasciculatae</i>	26Ab2		
<i>Puccinellietum capillaris</i>	26Ab3		
<i>Parapholido strigosae-Hordeetum marini</i>	26Ab4		
Armerion maritimae			
<i>Juncetum gerardi</i>	26Ac1	SM16*	<i>Juncus gerardi</i> group
<i>Armerio-Festucetum littoralis</i>	26Ac2		
<i>Junco-Caricetum extensae</i>	26Ac3		
<i>Blysmetum rufi</i>	26Ac4	SM19*	<i>Blysmus rufus</i> group
<i>Artemisietum maritimae</i>	26Ac5	SM17	
<i>Atriplici-Elytrigietum pungentis</i>	26Ac6	SM24,25,26	
<i>Oenanthe lachenalii-Juncetum maritimi</i>	26Ac7	SM15,18	<i>Oenanthe lachenalii</i> group
<i>Elymus repens</i> community		SM28	<i>Agrostis stolonifera</i> group
Saginion maritimae			
<i>Sagino maritimae-Cochlearietum danicae</i>	27Aa1		
Phragmition australis			
<i>Eleocharitetum uniglumis</i>		(SM20)*	<i>Eleocharis uniglumis</i> group
<i>Scirpetum tabernaemontani/maritimi</i>	8bb2, 8bb3d	S20	<i>Aster tripolium</i> group
Mediterranean			
<i>Arthrocnemum perenne</i> stands		SM7	
<i>Suaeda vera-Limonium binervosum</i>		SM21	
<i>Limonio vulgaris-Frankenietum laevis</i>		SM22	

* Target species of the following communities: SM13e, SM16f, SM19 and SM20, were not included for the Southern North-Atlantic region as they occur only in the Northern part of Great-Britain.



Checking for seedling emergence in the glasshouse (photo Sijbren Otto)

Soil seed bank and driftline composition along a successional gradient on a temperate salt marsh

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Applied Vegetation Science (2002) 5, 55-62.

The previous chapter showed that several target species established in restoration sites after de-embankment. But where did the species come from? The conceptual framework introduced in Chapter 1 identified the soil seed bank of the community species pool as a possible source of target species, provided that seeds are viable long enough to survive the period of embankment. The present chapter investigates the soil seed bank at different successional stages in a natural salt marsh and provides a longevity index based on the relative abundance of seeds in different depth layers of the soil. In addition, the potential role of tidal water in dispersing seeds homogeneously across the salt marsh is assessed from driftline material at different successional stages of the vegetation

Introduction

Salt marshes are ecologically very important because they provide a unique habitat for many plant and animal species. Throughout north-west Europe these ecosystems have been embanked and exploited for agricultural use since their origin c. 2500 years ago (Bakker *et al.* 1997; 2002). New salt marshes often developed in front of these embanked areas, but many of these are now threatened by globally rising sea level, insufficient sedimentation rates and inability to move inland (Allen & Pye 1992); a phenomenon called 'coastal squeeze' (Doody 2004). Along the coast of the UK, for example, loss of 40% of salt-marsh area in 15 yr has been attributed mainly to coastal squeeze (Burd 1992). On the eastern Dutch Wadden Sea coast, accretion rates of new salt marshes have been falling behind embankment rates for many years, resulting in a 50 km² deficit in salt-marsh area compared to 1600-1800 AD (Dijkema 1987). One approach to preventing further loss is to re-create salt marshes by breaching, or removing, the seawall around the embankments (Radley 1993; Williams 1994; Bakker *et al.* 1997; 2002).

The success of salt-marsh re-creation largely depends on (1) the presence of salt-marsh species in the target area, (2) the distance between this area and a source area harbouring the required salt-marsh plants (i.e. the species pool) and (3) the ability of the species to disperse into the target area (Morton & Law 1997; Zobel 1997; Willems & Bik 1998; Zobel *et al.* 1998). It is believed that while salt-marsh plants are absent from the vegetation of the target area their seeds may still be present in the soil seed bank, from which they can emerge when conditions are suitable (Fenner 1985). In cases where the species do not form a seed bank, or where the seeds are not viable long enough, they need to be dispersed into the target area. In these cases, the presence of barriers between the source and target areas and dispersal strategies become important (Zobel *et al.* 1998).

The importance of soil seed banks in determining the establishment of salt-marsh plants is not clearly understood (Ungar 1987), but the scarce seed bank records so far suggest short longevity of seeds of most salt-marsh species (Thompson *et al.* 1997). Therefore, successful salt-marsh restoration has to rely on seed dispersal from nearby source areas. Different studies on seed dispersal indicate that most salt-marsh species are able to float in the water column (Waisel 1972; Koutstaal *et al.* 1987; Huiskes *et al.* 1995) and are found in large quantities in driftline material (Gerlach 1999; Persicke *et al.* 1999). However, neither establishment nor viability of the seeds has been tested, so that the cited studies represent potential, rather than actual, dispersal success. The only example of actual seed dispersal identified shows that limited seed dispersal may be important in determining the species composition of the vegetation (Rand 2000). Hence there is an urgent need to investigate the exact mechanism of salt-marsh development in order to prevent disappointing results from future salt-marsh restoration projects.

We have studied a natural salt marsh to answer the following questions: (i) What is the composition of the viable soil seed bank? (ii) What is the composition of the viable driftline material? (iii) What is the longevity of the species in the soil seed bank? (iv) What is the composition of seeds in annually deposited sediment? (v) What is the importance of the seed bank of soil, driftline material or annually deposited sediment for species composition of the vegetation during different successional stages? (vi) What is the prospect of natural re-creation of salt marshes following de-embankment?

Methods

Study area

The salt marsh under investigation is located at the barrier island of Schiermonnikoog in the Dutch Wadden Sea (53° 30' N, 6° 10' E). This island is extending eastward because of sediment accretion and, consequently, a chronosequence representing different successional stages in salt-marsh vegetation exists along an east-west gradient.

At each stage there is an elevational gradient from low to high marsh (Olf *et al.* 1997). We examined the soil seed bank, seeds in driftline material and the established vegetation at five different successional stages ranging from 3 to 100 yr old. Distances between the sites are:

- 500 m between 3 and 10 yr old;
- 1500 m between 10 and 25 yr old;
- 1000 m between 25 and 35 yr old;
- 2500 m between 35 and 100 yr old.

The study sites for vegetation and seed bank sampling were at similar elevations, i.e. 20 cm to 40 cm above mean high tide (MHT). The sediment features a clay layer with a high nitrogen content (2 – 16 cm) on top of a sandy subsoil, which increases with salt-marsh age (Olf *et al.* 1997; van Wijnen & Bakker 1997). This sediment is deposited by tidal water along the entire chronosequence of ca. 6 km. Driftline material was collected higher up the marsh at ca. 50 m from the seed bank samples.

Vegetation and seed bank sampling

The established vegetation was monitored by recording the frequency of each species in ten subplots (0.4 m²) in each of ten plots (4 m²) per site during the summer of 1997.

The soil seed bank was sampled following the procedure developed by ter Heerdt *et al.* (1996). Six soil cores (7 cm diameter) were taken randomly in each of ten plots (1 m²) per site in November 1996. After removal of vegetative fragments the soil cores were divided into 0-5 cm and 5-10 cm layers and the layers for the six samples were pooled, resulting in ten replicates with a total sampled area of 231 cm² each. The upper 5 mm of soil, which corresponds to the annual accretion rate at this elevation (van Wijnen & Bakker 2001), was sampled in March 1997 by scooping ten replicate samples of soil from a 10 cm x 10 cm area at each site. All samples were stored in the dark at 5 °C for a month. After this stratification period, the samples were washed over a sieve (0.2 mm mesh) to reduce the amount of sand and clay. The remaining material was homogeneously distributed in a 2 mm layer over sterilized compost covered with 1 cm of sterile sharp sand in 25 cm x 25 cm x 10 cm plastic trays and placed in a glasshouse (15 °C at night (20.00 to 08.00); 25 °C or above during the day) and watered daily. Seedlings were identified, counted and removed as soon as possible after emergence. After six weeks, germination had ceased and the trays were left to dry for a week. This allowed the sample to be crumbled to expose deeper buried seeds to the light. After watering the samples for another two weeks, no new seedlings emerged. To ensure that no viable seeds remained in the soil, a subsample of one quarter of the total tray area was viewed under a microscope. Poking the seeds with a needle enabled us to distinguish between firm and empty seeds. The number of seeds that had remained in the soil accounted for only 1% to 3% of the total seed bank. No 'new' species were detected.

Classification of the seed bank and longevity of seeds

A comparison between the presence of a species in the vegetation and the number of seeds in the soil layers (0-5 cm and 5-10 cm depth) was used to determine the seed bank type of a species according to the classification key by Thompson *et al.* (1997). Species are classified as *transient* when they are present in the vegetation and either absent or only present in the upper 5 cm of the seed bank, *short-term persistent* when a higher number of seeds is found in the upper soil layer than the deeper layer and *long-term persistent* when there are at least as many seeds in the deeper layer as in the upper soil layer. A minimum of three seeds per layer was the standard used for a species to be recorded as present. A longevity index was calculated using the following equation (Bekker *et al.* 1998):

$$LI = \frac{SP + LP}{T + SP + LP}$$

where LI is the longevity index and SP, LP and T represent the number of sites in which a species was found to be short-term persistent, long-term persistent or transient respectively. The index ranges from 0 (strictly transient) to 1 (strictly persistent).

Driftline material

Driftline material was collected from the higher part of the salt marsh after storms in November 1996: ten 0.5 L samples from each of the five sites. The material was air-dried for a week and a random 10-g dry weight subsample was spread over a tray filled with sterilized compost topped with 1 cm of sterile sharp sand. The trays were covered with black plastic and placed outside for a stratification period of one month (daily temperature: -5 °C to 10 °C). After stratification, the samples were transferred to the glasshouse and analyzed as the seed bank material. It took at least two months for germination to stop.

Statistics

Prior to analysis, skewness and kurtosis measurements together with the Shapiro-Wilk test for normality and the Levene's test for homogeneity of variances were performed on all data. If data distribution was not normal, and if variances were not homogeneous, data were transformed (\log_{10} or $1/\sqrt{\cdot}$) after which the parametric one-way ANOVA and Tukey test were applied (Zar 1996) (Fig. 4.1). A Dunnett's C multiple comparison test followed the one-way ANOVA if a slight heterogeneity of variances was observed. In cases where data transformation could not prevent deviations from normality and homogeneity of variances, the Kruskal Wallis test followed by the Nemenyi test was applied. For each analysis, a 5% significance level was used. Spearman's correlation index (R^2) was calculated to determine the relationship between vegetation and the composition of the seed bank or driftline material and between the driftline and the upper 5 mm of soil. All correlations took into account the abundance of the species.

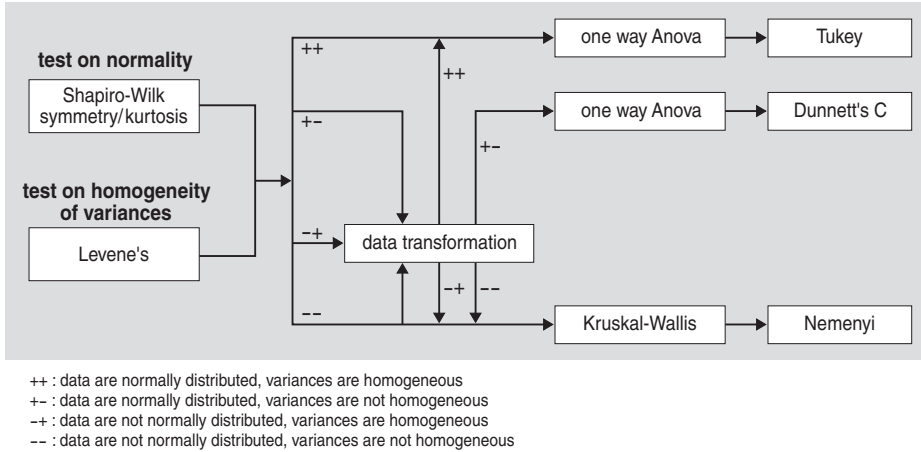


Figure 4.1. Statistical steps

Results

Seed bank classification and seed longevity

A longevity index was calculated for 21 salt-marsh species. There were 11 species which had seeds with low longevity, seeds of three species had intermediate longevity and seven species had seeds with high longevity (Fig. 4.2). *Agrostis stolonifera*, *Juncus gerardi* and *Spergularia media* were the only three species with a strictly persistent seed bank (Fig. 4.2).

Established vegetation

The successional trend in the vegetation showed that the 3-yr old transect was dominated by *Puccinellia maritima*, *Salicornia* spp., *Spergularia media* and *Suaeda maritima*, which were accompanied by *Aster tripolium*, *Atriplex portulacoides*, *Limonium vulgare* and *Plantago maritima* in the second successional stage (App. 4.1). The absence of pioneer species from the 25-yr old site is remarkable. These pioneer species were also absent from the 100 year-old transect.

The total number of species on 40 m² was lowest at the youngest site but increased rapidly in older successional stages with the exception of the 25-yr old transect (Table 4.1). This also holds for the mean number of species on 4 m².

Seed bank

The total number of species in the upper seed bank was smallest in the 3-yr old stage (Table 4.2), but doubled in the 10-yr old site. The mean number of species was significantly larger at the 25-yr old site compared to the younger stages. The mean number

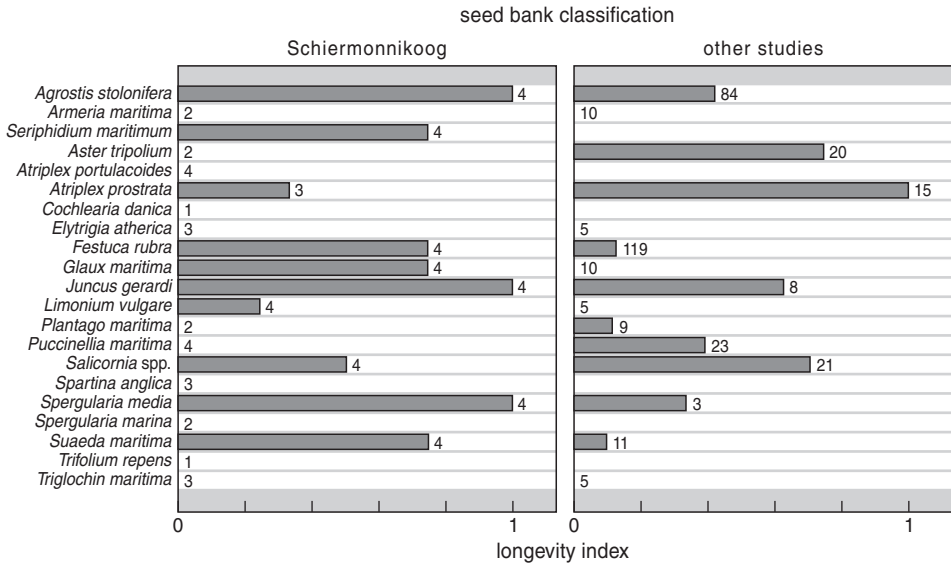


Figure 4.2. Comparison of longevity indices for salt-marsh species from Schiermonnikoog with other studies (Thompson et al. 1997), including the number of sites (Schiermonnikoog) or records (other studies) from which the index is calculated. 0 = strictly transient, 1 = strictly persistent.

of individuals was highest at the 100-yr old transect, but revealed no regular increase in different successional stages. The abundance of seeds was lower in the 5-10 cm and 0-0.5 cm layers compared to the 0-5 cm layer with the exception of the 25-yr old transect (Table 4.2). The seed bank was dominated by *Salicornia* spp., *Suaeda maritima* and *Spergularia media* during the first ten years of succession. These species were gradually replaced by *Seriphidium maritimum*, *Festuca rubra*, *Glaux maritima* and *Juncus gerardi* (App. 4.1) in later-successional stages.

Driftline

There was a more than twofold increase in species richness during the first seven years of succession (Table 4.3). Most species were found in the 10-yr and 25-yr old stages. Interestingly, many dune species were present in the driftline of these two sites (App. 4.1). The highest number of individuals was observed in the oldest stages.

Correlations

Correlation indices were calculated taking into account only the species from the local pool (i.e. those species indicated with an asterisk in App. 4.1). Significant correlations between vegetation and the 0-5 cm seed bank were observed for all sites except the youngest. Driftline and the 0-0.5 cm seed bank correlated best with vegetation of the three oldest stages (Table 4.4). Not surprisingly, correlations between vegetation and deeper soil layer were very weak and only significant for the oldest site. A significant

Table 4.1. Total and mean number with standard error ($n = 10$) of species in the vegetation at different successional stages. Different superscripts indicate significant differences ($P < 0.05$), assessed by a Tukey test after One-Way Anova.

	Successional age (years)				
	3	10	25	35	100
Total nr. of species (40m ²)	8	15	12	18	14
Mean nr. of species (4m ²)	6.2 ± 0.4 ^a	11.3 ± 0.5 ^c	7.5 ± 0.5 ^{ab}	10.7 ± 0.7 ^c	9.3 ± 0.5 ^{bc}

Table 4.2. Total number of species and mean number of species and individuals with standard error ($n = 10$) in four layers of the soil seed bank (sample area = 100 cm² for 0-0.5 cm and 231 cm² for 0.5 and 5-10 cm) for different successional ages. Means are analyzed for significant differences ($P < 0.05$), indicated by different superscripts, by a Tukey or Dunnett's C test after One-Way Anova or a Nemenyi test after Kruskal-Wallis.

	Successional age (years)				
	3	10	25	35	100
Total nr. of species					
0 – 0.5 cm	6	9	11	8	12
0 – 5 cm	9	16	15	14	12
5 – 10 cm	8	7	14	10	10
0 – 10 cm	11	16	17	14	14
Mean nr. of species					
0 – 0.5 cm	2.7 ± 0.3 ^a	3.7 ± 0.5 ^{ab}	3.6 ± 0.5 ^{ab}	3.9 ± 0.4 ^{ab}	5.7 ± 0.7 ^b
0 – 5 cm	4.9 ± 0.3 ^a	6.7 ± 0.5 ^{ab}	8.4 ± 0.5 ^{bc}	8.6 ± 0.6 ^c	8.2 ± 0.4 ^{bc}
5 – 10 cm	4.5 ± 0.3 ^{bc}	3.2 ± 0.3 ^{ab}	6.3 ± 0.3 ^d	5.2 ± 0.4 ^{cd}	3.1 ± 0.4 ^a
0 – 10 cm	5.6 ± 0.2 ^a	7.2 ± 0.5 ^{ab}	10.0 ± 0.3 ^c	9.1 ± 0.6 ^{bc}	9.0 ± 0.3 ^{bc}
Mean nr. of individuals					
0 – 0.5 cm	21.6 ± 4.9 ^a	70.5 ± 7.1 ^b	20.0 ± 7.2 ^a	16.4 ± 4.2 ^a	87.7 ± 15.5 ^b
0 – 5 cm	169.2 ± 23.3 ^b	414.2 ± 41.4 ^c	74.3 ± 6.8 ^a	99.7 ± 13.2 ^a	399.3 ± 68.4 ^c
5 – 10 cm	72.6 ± 11.4 ^b	59.0 ± 4.3 ^b	83.1 ± 10.6 ^b	28.7 ± 4.4 ^a	204.5 ± 35.8 ^c
0 – 10 cm	241.8 ± 22.3 ^{ab}	473.2 ± 41.7 ^b	157.4 ± 13.1 ^a	128.4 ± 13.2 ^a	603.8 ± 92.8 ^b

Table 4.3. Total and mean number with standard error ($n = 10$) of species in driftline material at different successional stages. Different superscripts indicate significant differences ($P < 0.05$) assessed by a Dunnett's C test and Tukey test respectively, after One-Way Anova.

	Successional age (years)				
	3	10	25	35	100
Total nr. of species	14	30	29	22	19
Mean nr. of species	12.1 ± 1.2 ^{ab}	18.0 ± 1.0 ^c	14.9 ± 0.9 ^{bc}	11.7 ± 1.1 ^{ab}	10.9 ± 0.6 ^a
Mean nr. of ind.	425.5 ± 81.3 ^a	337.9 ± 56.1 ^a	268.3 ± 33.4 ^a	780.0 ± 217.7 ^{ab}	1732.4 ± 315.5 ^b

Table 4.4. Spearman's correlations between vegetation and seed bank in different layers of the soil or driftline.

		Age	3	10	25	35	100	Seed bank 0-0.5 cm
vegetation	Age							
	3		0.38	0.42	-0.42	0.18	-0.13	
	10		0.44*	0.42	0.17	0.24	0.08	
	25		0.29	0.36	0.75**	0.63**	0.67**	
	35		0.31	0.35	0.49*	0.44*	0.30	
	100		-0.05	-0.01	0.60**	0.39	0.63**	
<hr/>								
		Age	3	10	25	35	100	Seed bank 0-5 cm
vegetation	Age							
	3		0.38	0.30	-0.11	0.15	-0.43	
	10		0.42	0.49*	0.06	0.21	0.12	
	25		0.28	0.33	0.56**	0.52*	0.59**	
	35		0.43*	0.42	0.25	0.42*	0.37	
	100		0.04	0.13	0.48*	0.31	0.50*	
<hr/>								
		Age	3	10	25	35	100	Seed bank 5-10 cm
vegetation	Age							
	3		0.38	0.38	-0.01	0.25	-0.20	
	10		0.22	0.35	0.05	0.29	-0.05	
	25		0.16	-0.08	0.30	0.42	0.50*	
	35		0.08	0.14	0.18	0.36	0.42	
	100		-0.20	-0.37	0.31	0.25	0.47*	
<hr/>								
		Age	3	10	25	35	100	Driftline
vegetation	Age							
	3		0.31	-0.12	-0.26	0.05	-0.17	
	10		0.62**	0.18	0.07	0.21	0.05	
	25		0.51*	0.48*	0.62**	0.86**	0.60**	
	35		0.46*	0.15	0.18	0.46*	0.14	
	100		0.26	0.37	0.51*	0.69**	0.54**	

* significant correlation, $P < 0.05$, ** significant correlation $P < 0.01$

Table 4.5. Spearman's correlations for salt-marsh species in driftline and soil seed bank (0-0.5 cm)

		Age	3	10	25	35	100	Seed bank 0-0.5 cm
Driftline	Age							
	3		0.77**	0.64**	0.66**	0.63**	0.59**	
	10		0.47*	0.38	0.69**	0.61**	0.74**	
	25		0.31	0.21	0.69**	0.45*	0.63**	
	35		0.38	0.32	0.73**	0.67*	0.75**	
	100		0.39	0.51*	0.68**	0.68**	0.68**	

* significant correlation, $P < 0.05$, ** significant correlation $P < 0.01$

relation between the upper 0.5 cm of soil and driftline material was observed for all but the 10-yr old site (Table 4.5). Interestingly, strong correlations were not only observed between the vegetation and upper soil layers or driftline of the same site but also when different successional sites were compared, especially between driftline material and the 0-0.5 cm soil layer.

Discussion

Seed bank classification and seed longevity

The classification of salt-marsh species in the present study reveals that the majority of species have a transient or short-term persistent seed bank. This conclusion was also derived from the database of Thompson *et al.* (1997). However, a comparison of the longevity index for each species shows that this could be predicted from the database for only five of 15 species (Fig. 4.2). It is difficult to explain why *Salicornia* spp. and *Atriplex prostrata* have a lower longevity index in this study compared to others. *Glaux maritima* is classified as having a long-term persistent seed bank in the present study whereas other studies give it longevity index of zero. This species is known to propagate from hibernacles (Yapp *et al.* 1917; Jerling 1988; Jerling & Elmgren 1996) which, unlike other vegetative fragments, were not removed from the samples.

One point of concern is that the classification of seed bank types starts from the assumption that older seeds are buried deeper than younger ones, because it takes time for the seeds to penetrate into the soil. This assumption might not hold for salt marshes, where bioturbation, sedimentation and erosion could affect the vertical distribution of seeds in the soil. The dissimilarity in seed bank classification may, therefore, be due to differences in sedimentation and invertebrate densities between various salt marshes. Bekker *et al.* (1998) counteracted this criticism by providing evidence of no difference in seed longevity between depth-derived and non-depth derived records. Salt marshes may provide a unique opportunity to relate depth of burial and age of buried seeds. Prerequisites are knowledge of the rate of sedimentation and the absence of soil disturbing animals.

Relation between established vegetation, seed bank and driftline

Some species present in the established vegetation are not, or only infrequently, found in the driftline material at the higher salt marsh at the same site, suggesting their seeds have poor floating capacity. These species are *Aster tripolium*, *Atriplex portulacoides*, *Puccinellia maritima*, *Spartina anglica* and *Triglochin maritima*. However, seeds of *S. anglica* and *T. maritima* were trapped in floating nets and seeds of *A. tripolium* in standing nets by Huiskes *et al.* (1995). Furthermore, especially the seeds of *T. maritima* have long flotation times (Koutstaal *et al.* 1987). Hutchings & Russell (1989) observed that the number of seeds of *A. tripolium* and *Puccinellia maritima* in the seed bank exceeded the actual seed production of these species at the same site and

concluded that immigration or redistribution of the seeds must be the cause. On the other hand, Milton (1939) observed a marked difference between the small number of viable seeds of *A. tripolium* in the soil compared with its abundance in the vegetation and Rand (2000) also remarked that *Aster* was rarely found in seed traps. In our study area it is most likely that, especially in younger successional stages, seed set is prevented by herbivores such as hares for *A. portulacoides* (van der Wal *et al.* 2000b) and geese for *Puccinellia maritima* and *T. maritima* (van der Wal *et al.* 2000a). This suggestion is supported by the results of the seed bank analysis, which reveals the absence of these species.

Spergularia media, *Salicornia* spp., *Suaeda maritima* and, to some extent, *Limonium vulgare* are present in the vegetation and upper 5 mm of soil. As these species are also found in the driftline material higher up the salt marsh at the same site, they are apparently able to spread by floating at least over small distances. *L. vulgare* seeds were also trapped in floating nets and *Spergularia* spp. seeds in standing nets by Huiskes *et al.* (1995). In the study by Hutchings & Russell (1989) the number of *Suaeda maritima* seeds in the soil exceeded the seed production at the same site

A large number of species are present as viable seeds in the driftline material at the high salt marsh, whereas these species are not always present in the recorded vegetation of the same site. This group includes *Agrostis stolonifera*, *Seriphidium maritimum*, *Atriplex prostrata*, *Elytrigia atherica*, *Glaux maritima*, *Juncus gerardi*, *Plantago coronopus* and *Plantago maritima*. These species are apparently able to float and cover larger distances than species of the previous group. *Plantago maritima* was assumed to be predated or dispersed by tides (Hutchings & Russell 1989). At the 10-yr and 25-yr old stages, the driftline material contains many low dune species. Their numbers reduce at older stages where *E. atherica* becomes dominant (Olf *et al.* 1997). This species outcompetes many other species, hence the decline in number of driftline species.

Another study at the island of Schiermonnikoog revealed many viable seeds of *Festuca rubra*, *Elytrigia atherica* and *Juncus gerardi* and few seeds of *Agrostis stolonifera*, *Seriphidium maritimum*, *Plantago maritima*, *Limonium vulgare*, *Suaeda maritima*, *Triglochin maritima* and *Salicornia* spp. in driftline material (Bakker *et al.* 1985). Waisel (1972) reported seeds of *Atriplex portulacoides*, *Limonium vulgare*, *Puccinellia maritima*, *Salicornia* spp. *Suaeda maritima*, *Triglochin maritima*, *Elytrigia atherica* and *Atriplex prostrata* in driftline material in the UK, but their viability was not tested. Along the mainland coast of Germany seeds of *Atriplex* spp., *Elytrigia* spp., *Phragmites australis* and *Triglochin maritima* were found (Persicke *et al.* 1999), but their viability was not tested. Seeds of *Elytrigia atherica* were trapped in floating nets by Huiskes *et al.* (1995) and they also reported that many seeds were trapped at the ebb tide. This suggests that seeds originating from the higher marsh could be dispersed towards the lower marsh but, as we do not find these seeds in the seed bank of the lower marsh, it seems that seeds trapped in floating and standing nets represent potential, rather than actual, dispersal. The present study further underlines the importance of dispersal of seeds of salt-marsh species by sea water.

A strong correlation exists between the established vegetation and the upper soil layer (0-0.5 and 0-5 cm). This suggests that the upper soil seed bank reflects the seed rain from the established vegetation rather than deposition of seeds imported from elsewhere by the sea. This agrees with Rand (2000). The youngest site is an exception, with more salt-marsh species entering the community than actually establishing in the vegetation. Salt stress might be an important factor limiting the germination of these species (Egan & Ungar 2000; Noe & Zedler 2001). The assumption that these species enter the seed bank via tidal water is supported by the exceptionally high correlation between driftline and seed bank at this site (Table 4.5).

Not surprisingly, the vegetation is least correlated with the deepest layer of the seed bank. One might expect a better relationship between the seed bank of this layer and the vegetation from one stage before, but the correlation indices show that this is not the case. This might be attributed to the transient and short-term persistent character of most salt-marsh species, preventing them from reaching the 5-10 cm soil layer.

Seed bank, driftline and vegetation succession

It has been mentioned above that most salt-marsh species can be dispersed by seawater and the inundating sea easily covers the 6 km distance between the youngest and oldest site. The complete local pool (Zobel *et al.* 1998) of salt-marsh species, which consists of all salt-marsh species present at Schiermonnikoog, therefore has the potential of entering the community species pool of each successional stage. However, the input of propagules, as sampled from the soil seed banks and driftline material is not the same along the chronosequence. *Aster tripolium* and *Atriplex portulacoides* were absent from seed banks of the 10-yr old site (App. 4.1). *Aster* was not present in the seed banks from the oldest site. *Puccinellia maritima* was only present in the seed banks of the two youngest sites and *Triglochin maritima* was only present in the 3-yr old site. The community species pool, including the established vegetation and the upper seed bank below it (Zobel *et al.* 1998) is not similar along the chronosequence. *Triglochin maritima*, *Plantago maritima*, *Elytrigia atherica*, *Atriplex prostrata* and *Armeria maritima*, are completely absent from the community pool at the 3-yr old stage (App. 4.1). All other salt-marsh species are represented in the upper seed bank and/or established vegetation in the 3-yr old stage, although often at low abundance. *Atriplex littoralis* is absent from all community pools, even though it is present in the driftline material at three sites. Interestingly, *Armeria maritima* and *Plantago maritima* are both absent from the 3-yr, 25-yr and 100-yr old sites whereas they appear in the 10-yr and 35-yr old sites.

It seems that the succession at the study area can be described as a wave, dispersing relatively large numbers of seeds that first float over the site and then become concentrated in the narrow zone of the driftline. Few seeds of this potential dispersal establish at their landing point on the low salt marsh, but once they develop into plants most of them build up a transient or short-term persistent seed bank that disappears again when the established vegetation has been replaced by late successional

salt-marsh species. Exceptions to this pattern are *Spergularia media* with a seed bank in later-successional stages and *Glaux maritima* and *Juncus gerardi* with large seed banks in early-successional stages.

Implications for management

What is the significance of this study for the natural restoration of salt-marsh communities in previously embanked agriculturally exploited areas? Our results indicate that it is unlikely that restoration is possible from a long-term persistent seed bank. Much better results are expected from seed dispersal by tidal water. However, herbivory in the source area may significantly reduce seed production and minimize potential seed dispersal to the target area. This can be prevented by establishing exclosures or abandoning cattle grazing at least one year prior to the restoration of the salt marshes. Deliberate planting of salt-marsh species, or direct seeding might be necessary in cases where source areas are far away, or where barriers are present which are likely to limit seed dispersal into the target area.

In the present study, much attention has been paid to the potential dispersal of salt-marsh plant species as derived from their presence in driftline material. However, the fate of viable seeds in this material is not known. The next step, therefore, is to monitor the establishment and survival of plants in driftlines. The actual dispersal, i.e. seeds deposited at a certain site, is derived from the upper 5 mm of the soil seed bank. This method can be applied on salt marshes such as Schiermonnikoog with a relatively constant accretion rate. However, where accretion rates vary considerably, e.g. in newly inundated areas, more accurate measurements of seed input are required.

Continuous monitoring of seed dispersal and species establishment after restoring tidal access to embanked areas is likely to contribute largely to our understanding of salt-marsh systems.

Summary

This study focused on the relationship between vegetation succession and soil seed bank composition on the Schiermonnikoog (the Netherlands) salt marsh, over 100 years. The importance of driftline material in the dispersal of seeds and the relationship with succession was also investigated. The results indicate that the majority of species have a transient or short-term persistent seed bank. Seeds of most species are able to float over the salt marsh, after which they become concentrated in the driftline higher up the marsh. After plants have established, a seed bank forms, which disappears when vegetation is replaced by later successional species. Exceptions are *Spergularia media* which is still present in the seed bank of late successional stages and *Juncus gerardi* and *Glaux maritima* which appear in the seed bank of early successional stages, while absent in the vegetation. Based on the results of this study the constraints and possibilities for salt-marsh restoration from summerpolders are discussed.

Acknowledgements

We would like to thank Bart Aerts, Yzaak de Vries and especially Geurt Verweij for their assistance in the field and Jacob Hogendorf for his help in the greenhouse. The contribution of participants of the 1997 Vegetation Dynamics course is gratefully acknowledged. The comments of the referees, Rob Marrs and Paul Adam, improved the manuscript.

References

- Allen, J. R. L. & Pye, K. (1992) Coastal salt marshes: their nature and importance. *Salt marshes, morphodynamics, conservation and engineering significance* (eds J. R. L. Allen & K. Pye), pp. 1-18. Cambridge University Press, Cambridge.
- Bakker, J. P., Dijkstra, M. & Russchen, P. T. (1985) Dispersal, germination and early establishment of halophytes and glycophytes on a grazed and abandoned salt marsh gradient. *New Phytologist*, **101**, 291-308.
- Bakker, J. P., Esselink, P., Dijkema, K. S., van Duin, W. E. & de Jong, D. J. (2002) Restoration of salt marshes in the Netherlands. *Hydrobiologia*, **478**, 29-51.
- Bakker, J. P., Esselink, P., van der Wal, R. & Dijkema, K. S. (1997) Options for restoration and management of coastal salt marshes in Europe. *Restoration Ecology and Sustainable development* (eds K. M. Urbanska, N. R. Webb & P. J. Edwards), pp. 286-322. Cambridge University Press, Cambridge.
- Bekker, R. M., Bakker, J. P., Grandin, U., Kalames, R., Milberg, P., Poschod, P., Thompson, K. & Willems, J. H. (1998) Seed size, shape and vertical distribution in the soil: indicators of seed longevity. *Functional Ecology*, **12**, 834-842.
- Burd, F. (1992) *Erosion and vegetation change on the salt marshes of Essex and North Kent between 1973 and 1988*. 42. Nature Conservancy Council, Peterborough, UK.
- Dijkema, K. S. (1987) Changes in salt-marsh area in the Netherlands Wadden Sea after 1600. *Vegetation between land and sea* (eds A. H. L. Huiskes, C. W. P. M. Blom & J. Rozema), pp. 42-49. Dr. W. Junk Publishers, Dordrecht.
- Doody, J. P. (2004) Coastal squeeze - an historical perspective. *Journal of Coastal Conservation*, **10**, 138.
- Egan, T. P. & Ungar, I. A. (2000) Similarity between seed banks and above-ground vegetation along a salinity gradient. *Journal of Vegetation Science*, **11**, 189-194.
- Fenner, M. (1985) *Seed ecology*. Chapman & Hall, London.
- Gerlach, A. (1999) Winter driftline debris on the Wadden island of Mellum, Germany; distribution, quantity and decomposition. *Abhandlungen Naturwissenschaftliches Verein Bremen*, **44**, 707-724.
- Huiskes, A. H. L., Koutstaal, B. P., Herman, P. M. J., Beeftink, W. G., Markusse, M. M. & de Munck, W. (1995) Seed dispersal of halophytes in tidal salt marshes. *Journal of Ecology*, **83**, 559-567.
- Hutchings, M. J. & Russell, P. J. (1989) The seed regeneration dynamics of an emergent salt marsh. *Journal of Ecology*, **77**, 615-637.
- Jerling, L. (1988) Population dynamics of *Glaux maritima* (L.) along a distributional cline. *Vegetatio*, **74**, 170.
- Jerling, L. & Elmgren, G. (1996) Phenotypic variation in clonal growth of *Glaux maritima* along an environmental cline. *Acta Botanica Neerlandica*, **45**, 367-380.
- Koutstaal, B. P., Markusse, M. M. & de Munck, W. (1987) Aspects of seed dispersal by tidal movements. *Vegetation between land and sea: Structure and processes* (eds A. H. L. Huiskes, C. W. P. M. Blom & J. Rozema), pp. 226-233. Dr. W. Junk Publishers, Dordrecht.
- Milton, W. E. J. (1939) The occurrence of buried viable seeds in soils at different elevations and on a salt marsh. *Journal of Ecology*, **27**, 149-159.

- Morton, R. D. & Law, R. (1997) Regional species pools and the assembly of local ecological communities. *Journal of Theoretical Biology*, **187**, 321-331.
- Noe, G. B. & Zedler, J. B. (2001) Spatio-temporal variation of salt marsh seedling establishment in relation to the abiotic and biotic environment. *Journal of Vegetation Science*, **12**, 61-74.
- Oloff, H., de Leeuw, J., Bakker, J. P., Platerink, R. J., van Wijnen, H. & de Munck, W. (1997) Vegetation succession and herbivory in a salt marsh: changes induced by sea level rise and silt deposition along an elevational gradient. *Journal of Ecology*, **85**, 799-814.
- Persicke, U., Gerlach, A. & Heiber, W. (1999) Zur botanischen Zusammensetzung von Treibsel der niedersächsischen Deichvorländer und Deichabsnitte. *Drosera*, **1**, 23-34.
- Radley, G. P. (1993) The environmental objectives of managed retreat. *Managed retreat. Putting theory into practice*. Conference proceeding, London Zoo conference and business venue.
- Rand, T. A. (2000) Seed dispersal, habitat suitability and the distribution of halophytes across a salt marsh tidal gradient. *Journal of Ecology*, **88**, 608-621.
- ter Heerdt, G. N. J., Verweij, G. L., Bekker, R. M. & Bakker, J. P. (1996) An improved method for seed bank analysis: seedling emergence after removing the soil by sieving. *Functional Ecology*, **10**, 144-151.
- Thompson, K., Bakker, J. P. & Bekker, R. M. (1997) *Soil seed banks of North West Europe: methodology, density and longevity*. Cambridge University Press, Cambridge.
- Ungar, I. A. (1987) Population Ecology of halophyte seeds. *The Botanical Review*, **53**, 301-334.
- Van de Meijden, R. (1996) *Heukel's flora van Nederland*. 22nd ed. Wolters-Noordhoff, Groningen.
- van der Wal, R., van Lieshout, S., Bos, D. & Drent, R. H. (2000a) Are spring staging brent geese evicted by vegetation succession? *Ecography*, **23**, 60-69.
- van der Wal, R., van Wijnen, H., van Wieren, S., Beucher, O. & Bos, D. (2000b) On facilitation between herbivores: how brent geese profit from brown hares. *Ecology*, **81**, 969-980.
- van Wijnen, H. J. & Bakker, J. P. (1997) Nitrogen accumulation and plant species replacement in three salt-marsh systems in the Wadden sea. *Journal of Coastal Conservation*, **3**, 19-26.
- van Wijnen, H. J. & Bakker, J. P. (2001) Long-term surface elevation change in salt marshes: a prediction of marsh response to future sea-level rise. *Estuarine, Coastal and Shelf Science*, **52**, 381-390.
- Waisel, Y. (1972) *Biology of halophytes*. Academic press, New York.
- Willems, J. H. & Bik, L. P. M. (1998) Restoration of high species density in calcareous grassland: the role of seed rain and soil seed bank. *Applied Vegetation Science*, **1**, 91-100.
- Williams, E. P. B. (1994) From reclamation to restoration - changing perspectives in wetland management. Wetland Management proceedings of the international conference (Eds. R.A. Falconer & P. Goodwin) pp. 1-19, London.
- Yapp, R. H., Johns, D. & Jones, O. T. (1917) The salt marshes of the Dovey estuary. *Journal of Ecology*, **5**, 65-102.
- Zar, J. H. (1996) *Biostatistical analysis*. Prentice Hall, London.
- Zobel, M. (1997) The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? *Trends in Ecology and Evolution*, **12**, 266-269.
- Zobel, M., van der Maarel, E. & Dupré, C. (1998) Species pool: the concept, its determination and significance for community restoration. *Applied Vegetation Science*, **1**, 55-66.

Appendix 4.1. Mean number of 0.4 m² plots in which species are present in the vegetation, mean number of seedlings that emerged from different soil layers (area is 100 cm² for 0-0.5 cm, 231 cm² for 0-5 and 5-10 cm) and mean number of seedlings that emerged from driftline material with a dry weight of 10-g per sample. Different superscripts indicate significant differences ($P < 0.05$) assessed by a Nemenyi test after Kruskal-Wallis ($n = 10$). T, SP and LP represent the number of sites in which a species is classified Transient, Short-term Persistent or Long-term Persistent. The 3-yr old site and layers with less than three seeds are omitted. An asterisk denotes species of the local pool.

		Successional age (yr)					Seed bank classification		
		3	10	25	35	100	T	SP	LP
Early successional species in the established vegetation									
* <i>Aster tripolium</i>	Vegetation	0.4 ^a	6.1 ^b	.a	2.1 ^{ab}	.a	2	-	-
	0-5 cm	-	0.1	0.2	0.1	0.1			
	5-10 cm	-	0.2	0.1	-	-			
	Driftline	0.9	-	0.7	1.1	-			
* <i>Atriplex portulacoides</i>	Vegetation	1.0 ^a	7.7 ^{bc}	0.9 ^a	9.1 ^c	3.1 ^{ab}	4	-	-
	Driftline	0.1	-	0.3	1.7	1.0			
* <i>Limonium vulgare</i>	Vegetation	1.2 ^a	10.0 ^c	7.8 ^{ab}	10.0 ^c	9.5 ^{bc}	3	-	1
	0-0.5 cm	-	-	0.6	-	1.1			
	0-5 cm	0.1 ^a	0.3 ^{ab}	.a	0.4 ^{ab}	1.3 ^b			
	5-10 cm	-	-	-	-	1.6			
	Driftline	6.1 ^{ab}	2.6 ^{ab}	10.9 ^{bc}	104.2 ^c	1.4 ^a			
* <i>Plantago maritima</i>	Vegetation	.a	7.2 ^b	.a	0.3 ^a	.a	2	-	-
	0-5 cm	-	0.1	-	-	-			
	5-10 cm	-	0.1	-	-	-			
	Driftline	3.8 ^{ab}	5.3 ^{bc}	19.7 ^c	0.5 ^a	1.4 ^{ab}			
* <i>Puccinellia maritima</i>	Vegetation	8.4 ^b	10.0 ^b	0.4 ^a	7.4 ^b	0.4 ^a	4	-	-
	Driftline	0.4	0.1	-	-	-			
	Vegetation	10.0 ^b	10.0 ^b	1.3 ^a	9.3 ^b	.a	2	2	-
* <i>Salicornia</i> spp.	0-0.5 cm	1.6	0.6	0.4	1.7	0.2			
	0-5 cm	75.6 ^c	32.7 ^{bc}	0.3 ^a	4.3 ^{ab}	0.4 ^a			
	5-10 cm	33.8 ^b	0.2 ^a	.a	0.4 ^a	0.1 ^a			
	Driftline	16.5 ^b	5.1 ^{ab}	2.4 ^a	8.9 ^{ab}	1.8 ^a			
	Vegetation	3.0 ^b	1.6 ^{ab}	.a	0.1 ^a	0.1 ^a	3	-	-
* <i>Spartina anglica</i>	Vegetation	6.4 ^{bc}	10.0 ^c	.a	1.0 ^{ab}	.a	-	3	1
* <i>Spergularia media</i>	0-0.5 cm	4.7 ^{bc}	9.8 ^c	.a	1.2 ^{ab}	0.4 ^{ab}			
	0-5 cm	69.4 ^{bc}	262.8 ^c	3.9 ^a	8.3 ^{ab}	4.9 ^a			
	5-10 cm	30.7 ^{bc}	51.4 ^c	22.8 ^{bc}	7.3 ^{ab}	.a			
	Driftline	10.6	0.5	-	1.6	2.3			
	Vegetation	10.0 ^c	10.0 ^c	6.5 ^{ab}	9.8 ^{bc}	2.2 ^a	1	3	-
* <i>Suaeda maritima</i>	0-0.5 cm	14.8 ^{bc}	58.5 ^c	0.3 ^a	6.4 ^{ab}	0.1 ^a			
	0-5 cm	20.6 ^b	107.6 ^c	7.4 ^{ab}	33.1 ^{bc}	1.1 ^a			
	5-10 cm	5.5 ^b	5.8 ^b	0.3 ^a	1.2 ^{ab}	.a			
	Driftline	143.4 ^c	13.0 ^{ab}	11.6 ^{ab}	41.4 ^{bc}	2.7 ^a			
* <i>Triglochin maritima</i>	Vegetation	.a	.a	1.4 ^{ab}	1.3 ^{ab}	3.3 ^b	-	3	-
	0-0.5 cm	-	0.3	0.2	-	0.2			
	0-5 cm	.a	.a	0.6 ^{ab}	0.4 ^{ab}	1.4 ^b			
	5-10 cm	-	-	0.1	-	0.1			
	Driftline	.a	0.1a	0.4 ^{ab}	3.8 ^b	0.2 ^{ab}			
Later successional species in the established vegetation									
* <i>Agrostis stolonifera</i>	vegetation	-	0.1	-	-	-	-	3	1
	0-0.5 cm	0.2	0.4	0.4	-	0.6			
	0-5 cm	2.1 ^{ab}	2.9 ^{ab}	4.3 ^b	3.1 ^{ab}	1.4 ^a			
	5-10 cm	1.6 ^{ab}	0.5 ^a	7.0 ^b	1.6 ^a	0.1 ^a			
	driftline	10.9 ^{bc}	56.4 ^c	21.6 ^c	0.7 ^a	0.7 ^{ab}			
* <i>Seriphidium maritimum</i>	vegetation	.a	1.6 ^a	9.9 ^b	8.7 ^b	10.0 ^b	1	3	-
	0-0.5 cm	0.2 ^a	0.5 ^a	13.3 ^b	3.0 ^{ab}	11.0 ^b			
	0-5 cm	0.2 ^a	0.3 ^{ab}	22.2 ^c	3.1 ^{ab}	5.0 ^{bc}			
	5-10 cm	-	-	1.2	0.8	0.9			
	driftline	132.2 ^b	3.4 ^a	22.0 ^{ab}	464.6 ^{bc}	1638.3 ^c	2	1	-
* <i>Atriplex prostrata</i>	vegetation	.a	.a	3.0 ^b	.a	4.0 ^b			
	0-0.5 cm	-	-	0.1	0.6	0.3			
	0-5 cm	-	-	0.9	0.8	0.7			
	5-10 cm	0.1	-	0.1	0.2	-			
	Driftline	0.8 ^a	14.3 ^{bc}	53.8 ^c	84.8 ^{bc}	7.0 ^{ab}			

		Successional age (yr)					Seed bank classification		
		3	10	25	35	100	T	SP	LP
Later successional species in the established vegetation									
* <i>Elytrigia atherica</i>	vegetation	.a	0.2 ^a	0.3 ^a	.a	5.5 ^b	3	-	-
	0-0.5 cm	-	-	-	-	0.1			
	0-5 cm	-	0.1	0.2	-	-			
	5-10 cm	-	-	-	-	0.1			
	driftline	5.3 ^a	3.2 ^a	14.8 ^{ab}	9.9 ^a	29.6 ^b			
* <i>Festuca rubra</i>	vegetation	.a	3.6 ^a	9.9 ^b	5.2 ^a	10.0 ^b	1	3	-
	0-0.5 cm	0.1 ^a	0.2 ^a	3.9 ^{bc}	1.5 ^{ab}	20.2 ^c			
	0-5 cm	.a	0.5 ^a	18.9 ^b	4.3 ^{ab}	20.6 ^b			
	5-10 cm	-	-	0.5	0.4	0.5			
	driftline	86.8 ^{bc}	12.7 ^a	89.8 ^c	30.6 ^{abc}	16.8 ^{ab}			
* <i>Glaux maritima</i>	vegetation	.a	4.6 ^{ab}	0.3 ^a	8.2 ^b	8.3 ^b	1	1	2
	0-0.5 cm	.a	.a	0.6 ^a	0.1 ^a	12.1 ^b			
	0-5 cm	0.2 ^a	0.8 ^a	10.9 ^b	4.5 ^{ab}	3.5 ^{ab}			
	5-10 cm	.a	.a	26.9 ^b	8.1 ^b	2.8 ^{ab}			
	driftline	5.6 ^a	53.6 ^b	2.7 ^a	2.6 ^a	2.2 ^a			
* <i>Juncus gerardi</i>	vegetation	.a	.a	2.1 ^{ab}	2.0 ^{ab}	7.3 ^b	-	3	1
	0-0.5 cm	.a	.a	0.1 ^a	1.9 ^{ab}	41.4 ^b			
	0-5 cm	0.8 ^a	5.3 ^{ab}	8.2 ^{ab}	39.7 ^{bc}	360.3 ^c			
	5-10 cm	0.7 ^a	0.8 ^a	11.9 ^{ab}	10.2 ^b	198.2 ^b			
	driftline	0.1 ^a	6.2 ^{ab}	3.2 ^{ab}	16.4 ^b	19.9 ^b			
Rare species									
<i>Arenaria serpyllifolia</i>	driftline	-	1.8	0.5	-	-			
* <i>Armeria maritima</i>	vegetation	-	0.5	-	1.5	-	2	-	-
	driftline	-	0.3	0.1	0.1	0.4			
* <i>Atriplex littoralis</i>	Vegetation	-	-	-	-	-			
	driftline	0.1 ^a	.a	.a	1.0 ^{ab}	3.4 ^b			
<i>Centaurium littorale</i>	0-5 cm	-	0.1	0.1	0.6	-			
	5-10 cm	-	-	-	0.1	-			
	driftline	-	4.7	0.7	-	-			
<i>Centaurium pulchellum</i>	0-5 cm	-	0.4	0.3	-	-			
	5-10 cm	.a	.a	18.8 ^b	.a	.a			
	driftline	-	-	0.8	-	-			
<i>Cerastium fontanum</i>	driftline	-	1.1	0.7	2.3	-			
<i>Chenopodium</i> spp	0-0.5 cm	-	0.1	-	-	-			
	5-10 cm	-	-	0.1	-	-			
	driftline	-	0.3	0.2	2.3	-			
* <i>Cochlearia danica</i>	vegetation	-	-	-	0.1	-	1	-	-
<i>Elytrigia farctus</i>	driftline	0.1	-	-	-	-			
<i>Leontodon saxatilis</i>	driftline	0.2 ^a	6.2 ^b	0.6 ^{ab}	.a	.a			
<i>Linaria vulgaris</i>	driftline	-	0.3	-	-	-			
<i>Tripleurospermum maritimum</i>	driftline	-	-	4.2	0.1	0.1			
<i>Odontites vernus</i>	driftline	-a	6.1 ^b	0.5 ^{ab}	.a	.a			
<i>Oenothera parviflora</i>	driftline	-a	7.3 ^b	0.3 ^a	0.2 ^a	.a			
<i>Plantago coronopus</i>	0-5 cm	-	0.1	-	-	-			
	driftline	1.3 ^{ab}	128.8 ^c	5.5 ^{bc}	.a	3.1 ^{ab}			
	driftline	0.1	0.2	-	1.1	-			
<i>Polygonum aviculare</i>	driftline	-	-	0.1	-	-			
<i>Potentilla anserina</i>	driftline	-	0.3	-	-	-			
<i>Sagina maritima</i>	driftline	-	-	-	-	-			
<i>Sagina procumbens</i>	0-0.5 cm	-	-	0.1	-	-			
	0-5 cm	0.2	-	-	-	-			
	5-10 cm	0.1	-	-	-	-			
driftline	0.1	0.7	-	-	-				
<i>Sedum acre</i>	driftline	0.3	3.5	-	-	-			
<i>Senecio jacobaea</i>	driftline	-	-	0.1	-	-			
<i>Senecio sylvaticus</i>	driftline	-	-	0.1	-	-			
<i>Sonchus arvensis</i>	driftline	-	0.1	-	-	-			
* <i>Spergularia marina</i>	vegetation	-	-	-	0.5	0.5	2	-	-
<i>Stellaria media</i>	0-5 cm	-	-	0.2	-	-			
	5-10 cm	-	-	0.1	-	-			
	driftline	-	-	-	0.5	-	1	-	-
* <i>Trifolium repens</i>	0-5 cm	-	-	-	0.1	-			
	5-10 cm	-	-	0.1	-	0.2			
	driftline	-	-	0.2	-	-			
<i>Typha angustifolia</i>	0-5 cm	-	0.1	-	-	-			
	5-10 cm	0.1	-	0.1	-	-			
<i>Urtica dioica</i>	driftline	-	-	-	-	0.1			

Composition of a soil seed bank before and after de-embankment

Mineke Wolters & Angus Garbutt

In Chapter 4 it was shown that the majority of salt-marsh species does not form a long-term persistent seed bank. It was therefore assumed that the seed bank does not play an important role in the restoration of salt-marsh vegetation after de-embankment. The present Intermezzo examines whether this assumption holds for a relatively recently reclaimed salt marsh and how long it takes for halophytes to build a seed bank and for glycophytes to disappear from the seed bank after de-embankment.

Introduction

In the past two decades, several previously reclaimed salt marshes in north-west Europe have been deliberately de-embanked with the aim of restoring salt-marsh vegetation (Wolters *et al.* 2005; Chapter 3). It is assumed that target plant species will colonize naturally once tidal water is allowed to re-enter the site. During the period of reclamation, the original established salt-marsh vegetation will often be replaced by glycophyte species. However, the salt-marsh species may still be present in the soil seed bank from which they may emerge when favourable conditions for their establishment return. A prerequisite is that the seeds are viable for long enough to survive the period of embankment. Previous studies on established salt marshes implied that the majority of salt-marsh species does not form a long-term persistent seed bank, as their abundance in deeper (and presumably older) soil layers is generally much lower compared with their abundance in the upper soil seed bank or in the above-ground vegetation (Thompson *et al.* 1997; Wolters & Bakker 2002; Chapter 4). However, it remains uncertain for how long the species are able to survive in the soil and hence what the potential of the soil seed bank for salt-marsh restoration is. Of the 37 de-embankment sites identified in north-west Europe that were monitored for plant species assemblages (Wolters *et al.* 2005; Chapter 3), only one site had information on the soil seed bank before de-embankment. The seed bank of this site, which was a summerpolder before de-embankment, contained seeds of six salt-marsh species, including *Suaeda maritima*, *Spergularia marina*, *S. media*, *Salicornia* spp., *Atriplex prostrata* and *Puccinellia maritima* (Bakker *et al.* 2001). These species may have entered the soil seed bank in winter when tides could have flooded over the low summerdike, rather than having survived the period of embankment.

Information on the composition of the soil seed bank is not only important with regard to the potential establishment of target species but also for determining the possibility of establishment of non-target species. The latter possibility becomes more important when sites have a relatively high surface elevation with respect to mean sea level and/or low soil salinity, in which case glycophytes are likely to outcompete halophytes for nutrients and light. In the present Intermezzo we examined the composition of the soil seed bank of a relatively recently reclaimed salt marsh before and after de-embankment. Specific questions that were addressed are: (i) does the soil seed bank contain any target species before de-embankment? (ii) how quickly do the target species form a soil seed bank after de-embankment? (iii) what is the relationship between the soil seed bank and the above-ground established vegetation? (iv) do glycophyte seeds retain their viability in the soil seed bank after de-embankment?

Methods

Study area

The Freiston managed-realignment site is located on the south-Lincolnshire Wash coastline, east England (Myatt *et al.* 2003). The 78 ha site was embanked between 1978 and 1982 for agricultural purposes, but because the reclamation was too far seaward, the embankment accidentally breached several times during construction and nearly breached in 1996. Since 1982, the sea had no access to the reclaimed land. In order to maintain coastal protection it was decided to deliberately breach the sea defence and re-establish an existing old seawall (English Nature 2002). Construction work consisted of strengthening the old sea defence and creating artificial channels and connecting them with creeks on the fronting salt marsh. The embankment was breached at three places (each 50 m wide) at the end of August 2002 (Symonds & Collins 2004).

Established vegetation

Prior to de-embankment, a survey of the vegetation was undertaken by walking through the site with two people. Species abundance was estimated and classified into five classes: dominant (D), abundant (A), frequent (F), occasional (O) and rare (R) (Tansley 1946). The presence of target species in the first and second year after de-embankment was recorded in 100 subplots (20 cm × 20 cm) randomly placed within a 10 m² plot at six locations in July/August.

Soil seed bank

The soil seed bank was sampled in the beginning of August 2002 (i.e. one month prior to de-embankment) and on 2,3 August 2003 and 16,17 July 2004 (i.e. the first two years after de-embankment). Ten samples of three (pre-breach) or four (post-breach) cores were taken from a 10 m² area in each of six locations within the restora-

tion site with a 5 cm diameter auger at 0-5 cm depth. In the pre-breach situation samples were also taken from the 5-10 cm layer, but data are not shown because species composition in this layer was comparable to the upper layer, although in general there were fewer seeds. The samples were treated according to the seedling emergence method described in ter Heerdt *et al.* (1996). The mean of the ten samples per 10 m² of the six locations was used to calculate a grand mean for the entire restoration site. Data are expressed per m² (i.e. multiplied by 169.49 for pre-breach samples and 127.39 for post-breach samples). Species that were present with fewer than 10 seeds per m² in any one year were omitted from the analysis.

Results

Established vegetation

The established vegetation prior to de-embankment was dominated by a dense sward of *Agrostis stolonifera* and *Lolium perenne* with large patches of *Cirsium arvense* and abundant stands of *Holcus lanatus*, *Cirsium vulgare* and *Senecio jacobaea* (Figure I1.1). The site was intersected by drainage ditches on the banks of which *Elytrigia repens* and *E. atherica* occurred. Both species, as well as *Agrostis* are considered target species of the southern North-Atlantic region (Wolters *et al.* 2005; Chapter 3). Five other target species were observed, including *Festuca rubra*, *Puccinellia maritima*, *Spergularia marina*, *Salicornia* spp. and *Suaeda maritima* (Figure I1.1). The latter four species occurred in a few isolated patches along a vehicle track. After de-embankment, the original vegetation was quickly killed by the inundating seawater.

Soil seed bank

Prior to de-embankment, the soil seed bank hardly contained any target species (Fig. I1.2). Exceptions were *Agrostis stolonifera*, which was also the dominant species of the established vegetation before de-embankment, and *Sagina maritima* and *Spergularia marina* which were present with only few seeds per m². *Agrostis* remained abundant in the soil seed bank for at least two years after de-embankment. *Salicornia* spp. and *Spergularia* were the only other salt-marsh species present in the seed bank after one year of restoration. *Suaeda* became abundant in the seed bank in the second year after de-embankment. In addition, seeds of *Puccinellia maritima* and *Sagina maritima* were found in low quantity. The abundance of *Salicornia* and *Suaeda* in the soil seed bank, two years after de-embankment, was representative of their abundance in the above-ground vegetation (Fig. I1.2).

Prior to de-embankment, 17 glycophyte species were present in the soil seed bank of which seven decreased sharply in abundance after de-embankment (Fig. I1.3). Species that remained abundant despite frequent inundation with seawater were *Poa trivialis*, *Poa annua*, *Sonchus asper* and *Cirsium arvense* with more than 100 seeds per m² in the seed bank two years after de-embankment.

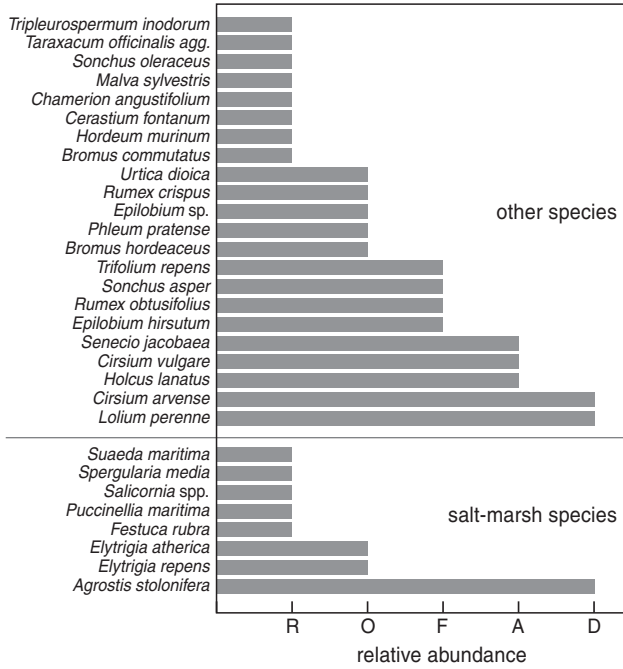


Figure II.1. Relative abundance of species in the vegetation before de-embankment (D, dominant; A, abundant; F, frequent; O, occasional; R, rare).

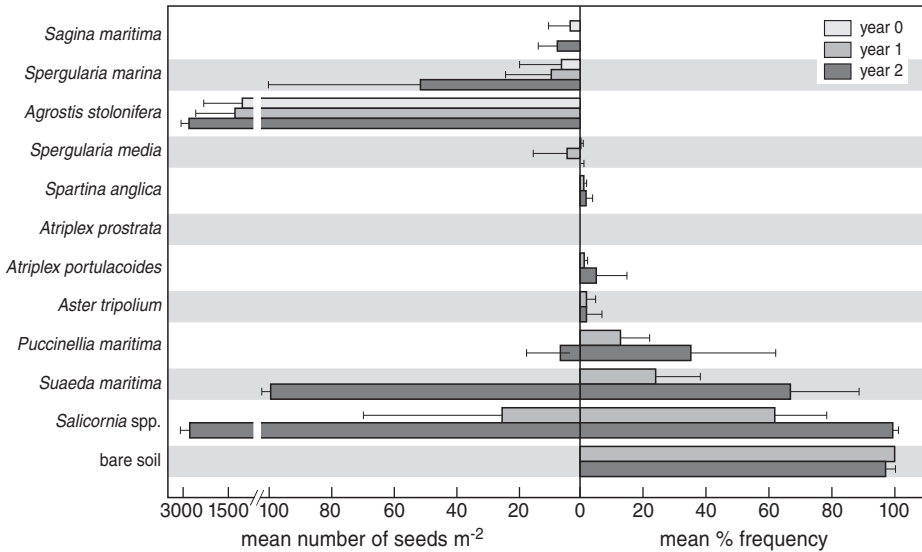


Figure II.2. Percentage frequency of occurrence of target species in the established vegetation and mean number of seeds per m² in the soil seed bank (0-5 cm) before and after de-embankment with standard deviation (n=6).

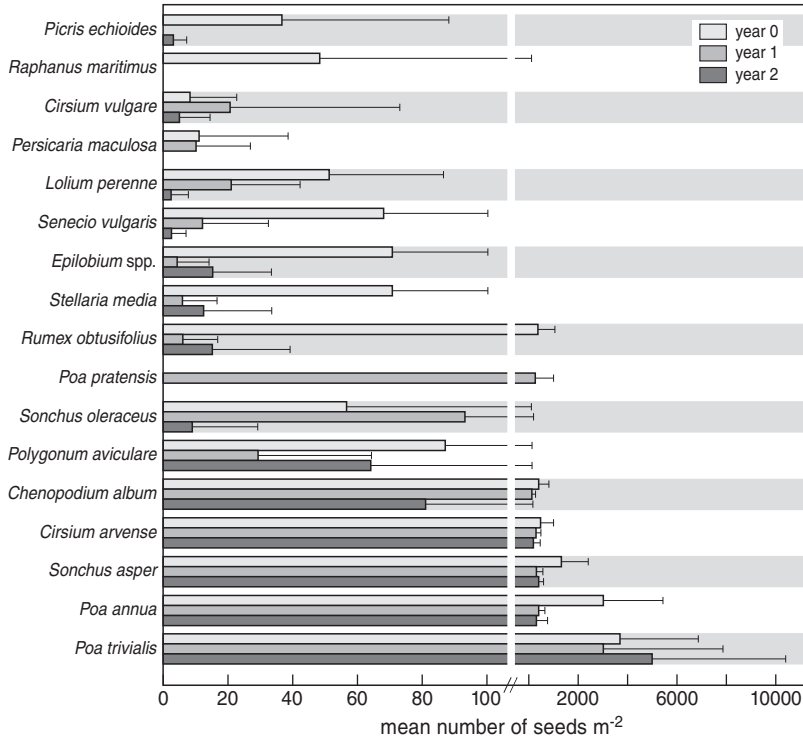


Figure 11.3. Mean number of seeds per m^2 with standard deviation ($n=6$) of glycyphytes in the soil seed bank (0-5 cm) before (year 0) and after (year 1,2) de-embankment.

Discussion

The main issue of the present Intermezzo was to determine whether the soil seed bank could play an important role in the establishment of salt-marsh species after de-embankment. The results show that, disregarding the abundance of *Agrostis* which was the dominant species in the pre-breach established vegetation, hardly any salt-marsh seed was present in the soil seed bank before de-embankment. These results imply that salt-marsh species are unable to survive a 30-year period of embankment and agricultural exploitation and support earlier conclusions that the majority of salt-marsh species does not form a long-term persistent seed bank (Thompson *et al.* 1997; Wolters & Bakker 2002; Chapter 4). Survival of seeds in the soil seed bank is of course affected by agricultural practices like ploughing, which may destroy the seeds or stimulate germination. When there is no fresh input of seeds, the soil seed bank may thus deplete over time despite the possibility of species having long-term persistent seeds.

A second issue involved the question of how quickly the target species would build a seed bank. The annual species *Suaeda maritima* and especially *Salicornia* became abundant in the seed bank within two years after de-embankment. Both species established in the vegetation within one year after de-embankment and presumably set seeds which either germinated in the following growing season or became incorporated in the soil seed bank. Seed bank formation proceeded much slower for the perennial species *Puccinellia maritima*, which was present in the established vegetation in the first year after de-embankment but occurred with less than 20 seeds per m² in the seed bank in the following year. *Aster tripolium*, *Atriplex portulacoides* and *Spartina anglica* did not yet form a seed bank despite having established in the vegetation. *Aster* (Clapham *et al.* 1942) and *Puccinellia* (Gray & Scott 1977) normally do not flower in the same year of seed germination and therefore do not contribute to the seed bank in that year. Seed production in *Atriplex* (Chapman 1950) and *Spartina* (Ranwell 1964) can be highly variable and the subsequent spread of these species may depend more on vegetative reproduction.

The third question was whether glycophyte seeds would retain their viability after de-embankment when the site became frequently inundated by seawater. There appear to be two distinct groups of species, the seed bank of the first group of species (*Poa annua*, *Poa trivialis*, *Sonchus asper*, *Cirsium arvense*, *Chenopodium album*, *Sonchus oleraceus*, *Polygonum aviculare* and *Poa pratensis*) did not change perceptibly after de-embankment, whereas the seed bank of the second group (*Rumex obtusifolius*, *Stellaria media*, *Epilobium* spp., *Senecio vulgaris*, *Lolium perenne*, *Raphanus maritimus* and *Picris echioides*) rapidly diminished during the first two restoration years. With the exception of *Cirsium arvense* and *Poa pratensis*, all species of the first group were classified as having a long-term persistent seed bank (i.e. surviving for at least five years) (Tamis *et al.* 2004). The second group included three species with a long-term persistent seed bank, one with a transient seed bank and three species that have not been classified (Tamis *et al.* 2004). Nearly all species of both groups have an Ellenberg indicator value for salinity of 0, which implies that they are absent from saline sites and non-persistent if subjected to saline spray or water (Hill *et al.* 1999). *Poa annua* and *Chenopodium album* are slightly salt tolerant and *Raphanus maritimus* is common in coastal sites. None of those three species, however, emerged from the soil seed bank. *Agrostis stolonifera* is also slightly salt tolerant, but despite its abundance in the soil seed bank and the established vegetation this species did not survive or re-establish after de-embankment.

Our results show that upon de-embankment, the original glycophyte vegetation is quickly killed by seawater. However, seeds of several glycophyte species remain viable in the soil seed bank for at least two years after de-embankment and thus have the potential to emerge when favourable environmental conditions (i.e. absence of saline water) occur. Annual salt-marsh species are the first to colonize the site and to form a soil seed bank. Establishment and seed bank formation proceeds much slower for perennial salt-marsh species, which may rely more on vegetative reproduction.

Summary

The restoration of salt-marsh vegetation after de-embankment relies on the assumption that target species will establish spontaneously. One possibility is establishment of target species from the soil seed bank of the restoration site, provided that seeds have survived the period of embankment. Our results show that most salt-marsh species have disappeared from the soil seed bank within three decades of embankment and agricultural exploitation. After de-embankment, the annual species *Salicornia* and *Suaeda* were the first to establish in the vegetation and subsequently to form a seed bank. Several glycophyte species remained abundant in the soil seed bank despite frequent inundation of the site with seawater. The majority of these species were classified as having a long-term persistent seed bank. For the successful restoration of salt-marsh vegetation target species have to be dispersed from a nearby source area. When sites are high in elevation with respect to sea level, establishment of glycophyte species from the persistent seed bank may negatively affect restoration success.

The assistance of Sijbren Otto with the fieldwork was much appreciated.

References

- Bakker, J.P., van den Brink, G., Verweij, G.L. & Esselink, P. (2001) Zaadvoorraad en dispersie bij een proefverkweldering in Noard-Fryslân Bûtendyks. *De Levende Natuur*, **102**, 19-23.
- Chapman V. J. (1950) Biological flora of the British Isles. *Halimione portulacoides*. *Journal of Ecology*, **38**, 214-222.
- Clapham A. R., Pearsall W. H., & Richards P. W. (1942) Biological flora of the British isles. *Aster tripolium*. *Journal of Ecology*, **30**, 385-395.
- English Nature (2002) *Reducing the risk of flooding by working with nature*. Press Release 11 October 2002. English Nature, Peterborough.
- Gray A. J. & Scott R. (1977) Biological flora of the British Isles. *Puccinellia maritima*. *Journal of Ecology*, **65**, 699-716.
- Hill, M. O., Mountford, J. O., Roy, D. B. & Bunce, R. G. H. (1999). Ellenberg's indicator values for British plants. pp. 1-46. Monks Wood, Institute of Terrestrial Ecology, UK.
- Ranwell, D. S. (1964) *Spartina* salt marshes in southern England. III Rates of establishment, succession and nutrient supply at Bridgewater Bay, Somerset. *Journal of Ecology*, **52**, 95-106.
- Symonds, A.M. & Collins, M.B. (2004) Sediment dynamics associated with managed realignment; Freiston Shore, the Wash, UK. Coastal Engineering, pp. 3173-3185. World Scientific Publishing Co. Pte.Ltd.
- Tansley, A.G. (1946) *Introduction to plant ecology*. Allen & Unwin, London.
- ter Heerdt, G.H.J., Verweij, G.L., Bekker, R.M. & Bakker, J.P. (1996) An improved method for seed bank analysis: seedling emergence after removing the soil by sieving. *Functional Ecology*, **10**, 144-151.
- Tamis, W.L.M., van der Meijden, R., Runhaar, J., Bekker, R.M., Ozinga, W.A., Odé, B. & Hoste, I. (2004) Standaardlijst van de Nederlandse flora 2003. *Gorteria*, **30**, 101-195.
- Thompson, K. Bakker, J.P. & Bekker, R.M. (1997) *Soil seed banks of North West Europe: methodology, density and longevity*. Cambridge University Press, Cambridge.
- Wolters, M., Garbutt, A. & Bakker, J.P. (2005) Salt-marsh restoration: evaluating the success of de-embankments in north-west Europe. *Biological Conservation*, **123**, 249-268.
- Wolters, M. & Bakker, J.P. (2002) Soil seed bank and driftline composition along a successional gradient on a temperate salt marsh. *Applied Vegetation Science*, **5**, 55-62.



Lunch break at Tollesbury, with Sijbren Otto waiting for the tide to turn before we can collect the astroturf mats

Astroturf seed traps for studying hydrochory

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Functional Ecology (2004) **18**, 141-147.

Chapter 4 showed that large quantities of seeds of different species were present in driftline material, deposited in a narrow zone after extreme weather and tidal conditions. It is not clear, however, whether and where the seeds are actually deposited on the salt-marsh surface after normal tidal flooding. The present chapter introduces the use of astroturf seed traps for studying hydrochory and tests the effectiveness of astroturf in trapping and retaining seeds of different salt-marsh species after tidal inundation. The aim of this chapter is to provide a technical study; the ecological aspects of using astroturf for studying hydrochory is the focus of the next chapter.

Introduction

Hydrochory, or diaspore dispersal by water, is an important aspect of the vegetation dynamics of plant species growing near streams, rivers, oceans and seas. It also plays an essential role in the restoration of wetlands. However, the development of reliable and fast methods for empirical studies on hydrochory remains a considerable challenge, largely because many dispersal units are too small, and movement of water too unpredictable, to trace sufficiently large numbers of seeds within a reasonable timespan. Several researchers have circumvented this problem by examining hydrochory indirectly. Examples of such studies include the use of seed mimics such as wooden blocks (Nilsson, Gardfjell, & Grelsson 1991; Andersson, Nilsson, & Johansson 2000), sunflower seeds (Koutstaal, Markusse, & De Munck 1987; Andersson *et al.* 2000) or plastic glitter (Levine 2001) to measure dispersal patterns. Other studies focus on dispersal traits such as seed buoyancy and morphology to explain the observed distribution of plant species along riverbanks (Morton & Hogg 1989; Johansson, Nilsson, & Nilsson 1996; Danvind & Nilsson 1997; Melcher, Bouman, & Cleef 2000; Nilsson *et al.*

2002). Hydrochory has also been measured through seed-addition experiments performed in the field (Schneider & Sharitz 1988; Orth, Luckenbach, & Moore 1994; Levine 2001; Lacap *et al.* 2002) or in highly sophisticated flume tanks (Merritt & Wohl 2002). All these studies provide valuable information on dispersal potential. However, they do not reveal what proportion of diaspores of which species actually land at a certain place at a specific time.

A more direct method for studying hydrochory is the sampling of drift material deposited along riverbanks (Skoglund 1990; Cellot, Mouillot, & Henry 1998) or coastlines (Bakker, Dijkstra, & Russchen 1985; Smith *et al.* 1990; Hacker 1990; Persicke, Gerlach, & Heiber 1999; Gerlach 1999; Bakker *et al.* 2001; Wolters & Bakker 2002). While this material will provide much insight into the composition and abundance of water-dispersed diaspores, a major drawback is that driftlines are generally formed only during unusually high tide events and/or storms, and therefore might not be representative of dispersal under ordinary circumstances. A solution to this problem is the use of seed traps which can measure hydrochory under normal circumstances at predefined locations and times. Floating buckets lined with netting have been used to study hydrochory in rivers (Schneider *et al.* 1988; Middleton 1995; Middleton 2000), and floating and standing nets were used to study seed dispersal by tidal water on salt marshes (Huiskes *et al.* 1995). However, these traps do not provide information on the deposition of seeds at the surface from which they may establish during the growing season. As far as we are aware, there are only two studies in which seeds have been trapped on the surface of (in both cases) a salt marsh. In these studies, Styrofoam plates covered with a resinous material (Tanglefoot) were fastened to the ground to estimate local dispersal (Ellison 1987; Rand 2000). The resinous material remained sticky after repeated inundation with seawater. Nevertheless on highly sedimentary coasts it is unlikely that the traps would capture seeds sufficiently, as only seeds in direct contact with the trapping surface would be retained. Also, the analysis of the captured seeds by microscope is time-consuming and does not provide information about the viability of the seeds. Clearly there is a need for an alternative or complementary method for studying hydrochory. Here we introduce the use of astroturf for trapping water-dispersed diaspores. The method has been tested successfully on salt marshes and has recently been tested by others on riverbanks (Goodson *et al.* 2003; Steiger *et al.* 2003). Here we have investigated the rate of deposition of diaspores after a few tidal inundations and compared it with the composition of the established vegetation. In addition, we examined the seed-retaining efficiency of the astroturf.

Methods

Natural diaspore dispersal

Seed traps were made from 45 x 45 cm polyethylene astroturf mats. Each mat contained \approx 1600 tufts with a diameter of 0.5 cm at the base and consisting of eight 2 cm

high shoots. The mats were fastened to the salt-marsh surface at four corners by 17 cm long stainless steel pegs. A plastic bag was placed under the astroturf mats to avoid seeds from the soil surface adhering to the bottom of the mat. Vegetation taller than 20 cm and within 2 m of the astroturf was cut and removed.

Replicates of five astroturf mats were placed on an ungrazed pioneer, low and high salt marsh (-0.10, 0.40 and 0.90 m + mean high tide, MHT, respectively) on 2 December 1999, when high water levels were predicted. The mats were collected two days later when the pioneer and low zone had been inundated four times and the high marsh twice. The number of tidal inundations was calculated afterwards from actual tide data recorded at the nearest tide gauge (data from www.waterbase.nl) with acknowledgements to the Ministerie van Verkeer en Waterstaat)

After tidal inundation, the mats were collected in separate bags and taken to the laboratory to be rinsed. This was done by placing a mat upright on a 0.212 mm mesh sieve and directing a jet of water from top to bottom. Depending on the amount of accumulated sediment, it took between 5 and 15 min to completely rinse one mat. Where necessary, the material collected on the sieve was washed gently to remove a surplus of fine sediment, which would pass through the 0.212 mm mesh sieve while the seeds would be retained. The remaining material was then spread in a thin layer (< 5 mm) on a tray filled with sterile potting soil and a 4 mm layer of sterile sand according to the method described by ter Heerdt *et al.* (1996). The samples were stored in a dark cold room at 4°C for one month to allow for cold stratification. After this period, the samples were transferred to a glasshouse (25°C day temperature, 15 °C night temperature, 15 h light period, automatic watering for 1 min twice a day). Emerging seedlings and tillering stolons were identified, counted and removed as soon as possible, or where there was difficulty with identification they were transferred to separate flowerpots and left to mature. After six weeks, germination had usually ceased. The samples were then left to dry out for a week, after which the top layer of sterile sand including the sample could be crumbled by hand, then watered and placed in the glasshouse for another two-week germination period. This procedure was applied to expose seeds buried deeper in the sample layer to the light and reduce the chance of seeds remaining dormant (ter Heerdt *et al.* 1996).

Vegetation

To determine whether all species present in the established vegetation were represented on the astroturf mats, the vegetation composition of the pioneer, low and high marsh zone was described in July 1999. In each zone the presence of a species was recorded in ten replicates of 2 x 2 m plots subdivided into ten subplots. A Sørensen similarity index (Jongman *et al.* 1995) was calculated for all species encountered in the established vegetation or on the astroturf mats, irrespective of their abundance; as

$$2C / (A + B),$$

where C is the number of species shared and A and B are the total number of species on the astroturf mats and in the vegetation, respectively. Nomenclature follows van der Meijden (1996)

Seed-retaining efficiency

To determine whether the seed-retaining ability of astroturf mats was different for different species, seeds of three common salt-marsh species (*Aster tripolium*, *Salicornia* spp. and *Suaeda maritima*) were added to the mats before tidal inundation. Prior to this experiment, the seed size, weight and flotation time were measured (Table 5.1). The weight of one seed was calculated from a sample containing 50 seeds. Flotation time was measured by placing four replicates of 50 seeds in plastic cups filled with full-strength seawater. To simulate water movement, the cups were placed in a shaking machine (shaking for 24 h day⁻¹, with a frequency of 75 times min⁻¹ and an amplitude of 1.5 cm). For the seed-retaining experiment, 20 seeds were placed in the centre of astroturf mats. Five sets of three mats containing 60 seeds (20 per species) were placed on pioneer, low and mid-marsh zones (-0.55, 0.55 and 0.85 m + MHT, respectively) of a salt marsh for which the extent and frequency of tidal inundation was highly predictable. A clean astroturf mat was placed with each replicate of three to control for natural seed dispersal. The first set of mats was collected after 6 h, when the tide had flooded and ebbed once. The other sets were picked up after 24 h, 30 h, 7 days and 28 days. The mats were rinsed as before and the remaining material was checked for the presence of seeds of the three species.

Table 5.1. Seed characteristics and flotation time: number of days after which 50% (T₅₀) and 100% (T₁₀₀) of seeds have sunk. Weight of one seed based on a sample containing 50 seeds. Seed size calculated as mean of ten seeds, measured over the longest axis.

Species	Weight (mg)	Size (mm)	Shape	T ₅₀ (days)	T ₁₀₀ (days)
<i>Aster tripolium</i>	3.70	6.64	Elongated	4	71
<i>Salicornia</i> spp.	0.422	1.40	Oval	1	26
<i>Suaeda maritima</i>	1.68	2.10	Disc	1	>90

Results

Natural diaspore dispersal

The astroturf mats were successful in trapping diaspores of different species. In the pioneer zone, for example, 745 propagules per m² of five different species emerged from material trapped during four tidal inundations (Table 5.2). Significantly more species were captured on the high marsh compared to the pioneer zone (Tukey's HSD, $\alpha = 0.05$), but there was no statistical difference among the number of diaspores captured in the three zones. Diaspores of *Salicornia* spp. were the most abundant of those

Table 5.2. Mean number (\pm SD, $n = 5$ for pioneer and low marsh, $n = 4$ for high marsh) of seedlings (I_{mean}) and species (S_{mean}) per m^2 emerging from material trapped on astroturf mats after four (pioneer and low marsh) or two (high marsh) inundations. Different superscripts indicate significant differences after Tukey's HSD multiple comparison test.

Zone	I_{mean}	S_{mean}
Pioneer	745 \pm 317 ^a	3.4 \pm 0.9 ^a
Low	644 \pm 373 ^a	5.6 \pm 0.9 ^{ab}
High	310 \pm 124 ^a	8.0 \pm 2.6 ^b

trapped on astroturf mats in the pioneer and low marsh zones followed by *Spergularia media* and *Suaeda maritima* (Table 5.3). Propagules of *Plantago maritima*, *Suaeda maritima*, *Atriplex prostrata* and *Tripleurospermum maritimum* dominated the astroturf mats in the high marsh zone (Table 5.3). Only *Puccinellia maritima* and *Agrostis stolonifera* had tillering stolons as vegetative diaspores.

Vegetation composition

The established vegetation of the pioneer zone was dominated by *Salicornia* spp., *Puccinellia maritima* and *Suaeda maritima* (Table 5.3). Seven more species were encountered, but at low frequency. The low marsh was dominated by the same three species as the pioneer marsh, with the addition of *Spergularia media* and *S. marina* (Table 5.3). Seven species occurred in more than 50% of the plots on the high marsh: *Agrostis stolonifera*, *Plantago maritima*, *Puccinellia maritima*, *Spergularia media*, *Festuca rubra*, *Aster tripolium* and *Glaux maritima* (Table 5.3).

In total, 17 different species were recorded in the vegetation, of which ten were also collected on the astroturf mats (Table 5.4). Five species (*Sagina procumbens*, *Cirsium arvense*, *Tripleurospermum maritimum*, *Poa annua* and *Lolium perenne*) were present on the astroturf mats, but absent from the vegetation (Table 5.3). The similarity indices between the composition of the established vegetation and generative and vegetative diaspores trapped on astroturf mats varied from 0.53 for the pioneer zone to 0.69 for the high marsh (Table 5.4). All zones combined resulted in a similarity index of 0.63 (Table 5.4).

Seed-retaining efficiency

A General Linear Model (SPSS 9.0) was used to assess whether the seed-retaining ability of the astroturf was different for different species. Location and species were entered as factor variables with the number of tides as a covariant. The percentage of seeds remaining on the astroturf mats was used as the dependent variable after arcsine transformation. All interactions, as well as individual factors, were tested. As expected, a significant interaction occurred between location and the number of tides ($P \leq 0.001$), hence these two variables were not tested individually. There was no sig-

Table 5.3. Classification of percentage frequency of species in the established vegetation in three classes: >50, 20-50 and <20 and mean number (\pm SD, $n = 5$ for pioneer and low marsh, $n = 4$ for high marsh) of seedlings emerging from material trapped on astroturf mats, after four (pioneer and low marsh) or two (high marsh) inundations.

Species	Percentage frequency in vegetation			Mean number diaspores m ⁻² astroturf
	>50	20-50	<20	
Pioneer				
<i>Puccinellia maritima</i>	*			
<i>Salicornia</i> spp.	*			670 \pm 313
<i>Suaeda maritima</i>	*			36.3 \pm 20.4
<i>Aster tripolium</i>			*	
<i>Atriplex portulacoides</i>			*	
<i>Atriplex prostrata</i>			*	
<i>Plantago maritima</i>			*	7.8 \pm 11.3
<i>Spartina anglica</i>			*	
<i>Spergularia media</i>			*	19.6 \pm 19.3
<i>Spergularia marina</i>			*	
<i>Sagina procumbens</i>				7.8 \pm 17.5
Low				
<i>Puccinellia maritima</i>	*			2.0 \pm 4.4
<i>Salicornia</i> spp.	*			249 \pm 156
<i>Spergularia media</i>	*			231 \pm 98.9
<i>Spergularia marina</i>	*			
<i>Suaeda maritima</i>	*			105 \pm 111
<i>Aster tripolium</i>		*		6.9 \pm 4.4
<i>Plantago maritima</i>		*		1.0 \pm 2.2
<i>Atriplex prostrata</i>			*	40.2 \pm 87.1
<i>Atriplex portulacoides</i>			*	
<i>Festuca rubra</i>			*	
<i>Glaux maritima</i>			*	
<i>Spartina anglica</i>			*	
<i>Cirsium arvense</i>				2.0 \pm 4.3
<i>Tripleurospermum maritimum</i>				1.0 \pm 2.2
<i>Poa annua</i>				1.0 \pm 2.2
<i>Sagina procumbens</i>				4.9 \pm 6.9
High				
<i>Agrostis stolonifera</i>	*			2.5 \pm 2.8
<i>Aster tripolium</i>	*			1.2 \pm 2.5
<i>Festuca rubra</i>	*			
<i>Glaux maritima</i>	*			
<i>Plantago maritima</i>	*			98.0 \pm 60.1
<i>Puccinellia maritima</i>	*			1.2 \pm 2.5
<i>Spergularia media</i>	*			8.6 \pm 10.9
<i>Atriplex prostrata</i>		*		61.3 \pm 27.0
<i>Elytrigia atherica</i>			*	
<i>Plantago major</i>			*	2.5 \pm 4.9
<i>Potentilla anserina</i>			*	
<i>Salicornia</i> spp.			*	6.1 \pm 2.5
<i>Spergularia marina</i>			*	
<i>Suaeda maritima</i>			*	69.8 \pm 39.9
<i>Triglochin maritima</i>			*	1.2 \pm 2.5
<i>Cirsium arvense</i>				2.5 \pm 2.8
<i>Lolium perenne</i>				1.2 \pm 2.5
<i>Tripleurospermum maritimum</i>				45.3 \pm 36.3
<i>Sagina procumbens</i>				8.6 \pm 17.2

Table 5.4. Number of species collected on astroturf (A); in the vegetation (B); and shared (C); and Sørensen similarity index between species in established vegetation and those trapped on astroturf mats in each salt-marsh zone after four (low and pioneer marsh) and two (high marsh) inundations.

Zone	A	B	C	Similarity index
Pioneer	5	10	4	0.53
Low	11	12	7	0.61
High	14	15	10	0.69
All	15	17	10	0.63

Table 5.5. Number of seeds found on control astro turfs after tidal inundation for 0.25 – 28 days.

Zone	species	Number of seeds found after time period (days):				
		0.25	1	1.25	7	28
Pioneer	<i>Aster</i>	0	0	0	0	0
	<i>Salicornia</i>	2	1	0	1	0
	<i>Suaeda</i>	0	0	0	1	0
Low	<i>Aster</i>	0	0	0	0	0
	<i>Salicornia</i>	29	1	1	4	0
	<i>Suaeda</i>	0	0	0	0	0
Mid	<i>Aster</i>	0	0	0	0	0
	<i>Salicornia</i>	0	2	2	5	0
	<i>Suaeda</i>	1	0	1	0	0

nificant effect of species on the seed-retaining ability ($P = 0.210$). With the first tidal inundation, seeds of all three species disappeared more readily from astroturf mats placed in the pioneer zone compared to mats in the low and mid-marsh zone (Tukey's HSD test, $\alpha = 0.05$) (Fig. 5.1). After one month (54, 24 and six tidal inundations for pioneer, low and mid-marsh, respectively) 15-34% of the *Aster tripolium* seeds, 29-50% of *Salicornia* spp. seeds and 10-24% of *Suaeda maritima* seeds were retrieved from the astroturf mats (Fig. 5.1). During the experiment, no seeds of *Aster tripolium* and one seed of *Suaeda maritima* on each of three occasions were trapped on the control mats ($n = 15$) (Table 5.5). In contrast, natural seed dispersal of *Salicornia* spp. resulted in an excess of seeds on astroturf mats in the low marsh during the first tidal inundation (Fig. 5.1), with 29 seeds being captured on a control mat (Table 5.5). The number of seeds of each species found on the control mats has been subtracted from the number left on the corresponding astroturf mats (Fig. 5.1).

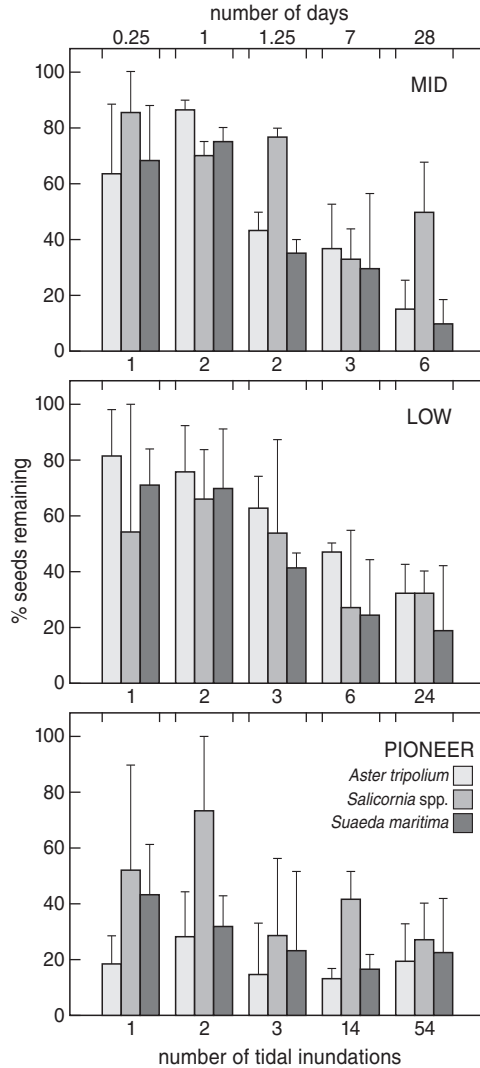


Figure 5.1. Mean percentage of seeds, with standard deviation ($n = 3$) of *Aster tripolium*, *Salicornia* spp. and *Suaeda maritima*, retained on astroturf mats on the mid-marsh, low marsh and pioneer zone after successive tidal inundations over a period of 28 days. Note the different x-axis scales.

Discussion

One of the main questions for this study was whether astroturf mats would effectively capture water-dispersed propagules. Our results demonstrate that this is the case with up to 745 seeds m^{-2} and a total of 15 different species being captured. Such yields are impressive, considering the astroturf mats were inundated only two or four times.

Approximately the same number of species (14), but many more viable seeds (13800 m⁻²) were encountered in driftline material collected from our study area in autumn 1996 (Bakker *et al.* 2001). This nearly fourfold increase was probably because the volume of driftline material sampled was much larger than that captured on the astroturf mats. On a different salt marsh, Huiskes *et al.* (1995) collected 2619 and 842 propagules of 14 and eight species, respectively, in their floating and standing nets during one tidal inundation in the same month in two successive years. The opening of the nets was 19.5 cm diameter for the standing nets and 68 × 24 cm (width × height) for the floating nets. Viability of the seeds was not tested. In a recent study, 24 × 36 cm astroturf traps were used to investigate the deposition of seeds within winter-flow deposited sediment along a river. In this study, a mean of 517 viable seeds m⁻² and a total of 73 species were captured over a five-month period. The number of species and seeds were positively related to the number of inundations (Goodson *et al.* 2003).

A second important question was whether all species present in the local vegetation were trapped on the astroturf mats. Our results show that of the 17 species recorded in the vegetation of the three salt-marsh zones combined, ten were collected on the astroturf mats (Table 5.4). However, when taking into account only those species that occurred in more than 50% of the plots in the vegetation (Table 5.3), 80% of those species was trapped on the astroturf mats. The absence of *Glaux maritima* and *Potentilla anserina* on the astroturf can be explained by the low seed production of these species during the study period. *Spergularia marina* could have been missed because seedlings of this species are easily confused with *S. media*. Nevertheless, a fraction of all seedlings that were left to mature in the glasshouse turned out to be exclusively *S. marina*. Seeds of *Spartina anglica*, *Puccinellia maritima* and *Atriplex portulacoides* were also rarely found in the seed bank or in driftline material at another salt marsh, even though these species were abundant in the vegetation (Wolters & Bakker 2002). It might be argued that these seeds could have remained dormant throughout the germination period, but the above study, in which the contents of a soil seed bank sample were viewed under a microscope after the six-week germination period, showed that no new species were detected and that the number of seeds remaining accounted for only 1-3% of the total seed bank (Wolters & Bakker 2002).

The similarity indices between vegetation and dispersed diaspores increased from pioneer to high marsh (Table 5.4). This pattern corresponds with studies comparing soil seed bank data with vegetation composition (Bekker *et al.* 2000; Wolters *et al.* 2002), where similarity increases with successional age. In a study where astroturf traps were used to study seed dispersal along a river, similarity indices between vegetation and deposited viable seeds varied between 0.558 and 0.603 for different sites (Goodson *et al.* 2003). As it was our objective to write a technical report and not an ecological study, it is beyond the scope of this paper to discuss these observations in detail. However, astroturf seed traps can be a helpful tool for studying fundamental questions about seed dispersal. For example, are seeds mainly dispersed locally, or are seeds of different species mixed and then distributed evenly by the inundating water?

The third question of our study was whether seeds would stay permanently on the astroturf mats, irrespective of the number of tidal inundations or the period of time. We focussed on three common salt-marsh species with different seed characteristics, to investigate whether this would influence the seed retention time. The results show that seeds added to the centre of the astroturf did not stay there permanently during multiple tidal inundations. The three species, irrespective of their seed size, weight or shape behaved similarly. Especially on the lowest elevation, seeds quickly disappeared from the mats after the first tidal inundation (Fig. 5.1). From this experiment it can be concluded that, apart from the frequency of tidal inundation, the duration and/or flow velocity appear to be important factors influencing hydrochory. In a flume channel experiment, Merritt & Wohl (2002) also demonstrated that flow regime is an important factor explaining differences in seed deposition. Natural seed dispersal measured via astroturf traps is therefore the result of the net transport of seeds by incoming and outgoing tides. Although the method underestimates the total rate of dispersal, astroturf mats are more efficient in retaining seeds compared to small (10 x 10 cm) pieces of lace placed on an intertidal flat and in a *Puccinellia maritima* stand. These pieces of lace retained between 1 and 3% of seeds of *Aster tripolium*, *Spergularia* spp., *Limonium vulgare*, *Triglochin maritima* and *Plantago maritima* after two tidal inundations (Dijkstra 1985).

Our results establish the astroturf mat as an effective and practical tool for investigating hydrochory. Not only can the traps be used to study fundamental questions related to population dynamics of salt-marsh and riverine species, but they will also be very useful in more applied research. In restoration ecology, for example, where management practices are aimed at re-establishing plant species, knowledge about actual seed dispersal in the field will be extremely useful (Bakker *et al.* 1996). So far, few empirical studies on seed dispersal are known, indicating a need for more field data. The method presented here will hopefully stimulate the research in this field.

We recommend the following protocol for using astroturf to study hydrochory:

- Put a plastic bag underneath the astroturf to avoid adherence of seeds from the soil surface to the bottom of the mats.
- Place astroturf mats (e.g. 45 x 45 cm) on the surface of the study site and fasten at four corners with at least 17 cm long stainless steel pegs.
- Collect the mats after one or more inundations and put them in separate bags for transportation.
- Rinse the mats by placing them upright on a 0.212 mm mesh sieve and directing a jet of water from top to bottom.
- To remove a surplus of sediment, gently wash the collected material .
- Spread the remaining material on trays filled with sterile potting soil, and place the trays in a glasshouse (daily watering, 15 h light period, 25°C day temperature, 15°C night temperature).
- Identify, count and remove seedlings as soon as possible.

- After c. six weeks leave the trays to dry, after which the top layer of sand including the sample can be crumbled to expose deeper buried seeds to the light. Water the trays for another two weeks after which germination has usually ceased.

It is recommended to store samples collected before the winter period, in a dark room at 4°C to allow for cold stratification.

Summary

Astroturf mats can effectively trap diaspores dispersed by tidal water. Within four tidal inundations, up to 745 propagules per m² and between three and eight different species per astroturf mat were trapped. Overall, 15 different species were collected on astroturf mats, ten of which were also present in the local established vegetation. The other five species must have come from further away, making the method also suitable for studying long-distance dispersal. The seed-retaining efficiency of the astroturf did not differ significantly for species with different seed characteristics.

The method will be useful for assessing actual seed dispersal at specific sites and over specific periods of time, and has particular relevance in predicting and evaluating the success of ecological restoration projects.

Acknowledgements

The assistance of Jacob Hogendorf in supplying the astroturf mats was much appreciated.

References

- Andersson, E., Nilsson, C., & Johansson, M.E. (2000) Plant dispersal in boreal rivers and its relation to the diversity of riparian flora. *Journal of Biogeography* **27**, 1095-1106.
- Bakker, J.P., Dijkstra, M., & Russchen, P.T. (1985) Dispersal, germination and early establishment of halophytes and glycophytes on a grazed and abandoned salt marsh gradient. *New Phytologist* **101**, 291-308.
- Bakker, J.P., Poschlod, P., Strykstra, R.J., Bakker, R.M. & Thompson, K. (1996) Seed banks and seed dispersal: important topics in restoration ecology. *Acta Botanica Neerlandica* **45**, 461-490.
- Bakker, J.P., van den Brink, G., Verwey, G.L., & Esselink, P. (2001) Zaaivoorraad en dispersie bij een proefverkweldering in Noard-Fryslân Bûtendyks. *De Levende Natuur* **102**, 19-23.
- Bekker, R.M., Verweij, G.L., Bakker, J.P. & Fresco, L.F.M. (2000) Soil seed bank dynamics in hayfield succession. *Journal of Ecology* **88**, 594-607.
- Cellot, B., Mouillot, F., & Henry, C.P. (1998) Flood drift and propagule bank of aquatic macrophytes in a riverine wetland. *Journal of Vegetation Science* **9**, 631-640.
- Danvind, M. & Nilsson, C. (1997) Seed floatation ability and distribution of alpine plants along a northern Swedish river. *Journal of Vegetation Science* **8**, 271-276.
- Dijkstra, M. (1985) *Enkele mogelijke oorzaken van verschillen in vegetatie tussen de onbeweide en de door jongvee beweide Oosterkwelder, Schiermonnikoog*. MSc thesis, University of Groningen.
- Ellison, A.M. (1987) Effects of competition, disturbance, and herbivory on *Salicornia europaea*. *Ecology* **68**, 576-586.

- Gerlach, A. (1999) Winter driftline debris on the wadden island of Mellum, Germany; distribution, quantity and decomposition. *Abhandlungen Naturwissenschaftliche Verein Bremen*, **44**, 707-724.
- Goodson, J.M., Gurnell, A.M., Angold, P.G., Morrissey, I.P. (2003) Evidence for hydrochory and the deposition of viable seeds within winter flow-deposited sediments: the river Dole, Derbyshire, UK. *River Research and Applications*, **19**: 317-334.
- Hacker, J.B. (1990) Drift seeds and fruit on Raine Island, northern Great Barrier Reef, Australia. *Journal of Biogeography*, **17**, 19-24.
- Huiskes, A.H.L., Koutstaal, B.P., Herman, P.M.J., Beeftink, W.G., Markusse, M.M., & De Munck, W. (1995) Seed dispersal of halophytes in tidal salt marshes. *Journal of Ecology*, **83**, 559-567.
- Johansson, M.E., Nilsson, C., & Nilsson, E. (1996) Do rivers function as corridors for plant dispersal? *Journal of Vegetation Science*, **7**, 593-598.
- Jongman, R.H.G., ter Braak, C.J.F. & van Tongeren, O.F.R. (1995). *Data analysis in community and landscape ecology*. Cambridge University Press, Cambridge.
- Koutstaal, B.P., Markusse, M.M., & De Munck, W. (1987) Aspects of seed dispersal by tidal movements. *Vegetation between land and sea: Structure and processes* (eds A.H.L.Huiskes, C.W.P.M.Blom, & J.Rozema), pp 226-233. Dr. W. Junk publishers, Dordrecht, NL.
- Lacap, C.D.A., Vermaat, J.E., Rollon, R.N., & Nacorda, H.M. (2002) Propagule dispersal of the SE Asian seagrasses *Enhalus acoroides* and *Thalassia hemprichii*. *Marine Ecology Progress Series*, **235**, 75-80.
- Levine, J.M. (2001) Local interactions, dispersal, and native and exotic plant diversity along a California stream. *Oikos*, **95**, 397-408.
- Melcher, I.M., Bouman, F., & Cleef, A.M. (2000) Seed dispersal in paramo plants: Epizoochorous and hydrochorous taxa. *Plant Biology*, **2**, 40-52.
- Merritt, D.M. & Wohl, E.E. (2002) Processes governing hydrochory along rivers: Hydraulics, hydrology, and dispersal phenology. *Ecological Applications*, **12**, 1071-1087.
- Middleton, B. (2000) Hydrochory, seed banks, and regeneration dynamics along the landscape boundaries of a forested wetland. *Plant Ecology*, **146**, 169-184.
- Middleton, B.A. (1995) Sampling devices for the measurement of seed rain and hydrochory in rivers. *Bulletin Torrey Botany Club*, **146**, 152-155.
- Morton, J.K. & Hogg, E.H. (1989) Biogeography of island floras in the Great Lakes. II. Plant dispersal. *Canadian Journal of Botany*, **67**, 1803-1820.
- Nilsson, C., Andersson, E., Merritt, D.M., & Johansson, M.E. (2002) Differences in riparian flora between riverbanks and river lakeshores explained by dispersal traits. *Ecology*, **83**, 2878-2887.
- Nilsson, C., Gardfjell, M., & Grelsson, G. (1991) Importance of hydrochory in structuring plant communities along rivers. *Canadian Journal of Botany*, **69**, 2631-2633.
- Orth, R.J., Luckenbach, M., & Moore, K.A. (1994) Seed dispersal in a marine macrophyte: implications for colonization and restoration. *Ecology*, **75**, 1927-1939.
- Persicke, U., Gerlach, A., & Heiber, W. (1999) Zur botanischen Zusammensetzung von Treibsel der niedersächsischen Deichvorländer und Deichabschnitte. *Drosera*, **1**, 23-34.
- Rand, T.A. (2000) Seed dispersal, habitat suitability and the distribution of halophytes across a salt marsh tidal gradient. *Journal of Ecology*, **88**, 608-621.
- Schneider, R.L. & Sharitz, R.R. (1988) Hydrochory and regeneration in a bald cypress water tupelo swamp forest. *Ecology*, **69**, 1055-1063.
- Skoglund, J. (1990) Seed dispersing agents in two regularly flooded river sites. *Canadian Journal of Botany*, **68**, 754-760.
- Smith, J.M.B., Heatwole, H., Jones, M., & Waterhouse, B.M. (1990) Drift disseminules on cays of the Swain Reefs, Great Barrier Reef, Australia. *Journal of Biogeography*, **17**, 5-17.
- Steiger, J., Gurnell, A.M., Goodson, J.M. (2003) Quantifying and characterizing contemporary riparian sedimentation. *River Research and Applications*, **19**, 335-352.
- ter Heerdt, G.N.J., Verwey, G.L., Bekker, R.M., & Bakker, J.P. (1996) An improved method for seed bank analysis: seedling emergence after removing the soil by sieving. *Functional Ecology*, **10**, 144-151.
- van der Meijden, R. (1996) *Heukels' flora van Nederland*. 22nd ed. Wolters-Noordhoff, Groningen.
- Wolters, M. & Bakker, J.P. (2002) Soil seed bank and driftline composition along a successional gradient on a temperate salt marsh. *Applied Vegetation Science*, **5**, 55-62.



Astroturf mat at Tollesbury with the breach in the embankment at the horizon

CHAPTER 6

Plant colonization after managed realignment: the relative importance of diaspore dispersal

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Journal of Applied Ecology (2005) **42**, 770-777.

In this chapter we investigate whether salt-marsh development may be constrained by limited diaspore dispersal. To assess diaspore dispersal at the salt-marsh surface, we use astroturf seed traps as discussed in the previous chapter.

Introduction

Managed realignment, or the deliberate breaching of sea defences, is frequently used for re-creating salt marshes on previously reclaimed land (Pethick 2002; Tabor 2003; Morris *et al.* 2004; Wolters, Garbutt & Bakker 2005, Chapter 3). Restoring regular tidal inundation is assumed to be sufficient to transform predominantly agricultural land into salt-marsh habitat (Meauchamp, Chauvelon, & Grillas 2002). However, recent studies have shown that it may take several years before the vegetation of a restoration site resembles that of a historical or nearby reference situation (Garbutt *et al.* 2002). This slow development may be because of dispersal constraints of the target species (Onaindia, Albizu, & Amezaga 2001; Bakker *et al.* 2002; Bischoff 2002; Bissels *et al.* 2004) or environmental conditions that are unsuitable for their establishment, such as a sediment deficit in combination with sea-level rise (Morris *et al.* 2004). Bioturbation and herbivory by invertebrates may also affect the establishment of pioneer species (Hughes & Paramor 2004; Paramor & Hughes 2004), although experiments so far remain inconclusive (Wolters *et al.* 2005, Chapter 2). In the present study we focused on the potential role of diaspore dispersal in the development of salt-marsh vegetation after managed realignment.

In managed realignment, regular tidal inundation is assumed to function as the key agent for dispersing diaspores. Laboratory studies have shown that seeds and fruits of various salt-marsh species can float in seawater for time spans varying from several hours up to several months (Koutstaal, Markusse, & De Munck 1987). Most seeds retain their viability during submergence in seawater (Koutstaal, Markusse, & De Munck 1987) and rapidly germinate upon transference to fresh water conditions (Woodell 1985). Both characteristics are likely to facilitate dispersal by tidal water.

Studies of the composition of driftline material deposited after storms and high tides show that although numerous propagules and vegetative parts occur in driftline material, the composition mainly resembles the local vegetation, suggesting limited dispersal distances (Bakker, Dijkstra, & Russchen 1985; Persicke, Gerlach, & Heiber 1999; Wolters & Bakker 2002, Chapter 4). On the other hand, Huiskes *et al.* (1995), using standing and floating nets to trap seeds at incoming and outgoing tide, showed a net export of floating propagules at intertidal flats compared with a net import at the salt marsh, indicating a potential exchange between different salt marshes. However, it is not clear whether the seeds are mainly floating over the salt marsh with the tide and becoming assembled in the driftline or actually settling at the salt-marsh surface.

In this study we assessed the deposition of diaspores in a salt-marsh restoration site by using seed traps. Our main objective was to determine whether salt-marsh development is constrained by limited diaspore dispersal. The specific aims of this study were to (i) examine temporal patterns in the dispersal of salt-marsh species in order to provide information on the appropriate timing of breaches during managed realignment for dispersal in the first year; (ii) compare the composition and abundance of diaspores trapped at different locations in the restoration site and adjacent marsh in order to identify possible barriers to dispersal such as elevation and distance to breach; (iii) relate the composition and abundance of the dispersed diaspores to the established vegetation of the restoration site and adjacent marsh in order to identify the main source of diaspores; and (iv) discuss the relative importance of diaspore dispersal for salt-marsh development after managed realignment.

Materials and methods

Study area

This study was performed at the Tollesbury managed-realignment site and adjacent marsh in the Blackwater Estuary, south-east England (51°46'N, 0°51'E) (Fig. 6.1). The 21-ha restoration site had originally been a salt marsh, but was reclaimed in the late 18th century, after which it was used for agriculture (Boorman *et al.* 1997). The old seawall surrounding the site was breached at one place in August 1995, leaving a 50-m wide opening that connects the site to Tollesbury Creek. Other construction work has involved the excavation of a channel to connect an existing drainage ditch to the

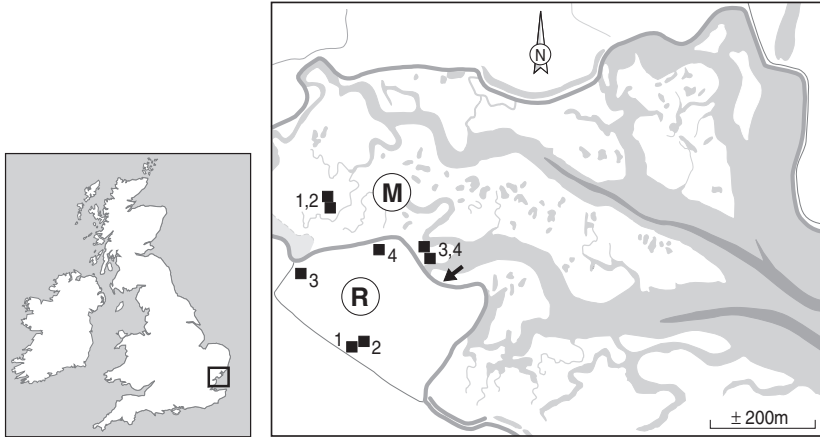


Figure 6.1. Study area with astroturf locations in restoration site (R1-4), adjacent marsh surface (M1, M3) and adjacent marsh creek banks (M2, M4). The arrow points to the breach made in the embankment in 1995.

breach and the construction of a new seawall landward of the old embankment to prevent flooding of the neighbouring arable fields. The elevation of the site ranges from 0.9 m to 3.0 m above Ordnance Datum (OD), with the major part of the site lying below 2.0 m OD (Garbutt *et al.* 2002). Mean high water neap (MHWN) and mean high water spring (MHWS) tide levels are 1.50 m and 2.60 m OD, respectively (Pye & French 1993).

Established vegetation of restoration site and adjacent marsh

Approximately 30% of the restoration site was vegetated in 2001, with the lower limit of the vegetation following the 1.5 m OD contour line (i.e. MHWN tide level). The dominant species is *Salicornia* spp. followed by *Suaeda maritima* and *Puccinellia maritima*. Ten other salt-marsh species have been recorded in the site, but with very low abundance (Garbutt *et al.* 2002).

Adjacent to the restoration site are the mature Old Hall and Tollesbury marshes (Fig. 6.1) which are characterized by numerous creeks that dissect the salt-marsh surface. The vegetation of the creek banks (average elevation 0.3 m + MHWN) is dominated by *Aster tripolium*, *Salicornia* spp. and *Suaeda maritima*, whereas the salt-marsh surface (average elevation 1.06 m + MHWN) is dominated by *Atriplex portulacoides*, *Puccinellia maritima* and *Limonium vulgare* (Garbutt *et al.* 2002). Data on species abundance in the established vegetation of the restoration site and adjacent marsh in 2001 were derived from Garbutt *et al.* (2002). In their study, the presence of a species in the restoration site was recorded in three transects of 125-m long and 20-m wide, divided into 2500 cells of 1 m². Species abundance at the adjacent marsh was recorded in 60 quadrats (43 salt-marsh surface, 17 creek bank) of 1m² divided into 100 subplots.

Diaspore dispersal

Four locations (R1-R4), representing different stages in the development of salt-marsh vegetation, were selected in the restoration site, and diaspore dispersal was assessed by placing five 45 × 45 cm astroturf mats, 1.5 m apart, at each of these four locations (Fig. 6.1). R1 and R3 were approximately 400 m from the breach at an elevation of 0.95 m and 0.93 m + MHWN. The established vegetation of the two sites was similar with *Salicornia* as the dominant species, frequent occurrences of *Suaeda* and some patches of *Puccinellia*, but the two sites were located at different angles from the breach, and might therefore have experienced different rates of diaspore dispersal. R2 was 15 m seaward of R1 at 0.87 m + MHWN and the established vegetation consisted almost entirely of *Salicornia* at high densities. R4 was located 160 m south-west of the breach at an elevation of -0.03 m + MHWN and here *Salicornia* was the only species present in the established vegetation at low densities. In order to compare dispersal in the restoration site with a reference site, four sets of five astroturf mats were placed on the adjacent marsh (M1-M4, Fig. 6.1). M1 and M2 were located at the interior marsh whereas M3 and M4 were close to the creek entering the restoration site. M2 and M4 were placed on the creek bank and M1 and M3 on the marsh surface to represent the two main plant communities of the adjacent marsh.

The astroturf mats were collected and replaced every month, starting 6 September 2001 with the final collection on 31 March 2002. In the first month (6 September - 12 October) only four out of the eight locations (i.e. R1, R2, M1, M2) were sampled and the results of this period have not been taken into account for statistical analysis. The material trapped during the sampling period was carefully rinsed from the mats onto a 0.212 mm mesh sieve, spread onto trays filled with sterilized soil and transferred to the glasshouse after a 4-6 week cold stratification period, according to the method described by Wolters *et al.* (2004) (Chapter 5). For every ten trays, a control tray without a sample was placed to check for seeds being blown into the glasshouse. Emerging seedlings and rooted vegetative parts were identified and removed as soon as possible, or transferred to separate flower pots in case flowering was needed for identification.

Statistical analysis

The first question we addressed was whether there were differences in number of diaspores between the four locations within the restoration site and within the adjacent marsh. Prior to statistical testing, screening of the data revealed a lack of normality and homogeneity of variances for the different groups, which only partly improved after different data transformations. Therefore, a non-parametric Kruskal Wallis test (SPSS11.5) was used to test for differences in the ranking of the mean number of diaspores trapped between different locations. The test was run separately for each salt-marsh species with a cumulative mean number of at least three diaspores per m² at any location over the period 12 October - 31 March. The Nemenyi multiple comparison test (i.e. the non-parametric analogue of the Tukey test; Zar 1996), was

used to determine which locations significantly differed from each other. A Sørensen similarity index (Jongman, ter Braak & van Tongeren 1995) was calculated to compare similarity in species composition between the established vegetation and diaspores trapped in the restoration site as well as on the adjacent marsh surface and creek banks.

Results

Total number of diaspores trapped

From 6 September 2001 to 31 March 2002 a total of 38 species was trapped at the astroturf mats, of which 18 were salt-marsh species (Appendix 6.1). Many of these species were present in very low numbers at any location and, in fact, only six salt-marsh species were found with more than three diaspores per m² per location. These species included *Aster*, *Limonium*, *Puccinellia*, *Salicornia*, *Spergularia media* and *Suaeda*.

Temporal patterns in diaspore dispersal

Temporal differences in number of trapped diaspores of all salt-marsh species indicate that the main dispersal period took place between October and December, both at the restoration site and the adjacent marsh (Fig. 6.2), but this pattern was mainly because of the abundance of *Salicornia*, which accounted for more than 95% of the diaspores trapped (Fig. 6.3). Some differences between the species could be observed with *Limonium*, *Puccinellia* and *Spergularia media* starting to be dispersed earlier than *Aster*, *Salicornia* and *Suaeda* (Fig. 6.3). Between September and October and between early February and late March hardly any diaspores were trapped.

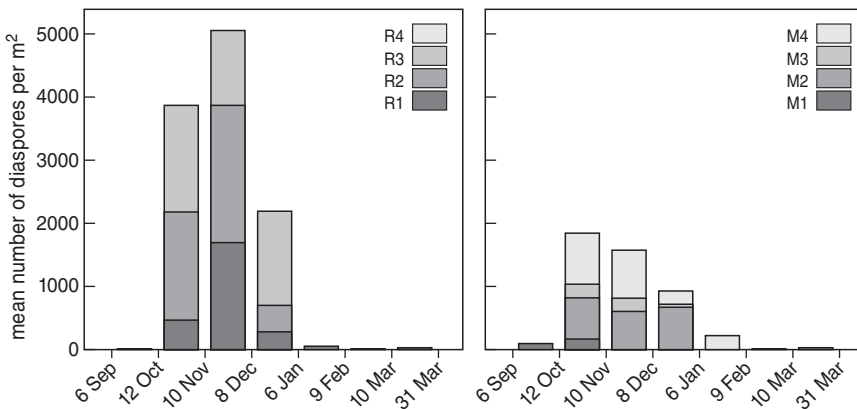


Figure 6.2. Temporal pattern in mean number of diaspores of salt-marsh species per m² for restoration site (R1-4) and adjacent marsh (M1-4).

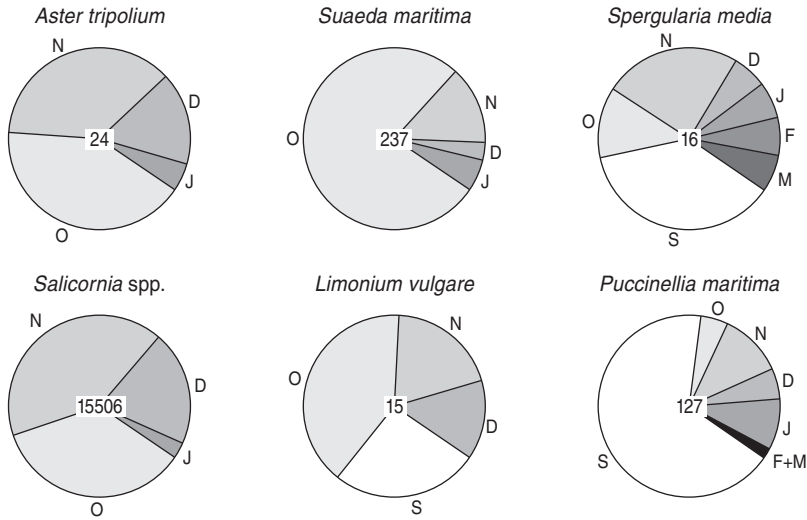


Figure 6.3. Temporal pattern in number of diaspores trapped in all locations combined. The number of diaspores trapped per m² in each period is expressed as a percentage of the sum of the means for the eight locations (number in centre of circle) over the entire sampling period for each species. Different periods are indicated by the first letter of the month in which the seed traps were placed, starting from September (S) to March (M). Note that for the period 6 September – 12 October only four out of eight locations were sampled.

Spatial patterns in diaspore dispersal

Over the period 12 October - 31 March, only five *Salicornia* seeds per m² and no other species were trapped in the restoration site at location R4 (i.e. closest to the breach at an elevation of -0.03 m + MHWN). No significant differences were detected between the other three locations within the restoration site for the six salt-marsh species and it was decided to pool the locations (R1, R2 and R3) to facilitate comparison with the adjacent marsh. On the adjacent marsh, significant differences between locations were found for *Aster* and *Salicornia* ($P < 0.05$), on the basis of which two groups were identified. The first group comprised the marsh surface locations (M1, M3) and the second group consisted of the creek bank locations (M2, M4). A non-parametric t -test (Mann-Whitney, SPSS 11.5) was applied to test for differences in number of diaspores between restoration site and marsh surface or creek bank for each of the six salt-marsh species (Fig. 6.4). Diaspores of *Aster* were trapped in significantly ($P < 0.05$) higher number on the adjacent marsh creek banks compared with the restoration site. No differences were observed between the restoration site and the adjacent marsh surface. *Limonium*, *Puccinellia*, *Spergularia media* and *Suaeda* were either absent or trapped in significantly lower number in the restoration site compared with the adjacent marsh surface and/or creek banks (Fig. 6.4). *Salicornia* was the only species with significantly more seeds trapped in the restoration site compared

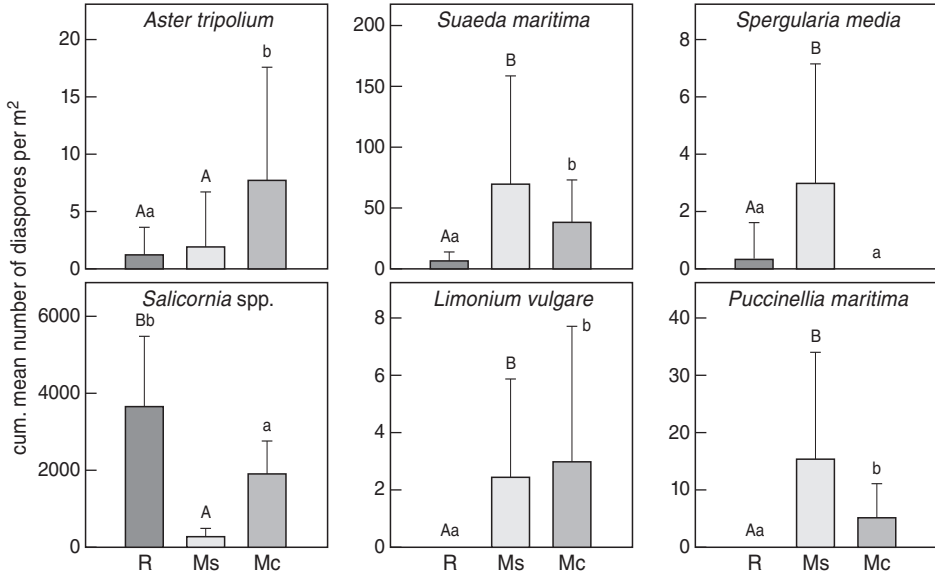


Figure 6.4. Cumulative mean number of diaspores per m^2 with standard deviation ($n = 15$ for the restoration site (R), $n = 10$ for the adjacent marsh surface (Ms) and creek banks (Mc)). Different letters indicate significant pairwise differences between the restoration site and adjacent marsh surface (capital letters) or between the restoration site and adjacent marsh creek banks (small letters) tested by a non-parametric t -test ($P < 0.05$). Note the differences in y-axis scale for different species.

with the adjacent marsh surface or creek banks. This species was by far the most abundant with almost 4000 seeds per m^2 trapped in the restoration site and 1900 seeds per m^2 on the adjacent marsh creek banks (Fig. 6.4).

Similarity between composition of vegetation and trapped diaspores

Out of the ten salt-marsh species trapped in the restoration site, six were recorded in the established vegetation of this site (Fig. 6.5), resulting in a similarity index of 0.52 (Table 6.1). Higher similarity in species composition (0.70) was found between diaspores and vegetation of the adjacent marsh surface, which had eight species in common. A much lower similarity (0.42 and 0.43) was calculated for the diaspores in the restoration site compared with the vegetation of the adjacent marsh surface and creek banks (Table 6.1). In particular, *Atriplex portulacoides* and *Triglochin maritima* showed a weak relationship between their abundance in the vegetation and the number of diaspores trapped (Fig. 6.5). Interestingly, diaspores of *Agrostis stolonifera*, *Leontodon autumnalis*, and *Sagina maritima* were trapped in the restoration site whereas they were not recorded in the established vegetation of this site or the adjacent marsh. *Plantago maritima*, which was also trapped in the restoration site but absent from the established vegetation, may have come from the adjacent marsh where it was recorded in 2.1 % of the plots.

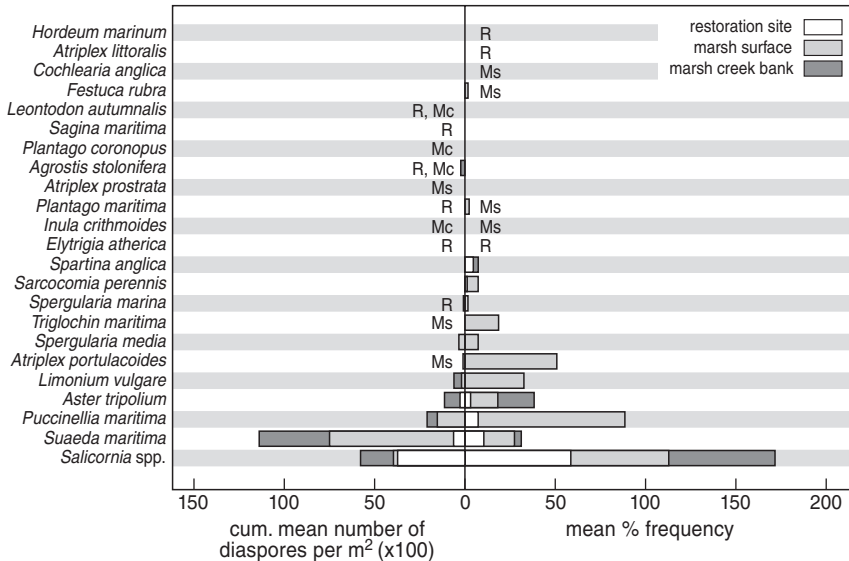


Figure 6.5. Comparison between species in the vegetation and species trapped on astroturf for the restoration site (R), adjacent marsh surface (Ms) and adjacent marsh creek banks (Mc). Letters indicate species occurring with a frequency of less than 3 % in the vegetation and species for which fewer than three diaspores per m² were trapped. Note that the number of diaspores of *Salicornia* should be multiplied by 100.

Table 6.1. Sørensen similarity indices comparing established vegetation and diaspores trapped on astroturf in the restoration site (R), and adjacent marsh surface (Ms) and creek bank (Mc).

Vegetation	Astroturf		
	R	Ms	Mc
R	0.52	0.64	0.45
Ms	0.42	0.70	0.43
Mc	0.43	0.46	0.46

Discussion

Total number of diaspores trapped

In our study a total of 18 salt-marsh species was trapped on astroturf mats, although only six with more than three diaspores per m². It could be argued that certain species might be more efficiently trapped than others because of morphological differences between their seeds. However, in an experiment specifically conducted to test the seed-retaining efficiency of the astroturf mats, no differences were found for three morphologically very different species Wolters *et al.* (2004) (Chapter 3). In compari-

son, Rand (2000) trapped a total of 346 diaspores per m² from six species over a three month period using styrofoam plates covered with a resinous material. This was 60 times less than the number of diaspores trapped on the astroturf mats in our study over the same period, although this was mainly because of the abundance of *Salicornia*. It should be noted that the number of diaspores retained by the astroturf mats in the present study was the net result of deposition and removal of diaspores by tidal water over the monthly replacement series. The results therefore represent a minimum rather than total number of diaspores dispersed during the sampling period. Dispersal by wind and birds may also have contributed to the number of diaspores trapped in our study. Huiskes *et al.* (1995) observed that a considerable number of propagules transported along the bottom of the water column with the flood tide returned to the same station with the ebb tide. However, the same was not found for propagules floating on the surface of the water column, suggesting different dispersal modes between species with different floating characteristics. Interestingly, four of the six most abundant species trapped on our astroturf mats turned out to be the same four species predominantly caught in standing nets by Huiskes *et al.* (1995), namely *Aster*, *Puccinellia Salicornia* and *Spergularia*. These species are characterized by relatively short flotation times of a few hours to a few days (Koutstaal, Markusse & De Munck 1987).

Temporal patterns in diaspore dispersal

One of the aims of this study was to examine temporal dispersal patterns in order to provide information on the appropriate timing of breaches for managed realignment. Our results show a peak in diaspore dispersal between September and December for *Limonium*, *Spergularia media*, and *Puccinellia* and between October and December for *Aster*, *Salicornia*, and *Suaeda*. These results agree with the study by Hutchings and Russell (1989) who observed that the latter three species as well as *Limonium* produced most of their seeds in September and October. However, *Puccinellia* was found to produce a majority of ripe seeds in July (Hutchings & Russell 1989) and to grow vegetative tillers at a faster rate from August to October (Gray & Scott 1977), suggesting that our study may have started too late to capture the dispersal peak for this species. Other species that may have been absent from our traps because of their dispersal peak occurring before the start of our study include *Armeria maritima*, *Festuca rubra*, *Juncus gerardi* and *Plantago*, which set seeds in July and August (Hutchings & Russell 1989). Except for *Plantago* these species were absent from the established vegetation of the restoration site and either absent or present in low frequencies on the adjacent marsh (Fig. 6.5), hence a limited local source of diaspores could also be an important reason for the absence of these species from our seed traps. Nevertheless, in order to take advantage of the peak in dispersal of salt-marsh species in the first year after breaching, it is recommended that breaching of sea defenses takes place in early September at the latest.

Spatial patterns in diaspore dispersal

An interesting result obtained from this study is the exceptionally low number of diaspores captured on seed traps located in the restoration site at low elevation (-0.03 m + MHWN) and relatively close to the breach (R4). It was expected that seeds would arrive at this location but fail to establish because of abiotic constraints related to the low elevation (Wiehe 1935). However, except for five *Salicornia* seeds per m² no diaspores were trapped during the entire study period. This could be because of the scarcity of a nearby source of diaspores (there were only few established *Salicornia* plants surrounding the seed traps) in combination with a predominantly short-distance dispersal of salt-marsh species as implied by the other results of this study. Another possibility is that diaspores may have been dispersed to this location but failed to settle on the seed traps because of strong tidal currents. Support for the latter possibility comes from a study where seeds of three salt-marsh species were added to astroturf mats placed at three different elevations. After one tidal inundation between 50 and 80 % of the seeds had disappeared from the mats at the lowest elevation compared to 20-50 % of the seeds from the mats at the higher elevations (Wolters *et al.* 2004, Chapter 5). In a seed dispersal experiment conducted in a flume channel designed with different fluvial features, Merritt and Wohl (2002) also found a smaller number of seeds deposited in areas of high velocity compared with areas of slow flow velocity. These results suggest that low elevation associated with high tidal flow velocities may not only constrain establishment but also arrival of salt-marsh plants.

Relationship between trapped diaspores and established vegetation

For most species, the number of diaspores trapped was representative of their abundance in the vegetation. Exceptions were *Atriplex portulacoides* and *Triglochin*, of which less than three diaspores per m² were trapped during the entire sampling period, although they occurred with a frequency of 50 and 18%, respectively, in the established vegetation of the adjacent upper marsh. The fruits of these two species have a flotation time exceeding four months (Koutstaal, *et al.* 1987), implying high potential for long-distance dispersal. Chapman (1950) and Davy (1991) also report a large potential for dispersal by tidal water for *A. portulacoides* and *Triglochin*, respectively, and both species were trapped in relatively high numbers in the study by Huiskes *et al.* (1995). One explanation for the absence of diaspores of these species from astroturf mats in our study may be herbivory of the plants. *A. portulacoides* for example, forms a food supply for shorelarks *Eremophila alpestris* (Dierschke 2002) and hares *Lepus europaeus* (van der Wal *et al.* 2000) and both *A. portulacoides* and *Triglochin* are eaten by snow bunting *Plectrophenax nivalis* (Dierschke 2002) and brent geese *Branta bernicla bernicla* (Summers *et al.* 1993; van der Wal *et al.* 2000). Of the latter species, between 400 and 900 individuals per year have been reported feeding at the Tollesbury site between 1996 and 1998 (Atkinson *et al.* 2001).

Another interesting observation is the trapping of *Agrostis stolonifera*, *Leontodon autumnalis* and *Sagina maritima* in the restoration site when none of these species

was present in the established vegetation of this site or the adjacent marsh. These species may have been transported over longer distances by tidal water, or they may have been blown onto the astroturf mats from nearby seawalls where they were observed to grow. All three species were classified as having a high potential for long distance dispersal (i.e. > 100 m) (Tamis *et al.* 2004) and they were described by Westhoff (1947) as anemochorous with potential dispersal distances of more than 1 km.

The much higher number of diaspores of *Salicornia* trapped in the restoration site compared to the adjacent marsh surface, while the percentage frequency of this species in the vegetation of the two sites was similar, could be explained by the fact that *Salicornia* occurred in much higher densities (i.e. higher percentage cover but not frequency) in the restoration site compared with the adjacent marsh surface. The absence of *Puccinellia* from seed traps in the restoration site is likely to be related to its low abundance in the vegetation of this site. This species was also absent from the creek bank vegetation, although it was trapped on astroturfs, but this could be explained by the fact that diaspores from the marsh surface may have landed on astroturf mats at the creek banks (which were directly below the marsh surface) but failed to establish because of abiotic constraints related to the low elevation (i.e. being 80 cm lower than the marsh surface).

Overall, our results indicate a predominantly local dispersal of salt-marsh species, despite the potential for long-distance transport and wide distribution by tidal water.

Implications for future managed realignment

Our results have shown that the peak dispersal of salt-marsh species occurs between September and early December, which is consistent with the data reported by Huiskes *et al.* (1995). It is important, therefore, that managed realignment should take place before this period in order to exploit the dispersal season. A relatively rapid establishment of pioneer and low-marsh species may be expected, as adult plants of these species are frequently inundated and their seeds stand more chance of being dispersed by seawater than those of high-marsh species. This is clearly the case for *Salicornia*, of which many seeds were trapped in our study and which has successfully established and maintained its abundance in the vegetation within three years of breaching the seawall (Garbutt *et al.* 2002). It is also probable that the seeds are dispersed via stepping stones, i.e. being initially deposited a short distance from the parent plant from whence they are transported further with subsequent tides. Spring tides and storms may be especially important in this respect, as discussed by Koutstaal, Markusse & De Munck. (1987). As a result of the predominant short-distance dispersal of salt-marsh species it is advantageous to have a well-developed salt-marsh in front of the restoration site as this will function as the source area. Usage of the restoration site by birds and the implementation of a livestock grazing regime in connection with the fronting marsh may further enhance seed dispersal into the site especially of species less adapted to hydrochory. In order to obtain rapid results and/or species absent from the source area, broadcasting seeds or driftline material

collected from high diversity marshes may be necessary (Hölzel & Otte 2003). However, as Morris *et al.* (2004) point out, positive sediment budgets will be a prerequisite, not only for salt marshes to keep up with rising sea levels, but also to increase the elevation of many realignment sites that have run into a sediment deficit during their period of embankment and are often below levels at which salt-marsh vegetation can develop.

Summary

Deliberate breaching of sea defences is frequently practiced with the aim of restoring salt-marsh vegetation on previously embanked land. However, experience so far has shown that it may take several years before salt-marsh vegetation is fully established, and it is possible that limited diaspore dispersal plays a role in this. In order to ascertain whether salt-marsh development may be constrained by limited diaspore dispersal, we have studied the dispersal of salt-marsh species by tidal water.

From October 2001 to the end of March 2002 a total of 38 species, of which 18 were salt-marsh species, were trapped in a restoration site and adjacent marsh. *Aster tripolium*, *Limonium vulgare*, *Puccinellia maritima*, *Salicornia* spp, *Spergularia media* and *Suaeda maritima* were the most abundant salt-marsh species, with more than three diaspores per m² trapped during the study period. For most species, the number of diaspores trapped was representative of their abundance in nearby vegetation. Hence despite the potential for long-distance transport by tidal water, our results indicate a predominantly local dispersal of salt-marsh species.

For the restoration of salt-marsh vegetation after de-embankment, relatively rapid colonization may be expected from pioneer and low-marsh species, provided they are present in a nearby source area and the restoration site is at the appropriate elevation. The establishment of species absent from the adjacent marsh may be dependent on the presence of birds or humans as the main dispersal agents. Breaching of sea defences should preferably take place before or during September in order to take advantage of the peak in dispersal of salt-marsh species in the first year after breaching.

Acknowledgements

We would like to thank Sijbren Otto for his help in the field, three anonymous referees for the useful comments to the manuscript, and we are grateful for the financial support of the Schure-Beijerinck-Popping fund to M. Wolters.

References

- Atkinson, P. W., Crooks, S., Grant, A., & Rehfish, M. M. (2001) *The success of creation and restoration schemes in producing intertidal habitat suitable for waterbirds*. English Nature, Peterborough, UK.
- Bakker, J. P., Dijkstra, M., & Russchen, P. T. (1985) Dispersal, germination and early establishment of halophytes and glycophytes on a grazed and abandoned salt marsh gradient. *New Phytologist*, **101**, 291-308.
- Bakker, J. P., Esselink, P., Dijkema, K. S., van Duin, W. E., & De Jong, D. J. (2002) Restoration of salt marshes in the Netherlands. *Hydrobiologia*, **478**, 29-51.
- Bischoff, A. (2002) Dispersal and establishment of floodplain grassland species as limiting factors in restoration. *Biological Conservation*, **104**, 25-33.
- Bissels, S., Hölzel, N., Donath, T. W., & Otte, A. (2004) Evaluation of restoration success in alluvial grasslands under contrasting flooding regimes. *Biological Conservation*, **118**, 641-650.
- Boorman, L. A., Garbutt, A., Barratt, D., Myhill, D., Eversham, B., Reading, C., Cox, R., & Rothery, P. (1997) *Large scale experimental managed realignment volume 1 at Tollesbury, Essex*. Institute of Terrestrial Ecology (Natural Environmental Research Council). Monks Wood, UK.
- Chapman, V. J. (1950) Biological flora of the British Isles. *Halimione portulacoides*. *Journal of Ecology*, **38**, 214-222.
- Davy, A.J. (1991) Biological flora of the British Isles. *Triglochin maritima*. *Journal of Ecology*, **79**, 531-555.
- Dierschke, J. (2002) Food preferences of shorelarks *Eremophila alpestris*, snow bunting *Plectrophenax nivalis* and twites *Carduelis flavirostris* wintering in the Waddensea. *Bird Study*, **49**, 263-269.
- Garbutt, R. A., Myhill, D. G., Barratt, D. R., Wolters, M., Cox, R., Mann, J. L & Rothery, P. (2002) Botanical and accretion studies at Tollesbury, Essex and Saltram, Devon. *Managed realignment at Tollesbury and Saltram. Final report*. (Eds C.J. Reading et al.), pp. 51-136. Defra project CSA2313. Centre for Ecology and Hydrology, Dorchester, UK.
- Gray, A. J. & Scott, R. (1977) Biological flora of the British Isles. *Puccinellia maritima*. *Journal of Ecology*, **65**, 699-716.
- Hölzel, N. & Otte, A. (2003) Restoration of a species-rich flood meadow by topsoil removal and diaspore transfer with plant material. *Applied Vegetation Science*, **6**, 131-140.
- Hughes, R.G. & Paramor, O.A.L. (2004) On the loss of saltmarshes in south-east England and methods for their restoration. *Journal of Applied Ecology*, **41**, 440-448.
- Huiskes, A.H.L., Koutstaal, B. P., Herman, P. M. J., Beeftink, W. G., Markusse, M. M., & De Munck, W. (1995) Seed dispersal of halophytes in tidal salt marshes. *Journal of Ecology*, **83**, 559-567.
- Hutchings, M. J. & Russell, P. J. (1989) The seed regeneration dynamics of an emergent salt marsh. *Journal of Ecology*, **77**, 615-637.
- Jongman, R.H.G., ter Braak, C.J.F. & van Tongeren, O.F.R. (1995) *Data analysis in community and landscape ecology*. Cambridge University Press. Cambridge.
- Koutstaal, B. P., Markusse, M. M., & De Munck, W. (1987) Aspects of seed dispersal by tidal movements. *Vegetation between land and sea: Structure and processes* (eds A.H.L. Huiskes, C.W.P.M. Blom & J. Rozema), pp. 226-233. Dr. W. Junk Publishers, Dordrecht, NL.
- Meauchamp, A., Chauvelon, P., & Grillas, P. (2002) Restoration of floodplain wetlands: opening of polders along a coastal river in Mediterranean France, Vistre marshes. *Ecological Engineering*, **18**, 619-632.
- Merritt, D.M. & Wohl, E.E. (2002) Processes governing hydrochory along rivers: Hydraulics, hydrology, and dispersal phenology. *Ecological Applications*, **12**, 1071-1087.
- Morris, R. K. A., Reach, I. S., Duffy, M. J., Collins, T. S., & Leafe, R. N. (2004) On the loss of saltmarshes in south-east England and the relationship with *Nereis diversicolor*. *Journal of Applied Ecology*, **41**, 787-791.
- Onaindia, M., Albizu, I., & Amezaga, I. (2001) Effect of time on the natural regeneration of salt marsh. *Applied Vegetation Science*, **4**, 247-256.
- Paramor O.A.L. & Hughes, R.G. (2004) The effects of bioturbation and herbivory by the polychaete *Nereis diversicolor* on the loss of saltmarsh in south-east England. *Journal of Applied Ecology*, **41**, 449-463.

- Persicke, U., Gerlach, A., & Heiber, W. (1999) Zur botanischen Zusammensetzung von Treibsel der niedersächsischen Deichvorländer und Deichabschnitte. *Drosera*, **1**, 23-34.
- Pethick, J. (2002) Estuarine and tidal wetland restoration in the United Kingdom: policy versus practice. *Restoration Ecology*, **10**, 431-437.
- Pye, K. and French, P. W. *Erosion and accretion on British Salt Marshes*. (1993) Cambridge Environmental Research Consultants Ltd. Database of British Saltmarshes, London.
- Rand, T. A. (2000) Seed dispersal, habitat suitability and the distribution of halophytes across a salt marsh tidal gradient. *Journal of Ecology*, **88**, 608-621.
- Summers, R. W., Stansfield, J., Perry, S., Atkins, C., & Bishop, J. (1993) Utilization, diet and diet selection by brent geese *Branta bernicla bernicla* on saltmarshes in Norfolk. *Journal of the Zoological Society London*, **231**, 249-273.
- Tabor, R. (2003) Turning the tide for saltmarshes. *British Wildlife*, **15**, pp. 10-19
- Tamis, W.L.M., van der Meijden, R., Runhaar, J., Bekker, R.M., Ozinga, W.A., Ode, B. & Hoste, I. (2004) Standaard lijst van de Nederlandse flora. *Gorteria*, **30**, 101-195.
- van der Wal, R., van Wijnen, H., van Wieren, S., Beucher, O., & Bos, D. (2000) On facilitation between herbivores: how brent geese profit from brown hares. *Ecology*, **81**, 969-980.
- Westhoff, V. (1947) *The vegetation of dunes and salt marshes on the Dutch islands of Terschelling, Vlieland and Texel*. University of Utrecht, Utrecht, NL.
- Wiehe, P. O. (1935) A quantitative study of the influence of tide upon the population of *Salicornia europaea*. *Journal of Ecology*, **23**, 323-333.
- Wolters, M. & Bakker, J. P. (2002) Soil seed bank and driftline composition along a successional gradient on a temperate salt marsh. *Applied Vegetation Science*, **5**, 55-62.
- Wolters, M., Geertsema, J., Chang, E. R., Veeneklaas, R. M., Carey, P. D., & Bakker, J. P. (2004) Astro turf seed traps for studying hydrochory. *Functional Ecology*, **18**, 141-147.
- Wolters, M., Garbutt, A. & Bakker, J.P. (2005) Salt-marsh restoration: evaluating the success of de-embankments in north-west Europe. *Biological Conservation*, **123**, 249-268.
- Wolters, M., Bakker, J.P., Bertness, M.D., Jefferies, R.L. & Möller, I. Salt-marsh erosion and restoration in south-east England: squeezing the evidence requires realignment. *Journal of Applied Ecology*, **42**, 844-851.
- Woodell, S.R.J. (1985) Salinity and seed germination patterns in coastal plants. *Vegetatio*, **61**, 223-229.
- Zar, J.H. (1996) *Biostatistical analysis*. Prentice Hall, London, UK.

Appendix 6.1. Mean number of trapped diaspores per m² per period and per location (R = restoration site, Ms and Mc = adjacent marsh surface and creek bank, respectively).

Period	6 Sep - 12 Oct			12 Oct - 10 Nov			10 Nov - 8 Dec			8 Dec - 6 Jan			6 Jan - 9 Feb			9 Feb - 10 Mar			10 Mar - 31 Mar			12 Oct - 31 Mar		
	R	Ms	Mc	R	Ms	Mc	R	Ms	Mc	R	Ms	Mc	R	Ms	Mc	R	Ms	Mc	R	Ms	Mc	R	Ms	Mc
Salt-marsh species																								
<i>Agrostis stolonifera</i>	1.2	-	-	-	-	-	0.3	-	0.5	0.3	-	-	-	-	-	-	-	-	-	-	-	0.7	-	1.0
<i>Aster tripolium</i>	-	-	-	0.7	1.5	2.5	0.3	-	4.0	0.3	-	1.5	-	-	-	-	-	-	-	-	-	1.3	2.0	7.9
<i>Atriplex portulacoides</i>	-	-	-	-	-	-	-	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.0
<i>Atriplex prostrata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.5
<i>Cochlearia anglica</i>	-	1.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Elytrigia atherica</i>	-	-	-	-	-	-	-	-	-	0.3	-	-	-	-	-	-	-	-	-	-	-	0.3	-	-
<i>Inula arithmoides</i>	-	-	-	-	-	0.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Leontodon autumnalis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.6
<i>Limonium vulgare</i>	-	4.0	-	-	1.0	2.0	-	1.5	-	-	-	1.0	-	-	-	-	-	-	-	-	-	0.3	-	0.5
<i>Plantago coronopus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.5
<i>Plantago maritima</i>	-	-	2.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.0
<i>Puccinellia maritima</i>	-	-	83.0	4.0	-	1.0	2.0	-	6.9	0.5	-	3.0	0.5	-	-	-	-	-	-	-	0.3	-	-	0.5
<i>Sagina maritima</i>	-	-	-	-	-	-	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	15.3
<i>Salicornia spp</i>	5.3	-	-	1286.2	127.4	696.8	1670.7	95.3	661.2	726.5	28.1	431.6	21.4	7.4	98.8	2.6	2.5	2.5	10.9	6.4	9.9	3718.3	267.1	1900.6
<i>Spergularia marina</i>	-	-	-	-	-	-	0.3	-	-	-	-	-	0.3	-	-	0.3	-	-	0.3	-	-	1.3	-	-
<i>Spergularia media</i>	-	4.9	1.0	-	1.0	-	-	1.5	-	0.3	0.5	-	-	-	-	-	-	-	-	-	-	0.3	-	3.0
<i>Suaeda maritima</i>	-	1.0	-	2.6	55.8	31.6	3.3	10.4	2.0	0.3	1.5	2.0	0.3	2.0	3.0	-	-	-	-	-	-	6.6	69.6	38.5
<i>Triglochin maritima</i>	-	-	-	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.5
Other species																								
<i>Buddleja davidii</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.3	-	-	-	-	-	0.3	-	-
<i>Carex spp</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8.9	-	-
<i>Cirsium arvense</i>	-	-	-	-	-	-	0.7	-	-	0.3	-	-	-	-	-	-	-	-	1.3	-	-	2.3	-	-
<i>Elytrigia repens</i>	-	-	-	-	-	0.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.6
<i>Epiobium spp.</i>	-	1.0	-	1.3	-	1.1	-	0.5	1.0	1.0	-	0.5	-	-	0.5	-	-	-	0.3	-	-	2.6	0.5	3.0
<i>Juncus effusus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.5
<i>Lolium perenne</i>	3.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.3	-	-	-	-	-	0.3	-	-
<i>Lythrum salicaria</i>	-	-	-	-	-	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.5
<i>Pieris echinoides</i>	0.6	-	-	-	-	-	0.3	-	-	0.3	-	-	-	-	-	-	-	-	-	-	-	0.7	-	-
<i>Plantago major</i>	-	-	-	-	-	-	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-	0.3	-	-	-
<i>Polygonum aviculare</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.3	-	-	-	-	-	0.3	-	-
<i>Pulicaria dysenterica</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.5
<i>Rumex acetosella</i>	-	-	-	-	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.5
<i>Rumex crispus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.3	-	-	-	-	-	0.7	-	-
<i>Samolus valerandi</i>	-	-	-	-	0.5	1.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.5	1.0
<i>Senecio vulgaris</i>	-	-	-	-	-	-	-	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.5
<i>Taraxacum officinale</i>	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Lypha angustifolia</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Urtica dioica</i>	0.5	-	1.0	0.3	0.5	-	1.0	1.0	-	0.3	-	-	0.3	-	0.5	-	-	-	1.0	-	-	1.3	-	-
<i>Veronica serpyllifolia</i>	-	-	-	-	-	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.0	1.5
																								0.5



Aerial photo of the Blackwater estuary with the Tollesbury managed realignment site
(acknowledgements to NERC)

Restoration of salt-marsh vegetation in relation to site suitability, species pools and dispersal traits.

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Submitted to *Journal of Applied Ecology*

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 north-west 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, south-east 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

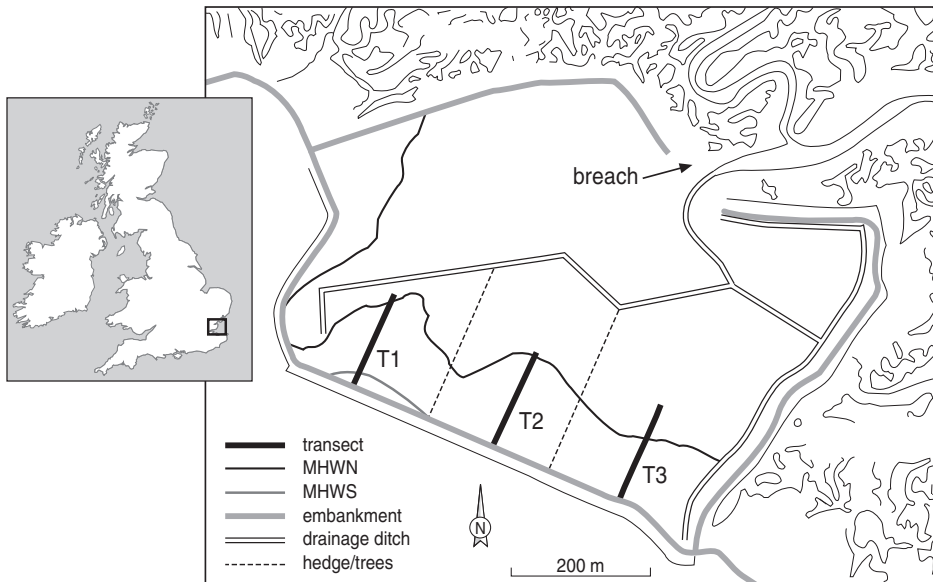


Figure 7.1. Study area with approximate location of transects and contour lines indicating mean high water spring (MHWS) and mean high water neap tide (MHWN).

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 × 10 cm.

The regional species pool is derived from Rodwell (2000) by selecting all salt-marsh 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 × 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

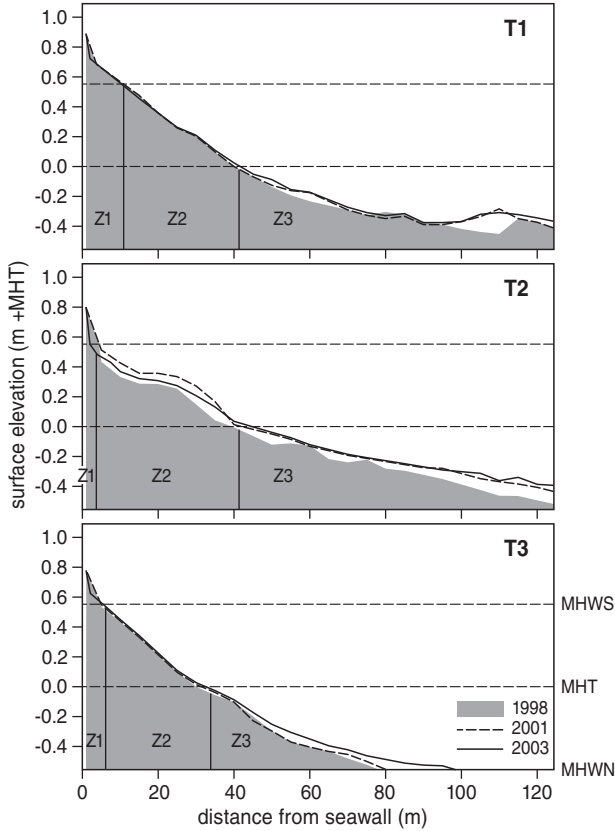


Figure 7.2. Surface elevation (in m + MHT) and elevation zones (Z1-3) of the three transects (T1-T3) in 1998, 2001 and 2003 with broken lines indicating mean high water spring (MHWS) and mean high tide (MHT) level.

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.

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*;

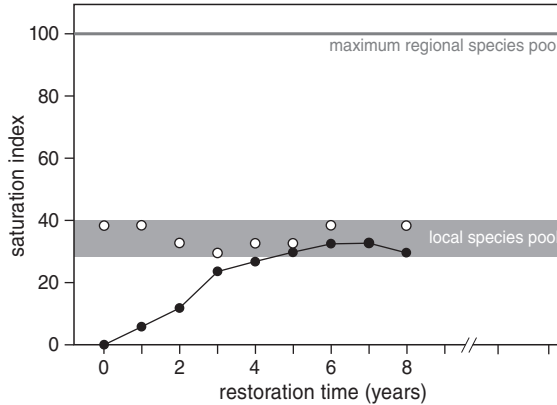


Figure 7.3. Saturation index, showing changes in number of target species in restoration site (black dots) and local species pool (open dots) over time as a percentage of the regional species pool (grey line).

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.

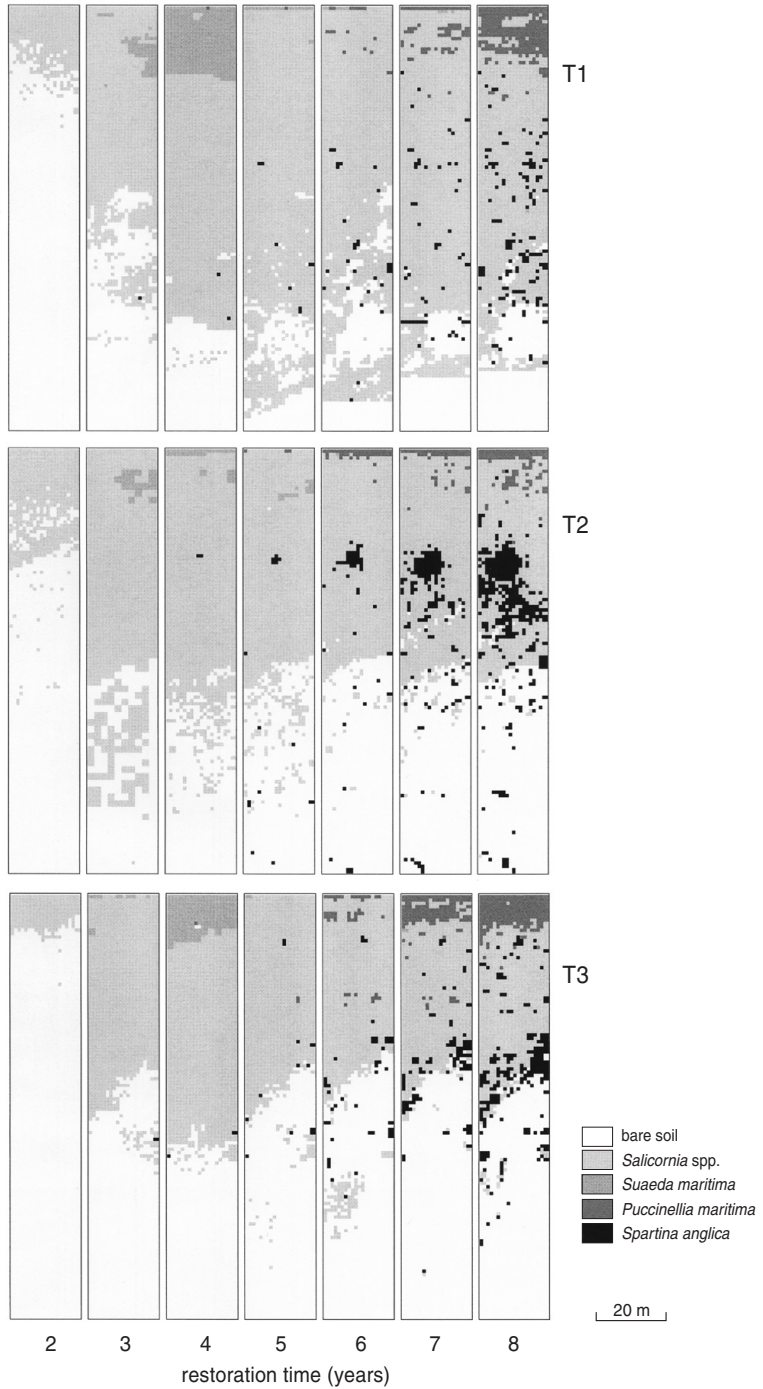


Figure 7.4. Distribution of dominant species in three transects (T1-T3) for seven years.

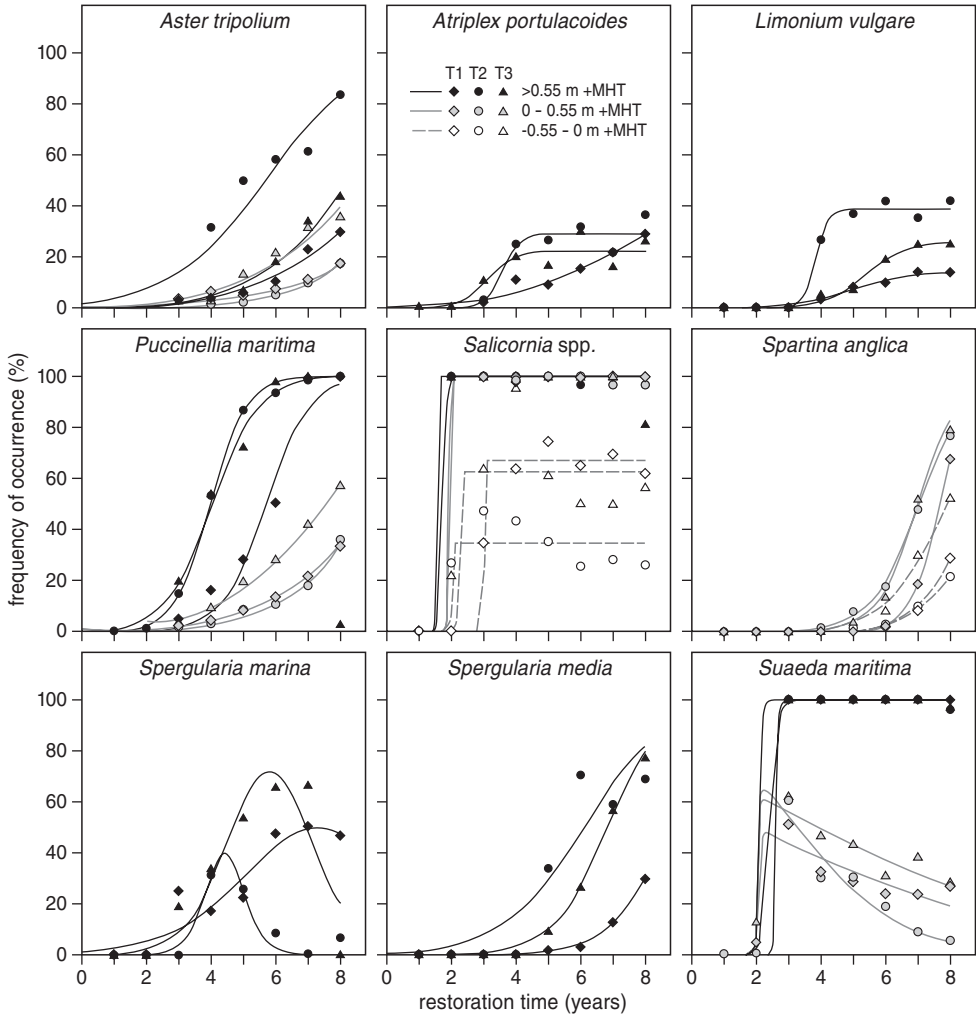


Figure 7.5. Response curves displaying temporal changes in frequency of occurrence for nine species with a minimum of 10 % occurrence for three consecutive years in three transects (T1, squares; T2, circles; T3, triangles) and 1- 3 elevational zones (> 0.55m + MHT, black; 0-0.55 + MHT, grey; -0.55-0 + MHT, white) .

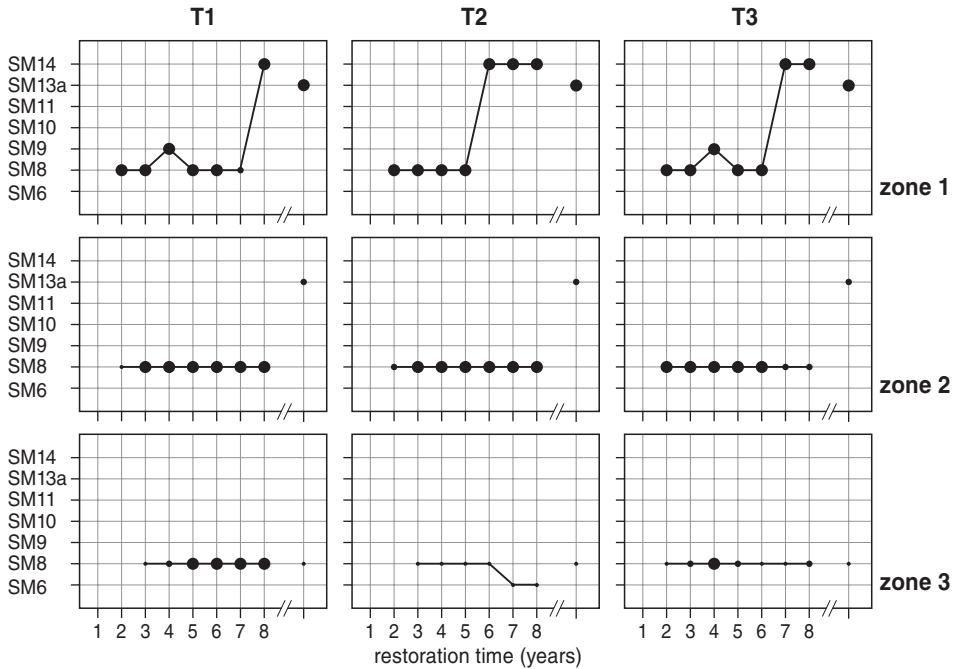


Figure 7.6. Goodness of fit to NVC communities in restoration site and adjacent marsh (after break in x-axis) for three different zones (zone 1: > 0.55 m + MHT, zone 2: $0 - 0.55$ m + MHT, zone 3: $- 0.55 - 0$ m + MHT) and three transects (T1-3). Only the best fit to a community is given, with the size 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
<i>Agrostis stolonifera</i>	Agrsto	4	93.52	0	0.05	6	6	1
<i>Armeria maritima</i>		4	68.98	0.03	0.93		7	3
<i>Aster tripolium</i>	Asttri	2	66.67	13.71	1.21	4 ^{1,2}	8	5
<i>Atriplex portulacoides</i>	Atrpor	2	59.26	50.08	3.69	6 ¹	8	6
<i>Atriplex prostrata</i>	Atrpro	4	90.74	0	3.31	1 ^{1,2}	7	2
<i>Bolboschoenus maritimus</i>	Bolmar	4	68.06	0	3.12	6	10	4
<i>Elytrigia atherica</i>	Elyath	3	71.30	0	4.20 ³	3 ^{1,2}	6	4
<i>Elytrigia repens</i>	Elyrep	4	77.31	0	2.56	3	5	2
<i>Festuca rubra</i>	Fesrub	4	62.96	0	0.94	3 ¹	5	2
<i>Frankenia laevis</i>		4	12.96	0	0.09 ⁴		8	5
<i>Glaux maritima</i>	Glamar	4	59.72	0	0.35	5 ²	7	4
<i>Inula crithmoides</i>		4	25.93	0	0.37		6	5
<i>Juncus gerardii</i>	Junger	4	65.74	0	0.03	1 ²	7	3
<i>Juncus maritimus</i>		4	43.06	0.02	0.03		8	5
<i>Leontodon autumnalis</i>		4	84.72	0	1.28		6	1
<i>Limonium bellidifolium</i>		4	0.46	0	0.73		8	5
<i>Limonium binervosum</i> agg.		4	24.07	0	0.56		8	5
<i>Limonium vulgare</i>	Limvul	3	44.44	15.63	0.84	1 ^{1,2}	8	6
<i>Oenanthe lachenalii</i>	Oenlac	4	45.37	0	1.13	3	8	3
<i>Plantago maritima</i>	Plamar	4	72.69	1.38	0.95	1 ^{1,2}	7	3
<i>Potentilla anserina</i>	Potans	4	86.57	0	0.89	1 ²	7	2
<i>Puccinellia distans</i>		4	46.30	0	0.27		8	4
<i>Puccinellia maritima</i>	Pucmar	2	53.70	61.23	0.72 ⁵	2 ¹	8	5
<i>Salicornia</i> spp.	Salspp	1	53.24	42.25	0.42 ⁶	1 ¹	8	9
<i>Sarcocornia perennis</i>		1	25.00	1.33			8	6
<i>Schoenoplectus tabernaemontani</i>	Schtab	4	48.15	0	1.33	3	10	3
<i>Seriphidium maritimum</i>	Sermar	4	39.81	0.02	0.75	1 ¹	7	5
<i>Spartina anglica</i>	Spaang	1	41.20	1.53	12.10 ³	4	9	7
<i>Spartina maritima</i>		4	12.96	0			9	6
<i>Spergularia marina</i>	Spemar	2	68.98	0	0.08	5 ²	8	5
<i>Spergularia media</i> ⁷	Spemed	3	59.26	3.49	0.13 ⁶	1 ^{1,2}	8	5
<i>Suaeda maritima</i>	Suamar	1	58.33	33.39	0.73	1 ^{1,2}	8	7
<i>Suaeda vera</i>		4	17.13	0			7	5
<i>Trifolium repens</i>		4	94.91	0	0.59		5	0
<i>Triglochin maritimum</i>	Trimar	4	59.26	12.2	0.50 ⁸	6 ¹	7	4

¹ (Koutstaal et al. 1987)² J. Geertsema, unpublished results³ Ecological flora of the British Isles at the University of York, www.york.ac.uk/res/ecoflora⁴ (Brightmore 1979)⁵ (Gray & Scott 1977)⁶ Personal observation⁷ *Spergularia media* was not regarded a target species in Wolters et al. (2005b)⁸ (Davy & Bishop 1991)

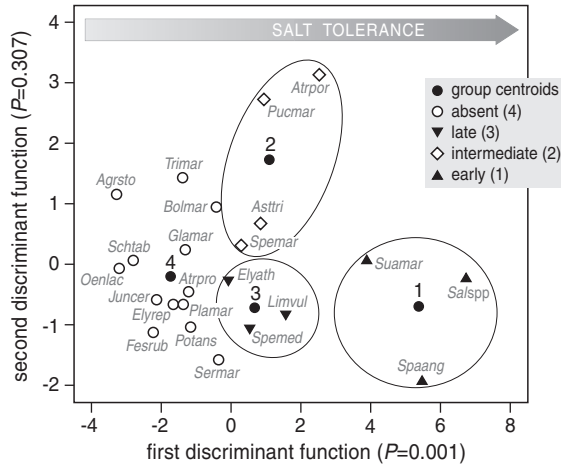


Figure 7.7. Discriminant analysis separating four groups of species differing in their sequence of establishment in the restoration site. Salt tolerance is highly correlated ($r = 0.664$) with the first discriminant function and abundance in the local species pool ($r = 0.674$) and flotation time ($r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

Acknowledgements

We would like to thank Dave Baratt, Laurie Boorman and Bill Meek for their assistance with the fieldwork. The help of Ruth Swetnam in converting cover data to dominance was much appreciated. Prof. Wim Wolff is kindly thanked for his comments on the manuscript. We are grateful for the financial support received from the Department of Environment, Fisheries and Rural Affairs.

References

- Adam, P. (1990) *Salt marsh ecology*. Cambridge University Press, Cambridge.
- Armstrong, W., Wright, E. J., Lythe, S. & Gaynard, T. J. (1985) Plant zonation and the effects of the spring-neap tidal cycle on soil aeration in a Humber salt marsh. *Journal of Ecology*, **73**, 323-339.
- Bakker, J. P. & Berendse, F. (1999) Constraints in the restoration of ecological diversity in grassland and heathland communities. *Trends in Ecology and Evolution*, **14**, 63-68.
- Belyea, L. R. & Lancaster, J. (1999) Assembly rules within contingent ecology. *Oikos*, **86**, 402-416.
- Bertness, M. D. & Hacker, S. D. (1994) Physical stress and positive associations among marsh plants. *American Naturalist*, **144**, 363-372.
- Bischoff, A. (2002) Dispersal and establishment of floodplain grassland species as limiting factors in restoration. *Biological Conservation*, **104**, 25-33.
- Bissels, S., Hölzel, N., Donath, T. W. & Otte, A. (2004) Evaluation of restoration success in alluvial grasslands under contrasting flooding regimes. *Biological Conservation*, **118**, 641-650.
- Boedeltje, G., Bakker, J. P., Bekker, R. M., van Groenendael, J. M. & Soesbergen, M. (2003) Plant dispersal in a lowland stream in relation to occurrence and three specific life-history traits of the species in the species pool. *Journal of Ecology*, **91**, 855-866.
- Boorman, L. A. (1967) *Limonium vulgare* Mill. and *L. humile* Mill. *Journal of Ecology*, **55**, 221-232.
- Boorman, L. A., Garbutt, A., Barratt, D. R., Myhill, D., Eversham, B., Reading, C., Cox, R. & Rothery, P. (1997) *Large scale experimental managed realignment volume 1 at Tollesbury, Essex*. T08074c5, 1-170. Institute of Terrestrial Ecology (Natural Environmental Research Council), Monks Wood, UK.
- Brightmore, D. (1979) Biological flora of the British Isles. *Frankenia Laevis*. *Journal of Ecology*, **67**, 1097-1107.
- Chapman, V. J. (1950) Biological flora of the British Isles. *Halimione portulacoides*. *Journal of Ecology*, **38**, 214-222.

- Chapman, V. J. (1974) *Salt-marshes and salt-deserts of the world*. Cramer, Lehre.
- Clarke, P. J., Kerrigan, R. A. & Westphal, C. J. (2001) Dispersal potential and early growth in 14 tropical mangroves: do early life history traits correlate with patterns of adult distribution? *Journal of Ecology*, **89**, 648-659.
- Cooper, A. (1982) The effects of salinity and waterlogging on the growth and cation uptake of salt marsh plants. *New Phytologist*, **90**, 263-275.
- Cornu, C. E. & Sadro, S. (2002) Physical and functional responses to experimental marsh surface elevation manipulation in Coos Bay's south Slough. *Restoration Ecology*, **10**, 474-486.
- Dalby, D. H. (1963) Seed dispersal in *Salicornia pusilla*. *Nature*, **199**, 197-198.
- Davy, A. J. & Bishop, G. F. (1991) Biological flora of the British Isles. *Triglochin maritima*. *Journal of Ecology*, **79**, 531-555.
- Davy, A. J., Bishop, G. F. & Costa, C. S. B. (2001) Biological flora of the British isles. *Salicornia L.* *Journal of Ecology*, **89**, 681-707.
- Diaz, S., Cabido, M., Zak, M., Martinez Carretero, E. & Aranibar, J. (1999) Plant functional traits, ecosystem structure and land-use history along a climatic gradient in central-western Argentina. *Journal of Vegetation Science*, **10**, 651-660.
- Ellison, A. M. (1987) Density dependent dynamics of *Salicornia europaea* mono cultures. *Ecology*, **68**, 737-741.
- Garbutt, R. A., Reading, C. J., Wolters, M., Gray, A. J. & Rothery, P. (2006) Monitoring the development of intertidal habitats on former agricultural land after the managed realignment of coastal defences at Tollesbury, Essex, UK. *Marine Pollution Bulletin (in Press)*.
- Goodman, P. J., Braybrooks, E. M. & Lambert, J. M. (1959) Investigations into the 'die-back' in *Spartina townsendii* agg. I. The present status of *Spartina townsendii* in Britain. *Journal of Ecology*, **47**, 651-677.
- Gray, A. J. & Scott, R. (1977) Biological flora of the British Isles. *Puccinellia maritima*. *Journal of Ecology*, **65**, 699-716.
- Hill, M. O. (1996) *Tablefit version 1.0, for identification of vegetation types*. Monks Wood, Institute of Terrestrial Ecology, UK.
- Hill, M. O., Mountford, J. O., Roy, D. B. & Bunce, R. G. H. (1999). *Ellenberg's indicator values for British plants*. 1-46. Monks Wood, Institute of Terrestrial Ecology, UK.
- Hölzel, N. & Otte, A. (2003) Restoration of a species-rich flood meadow by topsoil removal and diaspore transfer with plant material. *Applied Vegetation Science*, **6**, 131-140.
- Huisman, J., Olf, H. & Fresco, L. F. M. (1993) A hierarchical set of models for species response analysis. *Journal of Vegetation Science*, **4**, 37-46.
- Hutchings, M. J. & Russell, P. J. (1989) The seed regeneration dynamics of an emergent salt marsh. *Journal of Ecology*, **77**, 615-637.
- Keddy, P. A. (1992) Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science*, **3**, 157-164.
- Knevel, I. C., Bekker, R. M., Bakker, J. P. & Kleyer, M. (2003) Life-history traits of the Northwest European flora: The Leda database. *Journal of Vegetation Science*, **14**, 611-614.
- Koutstaal, B. P., Markusse, M. M. & de Munck, W. (1987) Aspects of seed dispersal by tidal movements. *Vegetation between land and sea: Structure and processes* (eds A. H. L. Huiskes, C. W. P. M. Blom & J. Rozema), pp. 226-233. Dr. W. Junk publishers, Dordrecht, NL.
- Langlois, E., Bonis, A. & Bouzille, J. B. (2003) Sediment plant dynamics in saltmarshes pioneer zone: *Puccinellia maritima* as a key species? *Estuarine, Coastal and Shelf Science*, **56**, 239-249.
- Levine, J. M., Brewer, J. S. & Bertness, M. D. (1998) Nutrients, competition and plant zonation in a New England salt marsh. *Journal of Ecology*, **86**, 285-292.
- Pennings, S. C., Selig, E. R., Houser, L. T. & Bertness, M. D. (2003) Geographic variation in positive and negative interactions among salt marsh plants. *Ecology*, **84**, 1527-1538.
- Preston, C. D., Pearman, D.A. & Dines, T.D. (2002) *New atlas of the British & Irish flora*. Oxford University Press, Oxford, UK.
- Pye, K. & French, P. W. (1993) Erosion and accretion on British salt marshes. ES19B(2). *Database of British saltmarshes*. Cambridge Environmental Research Consultants Ltd., London, UK.
- Pywell, R. F., Bullock, J. M., Hopkins, A., Walker, K. J., Sparks, T. H., Burke, M. J. W. & Peel, S. (2002) Restoration of species-rich grassland on arable land: assessing the limiting processes using a multi-site experiment. *Journal of Applied Ecology*, **39**, 294-309.

- Rand, T. A. (2002) Variation in insect herbivory across a salt marsh tidal gradient influences plant survival and distribution. *Oecologia*, **132**, 549-558.
- Ranwell, D. S. (1964) *Spartina* salt marshes in southern England. III Rates of establishment, succession and nutrient supply at Bridgewater Bay, Somerset. *Journal of Ecology*, **52**, 95-106.
- Reading, C. J., Gray, A. J., Paramor, O. A. L., Garbutt, R. A., Watts, C. W., Spearman, J. R., Barratt, D. R., Cheshier, T., Cox, R., Hughes, R. G., Mann, J. L., Myhill, D. G., Rothery, P., Semmence, J. & Wolters, M. (2002) *Managed realignment at Tollesbury and Saltram. Final report*. Defra project CSA2313, 1-199. Centre for Ecology and Hydrology, Dorchester, UK.
- Rodwell, J. S. (2000) *British plant communities. Maritime communities and vegetation of open habitats*. Cambridge University Press, Cambridge.
- Shumway, S. W. & Bertness, M. D. (1992) Salt stress limitation of seedling recruitment in a salt marsh plant community. *Oecologia*, **92**, 490-497.
- Snow, A. A. & Vince, S. W. (1984) Plant zonation in an Alaskan salt marsh. II. An experimental study of the role of edaphic conditions. *Journal of Ecology*, **72**, 669-684.
- Stace, C. (1997) *New Flora of the British Isles*. Cambridge University Press, Cambridge.
- Tamis, W. L. M., van der Meijden, R., Runhaar, J., Bekker, R. M., Ozinga, W. A., Odé, B. & Hoste, I. (2004) Standaardlijst van de Nederlandse flora. *Gorteria*, **30**, 101-195.
- Temperton, V. M., Hobbs, R. J., Nuttle, T., Fattorini, M. & Halle, S. (2004) Introduction: why assembly rules are important to the field of restoration ecology. *Assembly rules and restoration ecology. Bridging the gap between theory and practice* (eds V. M. Temperton, R. J. Hobbs, T. Nuttle & S. Halle), pp. 1-8. Island Press, Washington.
- Tessier, M. (2000) Factors affecting the population dynamics of *Suaeda maritima* at initial stages of development. *Plant Ecology*, **147**, 193-203.
- Tessier, M., Gloaguen, J.-C. & Bouchard, V. (2002) The role of spatio-temporal heterogeneity in the establishment and maintenance of *Suaeda maritima* in salt marshes. *Journal of Vegetation Science*, **13**, 115-122.
- Thom, R. M., Zeigler, R. & Borde, A. B. (2002) Floristic development patterns in a restored Elk River Estuarine marsh, Grays Harbor, Washington. *Restoration Ecology*, **10**, 487-496.
- Ungar, I. A. (1998) Are biotic factors significant in influencing the distribution of halophytes in saline habitats? *The Botanical Review*, **64**, 176-199.
- Watkinson, A. R. & Davy, A. J. (1985) Population biology of salt marsh and sand dune annuals. *Vegetatio*, **61**, 487-497.
- Watts, C. W., Tolhurst, T. J., Black, K. S. & Whitmore, A. P. (2003) In situ measurements of erosion shear stress and geotechnical shear strength of the intertidal sediments of the experimental managed realignment scheme at Tollesbury, Essex, UK. *Estuarine, Coastal and Shelf Science*, **58**, 611-620.
- Weiher, E. & Keddy, P. A. (1995) The assembly of experimental wetland plant communities. *Oikos*, **73**, 323-335.
- Wiehe, P. O. (1935) A quantitative study of the influence of tide upon the population of *Salicornia europaea*. *Journal of Ecology*, **23**, 323-333.
- Williams, P. B. & Orr, M. K. (2002) Physical evolution of restored breached levee salt marshes in the San Francisco Bay estuary. *Restoration Ecology*, **10**, 527-542.
- Wolters, M. & Bakker, J. P. (2002) Soil seed bank and driftline composition along a successional gradient on a temperate salt marsh. *Applied Vegetation Science*, **5**, 55-62.
- Wolters, M., Garbutt, A. & Bakker, J. P. (2005a) Plant colonization after managed realignment: the relative importance of diaspore dispersal. *Journal of Applied Ecology*, **42**, 770-777.
- Wolters, M., Garbutt, R. A. & Bakker, J. P. (2005b) Salt-marsh restoration: evaluating the success of de-embankments in north-west Europe. *Biological Conservation*, **123**, 249-268.
- Young, T. P., Chase, J. M. & Huddleston, R. T. (2001) Community succession and assembly. Comparing, contrasting and combining paradigms in the context of ecological restoration. *Ecological Restoration*, **19**, 5-18.
- Zobel, M., van der Maarel, E. & Dupré, C. (1998) Species pool: the concept, its determination and significance for community restoration. *Applied Vegetation Science*, **1**, 55-66.



Taking a distant view with Jan Bakker (Photo Willem van Duin)

Restoration of salt marshes : a synthesis

This final chapter sets out what the present thesis has contributed to our understanding of salt-marsh restoration and what the implications of this study are for the management of current and future de-embankment projects.

Introduction

The work described in the previous chapters centered on two aspects associated with salt-marsh restoration. The first aspect involved the evaluation of restoration success. Surprisingly little information is available on specific targets for salt-marsh restoration, obstructing not only the evaluation of restoration projects but also management decisions. The present chapter discusses our approach to evaluating restoration success and provides suggestions for improving measures of success. The second aspect focused on factors affecting salt-marsh restoration, with the central question: how do the target species arrive in the restoration site after de-embankment? A framework, summarizing the factors associated with salt-marsh development was introduced in Chapter 1 (see Fig. 8.1) and the present chapter will provide a critical analysis of the relative importance of these factors based on the work described in the previous chapters. Finally, a summary of management implications is provided at the end of this chapter.

Evaluating restoration success

Successful restoration of salt-marsh habitats involves many aspects, including structural components as well as ecosystem functioning (Box 8.1, www.ser.org, see also Ruiz-Jaen & Aide (2005)). The emphasis in this thesis has been on the establishment of salt-marsh vegetation. Other aspects of restoration success have been largely neglected, not because they are considered unimportant, but because by definition the

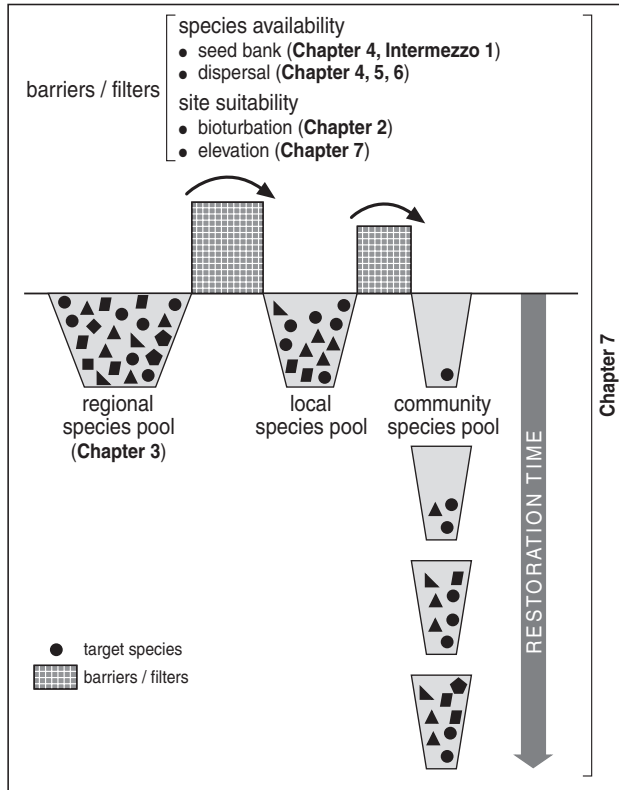


Figure 8.1. The framework used in the present thesis for elucidating the mechanisms behind salt-marsh development after de-embankment (see Chapter 1).

vegetation is the most important trophic level of a salt marsh and hence its restoration is a prerequisite for the occurrence of characteristic animals and for proper ecosystem functioning.

At the onset of the present study, no information was available as to what is considered a salt-marsh target species. Perhaps because it may appear trivial, i.e. a salt-marsh plant species is a species that tolerates salt, but what about *Agrostis stolonifera* or *Phragmites australis*, which can grow under brackish conditions but would probably not be regarded as characteristic salt-marsh species? There is clearly a need for an objective measure to select salt-marsh target species. In Chapter 3, the selection is based on phytosociological similarity between the target community and the regional flora, as advocated by Zobel *et al.* (1998). Target species were selected from National Vegetation Classification surveys, which list the frequency of occurrence of species characteristic or common to a certain community within the nation. A threshold level of more than 60 % frequency was used in Chapter 3 to ensure that non-typical salt-

marsh species were not selected, even though they may be present in a salt-marsh community. As an alternative, only constant or diagnostic species could have been included (see e.g. Bekker *et al.* (2002)), but this selection largely depends on the definition of constant or diagnostic which may differ between different countries. In both cases, the selection will be affected by the quality and detail of the National Vegetation Classification surveys and some typical salt-marsh species may fail to meet the selection criteria. A refinement of the selection procedure may involve the inclusion of a species' priority and vulnerability status (Rosenthal 2003). The assignment of priority status can be based on the rate of decline of a species (Rosenthal 2003), for example due to agricultural intensification or climate change. Vulnerability indices can be derived from red data lists or national floras (see e.g. Westhoff *et al.* (1993); Doody *et al.* (1993)). The use of the saturation index of Chapter 3 to evaluate restoration success can thus be improved by giving more weight to vulnerable or rapidly declining species. Another improvement involves information on species abundance and composition to identify whether a salt-marsh community has formed. The determination of salt-marsh communities is usually based on one or a few dominant species and, with the use of Global Positioning Systems (GPS), areas with similar species composition can easily be mapped in the field. In addition, data on species abundance and composition (preferably recorded on standard 2 m x 2 m plots) can be analyzed by computer programs specifically designed for identifying plant communities such as SALT 97 (de Jong *et al.* 1998) or Tablefit (Hill 1996) (see also Chapter 7).

Factors affecting salt-marsh restoration

The evaluation of current and historic de-embankments in north-west Europe has shown that many sites harbor less than 50 % of the regional target species (Chapter 3). As shown above, the regional species pool contains the sum of all target species occurring with a minimum frequency of 60 % in a particular salt-marsh community within the region. These target species have the potential to establish in a restoration site, but may not actually do so because they fail to reach the site or because site conditions are unsuitable for establishment. A framework summarizing the factors involved in salt-marsh restoration was presented in Chapter 1 (see Fig. 8.1). The following paragraphs will analyze how the results in the present thesis have contributed to our understanding of the factors involved in salt-marsh restoration.

Availability of target species

The first step in analyzing the mechanisms behind salt-marsh restoration involved identifying the source area of the target species and to ascertain their availability. Using the species pool concept, three species pools related to the same target community were distinguished at different spatial scales (Fig. 8.1; Chapter 1). The species pool concept postulates that species richness of one spatial scale is mainly determined

by the number of species at the next larger scale (Zobel 1997). In a restoration context, this implies that the probability of a target species establishing in the community species pool of the target area is highest when the species is present in the community species pool (including the established vegetation and below-ground diaspore bank), followed by the local species pool and finally the regional species pool (Fig. 8.1). Chapter 3 showed that between 48 and 100 % of the species present in the local species pool of the adjacent marsh established in the restoration sites within 1 to 13 years after de-embankment, compared to 26 to 64 % of the regional species pool. This agrees with the theory that species richness of one spatial scale is mainly determined by the number of species at the next larger scale (Zobel 1997). Other studies confirm that restoration success is largely affected by the abundance of target species in the established vegetation of a nearby source area (Boedeltje *et al.* 2003a; Donath *et al.* 2003).

Apart from the abundance of the target species in the local or regional species pool, the colonization potential will largely depend on a species' adaptation to dispersal and the presence of dispersal agents. A hypothetical graph of the rate at which species are expected to enter a restoration site after de-embankment is presented in Fig. 8.2, which is based on a species' main dispersal agent as derived from the Leda Traitbase (Knevel *et al.* 2003). The target species include all species of the regional species pool of the southern North-Atlantic region, as shown in Chapter 3. A certain proportion of target species from this regional species pool will have been present in the restoration site before it was embanked, but these species will have disappeared rapidly from the established vegetation once the area was reclaimed and exploited for agriculture. Upon de-embankment, the most rapid colonization is expected when the species are still present in the soil seed bank of the restoration site from which they may emerge when environmental conditions become suitable again (Fig 8.1). A prerequisite is that the seeds have retained their viability during the period of embankment. Chapter 4 showed that few salt-marsh species form a persistent seed bank and a salt-marsh restoration site that had been embanked for 30 years hardly contained any target species in the soil seed bank prior to de-embankment (Intermezzo 1). The contribution of the soil seed bank to species establishment during restoration may thus be neglected. This conclusion is not restricted to salt-marsh habitats (see Bakker *et al.* 1996b). Other studies have shown that the soil seed bank is unimportant in the restoration of species-rich dry alvar grassland (Bakker *et al.* 1996a), submerged aquatic vegetation in backwaters along a navigation channel (Boedeltje *et al.* 2003b) and hay meadows (Bekker *et al.* 2000).

The ecological significance of a persistent seed bank is that it allows the species to survive adverse conditions and to re-emerge from the soil when conditions become suitable. It has thus been postulated that persistent seed banks are an adaptation for species living in high disturbance or stressful areas (Harper 1977). Indeed, a database of soil seed banks of north-west Europe (Thompson *et al.* 1997) has shown that persistent soil seed banks are mainly associated with annual or biennial species that are

characteristic of disturbed habitats (Thompson *et al.* 1998). These species are generally small-seeded and require light to break their dormancy (Fenner 1985). When artificial gaps were created in perennial grassland vegetation, 36 % of the colonizing individuals originated from the soil seed bank (Kalamees & Zobel 2002). These studies, however, are centered on grassland species and arable weeds and the conclusions do not appear to extend to salt-marsh species (Chapter 4, Intermezzo 1) despite the stressful and disturbance-prone environment. The most likely explanation for this difference is that open space is amply available at the lower part of the salt marsh where most annuals occur. Germination of these species is therefore not usually inhibited by competition for light or resources from adult plants. Furthermore, the extent and period of tidal inundation is predictable, with neap tides followed by spring tides over a two-weekly period. Species like *Salicornia* spp. for example, use the period of neap tides to germinate and establish (Wiehe 1935). Were these species to have a persistent (dormant) seed bank, their seeds would soon be buried by accreting sediment after which the chance of germinating would be severely reduced.

It has also been suggested that a trade-off exists between the building of a persistent seed bank and adaptation to long-distance dispersal (Harper 1977; Venable & Brown 1988; Ehrlén & van Groenendael 1998), with the latter becoming more important for species of unpredictable and rare habitats. Four potential dispersal agents and their contribution to the dispersal of salt-marsh species have been distinguished in Fig. 8.2. Wind (anemochory) is considered an important dispersal agent as it is commonly available and can transport seeds over several kilometres (Soons & Ozinga 2005). However, very few salt-marsh species (e.g. *Aster tripolium*) appear to be adapted to wind dispersal. Much better colonization potential is expected via dispersal by water (hydrochory, Fig. 8.2), because the majority of salt-marsh species is able to remain afloat in seawater for several hours or days (Koutstaal *et al.* 1987) and salt marshes are inundated frequently. Finally, a small proportion of target species may have to rely on animals (externally: exozoochory, or internally: endozoochory) or unknown mechanisms for dispersal into the target area (Fig. 8.2). Dispersal of salt-marsh seeds by the feet or feathers of birds (Vivian-Smith & Stiles 1994) and via geese and hare (Chang *et al.* 2005) droppings or cattle dung (Bakker *et al.* 1985) has been demonstrated.

Chapter 4 has shown that large quantities of salt-marsh seeds of different species are dispersed via driftline material. However, propagules were not homogeneously distributed across a successional gradient (Chapter 4) and few species were actually trapped on the salt-marsh surface during restoration (Chapter 6). In contrast, studies of the colonization of atolls (Carlquist 1967) or volcanic islands in the Pacific Ocean (Harrison *et al.* 2001) and islands in the Great Lakes (Morton & Hogg 1989) indicate that water has been important in long-distance dispersal of seeds as many of the established species show adaptation to hydrochory. Furthermore, studies of drift material collected on isolated islands in the Indian Ocean (Green 1999) or on cays of the Great Barrier reef (Australia) (Smith *et al.* 1990) showed that many drift dis-

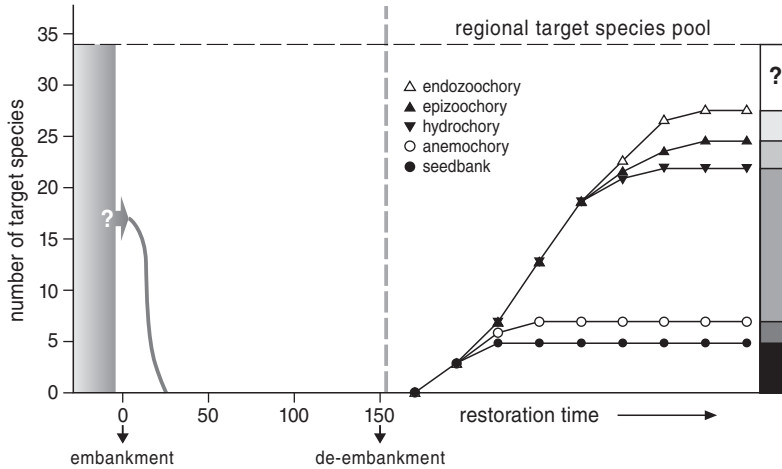


Figure 8.2. Hypothetical graph of colonization potential of regional target species after de-embankment, based on database information on dispersal traits (Leda Traitbase).

seminules did not belong to the local established flora and must have originated from source areas at least 300 km away (Hacker 1990). A large proportion of stranded seeds, however, failed to establish because they lost viability during immersion in seawater (Smith *et al.* 1990; Green 1999). Other studies have shown that dispersal of floating seeds is strongly related to the direction of ocean currents and the prevailing wind (Koutstaal *et al.* 1987; Smith *et al.* 1990; Hacker 1990; Huiskes *et al.* 1995). Floating seeds may thus behave similar to oil slick (Karafyllidis 1997) and the limited dispersal of salt-marsh species into the Tollesbury restoration site (Chapter 6) may be because of the prevailing offshore wind direction. Hence, despite the abundance of seeds in oceanic drift and the good flotation ability of many species, successful colonization appears to be determined mainly by environmental conditions (Porter 1976).

Site suitability

In Chapter 3 a significant relationship was found between the number of target species and surface elevational range in relation to sea level of different de-embankment sites. In addition, Chapter 7 has shown that colonization rates and species diversity were highest at the highest elevation of a restoration site. Superimposed on the importance of surface elevation is the effect of bioturbation and herbivory by the ragworm *Nereis diversicolor* (Chapter 2). Ragworms generally occur at the level of low intertidal flats up to the transition to pioneer salt marsh where vegetation is sparse. In this transition area they may have a negative effect on the survival of *Salicornia* seedlings, but the effect should be viewed in relation to physical parameters of tidal currents and soil properties (Chapter 2). In general it can be concluded that the higher the surface elevation relative to sea level the better the colonization potential for

salt-marsh species (see (Cornu & Sadro 2002; Williams & Orr 2002). However, competition from less salt-tolerant species will become increasingly important with increasing elevation. In this respect, land use before and after de-embankment may play a role in the establishment of salt-marsh species. A case study of a de-embanked summerpolder, for example, showed that several of the original non-halophytic species were able to survive and remain abundant at the highest areas for at least three years after the restoration of tidal inundation (van Duin *et al.* 2005). Colonization of these areas by salt-marsh species has proceeded much slower compared to lower-lying areas. Furthermore, cattle-grazed areas contained a higher number of halophytic species compared to exclosures (van Duin *et al.* 2005). Similar conclusions were derived from Chapter 3, which showed that the most successful de-embankment sites in terms of number of target species were those that had a grazing or management regime. This type of management is of course related to elevation, with only the higher areas with dense perennial vegetation being suitable for grazing or mowing. The importance of environmental conditions and management regimes on plant-community restoration has also been reported for grasslands (Walker *et al.* 2004) and heathlands (Bakker & Berendse 1999). However, the effect of site suitability on species establishment during community restoration has to be viewed in relation to seed dispersal constraints (Verhagen *et al.* 2001; Bakker *et al.* 2002a; Donath *et al.* 2003; Bissels *et al.* 2004).

In Chapter 7, the arrival order of different salt-marsh species has been tested against abundance in the regional and local species pool, dispersal traits and Ellenberg's indicator values for salinity and moisture. The indicator value for salinity was by far the most important factor explaining the arrival order of species during the first eight years of restoration. But does this mean that the target species are being dispersed into the restoration site but fail to establish due to unsuitable site conditions? Astroturf seed trap data for the Tollesbury managed-realignment site have shown that dispersal of late-successional or higher-marsh species is limited and that the diaspore pool is dominated by species that are abundant in the local vegetation (Chapter 6). But as with all dispersal studies, the tail of a dispersal curve is difficult to predict (Bullock & Clarke 2000) and rare species are easily missed as a result of restricted sampling effort. To disentangle the relative importance of site suitability and dispersal constraints, seed addition experiments can be applied. Several studies have shown that adding seeds will aid the establishment of species that failed to colonize naturally in inland grasslands (Pywell *et al.* 2002) and floodplains (Donath *et al.* 2003; Hölzel & Otte 2003). Very few seed addition experiments have been performed on salt-marsh systems (but see Bakker *et al.* (1985); Bakker & de Vries (1992); Rand (2000)), not least because of the inherent difficulties of retaining the seeds during tidal inundation. At Tollesbury for example, seeds of six salt-marsh species were sown at densities of 500 m⁻² and 5000 m⁻² at four different elevations within the restoration site, but no germination was observed (Reading *et al.* 2002; Garbutt *et al.* 2005). Seed trapping, seed addition and transplanting experiments should (continue to) be

performed on existing salt marshes and salt-marsh restoration sites in order to get a better understanding of the possibilities and constraints of seed dispersal in relation to site suitability.

Management implications

The present thesis has provided insight into the restoration of salt-marsh vegetation after de-embankment, with particular emphasis on seed dispersal. Many questions, however, remain unanswered and long-term results are still to be awaited. Nevertheless, the prospect for salt-marsh restoration after de-embankment is good, with target species coming in naturally and vegetation succession taking place. Pioneer and low-marsh species (in particular *Salicornia* and *Suaeda*) are the most successful colonizers after de-embankment (Chapter 3), not because they are better adapted to dispersal (based on flotation time and seed weight, Chapter 7) but more likely because their source areas are regularly inundated, thus increasing the chance of dispersal by tidal water. Moreover, chances of establishment are better because these species are relatively salt-tolerant and they do not need to compete with other species as established vegetation is initially absent. A prerequisite for successful restoration, therefore, is that sites are at a proper elevation with respect to tidal inundation for vegetation development (Cornu & Sadro 2002; Williams & Orr 2002; Morris *et al.* 2004; see also Chapters 3 and 7). When the surface elevation is high enough for the establishment of dense perennial vegetation, grazing and mowing regimes may be implemented to ensure higher species diversity. Otherwise, the tall-grass *Elytrigia atherica* may become dominant (Bakker *et al.* 2002b). In addition, the potential for seed dispersal into the restoration site is enhanced when target species are present in the local species pool of an adjacent marsh. The construction of drainage ditches will further enhance colonization rates by facilitating the distribution of species (Zedler & Callaway 2001; Eertman *et al.* 2002; Chapter 3). Furthermore, species can extend their lower elevational limits when the soil is well aerated (Bakker *et al.* 2002b). Drainage structures are especially important in sites that have been embanked for a long period and, as a result, feature over-consolidated surface soils that impede subsurface drainage (Crooks *et al.* 2002). The natural formation of creeks on these soils may take a long time.

In general, it can be concluded that de-embankment is a suitable means for the restoration of salt marshes on formerly reclaimed land and offers an excellent opportunity to study the initial stages of salt-marsh development and primary succession.

References

- Bakker, J. P., Bakker, E. S., Rosén, E., Verweij, G. L. & Bekker, R. M. (1996a) Soil seed bank composition along a gradient from dry alvar grassland to *Juniperus* shrubland. *Journal of Vegetation Science*, **7**, 165-176.
- Bakker, J. P. & Berendse, F. (1999) Constraints in the restoration of ecological diversity in grassland and heathland communities. *Trends in Ecology and Evolution*, **14**, 63-68.
- Bakker, J. P. & de Vries, Y. (1992) Germination and early establishment of lower salt marsh species in grazed and mown salt marsh. *Journal of Vegetation Science*, **3**, 247-252.
- Bakker, J. P., Dijkstra, M. & Russchen, P. T. (1985) Dispersal, germination and early establishment of halophytes and glycophytes on a grazed and abandoned salt marsh gradient. *New Phytologist*, **101**, 291-308.
- Bakker, J. P., Elzinga, J. A. & de Vries, Y. (2002a) Effects of long-term cutting in a grassland system: perspectives for restoration of plant communities on nutrient-poor soils. *Applied Vegetation Science*, **5**, 107-120.
- Bakker, J. P., Esselink, P., Dijkema, K. S., van Duin, W. E. & de Jong, D. J. (2002b) Restoration of salt marshes in the Netherlands. *Hydrobiologia*, **478**, 29-51.
- Bakker, J. P., Poschod, P., Strykstra, R. J., Bekker, R. M. & Thompson, K. (1996b) Seed banks and seed dispersal: important topics in restoration ecology. *Acta Botanica Neerlandica*, **45**, 461-490.
- Bekker, R. M., Strykstra, R. J., Schaminée, J. H. J. & Hennekens, S. M. (2002) Zaadvoorraad en herintroductie: achtergronden, spectra van plantengemeenschappen en voorbeelden uit de praktijk. *Stratiotes*, **24**, 27-48.
- Bekker, R. M., Verweij, G. L., Bakker, J. P. & Fresco, L. F. M. (2000) Soil seed bank dynamics in hay-field succession. *Journal of Ecology*, **88**, 594-607.
- Bissels, S., Hölzel, N., Donath, T. W. & Otte, A. (2004) Evaluation of restoration success in alluvial grasslands under contrasting flooding regimes. *Biological Conservation*, **118**, 641-650.
- Boedeltje, G., Bakker, J. P., Bekker, R. M., van Groenendaal, J. M. & Soesbergen, M. (2003a) Plant dispersal in a lowland stream in relation to occurrence and three specific life-history traits of the species in the species pool. *Journal of Ecology*, **91**, 855-866.
- Boedeltje, G., Bakker, J.P. & ter Heerdt, G.N.J. (2003b) Potential role of propagule banks in the development of aquatic vegetation in backwaters along navigation canals. *Aquatic Botany*, **77**, 53-69.
- Bullock, J. M. & Clarke, R. T. (2000) Long distance seed dispersal by wind: measuring and modelling the tail of the curve. *Oecologia*, **124**, 506-521.
- Carlquist, S. (1967) The biota of long-distance dispersal. V. Plant dispersal to Pacific Islands. *Bulletin of the Torrey Botanical Club*, **94**, 129-162.
- Chang, E. R., Zoxaya, E. L., Kuijper, D. P. J. & Bakker, J. P. (2005) Seed dispersal by small herbivores and tidal water: are they important filters in the assembly of salt-marsh communities? *Functional Ecology*, **19**, 665-673.
- Cornu, C. E. & Sadro, S. (2002) Physical and functional responses to experimental marsh surface elevation manipulation in Coos Bay's south Slough. *Restoration Ecology*, **10**, 474-486.
- Crooks, S., Schutten, J., Sheern, G. D., Pye, K. & Davy, A. J. (2002) Drainage and elevation as factors in the restoration of salt marsh in Britain. *Restoration Ecology*, **10**, 591-602.
- de Jong, D. J., Dijkema, K. S., Bossinade, J. H. & Janssen, J. A. M. (1998) *SALT97 een classificatieprogramma voor kweldervegetaties*. Rijkswaterstaat (RIKZ, Dir Noord Nederland, Meetkundige dienst) & IBN-DLO.
- Donath, T. W., Hölzel, N. & Otte, A. (2003) The impact of site conditions on seed dispersal and restoration success in alluvial meadows. *Applied Vegetation Science*, **6**, 13-22.
- Doody, J. P., Johnston, C. & Smith, B. (1993) Directory of the North sea coastal margin. Joint Nature Conservation Committee, Peterborough, UK.
- Eertman, R. H. M., Kornman, B. A., Stikvoort, E. & Verbeek, H. (2002) Restoration of the Sieperda tidal marsh in the Scheldt estuary, The Netherlands. *Restoration Ecology*, **10**, 438-449.
- Ehrlén, J. & van Groenendaal, J. M. (1998) The trade-off between dispersability and longevity - an important aspect of plant species diversity. *Applied Vegetation Science*, **1**, 29-36.
- Fenner, M. (1985) *Seed ecology*. Chapman & Hall, London, UK.

- Garbutt, R. A., Reading, C. J., Wolters, M., Gray, A. J. & Rothery, P. (2006) Monitoring the development of intertidal habitats on former agricultural land after the managed realignment of coastal defences at Tollesbury, Essex, UK. *Marine Pollution Bulletin*, In press.
- Green, P. T. (1999) Greta's Garbo: stranded seeds and fruits from Greta Beach, Christmas Island, Indian Ocean. *Journal of Biogeography*, **26**, 937-946.
- Hacker, J. B. (1990) Drift seeds and fruit on Raine Island, northern Great Barrier Reef, Australia. *Journal of Biogeography*, **17**, 19-24.
- Harper, J. L. (1977) *Population biology of plants*. Academic press, London, UK.
- Harrison, R. D., Banka, R., Thornton, I. W. B., Shanahan, M. & Yamuna, R. (2001) Colonization of an island volcano, Long Island, Papua New Guinea, and an emergent island, Mormot, in its caldera lake. II. The vascular flora. *Journal of Ecology*, **28**, 1311-1337.
- Hill, M. O. (1996) *Tablefit version 1.0, for identification of vegetation types*. Institute of Terrestrial Ecology, Huntingdon, UK.
- Hölzel, N. & Otte, A. (2003) Restoration of a species-rich flood meadow by topsoil removal and diaspore transfer with plant material. *Applied Vegetation Science*, **6**, 131-140.
- Huiskes, A. H. L., Koutstaal, B. P., Herman, P. M. J., Beefink, W. G., Markusse, M. M. & de Munck, W. (1995) Seed dispersal of halophytes in tidal salt marshes. *Journal of Ecology*, **83**, 559-567.
- Kalamees, R. & Zobel, M. (2002) The role of the seed bank in gap generation in a calcareous grassland community. *Ecology*, **83**, 1017-1025.
- Karafyllidis, I. (1997) A model for the prediction of oil slick movement and spreading using cellular automata. *Environment International*, **23**, 839-850.
- Knevel, I. C., Bekker, R. M., Bakker, J. P. & Kleyer, M. (2003) Life-history traits of the Northwest European flora: The Leda database. *Journal of Vegetation Science*, **14**, 611-614.
- Koutstaal, B. P., Markusse, M. M. & de Munck, W. (1987) Aspects of seed dispersal by tidal movements. *Vegetation between land and sea: Structure and processes* (eds A. H. L. Huiskes, C. W. P. M. Blom & J. Rozema), pp. 226-233. Dr. W. Junk Publishers, Dordrecht, the Netherlands.
- Morris, R. K. A., Reach, I. S., Duffy, M. J., Collins, T. S. & Leafe, R. N. (2004) On the loss of salt-marshes in south-east England and the relationship with *Nereis diversicolor*. *Journal of Applied Ecology*, **41**, 787-791.
- Morton, J. K. & Hogg, E. H. (1989) Biogeography of island floras in the Great Lakes. II. Plant dispersal. *Canadian Journal of Botany*, **67**, 1803-1820.
- Porter, D. M. (1976) Geography and dispersal of Galapagos Islands vascular plants. *Nature*, **264**, 745-746.
- Pywell, R. F., Bullock, J. M., Hopkins, A., Walker, K. J., Sparks, T. H., Burke, M. J. W. & Peel, S. (2002) Restoration of species-rich grassland on arable land: assessing the limiting processes using a multi-site experiment. *Journal of Applied Ecology*, **39**, 294-309.
- Rand, T. A. (2000) Seed dispersal, habitat suitability and the distribution of halophytes across a salt marsh tidal gradient. *Journal of Ecology*, **88**, 608-621.
- Reading, C. J., Gray, A. J., Paramor, O. A. L., Garbutt, R. A., Watts, C. W., Spearman, J. R., Barratt, D. R., Chesher, T., Cox, R., Hughes, R. G., Mann, J. L., Myhill, D. G., Rothery, P., Semmence, J. & Wolters, M. (2002) *Managed realignment at Tollesbury and Saltram*. Final report. Defra project CSA2313, 1-199. Centre for Ecology and Hydrology, Dorchester, UK.
- Rosenthal, G. (2003) Selecting target species to evaluate the success of wet grassland restoration. *Agriculture, Ecosystems and Environment*, **98**, 227-246.
- Ruiz-Jaen, C. & Aide, T. M. (2005) Restoration success: how is it being measured? *Restoration Ecology*, **13**, 569-577.
- Smith, J. M. B., Heatwole, H., Jones, M. & Waterhouse, B. M. (1990) Drift disseminules on cays of the Swain Reefs, Great Barrier Reef, Australia. *Journal of Biogeography*, **17**, 5-17.
- Soons, M. B. & Ozinga, W. A. (2005) How important is long-distance seed dispersal for the regional survival of plant species? *Diversity and Distributions*, **11**, 165-172.
- Thompson, K., Bakker, J. P. & Bekker, R. M. (1997) *Soil seed banks of North West Europe: methodology, density and longevity*. Cambridge University Press, Cambridge, UK.
- Thompson, K., Bakker, J. P., Bekker, R. M. & Hodgson, J. G. (1998) Ecological correlates of seed persistence in soil in the North-western European flora. *Journal of Ecology*, **86**, 163-169.

- van Duin, W., Esselink, P., Bos, D., Verweij, G., Wolters, M. & van Leeuwen, P.-W. (2005) *Monitoringsonderzoek proefverkweldering Noard Fryslân Bûtendyks*. Tussenrapportage 2004. Alterra, Texel, the Netherlands.
- Venable, D. L. & Brown, J. S. (1988) The selective interactions of dispersal, dormancy and seed size as adaptations for reducing risk in variable environments. *American Naturalist*, **131**, 360-384.
- Verhagen, R., Klooker, J., Bakker, J. P. & van Diggelen, R. (2001) Restoration success of low-production plant communities on former agricultural soils after top-soil removal. *Applied Vegetation Science*, **4**, 75-82.
- Vivian-Smith, G. & Stiles, E. W. (1994) Dispersal of salt marsh seeds on the feet and feathers of waterfowl. *Wetlands*, **14**, 316-319.
- Walker, K. J., Stevens, P. A., Stevens, D. P., Mountford, J. O., Manchester, S. J. & Pywell, R. F. (2004) The restoration and re-creation of species-rich lowland grassland on land formerly managed for intensive agriculture in the UK. *Biological Conservation*, **119**, 1-18.
- Westhoff, V., Hobohm, C. & Schaminée, J. H. J. (1993) Rote Liste der Pflanzengesellschaften des Naturraumes Wattenmeer unter Berücksichtigung der ungefährdeten Vegetationseinheiten. *Tuexenia*, **13**, 109-140.
- Wiehe, P. O. (1935) A quantitative study of the influence of tide upon the population of *Salicornia europaea*. *Journal of Ecology*, **23**, 323-333.
- Williams, P. B. & Orr, M. K. (2002) Physical evolution of restored breached levee salt marshes in the San Francisco Bay estuary. *Restoration Ecology*, **10**, 527-542.
- Zedler, J. B. & Callaway, J. C. (2001) Tidal wetland functioning. *Journal of Coastal Research*, **S127**, 38-64.
- Zobel, M. (1997) The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? *Trends in Ecology and Evolution*, **12**, 266-269.
- Zobel, M., van der Maarel, E. & Dupré, C. (1998) Species pool: the concept, its determination and significance for community restoration. *Applied Vegetation Science*, **1**, 55-66.

Box 8.1. Attributes for guiding the evaluation of ecological restoration success (from the Society for Ecological Restoration, www.ser.org)

1. the restored ecosystem contains a characteristic set of species that occur in the reference system
2. the restored ecosystem consists of indigenous species to the greatest practical extent
3. all functional groups necessary for the continued development and/or stability of the restored ecosystem are represented or have the potential to colonize
4. the physical environment of the restored ecosystem is capable of reproducing populations of the species necessary for its continued stability or development
5. the restored ecosystem functions normally for its ecological stage of development
6. the restored ecosystem is suitably integrated into a larger ecological matrix of landscape
7. potential threats to the health and integrity of the restored ecosystem from the surrounding landscape have been eliminated or reduced as much as possible
8. the restored ecosystem is sufficiently resilient to endure the normal periodic stress events in the local environment that serve to maintain the integrity of the ecosystem
9. the restored ecosystem is self-sustaining to the same degree as the reference ecosystem and has the potential to persist indefinitely under existing environmental conditions

Summary

This thesis focuses on the restoration of salt marshes in north-west Europe. Salt marshes are important habitats that need to be conserved. Not only do they provide a suitable environment for different plant and animal species, many of which are restricted to saline habitats, but they also function as a natural flood defence, reducing wave energy before the tidal water reaches constructed embankments.

Loss of salt marshes

For many centuries, salt marshes have been reclaimed from the sea by the construction of embankments and transformed into agricultural land. As a result, large areas of salt marsh have been lost. More recently, salt marshes are being lost because of erosion, which has been mainly attributed to a global rise in sea level as a result of climate change. In the United Kingdom, the combination of land reclamation and relative sea-level rise (i.e. land subsidence and eustatic sea-level rise) has received particular attention. This has resulted in the coastal squeeze hypothesis, which postulates that salt-marsh erosion is due to the presence of sea walls preventing landward migration of salt marshes in response to sea-level rise. This hypothesis has been refuted by scientists who argue that sediment accretion rates on salt marshes are sufficient to compensate for a rise in sea level. Instead, these scientists believe that the increased rate of salt-marsh erosion in recent decades is the result of bioturbation and herbivory by the ragworm *Nereis diversicolor*, causing instability of the sediment. A literature survey has been conducted in Chapter 2 to address the issues of salt-marsh erosion, coastal squeeze and the effect of *Nereis diversicolor* on erosion and plant establishment. The results of this survey show that although salt marshes may receive sufficient sediment to compensate for sea-level rise, lateral erosion of the salt-marsh edge will result in a net loss of salt-marsh area. This lateral erosion appears to be caused by a combination of physical factors, including strong winds, high tides and increased wave height, which in turn may be caused by climate change and human activities like land claim, dredging and canalization. In addition, laboratory studies have shown that bioturbation and herbivory from populations of *Nereis diversicolor* can lead to sediment instability and loss of pioneer plant species, such as *Salicornia* spp.

However, field studies were inconclusive and have been conducted at small spatial scales and the extent to which the ragworm may affect erosion at the regional scale remains uncertain.

De-embankment of salt marshes

Recently, reclamation of salt marshes for agricultural purposes has become financially less attractive, whereas nature conservation and coastal defence issues have become increasingly important. As a result, managed realignment, or de-embankment of formerly reclaimed land, has been introduced as a measure to compensate for salt-marsh loss by providing space for salt-marsh development land inward. The concept of de-embankment to re-create salt marshes is not new. In the past, several embankments accidentally breached during storm and high tides. In Chapter 3, a total of 70 accidental and deliberate de-embankments in north-west Europe have been identified and in several sites spontaneous development of salt-marsh vegetation has occurred. Many sites, however, have not been monitored for plant-species assemblages, so that we still know little about the process of colonization and subsequent establishment of salt-marsh plant species.

Establishment of salt-marsh species after de-embankment

A central question in the present thesis is how the target species can arrive in the restoration site after de-embankment. The first step in addressing this question is to identify what the target species are. In Chapter 3, target species were selected from national vegetation classification studies, which list the frequency of occurrence of species characteristic or common to a certain community within the nation. All species present in more than 60 % of the relevés of a specific community were selected to form the regional target species pool. A saturation index was calculated to express the number of target species that actually established in a restoration site as a percentage of the regional target species pool. This saturation index allowed the objective comparison of restoration success of many different sites based on the concept that all regional target species have the potential to establish in the restoration site, but may not actually do so because the site is unsuitable or inaccessible. Chapter 3 shows that of the 37 de-embankment sites with information on plant species assemblages, more than 30 sites contained less than 50 % of the regional target species. Factors affecting the saturation index included the size of the site, elevational range within the site and the age of the site. The pioneer species *Salicornia* was present in the majority of the sites, from which we conclude that even if bioturbation and herbivory by *Nereis* have occurred, overall the effects have been insufficient to restrict plant establishment on exposed sediment.

Species availability, dispersal and site suitability

In the present thesis, three potential source areas of the target species have been distinguished at different spatial scales, including the community, local and regional species pool. The fastest establishment is expected when the target species are present in the community species pool of the restoration site, which includes the vegetation and below-ground seed bank. It is unlikely that target species are present in the established vegetation of restoration sites that have been embanked for several decades. However, seeds that have been incorporated in the soil seed bank may have retained viability throughout the period of embankment. Seed longevity can be assessed by comparing the abundance of seeds in the upper (i.e. younger) soil layer with the deeper (i.e. older) soil layer. In Chapter 4, this method has been used to classify the seed bank of salt-marsh species along a successional gradient on an existing salt marsh. The results show that the majority of salt-marshes species do not form a long-term persistent seed bank. These results are in agreement with a case study of a restoration site that had been embanked for 30 years and which showed that prior to de-embankment hardly any salt-marsh seed was present in the soil seed bank (Intermezzo 1). Hence the soil seed bank of the community species pool is unlikely to play an important role in the establishment of target species after de-embankment and the target species have to be dispersed from nearby source areas into the restoration site.

It is expected that tidal water will play an important role in dispersal of salt-marsh species, as seeds of most species are able to float for some time in seawater and the salt marshes are regularly flooded. During extreme high tides, seeds can be accumulated into driftline material that is usually deposited at the upper part of a salt marsh or along the foot of the seawall. Chapter 4 describes the composition of driftline material along a successional gradient on the island of Schiermonnikoog. The results show that driftline material contains many seeds of different species. However, the composition of the material mainly resembles the local established vegetation and the seeds are not homogeneously distributed across different successional stages.

While driftline material provides essential information as to the possibilities of seed dispersal by tidal water, the occurrence of this material is spatially and temporally unpredictable and seedling survival tends to be low. Hence an alternative or complementary method is necessary to investigate whether seeds are actually deposited on the salt-marsh surface after normal tidal flooding. Chapter 5 introduces the use of astroturf seed traps for studying hydrochory. The mats were fastened to the salt-marsh surface and collected after one or multiple tidal inundations. After rinsing, the sampled material was placed in the greenhouse and checked for seedling emergence. The results of this technical study show that astroturf mats effectively trap diaspores dispersed by tidal water. The seed retaining ability of the astroturf did not differ significantly for species with different seed characteristics. Astroturf seed traps were used in Chapter 6 to ascertain whether salt-marsh development may be constrained

by limited diaspore dispersal. Seed traps were replaced monthly in the restoration site and on the adjacent marsh (i.e. local species pool) from October to March. Although a total of 38 species, including 18 salt-marsh species, were trapped in the restoration site and on the adjacent marsh, only six salt-marsh species occurred with more than three seeds per m². For most species, the number of diaspores trapped was representative of their abundance in the nearby established vegetation. Hence, despite the potential for long-distance transport by tidal water, our results indicate a predominantly local dispersal of salt-marsh species.

Chapter 7 investigates whether this outcome could be predicted from dispersal traits of the different species and their availability in the established vegetation of the local and regional species pool. Seed weight and flotation time were used as the main dispersal traits to predict the sequence of species arrival in a restoration site. The results show that dispersal traits or availability in the local or regional species pool are not the main factors determining the order of species arrival. Instead, salt tolerance of the species appears to be important with the most salt-tolerant species establishing first. These species occupy the lowest elevational zone, which is most frequently inundated and which may thus increase the chance of a species being dispersed into the restoration site from a nearby source area. In addition, chances for establishment of these species in the study site are higher because the majority of the site is at or below the elevation at which these species can grow, whereas less than 10 % of the site is high enough for less salt-tolerant species.

Conclusions

This thesis examined the possibilities of salt-marsh restoration after de-embankment. In north-west Europe, several de-embankment sites exist, but only few sites have information on salt-marsh development. This is partly because targets are absent or not well-defined. Setting clear targets is therefore the first step towards the evaluation of success of salt-marsh restoration projects. This brings along the need for monitoring of the sites and allows adjustment of construction measures and management regimes.

The prospect of salt-marsh restoration after de-embankment is good, with target species establishing spontaneously and vegetation succession taking place. Because most salt-marsh species are dispersed over short distances, it is important that a well-developed salt marsh is adjacent to the restoration site. Many sites, however, feature a relatively low surface elevation in relation to tidal inundation, which reduces the rate of salt-marsh development and species diversity. Proper surface elevation in relation to tidal inundation is therefore a prerequisite for the successful restoration of salt-marsh vegetation after de-embankment.

Samenvatting

Kwelders en hun betekenis voor natuurbehoud

Dit proefschrift gaat over het herstel van Europese kwelders na dijkdoorbraak. Kwelders (salt marshes) zijn met planten begroeide gebieden op de grens tussen land en zee. Deze gebieden ontstaan op plaatsen waar de golfslag van de zee gering is, zoals aan de Waddenzee kust of in rivier delta's. Door de geringe golfslag kunnen de fijne zand- en kleideeltjes die in het zeewater aanwezig zijn, bezinken. Hierdoor groeit het land langzamerhand aan. Is de golfslag te hoog, zoals aan de Noordzee, dan bezinken alleen de grovere zanddeeltjes en kan een zand-, of kiezelstrand ontstaan. De beweging van het zeewater is onderhevig aan getijden. In noord-west Europa is het tweemaal per dag hoogwater of vloed en zes uur na de vloed is het laagwater of eb. Hier bovenop komt een maandelijks ritme dat gestuurd wordt door de stand van de maan ten opzichte van de aarde. Is het volle of nieuwe maan, dan is die aantrekkingskracht het grootst en dat leidt tot een groot verschil in waterhoogte tussen eb en vloed. Dit wordt ook wel springtij genoemd. Bij halve maan is deze aantrekkingskracht veel geringer en komt het water bij vloed minder hoog en bij eb minder laag (doodtij). De waterhoogte is verder nog afhankelijk van seizoensinvloeden, het weer (met name de windrichting en kracht) en de vorm van het land (in een trechtervormig gebied kan het water bijvoorbeeld extra hoog opgestuwd worden).

Kwelderplanten zijn aangepast aan het leven in een wisselend getijdenregiem en het zoute zeewater. Deze aanpassing kost veel energie wat ten koste gaat van andere aspecten van hun stofwisseling, waardoor ze meestal niet lang kunnen overleven in gebieden waar het zeewater niet komt. Hier worden ze als het ware weggeconcentreerd door plantensoorten die veel sneller kunnen groeien en daardoor het licht voor de langzaam groeiende kwelderplanten wegnemen. Binnen de verschillende kwelderplanten speelt de wisselwerking tussen zouttolerantie en concurrentie ook een rol. Hierdoor staan soorten die kunnen overleven in regelmatig met zeewater overstroomde delen dichtbij de zee en de minder zouttolerante soorten staan verder weg. Het gevolg is dat er op een kwelder over de gradient van zee naar land verschillende zones voorkomen met elk een karakteristieke plantengroei. Dit wordt ook wel zonatie genoemd (Figuur S1).

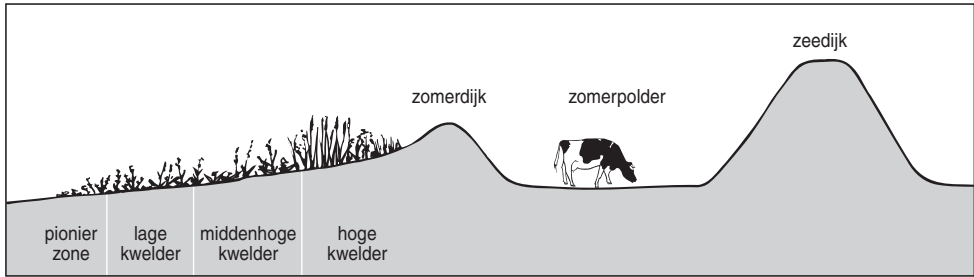


Figure S.1. Zonatie op een kwelder met daarachter een ingepolderde zomerpolder.

Doordat maar weinig planten en dieren aan het leven op de grens tussen land en zee zijn aangepast, is het voor de biodiversiteit van groot belang dat de kwelders behouden blijven. Met name in de winter zijn deze gebieden belangrijke voedselbronnen voor verschillende vogels, zoals ganzen, die komen om op te vetten voor ze terugkeren naar hun broedgebied in arctische streken. Daarnaast vormen kwelders een natuurlijke kustverdediging. De planten zorgen ervoor dat de golfslag afgeremd wordt en dat er zand-, en kleideeltjes uit het zeewater gezeefd worden, waardoor het land langzamerhand wordt opgehoogd. Deze ophoging is van belang om de zeespiegelstijging als gevolg van mondiale klimaatsverandering, bij te kunnen houden.

Verlies van kwelders

Zolang het financieel aantrekkelijk was zijn kwelders eeuwenlang beschouwd als gebied wat ingepolderd kon worden, zodat het geschikt werd voor landbouwkundig gebruik. Deze inpoldering geschiedde meestal door het bouwen van dijken of lage zomerkades zeewaarts van al bestaande dijken. Zomerkades hebben als functie het beschermen van het ingepolderde gebied (zomerpolder) tegen overstroming door zee-water in de zomer wanneer het gebied in landbouwkundig gebruik is en niet zozeer tijdens hoge stormvloeden die vaak in de winter plaatsvinden. Aan de noord Nederlandse en Duitse kust is de vorming van kwelders bevorderd door het aanleggen van sedimentatievakken op het kale wad. Dit zijn vakken van 400 m x 400 m omgeven door rijshouten dammen die de golfslag dempen, waardoor zand-, en kleideeltjes makkelijker kunnen bezinken. Wanneer er voldoende sediment is opgebouwd en het land niet meer bij elke vloed wordt overstroomd, kunnen de eerste kwelderplanten zich vestigen. Door het graven van sloten voor het verbeteren van de afwatering wordt deze vestiging bevorderd. De planten helpen daarna zelf verder mee aan bodemrijping.

Naast het verlies van kwelders door inpoldering heeft in de afgelopen decennia grootschalige afslag van kwelders plaatsgevonden, met name aan de zuidoost kust

van Engeland, maar ook aan de Friese en Groninger kust in Nederland waar het onderhoud van de sedimentatievakken sterk is gereduceerd. Deze erosie wordt wel toegeschreven aan de mondiale zeespiegelstijging als gevolg van klimaatsverandering, hoewel de meningen hierover in de literatuur sterk zijn verdeeld. In Engeland overheerst de theorie dat kwelders als het ware ingesloten worden tussen het stijgende zeewater aan de ene kant en bestaande dijken aan de andere kant. Door de bedijking kunnen kwelders niet landinwaarts opschuiven, wat in een natuurlijke situatie wel het geval is. Deze theorie is weerlegd door onderzoekers die stelden dat kwelders in staat zijn evenredig met het stijgende zeeniveau verticaal aan te groeien via sediment uit het zeewater. Hoewel deze onderzoekers hierin gelijk hebben, blijkt dat er veelal horizontale afslag van kwelders voorkomt, waarbij het vrijgekomen sediment vervolgens landinwaarts op dezelfde kwelder gedeponneerd kan worden. Uiteindelijk leidt deze horizontale afslag, ondanks de verticale ophoging, tot een verkleining van het kwelderareaal. Uit de literatuur is verder gebleken dat de oorzaak voor de toegenomen horizontale erosie een combinatie is van weersinvloeden (toegenomen frequentie en sterkte van stormen), toegenomen vloedhoogte en verhoogde golfslag. Deze factoren zijn beïnvloed door de mens, onder andere via landaanwinning, kustverdediging en kanalisering wat geleid heeft tot veranderingen in de zeestroming. In Hoofdstuk 2 van dit proefschrift wordt nader ingegaan op de verschillende factoren die een rol spelen in de grootschalige erosie van kwelders in zuidoost Engeland.

Ontpoldering

Nu het financieel minder aantrekkelijk is kwelders in te polderen voor landbouwkundige doeleinden, is hun functie voor kustverdediging en natuurbehoud prominent geworden. Hierdoor is besloten verschillende voormalig ingepolderde gebieden weer terug te geven aan de zee, middels het doorbreken van dijken of zomerkades. In Nederland spreekt men hierbij van ontpoldering, uitpoldering of verkweldering terwijl in Engeland de termen managed-realignment (opnieuw uitlijnen), managed-retreat (terugtrekken) en set-back (terugzetten) worden gebruikt. De engelse term die in dit proefschrift het meest gehanteerd wordt, is de-embankment (ontpoldering).

Het doorbreken van dijken is geen nieuw verschijnsel. In voorgaande eeuwen zijn meerdere malen door een combinatie van storm en springtij dijken doorgebroken, zoals bij de stormvloedramp van 1953. Een literatuuroverzicht in Hoofdstuk 3 van dit proefschrift leverde een totaal van 70 gebieden in noordwest Europa waar spontane of opzettelijke ontpoldering heeft plaatsgevonden. Wanneer de dijk niet gerepareerd werd, onstond vaak op den duur vanzelf een kwelder, zoals te zien is bij Peasemmerlannen (Peasens-Moddergat, noord-Friesland), waar de dijk in de jaren zeventig meerdere keren is doorgebroken. Helaas heeft men in de meeste gebieden het proces van kwelderopbouw niet direct gedocumenteerd, waardoor we nog steeds weinig weten over wanneer en hoe de verschillende plantensoorten zich vestigen.

Vestiging van kweldersoorten na dijkdoorbraak

Het onderzoek dat beschreven staat in dit proefschrift heeft als doel inzicht te krijgen in verschillende aspecten die een rol spelen bij de opbouw van kwelders na dijkdoorbraak. De centrale vraag is hoe de karakteristieke kwelderplantensoorten (doelsoorten of target species) zich in het ontpolderde gebied vestigen. Een eerste stap hierbij is het bepalen van de doelsoorten van een bepaalde regio. In Hoofdstuk 3 wordt een methode voorgesteld waarbij uit nationale vegetatieclassificatietabellen, soorten worden geselecteerd die met een frequentie van 60% of meer van het totaal aantal vegetatie-opnamen in bestaande kwelderplantengemeenschappen voorkomen. Vervolgens kan het aantal doelsoorten dat zich daadwerkelijk in het herstelgebied heeft gevestigd met deze regionale doelsoortenlijst worden vergeleken om een verzadigingsindex (saturation index) te berekenen. Naar verwachting zullen niet alle regionale doelsoorten in staat zijn zich in het doelgebied te vestigen, omdat ze het gebied niet kunnen bereiken of omdat het gebied (nog) niet geschikt is. Figuur 1.1 uit de inleiding geeft dit schematisch weer, waarbij drie bronnen (species pools) worden onderscheiden van waaruit de doelsoorten zich in het te herstellen gebied kunnen vestigen. De snelste vestiging wordt verwacht indien de soorten al of nog aanwezig zijn in de vegetatie of de zaadvoorraad in de bodem van het doelgebied (community species pool). Op iets grotere schaal kan gedacht worden aan verbreiding van zaden vanuit een bestaande kwelder grenzend aan het herstelgebied (local species pool). Dit kan door middel van getijdenwater (hydrochorie), dieren (via vacht, veren en poten: epizoöchorie; via keutels: endozoöchorie) of in mindere mate wind (anemochorie) (zie Figuur 8.2). Indien een goed ontwikkelde kwelder dichtbij het herstelgebied ontbreekt, zal de verbreiding van kweldersoorten over grotere afstand moeten plaatsvinden en kunnen de soorten uit de gehele noordwest Europese kust afkomstig zijn (regional species pool). De uiteindelijke vestiging van soorten uit de verschillende species pools in het doelgebied zal afhankelijk zijn van diverse factoren die als barrière of filter optreden. Zo kunnen sommige soorten zijn aangepast aan het langdurig overleven in de zaadbank, of ze hebben een goed drijfvermogen waardoor ze potentieel via het zeewater over lange afstand getransporteerd kunnen worden. Naast deze dispersiemechanismen zijn er ook factoren in het gebied zelf die invloed hebben op de vestiging. Zo kunnen grote aantallen Zeeduizendpooten (*Nereis diversicolor*) het sediment zo omwoelen dat zaden en kiemplantjes geen kans krijgen zich te vestigen. Daarnaast speelt de hoogteligging van het gebied een grote rol. Zoals in Figuur S1 is weergegeven, zijn sommige kweldersoorten beter aangepast aan de extreme omstandigheden dicht bij zee, terwijl hoger op de kwelder soorten voorkomen die minder bestand zijn tegen het zeewater.

Beschikbaarheid van soorten

Zoals in bovenstaande paragraaf vermeld, is de snelste vestiging van doelsoorten te

verwachten indien deze soorten nog in het gebied aanwezig zijn. Doordat de meeste ontpolderingsgebieden tientallen tot honderden jaren na de inpoldering als landbouwgebied in gebruik zijn geweest, zullen de kweldersoorten als gevolg van de gereduceerde bodemsaliniteit, intensieve bemesting en inzaaien van grassen of andere gewassen, uit de vegetatie verdwenen zijn. Ze kunnen echter nog wel als zaad in de bodem aanwezig zijn van waaruit ze kunnen opkomen wanneer de omstandigheden hiervoor geschikt zijn. Daarvoor moeten de zaden hun kiemkracht gedurende de periode van inpoldering behouden hebben. In de literatuur is een methode beschreven waarmee de zaden van plantensoorten geïncubeerd kunnen worden op basis van hun levensduur in de bodem. Deze methode gaat ervan uit dat zaden die dieper in de bodem (5 – 10 cm) voorkomen ouder zijn dan zaden die vooral in de ondiepe laag (0 – 5 cm) worden aangetroffen. In Hoofdstuk 4 van dit proefschrift is deze methode toegepast op de kwelder van Schiermonnikoog. Deze kwelder is interessant omdat het eiland door kustafslag in het westen en sedimentafzetting in het oosten langzaam naar het oosten opschuift. Hierdoor is de kwelder in het westen tientallen jaren ouder dan de kwelder in het oosten. Door dit verschil in leeftijd is er ook een verschil in samenstelling van de vegetatie (successie). In Hoofdstuk 4 is gekeken of de zaadbank een afspiegeling vormt van de bovengrondse vegetatie van verschillende successiestadia. Uit de resultaten blijkt dat, met uitzondering van de jongste kwelder, de soortensamenstelling in de ondiepe zaadbank sterk overeenkomt met de vegetatie. Daarentegen is er voor de verschillende successiestadia weinig overeenkomst tussen de diepe zaadbank en de vegetatie. Alleen op de 100-jaar oude kwelder is er een significante correlatie tussen diepe zaadbank en vegetatie, wat verklaard kan worden uit het feit dat hier weinig verandering in soortensamenstelling van de vegetatie optreedt (climax stadium). Uit de verhouding tussen het aantal zaden in de ondiepe en diepe zaadbank is verder gebleken dat de meeste soorten geen langlevende zaadbank opbouwen. Deze bevinding wordt ondersteund door een studie (Intermezzo 1) van de zaadbank van een relatief recent (30 jaar geleden) ingepolderde kwelder, waar vrijwel geen zaden van kweldersoorten in de bodem zijn aangetroffen. Beide studies leiden tot de conclusie dat de zaadbank geen belangrijke rol speelt in het herstel van kweldervegetatie na ontpoldering. De soorten zullen daarom uit het omringende gebied naar het doelgebied verbreid moeten worden. Naar verwachting zal het getijdenwater een belangrijke rol spelen bij de verbreiding van kwelderplanten aangezien kwelders regelmatig overstromd worden en de zaden uren tot maanden kunnen blijven drijven met behoud van hun kiemkracht. Verbreiding van zaden door getijdenwater kan op verschillende manieren worden vastgesteld. In Hoofdstuk 4 is gekeken naar de samenstelling van het vloedmerk, d.w.z. het materiaal dat na storm en hoogwater in een strook op hoge delen van de kwelder of aan de voet van de dijk wordt afgezet. Dit materiaal bevat een hoge dichtheid aan kiemkrachtige zaden en ander plantenmateriaal. Omdat bij extreem hoog water de hele kwelder onder water komt te staan, was de verwachting dat de samenstelling van het vloedmerk op verschillende locaties vrijwel gelijk is. Op de verschillende successiestadia van de kwelder van

Schiermonnikoog blijkt echter dat het vloedmerk veelal een afspiegeling vormt van de lokale vegetatie. Ondanks de reikwijdte van de zee lijkt het merendeel van de zaden dus over relatief korte afstand verbreid te worden.

De aanwezigheid van kweldersoorten in het vloedmerk geeft nog geen informatie over hun vestigingsmogelijkheden. Bovendien zijn de locatie en het tijdstip van afzetting van het vloedmerk niet vooraf te bepalen. Om een beter beeld te krijgen van de rol van water bij de verbreiding van kweldersoorten naar een doelgebied is het van belang regelmatig gedurende het zaadverspreidingsseizoen naar de zaadafzetting in het doelgebied te kijken. In Hoofdstuk 5 is een methode beschreven waarbij zaden op kunstgrasmatjes ingevangen kunnen worden. Deze matjes zijn op willekeurige locaties op een kwelder neergelegd en na één of meerdere getijden opgehaald. Het afgezette materiaal werd met een harde waterstraal van de matjes gespoeld en boven een fijnmazige zeef opgevangen. Dit materiaal is vervolgens in de kas te kiemen gezet. De resultaten gaven aan dat honderden zaden van verschillende soorten door het getijdenwater op de matjes zijn afgezet. Met name de pioniersoorten en soorten van de lage kwelder werden door het zeewater verbreid en hebben zich relatief snel in het doelgebied gevestigd (Hoofdstuk 6). Wederom blijkt echter dat de soortensamenstelling en de aantallen zaden grotendeels een afspiegeling vormen van de lokale vegetatie.

Geschiktheid van het gebied

Naast dispersie speelt de geschiktheid van het doelgebied een belangrijke rol voor de uiteindelijke vestiging van doelsoorten. In de literatuur wordt geargumenteed dat de vestigingskansen van pioniersoorten (met name Zeekraal, *Salicornia* spp.) na dijkdoorbraak sterk gereduceerd wordt door de aanwezigheid van de Zeeduizendpoot, die de bodem, en daarmee de zaden en kiemplantjes, omwoelt. Hoewel deze situatie inderdaad zichtbaar is op een schaal van enkele centimeters tot meters, is het effect op gebiedsniveau te verwaarlozen (Hoofdstuk 2). Uit een overzicht van verschillende ontpolderingsgebieden blijkt namelijk dat in vrijwel alle gebieden waarvoor een vegetatiebeschrijving beschikbaar is, pioniersoorten zijn aangetroffen (Hoofdstuk 3, Figuur 3.6; Tabel 3.1). Ook in Tollesbury (zuidoost Engeland), het belangrijkste studiegebied in dit proefschrift, vestigde Zeekraal zich als eerste in het gebied en breidde zich daarna het snelst uit (Hoofdstuk 7). De discrepantie tussen het waargenomen effect van de Zeeduizendpoot op kleine schaal en het uiteindelijk verwaarloosbaar effect op gebiedsniveau ligt voor een groot deel aan de invloed van de hoogteligging op het voorkomen van de Zeeduizendpoot en de vestigingskansen van kwelderplanten. De Zeeduizendpoot komt het meest voor op de overgang van het kale wad naar de begroeide kwelder die tweemaal per dag door de vloed overstromd raakt. Door de dagelijkse langdurige overstroming met zeewater en de werking van de golven is het hier een hard bestaan voor planten als Zeekraal. Uit het onderzoek op Tollesbury is te zien dat Zeekraal zich in eerste instantie op de hoogst gelegen delen van het

(kale) ontpolderingsgebied vestigt, waarna het zich zeewaarts uitbreidt (Hoofdstuk 7). Hebben de planten zich eenmaal gevestigd, dan is het sediment voor de worm minder geschikt vanwege de plantenwortels die het graafwerk belemmeren. Het belang van de hoogteligging voor het herstel van kweldervegetatie wordt ook in de literatuur onderschreven. Des te hoger het gebied binnen de invloedssfeer van het getijdenwater ligt, des te sneller is de vestiging van de vegetatie en des te groter de soortenrijkdom (Hoofdstuk 3, Figuur 3.7). Daarnaast is in Hoofdstuk 7 aangetoond dat de soorten met de grootste zouttolerantie zich het snelst hebben gevestigd in het verkwelderingsgebied van Tollesbury. Dispersie eigenschappen en beschikbaarheid van de soorten in de omgeving bleken van veel minder belang. Omdat het grootste deel van Tollesbury erg laag gelegen is, hebben de minder zouttolerante soorten maar een beperkte vestigingskans. Bovendien worden deze soorten in hun brongebied minder vaak overstromd wat hun kans op verbreiding via zeewater beperkt. Hoewel laaggelegen gebieden op den duur vanzelf opgehoogd kunnen worden via afzetting van sediment uit het zeewater, is een goede hoogteligging van het te verkwelderen gebied van groot belang voor een voorspoedige ontwikkeling van de vegetatie. De aanwezigheid van een goed afwateringssysteem kan deze ontwikkeling versnellen. Voor gebieden waar een dichte vegetatie aanwezig is, kan een begrazings- of maaibeheer nodig zijn om de soortendiversiteit te behouden of te vergroten.

Conclusies

In dit proefschrift is gekeken naar de mogelijkheden van kwelderontwikkeling na dijkdoorbraak. Hoewel er in noordwest Europa vele gebieden bekend zijn waar dijkdoorbraak heeft plaats gevonden, is van slechts een gering percentage bekend hoe de vegetatie zich heeft ontwikkeld. Dit heeft te maken met het feit dat de doelstellingen niet of nauwelijks omschreven zijn. Een goed gedefinieerde doelsoortenlijst is een eerste stap op weg naar een betere maatstaf voor het succes van verkwelderingsprojecten. Hieruit volgt de noodzaak van het monitoren van de vegetatie en de mogelijkheid het beheer van het gebied aan te passen. Uit verschillende onderzoeksgebieden waar de vegetatieontwikkeling is onderzocht, is gebleken dat er vestiging van kwelderplanten optreedt. Omdat de doelsoorten niet in de vegetatie of zaadbank van het doelgebied aanwezig zijn, moeten ze van buiten het gebied aangevoerd worden. Onderzoek naar de mogelijkheden van zaadverbreiding via getijdenwater laat zien dat zaden door het zeewater verbreed kunnen worden. De meeste zaden worden echter over korte afstand getransporteerd. Het is daarom van belang dat een goed ontwikkelde kwelder in de buurt van het doelgebied ligt. De hoogteligging van het gebied speelt een belangrijke rol bij de vestiging van de soorten. Daarnaast hebben een goede afwatering en begrazings- of maaibeheer een gunstige invloed op de soortenrijkdom.



2000 m above sealevel (Photo Sijbren Otto)

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List of publications

International journals

- Wolters, M., Garbutt, A., Bekker, R.M., Bakker, J.P. & Carey, P.D. Restoration of salt-marsh vegetation in relation to site suitability, species pools and dispersal traits. *Submitted to Journal of Applied Ecology*.
- Garbutt, R.A., Reading, C.J., Wolters, M., Gray, A.J. & Rothery, P. (2006). Monitoring the development of intertidal habitats on former agricultural land after the managed realignment of coastal defences at Tollesbury, Essex, UK. *Marine Pollution Bulletin*, *in press*.
- Wolters, M., Bakker, J.P., Bertness, M.D., Jefferies, R.L. & Möller, I. (2005). Saltmarsh erosion and restoration in south-east England: squeezing the evidence requires realignment. *Journal of Applied Ecology*, **42**, 884-851.
- Wolters, M., Garbutt, A. & Bakker, J.P. (2005). Plant colonization after managed realignment: the relative importance of diaspore dispersal. *Journal of Applied Ecology*, **42**, 770-777.
- Wolters, M., Garbutt, A. & Bakker, J.P. (2005). Salt-marsh restoration: evaluating the success of de-embankments in north-west Europe. *Biological Conservation*, **123**, 249-268.
- Wolters, M., Geertsema, J., Chang, E.R., Veeneklaas, R.M., Carey, P.D., Bakker, J.P. (2004). Astroturf seed traps for studying hydrochory. *Functional Ecology* **18**, 141-147.
- Wolters, M. & Bakker, J.P. (2002). Soil seed bank and driftline composition along a successional gradient on a temperate salt marsh. *Applied Vegetation Science* **5**, 55-62

National journals, books, conference proceedings & reports

- Wolters, M., Hogendorf, J. Willemsse, L.M. & Bakker, J.P. (2006) Verbreiding van zaden van kwelderplanten in de Waddenzee. *De Levende Natuur*, *in press*.
- van Duin, W., Esselink, P., Bos, D., Verweij, G., Wolters, M. & van Leeuwen, P.-W. (2005). Monitoringsonderzoek proefverkweldering Noard Fryslân Bûtendyks. Tussenrapportage 2004. Alterra Texel.
- Reading, C.J., Garbutt, R.A., Watts, C.W., Saunders, J. and Wolters, M. (2004) Managed realignment at Tollesbury. Annual report to Defra. Centre for Ecology and Hydrology, Dorchester, UK.
- Garbutt, A., Gray, A., Reading, C., Brown, S. & Wolters, M. (2003) Saltmarsh and mudflat development after managed realignment. Proceedings of the 38th Defra flood and Coastal Management Conference.
- Reading, C.J., Gray, A.J., Paramor, O.A.L., Garbutt, R.A., Watts, C.W., Spearman, J.R., Barratt, D.R., Chesher, T., Cox, R., Hughes, R.G., Mann, J.L., Myhill, D.G., Rothery, P., Semmence, J. & Wolters, M. (2002) Managed realignment at Tollesbury and Saltram. Final report to Defra. Centre for Ecology and Hydrology, Dorchester, UK.
- Reading, C.J., Paramor, O.A.L., Garbutt, R.A., Chesher, T., Hall, J.R., Hughes, R.G., Mann, J.L., Masters, N.D., Myhill, D.G., Rothery, P., Spearman, J.R., Stevenson, J.R., Wolters, M. & Gray, A.J., (2001) Managed realignment at Tollesbury and Saltram. Annual report to Defra. Centre for Ecology and Hydrology, Dorchester, UK.
- Möller, I., Garbutt, A.G. & Wolters, M. (2001) Managed realignment of sea defences and the re-creation of salt marshes in south-east England. In: Green, R.E., Harley, M., Spalding, M. & Zockler, C. Impact of climate change on wildlife. Royal society for the protection of birds, Sandy.