

**The role of dispersal constraints
in the assembly of salt-marsh communities**

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The role of dispersal constraints in the assembly of salt-marsh communities

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Chapter 1

Introduction

Dynamics of Community Assembly

The study of constraints on community development has a long history dating back to the early twentieth century, when ecologists such as Clements (1916; 1936) and Gleason (1917; 1926) were already debating ‘organismic’ vs. ‘individualistic’ models of community development (Booth & Larson 1999). The dichotomies in their debate (deterministic vs. stochastic processes, local vs. regional scales) are still echoed in the current discussion on this subject in community ecology. After decades of investigating community structure in relation to local physical conditions and consequent influences on species interactions, ecologists are returning to the idea that local communities must be considered within the larger geographical and historical scales in which they are embedded in order to be fully understood (Ricklefs 1987). In this thesis, community structure is defined as patterns of species composition and species abundance in communities.

Dispersal filters may influence community assembly *per se* or through interactions with internal dynamics (*i.e.* species interactions) (Belyea & Lancaster 1999). The dispersal of some species may be dependent on close physical association with other species, so that the arrival of co-dispersers may not be independent (Chambers & MacMahon 1994; Belyea & Lancaster 1999). Species may be able to overcome constraints of dispersal over space by producing a bank of dormant propagules, which may remain viable for long periods of time (Thompson *et al.* 1997). Chance events during dispersal and the unique historical circumstances of sequence of arrival at a site may strongly affect species composition of communities through priority effects (Morin 1984; Barkai & McQuaid 1988; Drake *et al.* 1993; Grover 1994; Law & Morton 1996; Blaustein & Margalit 1996; Wilbur 1997; Belyea & Lancaster 1999). Even given identical conditions, communities with different histories may not converge (Drake 1990). In this Introduction, I will briefly discuss some current conceptual models of community assembly and show how I will use adaptations of these models as a framework to explore dispersal filters on the assembly of coastal salt-marsh communities.

In a simple conceptual model proposed by Keddy (2000), communities are generated from a pool of potential colonists (*i.e.* species pool) through a filtering process (Fig. 1.1). The filters, or hierarchy of filters, select for or against certain traits and ‘assembly rules’ specify which set of traits will be filtered out in a specified habitat. Biotic filters may include species interactions such as competition and predation/herbivory (Diamond 1975; Belyea & Lancaster 1999), whereas abiotic filters are characterized by the physical environment (Keddy 2000). The formation of the species pool, a large-scale process which is determined by rates of speciation and extinction, is considered to lie outside community ecology in the realm of evolutionary ecology in this model and the emphasis lies on the role of local filters in determining community structure.

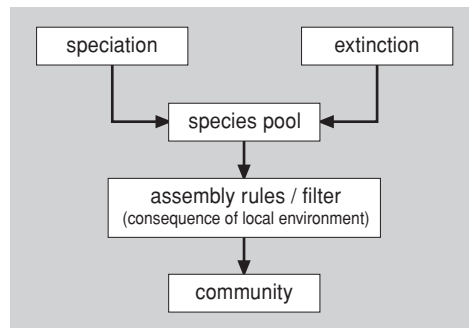


Figure 1.1 Conceptual model of community assembly, where the local environment filters out species from the species pool, thereby creating a community (after Wiens 1983; Keddy 2000).

In contrast, the species-pool concept (Pärtel *et al.* 1996; Zobel 1997; Zobel *et al.* 1998) explicitly addresses scale and scale-dependent dispersal of species. Pools of potential colonists are hierarchically arranged by the spatial scale over which they operate: regional, local and community (Fig. 1.2). The regional scale theoretically encompasses the geographical distribution of the community of interest (*i.e.* target

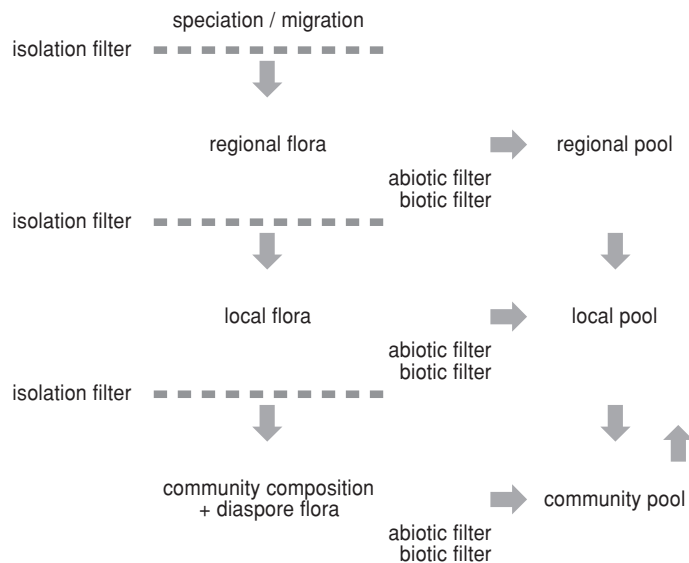


Figure 1.2 Diagram of species-pool concept showing the role of processes at different scales in determining community composition (after Zobel 1997).

community). The local scale covers a single landscape type and species from the local species pool are assumed to disperse relatively quickly into the target community. The species associated with a community are referred to as the community species pool and it includes the species present in a community as well as the diaspore bank and rain. Species pools at all scales are pre-sorted in that they only include species which are capable of coexistence within the target community. However, the actual determination of species pools is still in its infancy and can be difficult to apply (Zobel *et al.* 1998; Srivastava 1999; Wolters *et al.* 2005b).

Of course, all species in a species pool do not normally arrive simultaneously at a given site but usually arrive sequentially, one or a few species at a time (Morton & Law 1997). Community assembly can be viewed from a historical perspective, incorporating turnover of species as invaders arrive and residents disappear over time. By considering the production of an existing community state through intermediate states, community organization can be explored as it emerges (Drake 1990). Thus, the concept of community assembly is integrated with the older but clearly related concept of succession.

Dispersal filters in the assembly of plant communities

One seemingly straight-forward way to detect the effects of dispersal constraints on the species composition of plant communities is to disperse seeds artificially into sites and then to examine the consequences as is done in seed sowing experiments. Seed-sowing experiments can manipulate effects of seed limitation on species abundance or species distribution (seed augmentation and seed introduction, respectively, in Turnbull *et al.* 2000). In a review of seed sowing experiments, around 50 % of 27 seed-augmentation studies indicated constraints of seed limitation on species abundance (Turnbull *et al.* 2000). Seed limitation tended to occur more often in early-successional communities and species typical of the early-successional stages (Turnbull *et al.* 2000). However, seed limitation can result from multiple causes, such as poor distribution of seed sources (adult plants), low density of seed sources and low seed production (all of which are filters at the community scale), in addition to poor dispersal (Levine & Murrell 2003). Seed-augmentation experiments alone cannot distinguish between these potential causes. Results are easier to interpret for seed-introduction studies, where the seed sources are absent from communities. In 13 studies of seed introductions incorporating data from approximately 100 species, 53% of them indicated seed limitation on the distribution of species (Turnbull *et al.* 2000). Thus, about half of the seed-addition experiments reviewed in Turnbull *et al.* (2000) indicated possible dispersal constraints on both species abundance and composition in plant communities.

Filters in the assembly of salt-marsh communities

Salt-marsh communities have been used to demonstrate both biotic and abiotic filters in community assembly. Wilson and Whittaker (1995) suggested that the assembly rule of guild proportionality was demonstrated in a Welsh salt marsh. Members of the same guild or functional group are assumed to compete more with each other than with species in another guild (Pianka 1980). Consequently, the proportion of species from different guilds tends to remain constant (Wilson & Roxburgh 1994; Morris & Knight 1996). Competition between species in the canopy for light, and the different functional roles of broad and narrow leaves in canopy structure, was an important biotic filter in salt-marsh communities.

Keddy (2000) suggested another important filter, salinity, on the species composition of salt-marsh communities. When considering salinity as an abiotic filter, species can be screened and then ranked in relation to a single trait: salinity tolerance. If the salinity level of a local site is known, it is possible to predict which species from the species pool could potentially become established. However, both the studies described above concentrated solely on local processes and did not explore the potential role of dispersal filters in structuring salt-marsh communities.

Despite evidence that tidal action can disperse seeds considerable distances (action radius of tens of kilometers in Koutstaal *et al.* 1987), the few empirical studies conducted on seed dispersal in salt marshes indicate that the species composition of plant communities are potentially constrained by dispersal (Rand 2000; Wolters *et al.* 2005a). Further support of this conclusion comes from results of salt-marsh restoration sites, where former reclaimed lands were re-exposed to tidal inundation when sea walls were breached. When salt-marsh species were present locally, restoration sites generally acquired more of these species than when potential donor communities were located far away (Wolters *et al.* 2005b).

Salt-marsh chronosequence as model system

Salt marshes on the Dutch island of Schiermonnikoog provide a unique opportunity to study the dynamics of community assembly due to a well-developed chronosequence reconstructed from aerial photographs and old maps (Olf *et al.* 1997). Sea currents and resulting erosion/sedimentation patterns have caused the island to move eastwards over time so that salt-marsh communities of progressive ages are found adjacent to each other (Fig. 1.3). The topography of these coastal barrier marshes is determined primarily by relief patterns in the sandy subsoil, which were formed by wind processes and subsequently fossilized, rather than sedimentary processes influenced by tidal water (de Leeuw *et al.* 1993). The eleva-

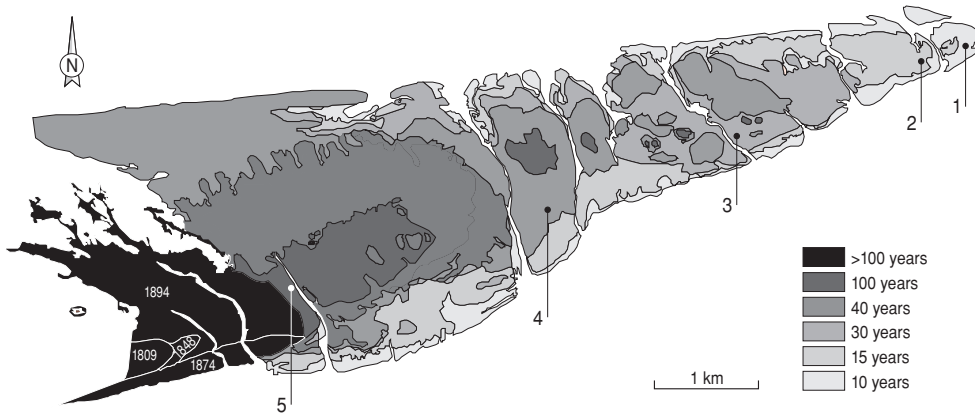


Figure 1.3 Map of chronosequence of salt-marsh communities on Schiermonnikoog. Numbers represent location of communities of different ages: 10 years, 15 years, 30 years, 40 years and 100 year.

tion of the sandy subsoil ranges from 25 cm to 125 cm above mean high tide, whereas the sedimentary layer that lies above the sandy subsoil is only 2 cm to 16 cm in depth (Olff *et al.* 1997). Successional dynamics in species composition differ between elevational ranges (Olff *et al.* 1997) so that a proper chronosequence is observed by comparing sites at the same base elevation (sandy layer).

Studies of the species composition of salt-marsh communities at this site have concentrated on possible effects of biotic filters (*e.g.* competition, herbivory), abiotic filters (*e.g.* nutrient availability) and interactions between these two groups (*e.g.* herbivory and nitrogen mineralization, fertilization by faeces) (van de Koppel *et al.* 1996; Olff *et al.* 1997; van Wijnen & Bakker 1997; van Wijnen & Bakker 1999; van Wijnen *et al.* 1999; Kuijper *et al.* 2005; Kuijper & Bakker 2005; van der Graaf 2006). In short, most of these studies have concentrated on the effects of local filters on community development. However, results of a study on soil seed banks and seed composition of driftlines suggested that dispersal filters occur over both space and time (Wolters & Bakker 2002).

Outline of thesis

Using the chronosequence of salt-marsh communities on Schiermonnikoog, I will examine the role of different dispersal filters in the dynamics of community assembly in this thesis. For many plant species, dispersal often occurs at the stage of the seed, although dispersal through vegetative propagules is also possible.

Dispersal filters over space can operate at both the regional (A in Fig. 1.4) and local scales (B in Fig. 1.4). The production of seeds can reinforce and maintain the membership of a species once it joins a community (C in Fig. 1.4). Dispersal filters over time are influenced by the burial, survival and exhumation processes of seed reserves in the soil (D in Fig. 1.4). Once a seed reaches a community, local filters governing a myriad of processes, such as seed retention, germination, competition, facilitation, herbivory, attack by pathogens, abiotic stress and disturbance, will determine whether that species will establish in the community or not (E in Fig. 1.4).

The regional scale is defined as that covering the central North-Atlantic region in Europe, that spans from Scotland and southern Scandinavia to northern France following Dijkema *et al.* (1984) and Wolters *et al.* (2005b) (Fig. 1.5). The salt-marsh communities on the south-eastern coast of Schiermonnikoog (*Oosterkwelder*), which are not grazed by livestock, delineate the local scale. Multiple communities along the chronosequence will be used to study the community scale.

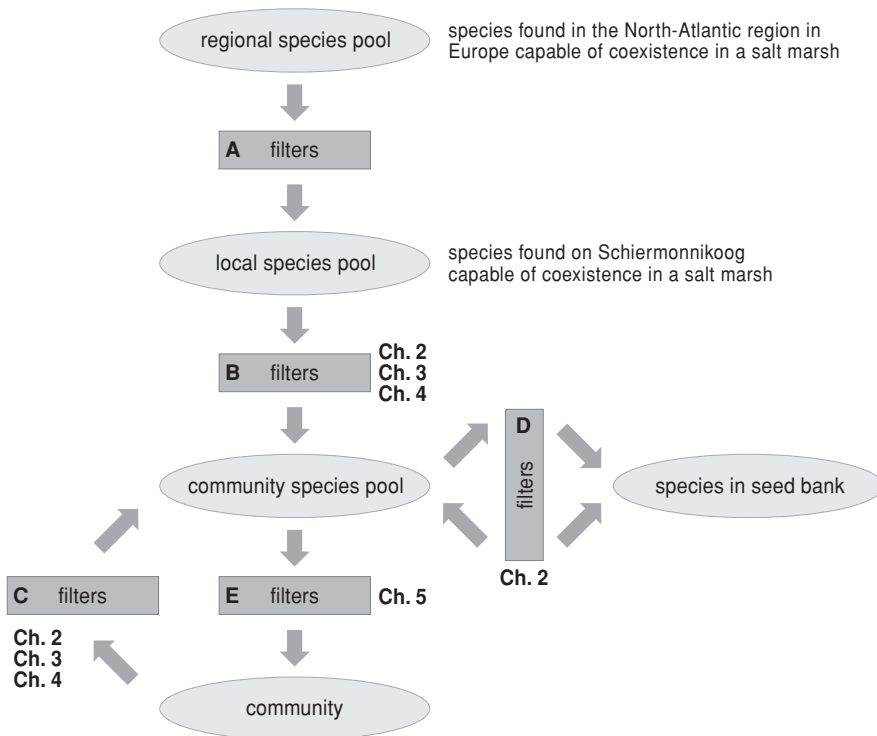


Figure 1.4 Conceptual framework for exploring constraints in the assembly of salt-marsh communities.

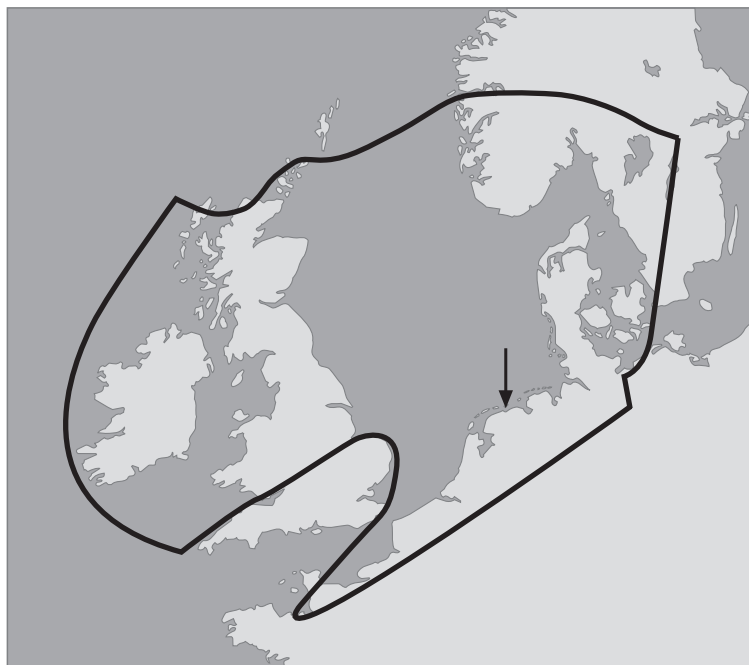


Figure 1.5 Biogeographical area for which the regional species pool is defined (after Dijkema *et al.* 1984; Wolters *et al.* 2005b). Arrow refers to the position of Schiermonnikoog.

In Chapter two, I explain how the relationship between the species composition and species abundance of the community (established vegetation) and soil seed bank can be used to predict constraints on community assembly. A descriptive approach, using surveys of the vegetation, soil seed banks and seed production along the chronosequence, is combined with results from a burial experiment in order to examine the relative strength of filters on community assembly involved in dispersal (B in Fig. 1.4), seed burial and survival (D in Fig. 1.4) and seed production (C in Fig. 1.4).

In Chapter three, the potential roles of biotic (hares, geese) and abiotic (tidal water) filters in constraining dispersal are compared. I will use a descriptive approach, comparing the seeds found in the droppings of hares and geese to those caught on seed traps along the chronosequence, to study the effectiveness of these dispersal vectors. In addition, I will use an experimental approach with feeding trials of captive animals to study the effect of ingestion by these small herbivores on seed survival and germinability. Seeds found in droppings and on seed traps may reflect seed sources available in the community as well as those that result from local dispersal (B & C in Fig. 1.4).

I explore further the factors constraining movement of seeds by tidal water in Chapter four by comparing the effect of normal tides (deterministic) and storm surges (stochastic) on seed-rain patterns along the chronosequence. Mainly descriptive methods are used, supplemented by an experiment on the differential effects of water movement originating from the sea coast and creeks on seed movement. As in Chapter three, dispersal filters (B in Fig. 1.4) as well as community-level filters on seed availability (C in Fig. 1.4) are examined.

In Chapter five, I study the factors that influence seed retention, the opposite but complementary process to that examined in Chapter four. Experiments were conducted both in a field and laboratory setting to explore the process by which morphological traits of seeds are filtered by abiotic (tidal water) and biotic factors (vegetation structure of a community) (E in Fig. 1.4). Vegetation structure, as opposed to community structure, refers to physical properties such as height, biomass, shoot density and stiffness.

Finally, the synthesis in Chapter six will use data presented in Chapters two to five to evaluate the role of dispersal filters in constraining the composition and abundance of salt-marsh communities.

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Chapter 2

Relationship between the vegetation and soil seed bank in a coastal salt marsh: predicting constraints in community assembly

E.R. Chang, M. Wolters & J.P. Bakker

Summary

Three relationships between the vegetation and soil seed bank along a community sequence, and accompanying predictions for constraints in community assembly, are proposed: a) patterns in the soil seed bank follow patterns in the vegetation; b) the soil seed bank is dominated by early-successional species for the entire sequence; c) the soil seed bank remains similar along the sequence and is composed of species from across the community sequence.

Multivariate analysis indicated that the most important factor in explaining species variance in the vegetation (75.1 %) and soil seed bank (61.4 %) in coastal, temperate salt-marsh communities was the age of the community. Also, the positions of species along the age gradient were similar for the vegetation and soil seed bank, indicating similar trends in abundance of species both above-and-below ground. The relationship between the vegetation and soil seed bank also was influenced by differential seed production and seed longevity between species. Most species appear to have transient or short-term persistent seed banks and this was confirmed by a seed burial experiment. The relationship between the vegetation and soil seed bank most closely resembles the first proposed relationship, thus predicting strong dispersal constraints on community assembly. Despite regular tidal inundation, the results indicate that seeds of some species may not reach all communities. The importance of seed limitation on community structure, especially when placed in a regional or historical context, is strongly indicated by our results.

Introduction

The relationship between vegetation and the soil seed bank is influenced by ecological processes that strongly affect survival traits of seeds (Leck *et al.* 1989; Baskin & Baskin 1998) and community development. Community assembly can be conceptualised as a process whereby species, which are members of a species pool for a given region, are ‘sieved out’ as they pass through a hierarchy of filters, specific to a habitat, that select for or against certain traits (Wiens 1983; Keddy 2000). Species pools can be constrained by dispersal which acts as a filter at different spatial scales (Pärtel *et al.* 1996; Zobel *et al.* 1998). Species present at the landscape level (local species pool) may have to pass through dispersal filters to become members of the community species pool. Species present in the soil seed bank are members of the community species pool (Zobel *et al.* 1998) but they are often present in an inactive state and require passage through additional filters to join the active community species pool (Fig. 2.1).

A consideration of the development of extant communities can reveal mechanisms that regulate expression of community patterns (Drake 1990). Three relationships between the vegetation and soil seed bank along a community sequence can be recognised in relation to underlying ecological processes of community assembly: 1) the seed bank composition varies, reflecting changes in established

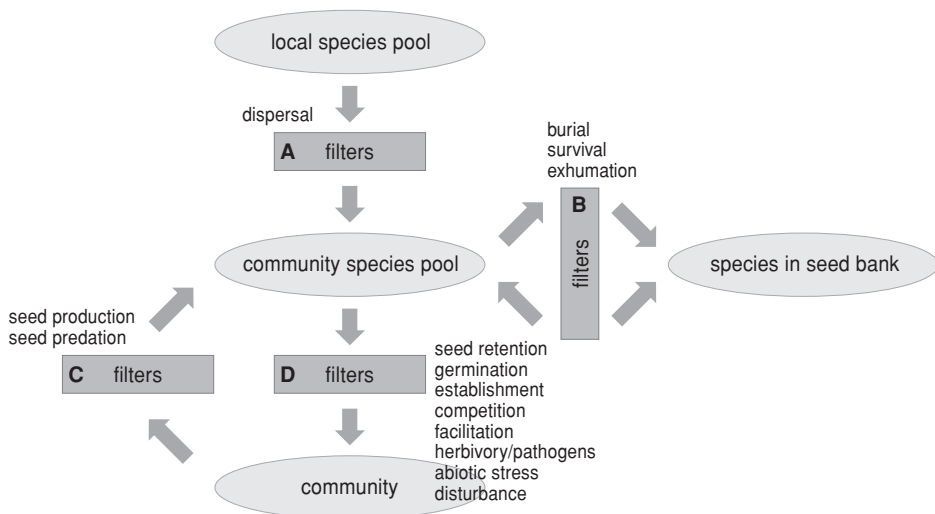


Figure 2.1 Conceptual model of community assembly. Species belonging to species pools at the local and community scale, represented by arrows, are sieved out as they pass through filters at different stages.

vegetation along the community sequence (succession); 2) the seed bank composition is composed of early successional species that produce many seeds that persist along the sequence of communities; 3) the seed bank composition remains similar along the sequence and contains a mixture of species found in the different communities. Access to a common local species pool is assumed for all communities along the chronosequence.

The first case clearly implies that filters between the local species pool and the community species pool impose strong constraints on community assembly (Fig. 2.1A). Species composition of the vegetation and soil seed bank reflect each other along the community sequence as seed production, burial and survival in the soil are not limiting for establishment of species. Similarity between the composition of the vegetation and seed bank is predicted to be high along the chronosequence. Early successional species become lost from the soil seed bank as they disappear from the vegetation, whereas seeds of species appearing later in succession become incorporated into the soil (Bossuyt & Hermy 2004). Studies of primary succession of coastal habitats (Looney & Gibson 1995; Bossuyt & Hermy 2004) and secondary succession of hayfields (Bekker *et al.* 2000) have demonstrated this close relationship between species composition of vegetation and the soil seed bank.

In the second case, filters between the community species pool and species in the seed bank (Fig. 2.1B) and between the plant community and the community species pool (Fig. 2.1C) impose constraints that shape community composition over time. Composition of the soil seed bank is determined mostly by differential seed production, and burial and survival rates of propagules of different species. The strength of filters affecting seed production and/or seed survival increases over time. It is necessary to distinguish the effects of filters on seed production (C) and those affecting seed survival stages (B) (Fig. 2.1) in order to distinguish the relative contribution of the respective filters. Similarity is predicted to decrease during community succession. Studies of primary succession in a habitat created by isostatic rebound (Grandin 2001) and of secondary succession in species-rich meadows (Kalamees & Zobel 1998) and old fields (Lavorel *et al.* 1993) have demonstrated this second relationship.

Filters between the community species pool and the community impose strong constraints in the third case (Fig. 2.1D). Species are available, in both space and time, to colonise newly available habitats and only environmental filters and/or biotic interactions between species determine community assemblages. The similarity between the vegetation and seed bank is predicted to be low. This third relationship, to our knowledge, has not been demonstrated in any empirical study and, in this study, it represents a null model where no seed limitations (either from dispersal, seed production or the soil seed bank) restrict plant establishment and community assembly, in contrast to the first two relationships which imply some degree of seed limitation.

In this study, the following questions are posed: 1) What is the relationship between the vegetation and soil seed bank in a temperate, coastal salt marsh across a community development sequence? 2) What are the underlying processes and the relative importance of different abiotic and biotic filters, as communities develop? 3) Are these conclusions supported by data of seed production and survival following burial?

Materials and methods

Site and vegetation description

The studies were conducted on the coastal-barrier island of Schiermonnikoog, the Netherlands (53° 30' N, 6° 10' E). Schiermonnikoog is extending eastward due to changing sea currents and sediment accretion (Olf *et al.* 1997). The salt marshes form a gradient in age on the southern shore of the island, resulting in a well-developed chronosequence (de Leeuw *et al.* 1993; Olf *et al.* 1997). Soils consist of a basal sandy layer and an upper layer of clay (2 – 16 cm), deposited by tidal water. Four communities were studied along the chronosequence that initially established in 1913, 1974, 1986 and 1993. These communities were sampled at low-elevation sites at the same base elevation (sand layer) of 20 to 40 cm above MHT (Mean High Tide).

The developmental sequence of salt-marsh communities on this island is described in detail by Olf *et al.* (1997). After 10 years of community development, the vegetation is dominated by *Spergularia media*, *Suaeda maritima*, *Limonium vulgare* and *Puccinellia maritima*. Plant nomenclature follows van der Meijden (1996). As development continues, *L. vulgare* remains dominant in the community whereas the remainder of these species decrease in frequency. *Festuca rubra*, *Glaux maritima* and *Seriphidium maritimum* (*Artemisia maritima* L.) all increase in frequency over time. The frequency of *Juncus gerardi* increases after 40 years and it becomes one of the most dominant species in later stages of development. *Atriplex portulacoides* shows a clear peak in presence and dominance between 40 and 60 years of community development. *Elytrigia atherica* is never a very abundant species at this low elevation although its frequency increases with community age.

Collection of vegetation, seed bank and seed production data

Vegetation data were collected from permanent transects located in all four communities in June of 1997 and 2001. Each transect consisted of a grid of 10 columns, oriented parallel to the elevation gradient, and five rows of 1 m² sub-plots. Due to the interaction between the chronosequence and zonation gradients, only relatively restricted areas represent communities established at the same base elevation between marshes. For each sub-plot, four species with the highest per-

centage cover (determined subjectively) were given dominance scores: the species with highest percentage cover received a dominance score of 4, the next received a score of 3 and so on (modified version of scale described in Tansley 1939). The dominance scores were pooled for each column, resulting in scores for 10 plots of 5 by 1 m² ($n = 10$).

The soil seed bank was sampled in November 1996 from 10 plots of 1 m² within the four communities close to the permanent transects and at the same elevation using procedures given in Wolters & Bakker (2002). The seed bank was resampled five years later (June and July, 2001) in 10 different plots within each community in a similar way. The samples were assayed for seed content using a technique combining concentrating seeds in the sample and seedling emergence (ter Heerdt *et al.* 1996). In summary, soil samples were divided into two layers (0 – 5 cm and 5 – 10 cm), rinsed through a 0.212 mm sieve, placed in a glasshouse and monitored for seedling emergence. Seedling emergence usually ceased after six weeks. The residual soil was checked for remaining seeds in 1996 by viewing one quarter of the total tray area under a microscope and probing seeds with a needle in order to distinguish between firm and empty seeds. Since the number of seeds that remained in the soil after processing accounted for only 1 to 3 % of the seed bank and no additional species were detected, this procedure was not repeated in 2001.

Six plots of 1 m² were used to measure seed production within each community. These plots also were located close to the permanent transects. Flowering and fruiting inflorescences were counted for all species present in each plot between mid-to-late October, 2002. The average number of seeds per inflorescence was estimated by haphazardly collecting 50 fruiting inflorescences per species at each community and counting seeds of each sample. Seed production was estimated only once because seeds of most species ripen in late September/early October and are retained until the marshes are flooded by autumnal tides. However, a few species ripen and disperse earlier in the summer (*e.g.* *Armeria maritima*, *Festuca rubra*) and seed production by these species was not estimated.

Seed burial experiment

Seeds of *Elytrigia atherica*, *Plantago maritima*, *Salicornia europaea*, *Seriphidium maritimum* and *Suaeda maritima* were buried in the young community (established 1993) and an intermediate-aged community (established 1974) at similar base elevations (20 to 40 cm above MHT). Five plots of 2 m x 2 m were chosen at both communities using a priori criteria based upon long-term monitoring of the abundance of selected species considered typical for each community. The mean distance between plots was 38 m \pm 3.6 m (s.e.). Each plot was divided into 16 sub-plots of 50 cm x 50 cm and at 15 of these 16 sub-plots, five nylon mesh bags were buried at a depth of 10 cm below the surface. Each bag contained local soil that had been

sterilized and seeds of one of the five species listed above. Groups of 50 seeds were used for *Seriphidium maritimum* and *Spergularia maritima*, and groups of 30 seeds were used for the remaining three species. All bags in three sub-plots of each of the 10 plots were exhumed every six months for two years and results were pooled within each plot for each species ($n = 5$ per sampling period). Three sub-plots at each of the 10 plots were left intact in the soil to be exhumed after five years, which is regarded as the boundary between short and long-term persistence (Thompson *et al.* 1997).

After exhumation, surviving seeds were placed in cold storage (6 °C) for a minimum of eight weeks (only if exhumed in the autumn and did not undergo natural cold-stratification), sorted by species and their condition (firm or empty) determined under a magnifying glass before counting. They were transferred to Petri dishes lined with damp filter paper and kept in a growth chamber for 30 days (12 h light period, 25°C day temperature and 15°C night temperature). Seedlings were counted and removed once germination had occurred. Ungerminated seeds were pricked with a pin to check for a firm endosperm.

Data analyses

Soil seed bank and vegetation data were analysed using multivariate methods and Monte Carlo permutation tests using the software program, CANOCO for Windows 4.52 (ter Braak & Šmilauer 1998). Data from all 21 species found in the soil seed bank were used simultaneously to construct an ANOVA table, partitioning all the variance explained by different sources in the model (three-way factorial ANOVA).

Soil seed bank data were first \log_{10} transformed in order to improve homogeneity of variance in multivariate space. The sampling design was encoded using dummy variables of 0 and 1. Partial redundancy analysis (RDA) was used instead of partial canonical correspondence analysis (CCA) because we were interested in measures of absolute rather than relative abundance of species in the soil seed bank, and partial RDA resulted in better homogeneity of variance in multivariate space than partial CCA. Eight separate significance tests using Monte Carlo simulations were run for each ANOVA, including one for the full model (4 by 2 by 2 full factorial), three main effects (year of community establishment, year of sampling, soil depth), three 2-way interactions and one 3-way interaction. For the permutation tests when assessing main effects, the factor in question was used as the environmental variable and the other two factors were used as covariables. Permutations were restricted by blocks defined by all covariables. In the case of 2-way interaction tests, all three factors were listed as covariables and for the 3-way interaction test, all three factors plus all three 2-way interactions were used as covariables. Permutations for interaction effects were unrestricted. When a factor is used as a covariable in an analysis, only the variance explained by the environ-

mental variables after subtracting overlapping variance attributable to the covariables is considered.

For the vegetation data, analyses parallel to a repeated-measures ANOVA (repeated-measures analysis of inertia) were used. A partial DCCA was applied because the vegetation measurement we used (dominance) is a relative measure. The detrending method used second-order polynomials. The between-subject factor was year of community establishment and the within-subject factors were the year of sampling and interactions between the year of community establishment and year of sampling. Permutation tests were conducted under the split-plot framework in CANOCO (Lepš & Šmilauer 2003). Because data from permanent transects were used, we accounted for spatial autocorrelation by linear detrending *i.e.* using a covariable file listing the position of the plots.

Response curves of species dominance (vegetation, upper seed bank and lower seed bank) to community age were produced for five representative species. Data from both sampling years were used and the age of the community at time of sampling was calculated. Curves were fitted using the regression function of the software program, Sigmaplot 8.0 (Sigmaplot 2002). The abundance values of seed bank samples were first converted into dominance values. The simplest model (lowest number of parameters) yielding the highest model fit (coefficient of determination or R^2) was selected in order to calculate each curve. Response curves were similarly calculated between seed production, upper and lower seed bank, and age of community for five species for which there were sufficient data. Seed production and seed bank data were first transformed ($y = \log_{10}(x + 0.01)$).

For the burial experiment, t-tests were used to compare the mean germination of young and intermediate-aged communities for each of five species exhumed at the end of two years. In order to avoid inflation of type 1 error, a Bonferroni correction was applied. The null hypothesis of no difference between means was rejected at $\alpha = 0.01$.

Results

Vegetation

When multivariate data for 18 species are considered, the sampling design (repeated-measures analysis of inertia with one between-subject factor and one within-subject factor) explains 75.1 % of the variation in the species distribution. The year of community establishment is a highly significant between-subjects factor ($F = 48.69$, $p < 0.01$) and accounts for 65.8 % of the variation in the species data. The first DCCA axis most likely represents an age gradient. The sequence of species on this first DCCA axis is similar to the developmental sequence of species described in Olff *et al.* (1997) (Fig. 2.2A). Pioneer species, such as *Spartina anglica*,

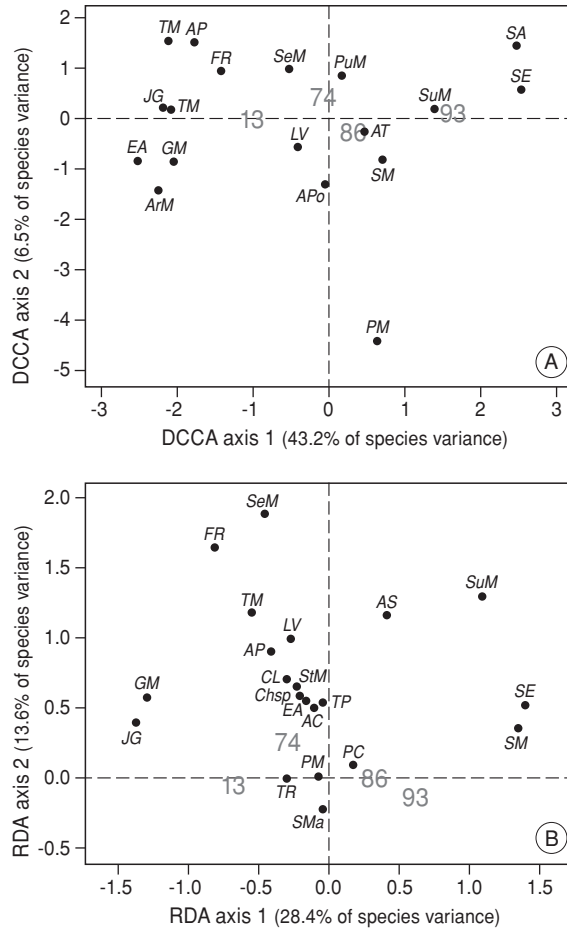


Figure 2.2 Plots of species and sample group centroids illustrating between-subjects factor, year of community establishment, in multivariate (A) analysis of inertia of vegetation data and (B) ANOVA of soil seed bank data. Partial detrended canonical correspondence analysis (DCCA) was used based upon vegetation data constrained by the sampling design (repeated-measures analysis of inertia). Partial redundancy analysis (RDA) was used based upon seed bank data constrained by sampling design (3-way factorial ANOVA). The parsimonious models were used to produce Figures. Seed bank data were \log_{10} -transformed. Species abbreviations are: ArM = *Armeria maritima*, AS = *Agrostis stolonifera*, AT = *Aster tripolium*, APo = *Atriplex portulacoides*, AP = *Atriplex prostrata*, CL = *Centaurium littorale*, CP = *Centaurium pulchellum*, Chsp = *Chenopodium* sp., EA = *Elytrigia atherica*, FR = *Festuca rubra*, GM = *Glaux maritima*, JG = *Juncus gerardi*, LV = *Limonium vulgare*, PC = *Plantago coronopus*, PM = *Plantago maritima*, PuM = *Puccinellia maritima*, SE = *Salicornia europaea*, SeM = *Seriphidium maritimum*, SA = *Spartina anglica*, SM = *Spergularia media*, SMa = *Spergularia marina*, StM = *Stellaria media*, SuM = *Suaeda maritima*, TM = *Triglochin maritima*, TR = *Trifolium repens*. Numbers represent centroids of samples from different communities. 13 = community established in 1913, 74 = 1974, 86 = 1986, 93 = 1993.

Salicornia europaea, *Suaeda maritima* and *Spergularia media* are strongly associated with the youngest community. *Atriplex portulacoides*, *Limonium vulgare* and *Seriphidium maritimum* are associated with intermediate-aged communities. On the other end of the axis, species such as *Elytrigia atherica*, *Juncus gerardi*, *Glaux maritima* and *Festuca rubra* are associated with the oldest community established in 1913.

Both within-subjects factors, year of sampling and the interaction between year of sampling and year of community establishment, are highly significant but explain little of the species variation in comparison to year of community establishment. The year of vegetation sampling explains 3.0 % of the variation in species distribution ($F = 2.37$, $p < 0.01$) and the interaction factor explains 6.0 % of the species variation ($F = 13.07$, $p < 0.01$).

Soil seed bank

Twenty-one species were recorded in the soil seed bank. When multivariate data are considered, factors in the sampling design explain 61.4% of the variation in the species distribution. All factors are highly significant ($p < 0.01$) but the year of community establishment explains more than half of the variation accounted for by the full model (33.7% of species variation). The ordination of the main effects of year of community establishment for the soil seed bank data along the first RDA axis is very similar to the ordination resulting from vegetation data (Figs. 2A & b). The ordination of the species found in the soil seed bank along the first RDA axis is also very similar to the ordination of species found in the vegetation along the first DCCA axis, even though different ordination techniques were used.

As noted before, all two-way and three-way interaction factors are highly significant but account for very little of the species variation in comparison to the main effect of year of community establishment.

Relationship between vegetation, seed production and soil seed bank

Of the 18 species recorded in the vegetation, three species were not found in the seed bank (*Atriplex portulacoides*, *Puccinellia maritima* and *Spartina anglica*). For the soil seed bank, seven out of 21 recorded species were not found in the vegetation (*Agrostis stolonifera*, *Centaureum littorale*, *Centaureum pulchellum*, *Chenopodium* sp., *Plantago coronopus*, *Stellaria media*, *Trifolium repens*).

When considering qualitative data (species presence/absence), the similarities in species composition between established vegetation and the soil seed bank (0 – 10 cm) are intermediate to high within communities. The Sørensen similarity index comparing vegetation and seed bank of the same communities ranges from 0.47 to 0.73 (Table 2.1). Both short-term (year of sampling) and long-term temporal effects (year of community establishment) on the similarity between the vegetation and seed bank do not show trends.

Table 2.1 Sørensen similarity indices between the vegetation and soil seed bank (0-10 cm) sampled at different communities along the chronosequence in two different years (1996/1997 and 2001).

		Vegetation			
	Year of establishment	1993	1986	1974	1913
A) Sampled 1996/1997					
Soil seed bank (0-10 cm)	1993	0.47	0.58	0.64	0.56
	1986	0.43	0.73	0.64	0.52
	1974	0.32	0.56	0.67	0.54
	1913	0.45	0.69	0.80	0.67
B) Sampled 2001					
Soil seed bank (0-10 cm)	1993	0.54	0.50	0.62	0.62
	1986	0.64	0.50	0.62	0.62
	1974	0.64	0.59	0.69	0.69
	1913	0.40	0.45	0.58	0.58

The response curves of species (Fig. 2.3) illustrate three types of responses with respect to time: species with decreasing dominance (*Salicornia europaea*, *Spergularia media*), species which reach a peak or saturation level in dominance (*Seriphidium maritimum*, *Festuca rubra*); and species with increasing dominance (*Juncus gerardi*). For the decreasing species, dominance of species in the upper and lower seed bank can track but lag behind their dominance in the vegetation (*S. europaea*). Alternatively, species can dominate the seed bank earlier than in the vegetation (*S. media*). The lower seed bank reflects the shape of the curve formed by the upper seed bank but either it lags behind (*S. europaea*) or precedes dominance (*S. media*) in the upper soil layers. Species which reach a peak or saturation level of dominance in the vegetation either do not form or form an extremely small seed bank (e.g. *L. vulgare* which is not shown in Fig. 2.3) or show a marked seasonal response (*S. maritimum*, *F. rubra*). *S. maritimum* is much less dominant in the seed bank than might be predicted from its vegetation dominance. The upper soil seed bank loosely tracks the vegetation but seeds are present in the lower layers only in the autumn. The seed bank of *F. rubra* formed in the upper layers of the soil during the autumn is much more dominant than that found in the spring whereas dominance in the lower seed bank is consistently low. For the increasing species, dominance in the seed bank either greatly precedes dominance in the vegetation (*J. gerardi*) or a seed bank is almost missing (e.g. *E. atherica* which is not shown in Fig. 2.3). All regressions were significant ($p < 0.05$).

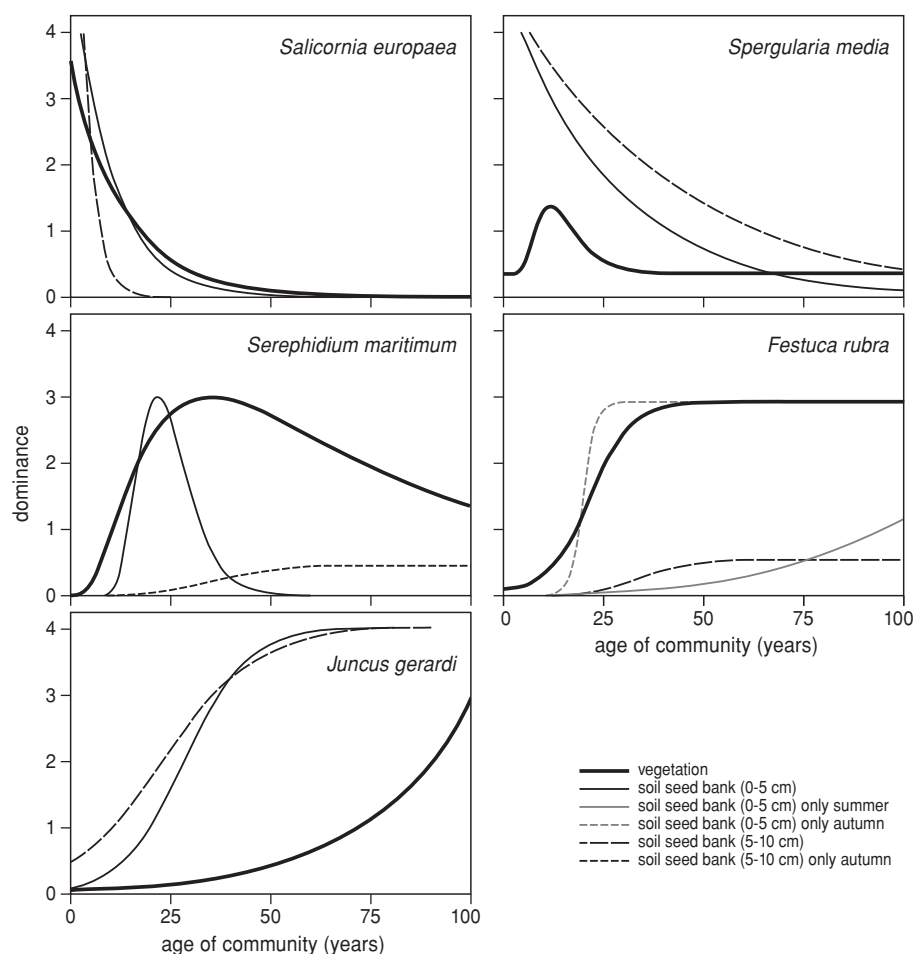


Figure 2.3 Graphs illustrating regressions between dominance scores of species (1 to 4) in the vegetation, upper and lower soil seed bank, and age of the community. Five representative salt-marsh species are shown. The p -value of all regressions were < 0.05 . R^2 values are given in Appendix 2.3. Explanation of the different curves are given in the inset key. Unless indicated, the regressions combined data collected in 1996/1997 and 2001. Data from only the autumn were collected in 1996. Data from only the summer were collected in 2001.

With respect to seed production, *S. europaea* and *S. media* show very similar trends to their dominance in the vegetation and the seed bank over time (Fig. 2.4). However, *S. media* shows higher seed production in younger communities than might be expected from its corresponding dominance values in the vegetation. *Suaeda maritima* shows similar trends to *S. europaea*. *L. vulgare* shows decreasing seed production as communities age. The density of the upper soil seed bank,

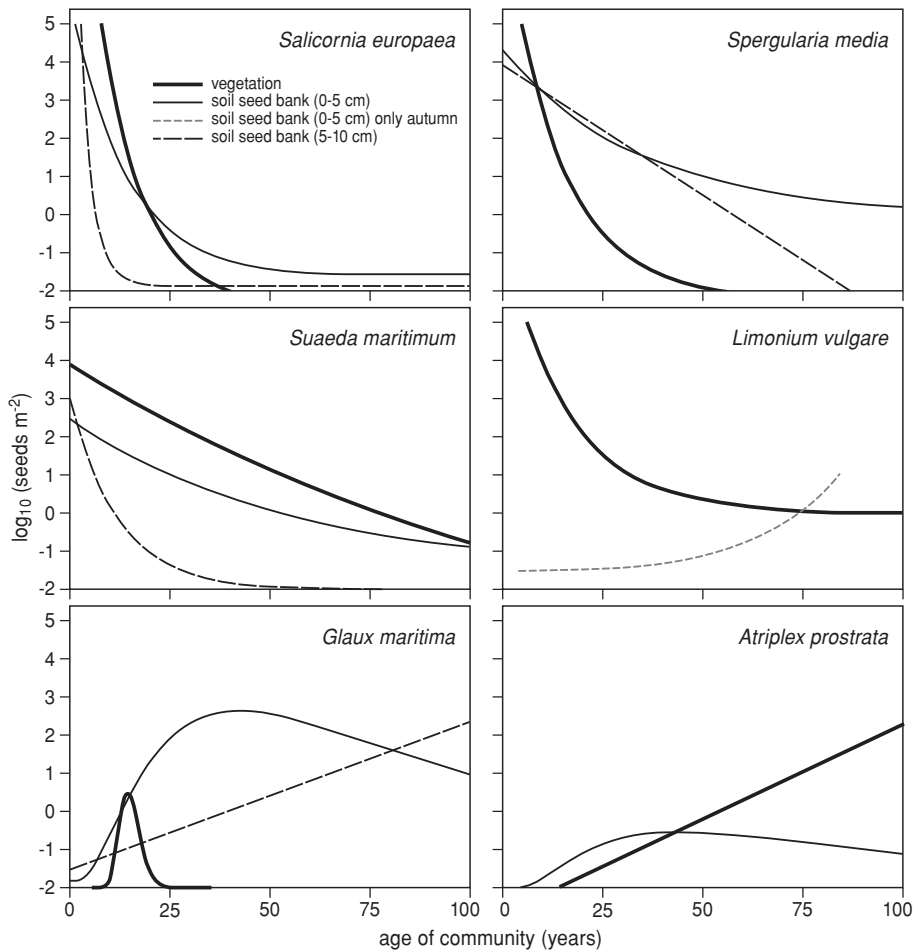


Figure 2.4 Graphs illustrating regressions between seed production, upper and lower soil seed bank, and age of the community. Six representative salt-marsh species are shown. The p-value of all regressions were < 0.05 . R^2 values are given in Appendix 2.4. Explanation of the different curves are given in the inset key. Unless indicated, the regressions combined data collected in 1996/1997 and 2001. Data from only the autumn were collected in 1996.

however, increases with age of the community. *G. maritima* shows a peak in seed production early in time. This peak is magnified and elongated in the upper seed bank over time unlike the density of the lower seed bank, which increases steadily over time. *A. prostrata* shows increasing seed production over time. However, seeds are only present in the upper layers of the soil and density peaks in intermediate-aged communities.

Seed survival in the soil after burial

The difference in means between percentage of seeds that germinated and those with a firm endosperm is with few exceptions less than 5 %. Therefore, only the values for germinable seeds are presented. The percentage of buried seeds that germinate decreases over time for all species and for both young and intermediate-aged communities (Fig. 2.5). At the end of two years, mean germination ranges between 30.6 % to 54.0 %, except for *Salicornia europaea* and *Elytrigia atherica* seeds buried in the young community. For these groups, very few of the originally buried

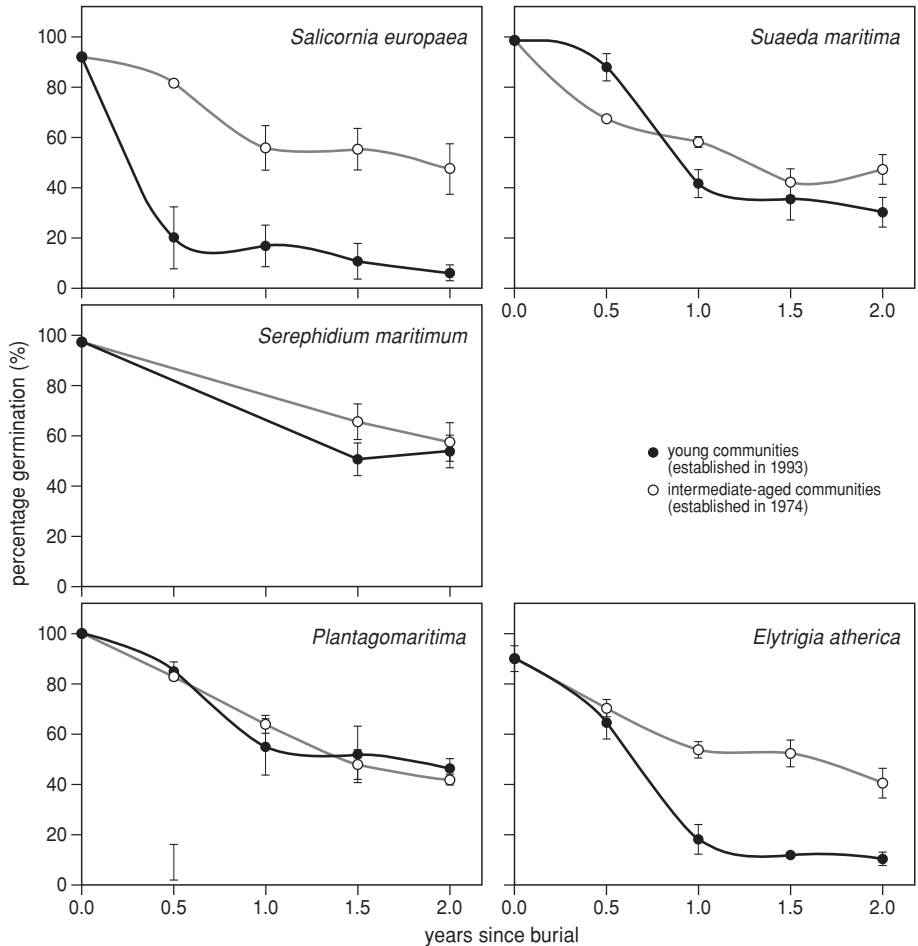


Figure 2.5 Germination of seeds artificially buried and exhumed after 0.5 to 2 years. Seeds of five species were buried under a young and intermediate-aged communities. Symbols and lines are explained in the inset key. Error bars represent standard errors.

seeds survived and germinated after two years (6.2 % and 10.6 % respectively for *S. europaea* and *E. atherica*). Germination is significantly lower in the young community compared to the intermediate-aged community for *E. atherica* (t-test, $t_8 = -4.742$, $p = 0.001$) and this difference is almost significant for *S. europaea* due to the Bonferroni correction (t-test, $t_{4.669} = -3.886$, $p = 0.013$).

Discussion

Patterns in relationship between the vegetation and soil seed bank

Overlap between species presence in the vegetation and soil seed bank at the same point in space and time ranged between 47 to 73 % and did not show a trend as communities aged. The similarity between the vegetation and soil seed bank was comparable to values found in some salt-marsh studies (Hutchings & Russell 1989; Egan & Ungar 2000) but higher than values found in salt marshes in south Wales (Ungar & Woodell 1996) and an annual-dominated Mediterranean salt marsh (Marañón 1998). Part of the discrepancy may be due to a delay between appearance in the vegetation and incorporation of seeds into the soil seed bank. Some species present in the vegetation were absent from the seed bank along the entire chronosequence and *vice-versa*. Grazing by herbivores, such as geese on *Puccinellia maritima* (van der Wal *et al.* 2000a) and hares on *Atriplex portulacoides* (van der Wal *et al.* 2000b), may act as filters by preventing seed set (Fig. 2.1C) (Wolters & Bakker 2002). In this study, both species occur frequently in the vegetation but are absent from the soil seed bank. This situation was also found in some British salt marshes (Ungar & Woodell 1993; Ungar & Woodell 1996), of which some were heavily grazed by livestock. In contrast, seeds of *Puccinellia maritima* were recorded, sometimes in high densities, in the soil (347 ± 53 to 6627 ± 224 seeds m^{-2}) of an ungrazed salt marsh in Sussex, U.K. (Hutchings & Russell 1989). *Plantago maritima*, although present in the vegetation of intermediate-aged communities, was found in the soil seed bank at very low densities and occurred only in four samples. For this species, intense grazing by Brent geese (Prins *et al.* 1980) may decrease seed production as was found when this species was grazed by cattle (Jerling & Andersson 1982). Viable seed set in *Spartina anglica* may be affected by high incidence of a pre-dispersal pathogen attack (Raybould *et al.* 1998). Most of the species present in the soil seed bank but absent from the vegetation (*Agrostis stolonifera*, *Centaureum littorale*, *Centaureum pulchellum*, *Plantago coronopus*, *Stellaria media*, *Trifolium repens*) are species that are generally found at higher elevations near the dunes rather than in the lower, more frequently inundated zone. These are species that are unlikely to pass through the environmental filters of a low salt-marsh habitat (Fig. 2.1D) such as high salinity, frequent inundation and sedimentation.

Support from seed production and burial data

Densities of seeds in the soil seed bank generally tracked changes in the production of seeds for three early-successional species: *Salicornia europaea*, *Spergularia media* and *Suaeda maritima* (Fig. 2.4). The relationship between densities in seed production and soil seed bank closely mirrored the relationship seen between dominance in the vegetation and soil seed bank, suggesting that seed production is not a constraining factor.

For both *Limonium vulgare* and *Glaux maritima*, seed production did not seem to limit abundance in the soil seed bank as seed numbers built up in the soil even though production showed an early peak or decreased over time. The relationship between seed production and the seed bank for *L. vulgare* suggested that seed longevity in soil may be the constraining factor for this early-to-mid successional species. This was clearly not the case for *G. maritima*, which displayed a long-term persistent seed bank (>5 years; Thompson *et al.* 1997).

Atriplex prostrata displayed increasing seed production over time, reflecting its patterns of dominance in the vegetation, but this increase was not reflected in the soil seed bank. Also, seeds of this species were mostly limited to the upper layers of soil, suggesting a transient seed bank (<1 year; Thompson *et al.* 1997) although studies at 15 other sites concluded that, in general, this is a persistent species (Wolters & Bakker 2002). *A. prostrata* is known to have dimorphic seeds: large, brown, transient seeds and small, black seeds with potential for long-term persistence (Carter & Ungar 2003). Dimorphic seeds may be formed in variable proportions (Wertis & Ungar 1986) and at our site, *A. prostrata* produced a much greater proportion of transient, large seeds. Haphazard samples which were pooled contained 13 % small seeds and 86 % large seeds ($n = 738$ seeds).

With the exception of *Glaux maritima*, *Juncus gerardi* and *Spergularia media*, most species in these communities possessed transient (<1 year) or short-term persistent (at least 1 year but <5 years) soil seed banks when the relationship between the vegetation, and upper and lower layers of the soil was examined (Thompson *et al.* 1997). These indirect, “depth-derived” observations are supported by results from the burial experiment. At the end of two years, less than half of the originally buried seeds for all five species survived and germinated. If depletion from the seed bank continues at the same rate, no seeds are predicted to survive beyond five years.

For two species, site conditions possibly had an impact on seed survival. Seeds of *Salicornia europaea* and *Elytrigia atherica* displayed lower survival in the youngest community than in the intermediated-aged community. Perhaps the more frequent and longer inundations at the younger site resulted in conditions that negatively affected their survival. Survival of *E. atherica* seeds that were artificially buried in the intermediate-aged community ($40.8 \% \pm 5.8$ at the end of two years) was much higher than that predicted by the survey data (<1 year). However, artificial burial experiments can exaggerate seed longevity because they bypass the

crucial step of natural burial mechanisms (Thompson *et al.* 1997). Seeds of *E. atherica* are relatively large and heavy (~ 0.004 g) and remain attached to bracts after detachment. Due to their relatively large size, seeds of this species are unlikely to percolate downwards through the soil as smaller seeds are more likely to be buried (Peart 1984; Thompson *et al.* 1994).

For the few species for which we managed to collect sufficient data, seed production filters (Fig. 2.1C) did not appear to impose strong constraints. However, it is possible that seed production is limiting for *Puccinellia maritima* and *Spartina anglica*, due to effects of herbivores and pathogens. Also, despite the higher proportion of perennial species in later communities, seed production did not generally appear to decrease over time. More species may be constrained by filters affecting seed longevity (Fig. 2.1B). Very few species appeared to possess long-term persistent seed banks. However, patterns observed in seed longevity for different species did not match those predicted for the second proposed relationship between the vegetation and seed bank *i.e.* increasing strength of filters controlling seed longevity over time. Most species, across the entire community sequence, possessed either transient or short-term persistent seed banks. Of the three possible exceptions, *Spergularia media* is an early-successional species, *Glaux maritima* is a mid-to-late successional species and *Juncus gerardi* is a late-successional species, and thus individual cases of long-term persistence ranged across the entire community sequence.

Predictions for constraints in community assembly

Of the three relationships between the vegetation and the soil seed bank proposed in the introduction, the situation at our site most resembles the first relationship, where the seed bank composition varies, reflecting changes in the vegetation over time. An intermediate to high similarity remained throughout and showed no trend as communities aged. The prediction for community assembly is that strong constraints exist in dispersal between the local species pool and the community species pool although regular tidal inundation from the Wadden Sea would be expected to lead to relatively rapid migration. Tidal inundation covers the 6 km distance between the youngest and oldest sites but many species are found much closer than suggested by their patterns along the chronosequence due to zonation of species along the elevation gradient. For example, *E. atherica* is not present in young sites at low elevations but is present in the high-elevation sites near the dunes tens of metres away. This may indicate a net upward transport of seeds by tidal flow along the zonation gradient (Huiskes *et al.* 1995), which is supported by the high density and species richness of seeds found in driftlines at the foot of the dunes (Wolters & Bakker 2002). Seed trap and driftline studies at this same site also support this possibility (Chapter four). However, successful establishment of salt-marsh species in the driftline has not been observed during the

course of this study. Thus, successful dispersal of seeds from the local species pool to the community species pool in the low marsh may be constrained by low rates of seed retention as most seeds float over the site and become concentrated in the driftlines, where they are effectively lost from the system.

Seed limitation has a strong influence on community membership and structure of many systems including grasslands (Tilman 1997; Zobel *et al.* 2000), coastal dunes (Lichter 2000), oak savannas (Foster & Tilman 2003) and frequently flooded riparian wetlands (Xiong *et al.* 2003). In a review, Turnbull *et al.* (2000) concluded that about 50% of reviewed seed-addition experiments showed evidence of seed limitation. The results of this study indicate that seeds of many species may not reach all communities and, therefore, seed limitation may be a constraint in community assembly.

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Appendix 2.1 Mean dominance scores for species (\pm standard error) found during vegetation surveys of permanent transects. Permanent transects were located at four stages of community development and were sampled twice (in 1997 and 2001). A dominance score of 4 indicates most abundant species in a sub-plot; 3, the next most abundant species and so on. The dominance scores of a maximum number of four species was recorded for each sub-plot. $n = 10$

Species	Year of community establishment				1913			
	1993		1986		1974		1974	
	Sampled in 1997	Sampled in 2001	Sampled in 1997	Sampled in 2001	Sampled in 1997	Sampled in 2001	Sampled in 1997	Sampled in 2001
<i>Armeria maritima</i>	0	0	0.06 \pm 0.04	0.02 \pm 0.02	0	0	0.40 \pm 0.06	0.38 \pm 0.06
<i>Aster tripolium</i>	0.02 \pm 0.02	0.18 \pm 0.05	0.64 \pm 0.07	0.98 \pm 0.02	0.26 \pm 0.11	0.90 \pm 0.33	0	0.04 \pm 0.04
<i>Atriplex portulacoides</i>	0.12 \pm 0.04	0.38 \pm 0.11	1.70 \pm 0.16	2.34 \pm 0.24	0.78 \pm 0.20	0.98 \pm 0.28	0.88 \pm 0.05	0.86 \pm 0.04
<i>Atriplex prostrata</i>	0	0	0	0	0.12 \pm 0.07	0.60 \pm 0.14	0.60 \pm 0.07	0.68 \pm 0.06
<i>Elytrigia atherica</i>	0	0	0	0	0	0.04 \pm 0.03	0.62 \pm 0.06	0.86 \pm 0.05
<i>Festuca rubra</i>	0	0	0.76 \pm 0.16	0.52 \pm 0.14	1.46 \pm 0.45	2.28 \pm 0.46	2.58 \pm 0.12	3.18 \pm 0.18
<i>Glaux maritima</i>	0	0	0.16 \pm 0.08	0.24 \pm 0.10	0.28 \pm 0.10	0.04 \pm 0.03	2.00 \pm 0.11	1.14 \pm 0.05
<i>Juncus gerardi</i>	0	0	0	0	0.04 \pm 0.04	0.68 \pm 0.14	1.32 \pm 0.10	2.02 \pm 0.27
<i>Limonium vulgare</i>	0.10 \pm 0.06	1.16 \pm 0.13	3.60 \pm 0.10	3.72 \pm 0.07	2.80 \pm 0.34	2.08 \pm 0.20	3.70 \pm 0.07	2.58 \pm 0.09
<i>Plantago maritima</i>	0	0	0.98 \pm 0.02	0.94 \pm 0.03	0	0.10 \pm 0.04	0	0
<i>Puccinellia maritima</i>	0.40 \pm 0.09	1.02 \pm 0.06	1.24 \pm 0.13	1.00 \pm 0	1.36 \pm 0.40	1.66 \pm 0.39	0.94 \pm 0.03	0.76 \pm 0.04
<i>Salicornia europaea</i>	2.42 \pm 0.10	2.74 \pm 0.09	1.00 \pm 0	1.00 \pm 0	0.68 \pm 0.15	0.66 \pm 0.14	0	0
<i>Spartina anglica</i>	0.34 \pm 0.10	0.76 \pm 0.13	0.14 \pm 0.08	0.10 \pm 0.04	0.20 \pm 0.12	0.16 \pm 0.10	0	0
<i>Seriphidium maritimum</i>	0	0	1.50 \pm 0.21	1.82 \pm 0.24	2.62 \pm 0.35	2.68 \pm 0.39	1.24 \pm 0.09	2.08 \pm 0.14
<i>Spergularia marina</i>	0	0.22	0	0	0	0	0	0
<i>Spergularia media</i>	0.26 \pm 0.10	0.96 \pm 0.09	1.34 \pm 0.07	1.24 \pm 0.08	0.52 \pm 0.15	0.68 \pm 0.12	0.42 \pm 0.12	0.32 \pm 0.08
<i>Suaeda maritima</i>	2.48 \pm 0.07	1.22 \pm 0.08	2.12 \pm 0.18	1.00 \pm 0	1.28 \pm 0.30	0.92 \pm 0.04	0.48 \pm 0.07	0.24 \pm 0.06
<i>Triglochin maritima</i>	0	0	0	0.02 \pm 0.02	0.16 \pm 0.05	0.20 \pm 0.04	0.80 \pm 0.03	0.80 \pm 0.04

Appendix 2.2 Mean density of seeds found in the soil (seeds m⁻²) along a community sequence. Soil samples were separated into an upper (0-5 cm depth) and a lower layer (5-10 cm depth). Communities were established in 1993, 1986, 1974 and 1913 and were sampled in 1996 and five years later in 2001.

Species	Year of community establishment					
	1993			1986		
	Upper layer		Lower layer	Upper layer		Lower layer
	Sampled in 1996	Sampled in 2001	Sampled in 1996	Sampled in 1996	Sampled in 2001	Sampled in 1996
<i>Agrostis stolonifera</i>	91 ±18	35 ±20	69 ±23	126 ±27	40 ±19	22 ±12
<i>Aster tripolium</i>	0	5.0 ±5.0	0	4.3 ±4.3	5.0 ±5.0	8.7 ±8.7
<i>Atriplex prostrata</i>	0	5.0 ±5.0	4.3 ±4.3	0	30 ±17	0
<i>Centaurium littorale</i>	0	0	0	0	0	4.3 ±4.3
<i>Centaurium pulchellum</i>	0	0	0	810 ±330	0	17 ±9.6
<i>Chenopodium</i> sp.	0	0	0	0	0	0
<i>Elytrigia atherica</i>	0	0	0	4.3 ±4.3	0	0
<i>Festuca rubra</i>	0	5.0 ±5.0	0	22 ±9.7	0	0
<i>Glaux maritima</i>	8.7 ±5.8	9.9 ±9.9	0	35 ±30	640 ±310	0
<i>Juncus gerardi</i>	35 ±14	20 ±15	30 ±9.2	230 ±42	270 ±160	35 ±14
<i>Limonium vulgare</i>	4.3 ±4.3	0	0	13 ±6.6	0	0
<i>Plantago coronopus</i>	0	5.0 ±5.0	0	4.3 ±4.3	0	0
<i>Plantago maritima</i>	0	0	0	4.3 ±4.3	0	4.3 ±4.3
<i>Salicornia europaea</i>	3300 ±540	940 ±320	1500 ±440	1400 ±320	140 ±40	8.7 ±5.8
<i>Seriphidium maritimum</i>	8.7 ±8.7	0	0	13 ±6.6	180 ±46	0
<i>Spergularia marina</i>	0	0	0	0	5.0 ±5.0	0
<i>Spergularia media</i>	3000 ±820	10000 ±2400	1300 ±230	11000 ±1800	1900 ±480	2200 ±180
<i>Stellaria media</i>	0	0	0	0	0	0
<i>Suaeda maritima</i>	890 ±180	40 ±14	240 ±100	4700 ±270	390 ±260	250 ±81
<i>Trifolium repens</i>	0	0	0	0	0	0
<i>Triglochin maritima</i>	0	0	0	0	0	0

Appendix 2.2 Continued

Species	Year of community establishment						
	1974			1913			
	Upper layer		Lower layer	Upper layer		Lower layer	
	Sampled in 1996	Sampled in 2001	Sampled in 1996	Sampled in 2001	Sampled in 1996	Sampled in 2001	
<i>Agrostis stolonifera</i>	190 ± 39	45 ± 12	300 ± 77	60 ± 34	61 ± 38	4.3 ± 4.3	0
<i>Aster tripolium</i>	8.7 ± 5.8	40 ± 28	4.3 ± 4.3	0	4.3 ± 4.3	0	0
<i>Atriplex prostrata</i>	39 ± 20	45 ± 25	4.3 ± 4.3	0	30 ± 11	15 ± 7.6	0
<i>Centaurium littorale</i>	4.3 ± 4.3	0	22 ± 9.7	0	0	0	0
<i>Centaurium pulchellum</i>	13 ± 9.2	5.0 ± 5.0	160 ± 120	130 ± 73	0	0	0
<i>Chenopodium</i> sp.	0	0	4.3 ± 4.3	0	0	0	0
<i>Elytrigia atherica</i>	8.7 ± 5.8	0	0	0	0	4.3 ± 4.3	0
<i>Festuca rubra</i>	820 ± 220	0	22 ± 13	5.0 ± 5.0	890 ± 160	22 ± 13	25 ± 13
<i>Glaux maritima</i>	470 ± 140	940 ± 690	1100 ± 260	1000 ± 300	150 ± 54	120 ± 32	720 ± 370
<i>Juncus gerardi</i>	360 ± 150	2200 ± 1100	520 ± 180	650 ± 190	16000 ± 2900	12000 ± 1700	8600 ± 1500
<i>Limonium vulgare</i>	0	0	0	0	56 ± 13	0	69 ± 69
<i>Plantago coronopus</i>	0	0	0	0	0	0	0
<i>Plantago maritima</i>	0	5.0 ± 5.0	0	0	0	9.9 ± 9.9	0
<i>Salicornia europaea</i>	13 ± 6.6	30 ± 30	0	5.0 ± 5.0	17 ± 7.1	0	4.3 ± 4.3
<i>Seriphidium maritimum</i>	960 ± 170	290 ± 93	52 ± 19	0	217 ± 65	0	39 ± 22
<i>Spergularia marina</i>	0	0	0	15 ± 11	0	0	0
<i>Spergularia media</i>	170 ± 92	340 ± 160	990 ± 180	640 ± 180	210 ± 65	55 ± 23	0
<i>Stellaria media</i>	8.7 ± 5.8	0	4.3 ± 4.3	0	0	0	0
<i>Suaeda maritima</i>	320 ± 100	65 ± 27	13 ± 9.2	5.0 ± 5.0	48 ± 16	5.0 ± 5.0	0
<i>Trifolium repens</i>	0	0	4.3 ± 4.3	0	0	0	8.7 ± 8.7
<i>Triglochin maritima</i>	26 ± 22	0	4.3 ± 4.3	0	61 ± 16	0	4.3 ± 4.3

Appendix 2.3 Results of non-linear regression between age of community and dominance of species in the vegetation (V), upper soil seed bank (USB) and lower soil seed bank (LSB). $p < 0.05$ for all regressions.

Species		Curve family	Parameters	R^2
<i>Salicornia europaea</i>	V	Exponential decay	2	0.79
	USB	Exponential decay	2	0.77
	LSB	Exponential decay	2	0.84
<i>Spergularia media</i>	V	Log-normal	4	0.55
	USB	Exponential decay	2	0.50
	LSB	Exponential decay	2	0.80
<i>Seriphidium maritimum</i>	V	Log-normal	3	0.58
	USB	Log-normal	3	0.55
	LSB	Gaussian	3	0.25
<i>Festuca rubra</i>	V	Sigmoidal	3	0.65
	USB (Fall)	Sigmoidal	3	0.85
	USB (Summer)	Sigmoidal	3	0.24
	LSB	Sigmoidal	3	0.17
<i>Juncus gerardi</i>	V	Exponential growth	2	0.74
	USB	Sigmoidal	3	0.74

Appendix 2.4 Results of non-linear regression between age of community and seed production (SP), upper soil seed bank (USB) and lower soil seed bank (LSB). Density of seeds (seeds m^{-2}) were transformed before analysis ($y = \log_{10}(x + 0.01)$). $p < 0.05$ for all regressions.

Species		Curve family	Parameters	R^2
<i>Salicornia europaea</i>	SP	Exponential decay	3	0.72
	USB	Exponential decay	3	0.64
	LSB	Exponential decay	3	0.70
<i>Spergularia media</i>	SP	Exponential decay	3	0.69
	USB	Exponential decay	2	0.36
	LSB	Polynomial, linear	2	0.97
<i>Suaeda maritima</i>	SP	Exponential decay	3	0.32
	USB	Exponential decay	3	0.20
	LSB	Exponential decay	3	0.38
<i>Limonium vulgare</i>	SP	Exponential decay	2	0.50
	USB (Fall)	Exponential growth	5	0.34
<i>Glaux maritima</i>	SP	Log-normal	4	0.34
	USB	Log-normal	4	0.32
	LSB	Polynomial, linear	2	0.32
<i>Atriplex prostrata</i>	SP	Polynomial, linear	2	0.77
	USB	Log-normal	4	0.11



Chapter 3

Seed dispersal by small herbivores and tidal water: are they important filters in the assembly of salt-marsh communities?

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Summary

Characteristics of internal seed dispersal (endozoochory) by European brown hares were compared to similar dispersal by brent geese. Hares deposited more seeds of mid-successional, perennial, high-marsh species than geese, which deposited more seeds of early-successional, annual, low-marsh species. Seed survival and germination of salt-marsh species were higher after ingestion and passage through the digestive system of hares compared to geese. Both hares and geese had a negative effect on the percentage of seeds that germinated in comparison with uningested seeds. Small herbivores (hares and geese) dispersed two orders of magnitude fewer seeds than those dispersed by tidal water. Thus, they are not likely to be important filters (constraints) in community assembly at this salt-marsh site on a coastal island in the Netherlands.

Introduction

Community assembly can be conceptualized as a process whereby members of a species pool are eliminated as they pass through a hierarchy of biotic and abiotic filters (Wiens 1983; Keddy 2000). The filters select for certain traits and the species, which form a community, are those with traits that have enabled them to survive passage through the filters. In the case of salt-marsh communities, most research has focussed either on the roles of environmental filters such as salinity (Keddy 2000), or interactions between individuals of the different species such as competition (Wilson & Whittaker 1995; Keddy 2000). Less attention has been paid to the processes that control membership of the species pool.

Dispersal of vegetative diaspores, fruits or seeds is dependent on abiotic (*e.g.* wind, water, rain splatter) and biotic vectors (*e.g.* animals and people). As vectors of seed dispersal, can small herbivores act as important dispersal filters in the assembly of plant communities by determining species pool membership? Studies on the internal dispersal of seeds (endozoochory) by hares, for example, indicate that passage through the digestive system may break dormancy and highly enhance germination in species with hard seed coats (Izhaki & Ne'eman 1997). Rabbits may provide directed dispersal to particularly favourable microhabitats (*c.f.* Howe & Smallwood 1982) in fragmented vegetation communities such as transient wetlands (Zedler & Black 1992). Similarly, mammals and birds disperse seeds of isolated patches of bush-pocket vegetation in dune fields (Castley *et al.* 2001). Rabbits may also facilitate colonization of new habitats such as small disturbances in pastures (Malo *et al.* 1995) and open ground in dune systems (Calviño-Cancela 2002). Endozoochory may be important where high numbers of animals are present, even if the probability of dispersal per individual animal is low, such as is the case with duck species during autumn migration (Charalambidou *et al.* 2003). It may also be important if no other dispersal vector for long distances is available (D'Antonio 1990; Zedler & Black 1992; Milton & Dean 2001).

The effectiveness of endozoochory by small herbivores may change as communities develop and mature. It is predicted that effectiveness will be greater in younger communities where a greater proportion of species are annuals, which depend upon recruitment solely from seed sources, and seed limitation of recruitment is likely to be more prevalent (Turnbull *et al.* 2000). Where other dispersal vectors are present, the importance of endozoochory by small herbivores must be evaluated in relation to the effectiveness of dispersal provided by other vectors. We posed three questions in this study: 1) Do hares and geese differ in their effectiveness as vectors of seed dispersal? 2) Does the effectiveness of hares and geese as seed dispersers change during community development? 3) How effective is endozoochory compared to dispersal by tidal water in an intertidal salt marsh?

Materials and Methods

Site description

The studies were conducted on the barrier island of Schiermonnikoog, the Netherlands (53° 30' N, 6° 10' E). The island is extending eastward as a consequence of changing sea currents and sediment accretion (Olff *et al.* 1997). Salt marshes form an age gradient on the southern shore of the island, resulting in a well-developed chronosequence (de Leeuw *et al.* 1993; Olff *et al.* 1997). Five salt-marsh communities were studied that were characteristic of 10, 15, 30, 40 and 100 year-old marshes. A second gradient, elevation, rises from the intertidal mud flats, across the salt marshes, to the dunes (Olff *et al.* 1997). Sediments consist of a sandy sub-layer with an upper clay layer (2-16 cm), which increases with community age. Low marshes occur at a sand-layer elevation between 20 - 40 cm above MHT (mean high tide). During the period when this study was conducted, the inundation frequency varied from every few days for young marshes to weekly or bi-weekly for intermediate-aged marshes to infrequent for old marshes. High marshes occur at a sand-layer elevation between 60 - 80 cm above MHT and inundation is infrequent.

About 3000 brent geese (*Branta bernicla bernicla* L.) are residents on Schiermonnikoog between October and late May (Bos & Stahl 2003). Brent geese feed mainly in agricultural pastures but they also graze on the natural salt marshes during the study period in November to December. A range of 30 to 620 brent geese were tallied in this area during monthly counts between October to December from 2001 to 2004 (SOVON Waterfowl counts, Klaas van Dijk & Julia Stahl, unpublished data). Other birds which occur frequently in the area and potentially consume seeds include ducks, such as wigeons (*Anas penelope*), common teals (*Anas crecca*) and mallards (*Anas platyrhynchos*), and passerines, such as snow buntings (*Plectrophenax nivalis*), twites (*Carduelis flavirostris*) and horned larks (*Eromophila alpestris*). About 500 European brown hares (*Lepus europaeus* Pallas) are resident on the natural salt marshes throughout the year (Kuijper 2004).

Endozoochorous dispersal by hares and geese

Seed dispersal in the faeces of hares and geese was estimated by collecting droppings at six sites (three high-elevation and three low-elevation) within each of the five stages of community development. Mean distance between sites was 42 m (± 25 standard deviations) and minimum distance was 12 m. At each of the six sites, five marking sticks were placed using *a priori* criteria: high-density patches of *Festuca rubra* for high marshes and high-density patches of *Puccinellia maritima* for low marshes. Plant nomenclature follows van der Meijden (1996). Dropping densities of hares and geese are generally very low and clustered in distribution, and

there is a lot of spatial heterogeneity in structure of the salt marshes. The *a priori* criteria were used to select similar patches, which could be consistently compared along the chronosequence and were feasible candidates to be influenced by endozoochory. For each sampling date, all hare droppings present within a radius of 1.3 m (area = 4 m²) from each stick were collected, resulting in a total sampling area of 20 m² for each site. Goose droppings were sampled differently from hare droppings due to a lower incidence of occurrence and less even distribution. Goose droppings present within 1.5 m from a direct path between each of the sticks were taken for an average area of 76.24 m² sampled for each site. The five sub-samples for each site were pooled. All plots were cleared of droppings on 12 November, 2002. Fresh droppings were counted and collected on 29 November and 12 December, 2002. Data from both sampling dates were pooled and used for all analyses.

Samples were assessed for seed content using a modified seedling emergence technique (ter Heerdt *et al.* 1996). After exposure to a minimum of five weeks of cold stratification (6°C) in order to simulate winter conditions, the samples were transferred to a greenhouse (25°C day temperature, 15°C night temperature, 15-hour light period) and monitored for germination. An additional sample of 100 droppings each for hares and geese was collected and dried in an oven (48 hours, 70°C) in order to express endozoochory samples on a dried mass basis.

Feeding experiments using captive animals

Five European brown hares born in captivity were used for the feeding experiments. The animals were kept in outdoor pens of 1.5 m x 1 m with a wooden box for shelter and a mesh-wire floor (around 1 cm mesh size) through which droppings could fall onto a net suspended under each cage.

Portions of food were prepared by embedding seeds in a matrix, made of commercial rabbit food pellets softened by immersion in water, and rolling the resulting mixture into a ball. One portion of food was fed to each hare on 16 July, 2002. 50 seeds each of *Suaeda maritima*, *Seriphidium maritimum*, *Glaux maritima* and 30 seeds each of *Elytrigia atherica*, *Plantago maritima* and *Salicornia europaea* were added to each portion. Hares were observed to consume the entire portions. To ensure that all seeds fed to the hares had been excreted, all faeces produced by each hare for one week were collected (Hirakawa & Okada 1995; Hirakawa 2001; Kuijper *et al.* 2004). The droppings collected from the captive hares were processed identically to those collected from the salt marshes. Three control samples of 50 uningested seeds for each plant species were germinated in Petri dishes (similar environmental conditions as ingested samples).

Data obtained from feeding experiments with captive hares were compared to feeding trial data collected from barnacle geese (*Branta leucopsis* L.) on seeds of the same salt-marsh species (Geertsema 2000). Barnacle geese (1780 g) are only

slightly larger than brent geese (1564 g) and share similar food resources (Stahl 2001). About 12 000 barnacle geese reside on Schiermonnikoog between October and early April (Bos & Stahl 2003) but they do not forage on the natural salt marshes between October and December. To our knowledge, no experimental feeding trial data on the effect of brent geese on seed survival and germination exist. Brent geese do not breed in captivity and captive birds are highly susceptible to stress.

Seed dispersal by tidal water

During approximately the same period when droppings were collected, seed traps were used to measure seed dispersal by tidal water (hydrochory). Seed traps were made of squares of Astroturf® (45 cm x 45 cm) and their efficacy as seed traps is documented in Wolters *et al.* (2004). Seed traps were fastened to the ground using stainless steel pegs.

Ten seed traps were placed at least 10 m apart at each of four stages of community development (40 year-old marsh not sampled) using *a priori* criteria. They were placed in a row parallel to the coastline in the low-elevation sites from where the endozoochorous samples were collected. The traps were set out on 1 November, 2002 and collected seven weeks later on 20 December. After collection, the seed traps were rinsed with water over a 0.212 mm mesh sieve. Very few droppings were observed on the seed traps. The resulting sediment and seed mixtures were then processed identically to the procedure used for dropping samples. In order to facilitate comparisons with endozoochory data, the mean number of seeds collected per 28 days was calculated.

Data analyses

Germinable seeds recovered from the droppings of hares and geese, and seed traps were analysed using multivariate methods and Monte Carlo permutation tests using the software program, CANOCO for Windows 4.52 (ter Braak & Šmilauer 1998). These analyses parallel analysis of variance (ANOVA). Data from all 14 species found in the droppings were used simultaneously to construct an analysis of variance table, partitioning all the variance explained by sources in the model. Such a table could be conceptually obtained by carrying out an ANOVA on each of the 14 species, totalling the sums of squares (SS) of each ANOVA source across the 14 species, and dividing the resulting sums by the total sum (ter Braak & Šmilauer 1998). The use of Monte Carlo permutations to test the significance of each ANOVA source frees us from an assumption of conventional ANOVA, that of normal distribution, as this is a statistical technique that does not assume a particular distribution. The observed value of a test statistic (F-ratio) for a factor is assessed by comparison to a frequency distribution of expected values under the null hypothesis that is generated by randomly reordering the actual data using some assumed model, not to a theoretical distribution (Manly 1997). The sam-

pling design will determine the assumed model and how data are reordered (permuted). However, the assumption of homogeneity of variance remains.

The sampling design was encoded using dummy variables of 0 and 1. Partial redundancy analysis (RDA) was used instead of partial canonical correspondence analysis (CCA) because partial RDA resulted in better homogeneity of variance in multivariate space, when coupled with a square root transformation, than the partial CCA. Eight separate significance tests using Monte Carlo simulations were run for each analysis, including one for the full model (2 by 5 by 2 full factorial), three main effects (animal type, community state, elevation), three 2-way interactions and one 3-way interaction. For the permutation tests when assessing the main effects, the factor in question was used as the environmental variable and the other two factors were used as covariables. Permutations were restricted by blocks defined by all covariables. In the case of the 2-way interaction tests, all three factors were listed as covariables in the analyses and for the 3-way interaction test, all three factors plus all three 2-way interactions were used as covariables. Permutations for interaction effects were unrestricted. When a factor is used as a covariable in an analysis, only the variability explained by the environmental variables after subtracting overlapping variance explained by the covariables is considered. For figures illustrating significant factors, parsimonious models are shown. A practical guide to setting up similar analyses in CANOCO is given in this paper. For more technical and theoretical discussions, consult ter Braak & Šmilauer (1998) and Lepš & Šmilauer (2003). For further discussions on Monte Carlo tests, consult Manly (1997) and Edgington (1986).

When the distribution of a data set is non-normal, one can either transform the data to meet the model assumptions or one can conversely mould the model to meet the data characteristics, which is what occurs in generalized linear models (Crosbie & Hinch 1985). For the feeding trials, a general linear model ANOVA was used with animal type and seed species as fixed factors using SPSS 12.0.1 for Windows (2003). A square-root transformation was used to meet model assumptions. For endozoochorous and hydrochorous data, generalized linear models using Poisson distribution were used to analyse univariate data pooled for all species using S-Plus 6 Professional (2001).

Results

Endozoochorous dispersal by hares and geese

Hares deposited a significantly higher number of droppings per unit area than geese (Fig. 3.1A) (generalized linear model, $F_1 = 67.4$, $p < 0.01$). More droppings were found in high marshes than in low marshes per unit area (generalized linear model, $F_1 = 6.1$, $p = 0.02$).

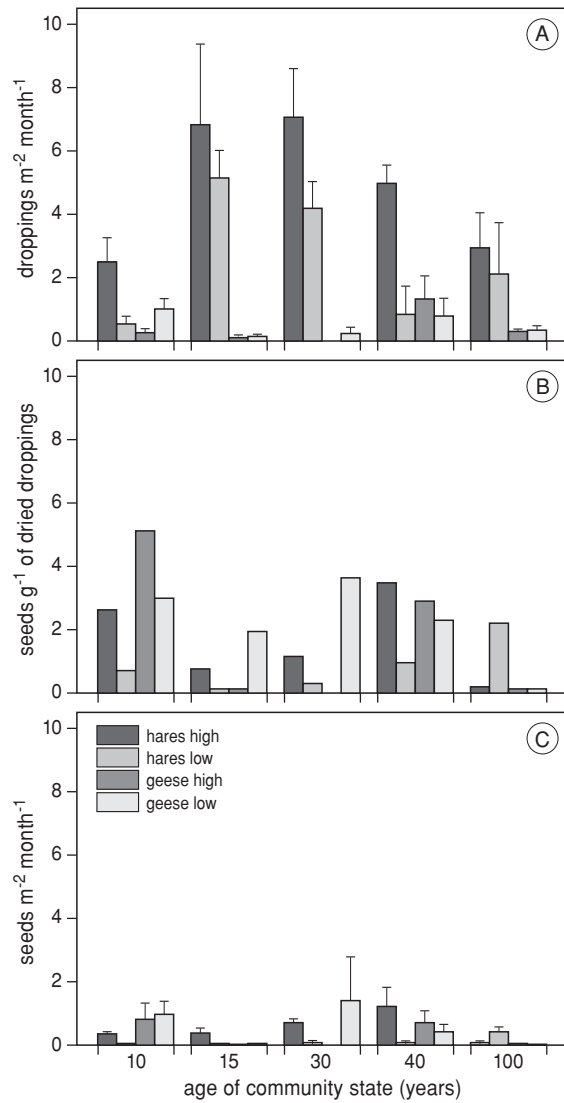


Figure 3.1 Distribution of hare and goose droppings, and seeds found in these droppings along a chronosequence of plant communities at high and low elevations; error bars represent standard errors: A) mean number of droppings per square metre deposited in a month (28 days); animal type and the elevation were significant factors, B) mean number of seeds (all species pooled) found per gram of dried hare and goose droppings; no factors were found to be significant, and C) mean number of seeds (all species pooled) found per square metre in a month; only the interaction factor between animal type and elevation was significant.

When the data for all plant species were pooled, no significant trends were seen in the number of seeds found per gram of dried hare and goose droppings (Fig. 3.1B). However, when multivariate data were considered, there was a highly significant difference between the composition of germinable seeds found per gram of dried hare and goose droppings ($SS = 0.15$, $F_{1,46} = 10.28$, $p < 0.01$), a highly significant effect of where the seeds occurred along the community state sequence ($SS = 0.15$, $F_{4,49} = 2.46$, $p < 0.01$) and also a significant interaction effect between community state and animal type ($SS = 0.10$, $F_{4,44} = 1.70$, $p = 0.04$). Except for the 10 year-old community state, the most abundant species found in hare droppings was *Seriphidium maritimum* (Table 3.1). Seeds found in goose droppings were dominated by annuals such as *Salicornia europaea* and *Suaeda maritima* except for samples taken from the oldest community state.

When data were pooled for all species, the average number of seeds found per square metre showed only a significant interaction effect between animal type and elevation (generalized linear model, $F_1 = 4.68$, $p = 0.04$) (Fig. 3.1C). Hares deposited more seeds in high marshes than in low marshes, in contrast to geese which deposited more seeds in low marshes. When multivariate data were considered, there was a highly significant difference in species composition between seeds deposited by hares and by geese ($SS = 0.12$, $F_{1,54} = 8.59$, $p < 0.01$). Hares deposited more seeds of mid-successional, perennial, dicotyledonous species such as *Seriphidium maritimum* and *Plantago maritima*. In contrast, geese dispersed more seeds of early-successional, annual, dicotyledonous species such as *Salicornia europaea* and *Suaeda maritima* (Table 3.1) (Fig. 3.2B). There was also a highly significant effect of community state on the species composition of the deposited seeds ($SS = 0.13$, $F_{4,57} = 2.28$, $p < 0.01$). The first RDA axis (Eigen-value = 0.171), which is much stronger than the second axis (Eigenvalue = 0.046), separated the samples found in the youngest community state from the other community states (Fig. 3.2B). Droppings deposited on the youngest community state were mostly composed of the early-successional, annual species listed above. All older community states (age 15 to 100) could not be readily distinguished from each other based upon seeds dispersed by hares and geese.

Feeding experiments using captive animals

Relative germination percentage (absolute mean germination percentage / mean germination percentage of control seeds) was used to compare the feeding trial data collected from hares and geese because different control samples were used in the two experiments. A significantly greater percentage of seeds survived passage through the digestive system of European brown hares compared with that of barnacle geese (Fig. 3.3) (ANOVA, $F_{4,33} = 35.98$, $p < 0.01$). There were no significant differences in survival between seeds of the five species.

Table 3.1 Density of germinable seeds found in brent goose and European brown hare droppings (seeds m⁻² month⁻¹ ± standard error) in five stages of community development. Both high-elevation and low-elevation marshes were sampled at each of the five stages. *n* = 3

Species	10 year-old community				15 year-old community				30 year-old community			
	Hares		Geese		Hares		Geese		Hares		Geese	
	High	Low	High	Low	High	Low	High	Low	High	Low	High	Low
<i>Agrostis stolonifera</i>	0	0	0.13 ±0.013	0	0	0	0	0	0.17 ±0.12	0	0	0
<i>Aster tripolium</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Atriplex prostrata</i>	0.033 ±0.033	0	0	0	0	0	0	0	0.12 ±0.093	0	0	0
<i>Elytrigia atherica</i>	0	0	0.0043 ±0.0043	0	0	0	0	0	0	0	0	0
<i>Festuca rubra</i>	0	0	0	0	0	0	0	0	0.017 ±0.017	0	0	0
<i>Glaux maritima</i>	0.15 ±0.10	0	0.017 ±0.017	0	0.033 ±0.017	0	0.0051 ±0.0051	0	0	0	0	0
<i>Juncus gerardii</i>	0	0	0	0	0	0	0	0	0	0	0.0043 ±0.0043	0.013 ±0.0075
<i>Limonium vulgare</i>	0	0	0	0.0097 ±0.0048	0	0.017 ±0.017	0	0	0	0	0	0
<i>Plantago maritima</i>	0	0	0.017 ±0.011	0	0.083 ±0.017	0	0	0	0.12 ±0.093	0.017 ±0.017	0	0
<i>Salicornia europaea</i>	0.05 ±0	0.03 ±0.03	0.16 ±0.090	0.87 ±0.37	0	0	0	0.027 ±0.027	0.017 ±0.017	0	1.0 ±1.0	0.10 ±0.10
<i>Seriphidium maritimum</i>	0.13 ±0.13	0	0	0	0.23 ±0.18	0.017 ±0.017	0	0	0.22 ±0.060	0.05 ±0.029	0	0
<i>Spergularia media</i>	0.017 ±0.017	0	0.43 ±0.34	0.073 ±0.073	0.017 ±0.017	0	0	0	0	0	0	0
<i>Suaeda maritima</i>	0	0	0.18 ±0.13	0.0097 ±0.0097	0	0	0	0	0.033 ±0.033	0	0	0.25 ±0.25

Table 3.1 Continued

Species	40 year-old community				100 year-old community			
	Hares		Geese		Hares		Geese	
	High	Low	High	Low	High	Low	High	Low
<i>Agrostis stolonifera</i>	0	0	0	0	0.017 ±0.017	0	0	0
<i>Aster tripolium</i>	0	0	0	0	0	0	0	0.010 ±0.010
<i>Atriplex prostrata</i>	0.017 ±0.017	0	0.012 ±0.0070	0.0043 ±0.0043	0.017 ±0.017	0	0	0
<i>Elytrigia atherica</i>	0	0	0	0	0	0	0	0
<i>Festuca rubra</i>	0	0	0	0	0	0	0	0
<i>Glaux maritima</i>	0	0	0	0	0	0.017 ±0.017	0	0
<i>Juncus gerardii</i>	0.017 ±0.017	0	0.10 ±0.098	0.035 ±0.019	0	0	0	0
<i>Limonium vulgare</i>	0	0	0.0084 ±0.0084	0.013 ±0.0075	0	0.017 ±0.017	0	0
<i>Plantago maritima</i>	0	0	0	0	0	0	0	0
<i>Salicornia europaea</i>	0	0	0.48 ±0.26	0.31 ±0.23	0	0	0	0.01 ±0.01
<i>Seriphidium maritimum</i>	1.1 ±0.65	0.067 ±0.017	0.059 ±0.041	0	0.017 ±0.017	0.30 ±0.18	0	0
<i>Spergularia media</i>	0.033 ±0.033	0	0	0	0	0.017 ±0.017	0	0
<i>Suaeda maritima</i>	0.017 ±0.017	0	0.067 ±0.034	0.022 ±0.022	0	0.05 ±0.05	0	0.021 ±0.021

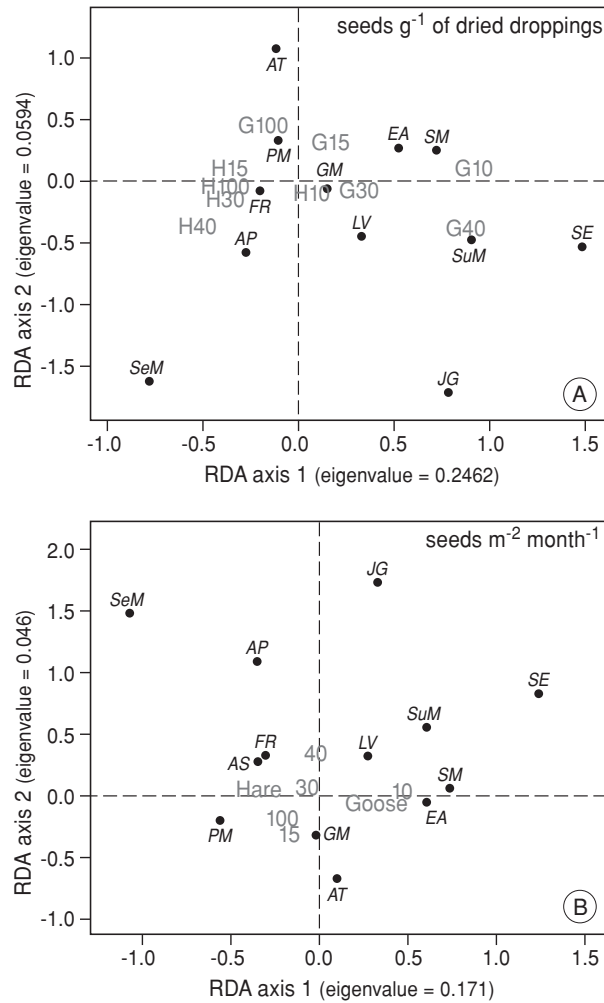


Figure 3.2 Biplots of species and environmental centroids illustrating significant factors in two multi-species analyses of variance (ANOVA). Partial redundancy analysis (RDA) was used based upon seed data constrained by the design (3-way ANOVA). The parsimonious models are shown. Seed data were transformed using $y = \sqrt{x}$. Species abbreviations are: AS = *Agrostis stolonifera*, AP = *Atriplex prostrata*, AT = *Aster tripolium*, EA = *Elytrigia atherica*, FR = *Festuca rubra*, GM = *Glaux maritima*, JG = *Juncus gerardii*, LM = *Limonium vulgare*, PM = *Plantago maritima*, SE = *Salicornia europaea*, SeM = *Seriphidium maritimum*, SM = *Spergularia media*, SuM = *Suaeda maritima*. A) Ordination diagram of mean number of seeds found per gram of dried droppings. Animal type, community state and their interactions were found to be significant. Only the interaction factors are shown: H = hare, G = goose; numbers refer to age of community. B) Ordination diagram of mean number of seeds found per square metre. Only the main effects of animal type and community state were found to be significant. Numbers refer to the age of the community.

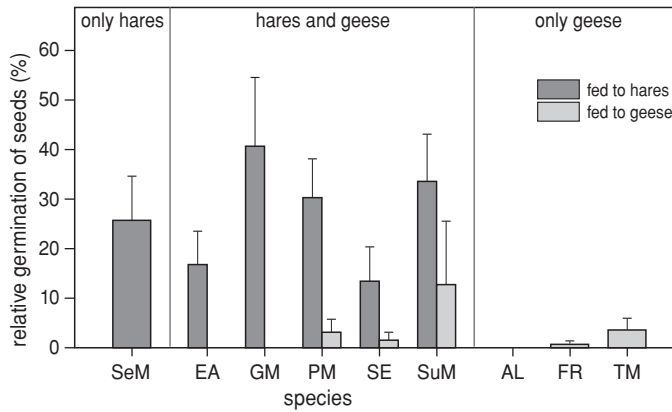


Figure 3.3 The germination of seeds after passage through the digestive systems of captive European brown hares and barnacle geese. Seeds of some species were fed only to hares, others to the geese and five species were fed to both. The mean germination percentages were corrected by dividing by the percentage of uningested seeds germinating for each species. Error bars represent standard errors. In addition to the species abbreviations used in Figure 3.2: AL = *Atriplex littoralis*, TM = *Triglochin maritima*.

Table 3.2 Density of seeds dispersed by tidal water (seeds $\text{m}^{-2} \text{month}^{-1} \pm$ standard error) in four stages of community development. Only low-elevation marshes were sampled. $n = 10$

Species	10 year-old community	15 year-old community	30 year-old community	100 year-old community
<i>Aster tripolium</i>	0.55±0.37	6.9±4.5	1.1±0.84	0
<i>Glaux maritima</i>	0.28±0.28	0.28±0.28	0.28±0.28	
<i>Juncus gerardii</i>	0	0.28±0.28	0	0.28±0.28
<i>Limonium vulgare</i>	74±19	28±15	6.9±6.0	24±17
<i>Plantago maritima</i>	0.28±0.28	1.4±1.4	0	0.28±0.28
<i>Salicornia europaea</i>	310±99	3.3±1.5	14±13	10±9.9
<i>Seriphidium maritimum</i>	0	280±150	590±100	130±85
<i>Spergularia media</i>	14±5.5	0.55±0.37	0	0.55±0.55
<i>Suaeda maritima</i>	130±71	2.2±1.2	65±38	8.0±6.4

Comparison of seeds dispersed by endozoochory and tidal water

The type of dispersal vector had a highly significant effect upon numbers and composition of dispersed seeds ($SS = 0.24$, $F_2 = 14.03$, $p < 0.01$). Many more seeds were dispersed by hydrochory than were dispersed by endozoochory (Tables 3.1 & 3.2). The community state where seeds were dispersed also had a significant effect, both when considering pooled data for all species (generalized linear

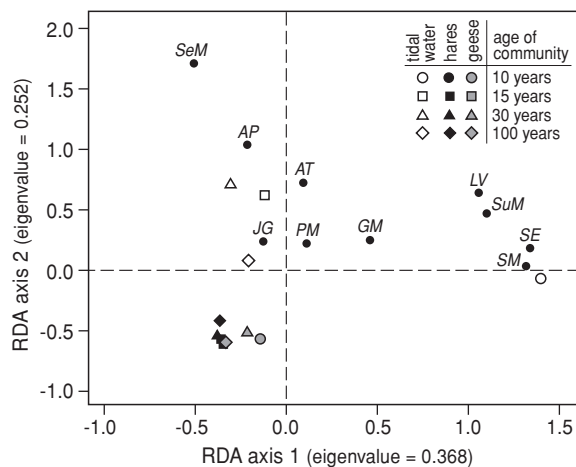


Figure 3.4 Biplot of species and environmental centroids illustrating significant factors in a multi-species analysis of variance (ANOVA) comparing seed dispersal by hydrochory and those dispersed internally by hares and by geese. Partial redundancy analysis (RDA) was used based upon seed data constrained by the design (2-way ANOVA). The parsimonious model is shown. Seed data were transformed using $y = \log_{10}(x + 0.01)$. Species abbreviations are the same as in Figure 3.2. The vector type, the community state where the seeds were found and their interactions were found to be significant. Only the interaction factors are shown. See inset key for explanation of symbols.

model, $F_2 = 5.04$, $p = 0.03$) and when considering the multivariate data ($SS = 0.261$, $F_3 = 10.12$, $p < 0.01$). When using multivariate data for all species, there was also a highly significant interaction effect between vector type and community state ($SS = 0.14$, $F_6 = 3.32$, $p < 0.01$); *i.e.* there was a significant effect of community state for hydrochorous samples but not for endozoochorous samples. The first RDA axis separated samples dispersed by tidal water at the 10 year-old community state from the rest of the samples (Fig. 3.4). These samples contain many seeds of annual species such as *Salicornia europaea*, *Spergularia media* and *Suaeda maritima*. The second RDA axis distinguished three groups: samples dispersed by hydrochory at intermediate community states (15 and 30 year-old) containing many seeds of *Seriphidium maritimum*, samples dispersed by hydrochory at the youngest and oldest community states (10 and 100 year-old) and samples dispersed by endozoochory. For the samples dispersed by hydrochory, the community state has an important effect upon both seed number and species composition unlike samples dispersed by endozoochory. Note that all species in the biplot are associated with centroids of hydrochorous sample groups rather than with endozoochorous sample groups, signifying that small amounts of seeds of all species are dispersed by endozoochory in comparison with hydrochory.

Discussion

Differences in effectiveness of seed dispersal by hares and geese

When considering all the salt-marsh communities together, hares and geese dispersed similar quantities of seeds. However, they dispersed seeds of different species and to different types of habitats. The most common species found in hare droppings was *Seriphidium maritimum*, a mid-successional, perennial species. In contrast, goose droppings contained mostly early-successional, annual species such as *Salicornia europaea* and *Suaeda maritima*. Hares deposited seeds more often in high marshes, whereas geese deposited seeds more often in low marshes reflecting their grazing preferences. For example, brent geese feed on *Salicornia europaea* in autumn (Summers *et al.* 1993; Bruinzeel *et al.* 1997). In studies conducted at Schiermonnikoog, brent geese graze preferentially in low-elevation *Puccinellia maritima* marshes (van der Wal *et al.* 1998) of intermediate age (Olf *et al.* 1997) whereas hares graze more often on higher *Festuca rubra* marshes (van der Wal *et al.* 1998). Whereas patterns in endozoochory reflected the grazing preferences of the animals, they did not directly correspond to the plant distribution along the community state sequence suggesting that these small herbivores are selective grazers. Regressions between seed density of droppings and both frequency in the vegetation and seed production yielded non-significant results.

An important component used to determine the quality of seed dispersal by animals is the treatment of seeds in the mouth and gut. The experimental feeding trials indicate that seeds suffer from less damage in the digestive system of European brown hares than that of barnacle geese. The relative percentage of seeds that germinated after passage through hares ranged from 13.6 % to 42.3 %. When compared to studies using rabbits, these numbers are much higher than the percentages reported for species found in North American sagebrush-grasslands and salt-deserts (0 - 5.2 %) (Lehrer & Tisdale 1956) but comparable to species found in temperate West European grasslands (1.2 - 30.5 %) (Cosyns *et al.* 2005). In comparison with hares, a lower percentage of seeds germinated after ingestion by geese (0% to 12.8%). In a recent review on feeding trials of waterbirds, the effects of digestion on the seeds of aquatic and wetland species were found to be highly variable (Charalambidou & Santamaria 2002). Although hares physically damage their food by chewing and reingesting their faeces for a second time (Hirakawa 2001), seeds passing through the digestive systems of geese receive the most physical damage in the gizzard (Charalambidou & Santamaria 2002). Apparently, seeds are more damaged passing once through the gizzards of geese than being chewed and digested multiple times by hares. This is a surprising result as geese show less efficient digestion of food (10 to 40 % for cellulose, 25 to 40 % for protein) (Bruinzeel *et al.* 1997) than hares (40% and 60% respectively for dry matter and nitrogen) (Kuijper *et al.* 2004).

Changes in effectiveness of seed dispersal as communities develop

At early stages of community development, geese were more effective as dispersal vectors relative to hares. The composition of seeds found in the droppings of geese dominated the droppings found at the 10 year-old community state as hare droppings were uncommon (Fig. 3.2B). The predominantly annual species dispersed by geese are obliged to recruit from seeds in order to persist in these community states. Seeds of perennial species associated with goose droppings, such as *Limonium vulgare* and *Elytrigia atherica*, were present in very low numbers. Hares were relatively more important than geese in intermediate and older community states as dispersal agents. The predominantly perennial species dispersed by hares, however, are less dependent on seed input for persistence in these communities because of clonal growth. The only exception was *Atriplex prostrata*, an annual species found in older, more nutrient-rich community states but it occurred in very low numbers in droppings.

Species may be present in the actual or community species pool (Zobel *et al.* 1998) as an adult plant, in a diaspore bank or in the diaspore rain. During the assembly process of young communities, community species pool membership may be more constrained by seed input than in older communities. Thus, geese were judged to be more effective as dispersal vectors than hares.

As young, low communities were more frequently inundated than other communities, it is possible that there was an under-estimation of endozoochory to these sites. Faeces may dissolve or be re-dispersed more quickly than the time between sampling dates (two weeks). In this case, however, the conclusion that geese were more effective dispersal vectors than hares would only be reinforced.

Seed dispersal by small herbivores versus dispersal by tidal water

When considering the quantity of germinable seeds dispersed, small herbivores dispersed fewer seeds than numbers dispersed by tidal water on the low marshes by two orders of magnitude (Tables 3.1 & 3.2). Also, there is no evidence that small herbivores dispersed any species that were not dispersed by tidal water (Tables 3.1 & 3.2) (Fig. 3.4). All the species in the species-environmental centroids biplot are associated with the seed trap sample groups rather than with the endozoochorous sample groups.

Is there any indication that small herbivores provide better quality of seed dispersal with respect to seedling establishment than tidal water? Izhaki & Ne'eman (1997) concluded that the small amount of dry matter in faeces produced by hares in a sandy, coastal plain environment did not provide sufficient nutrients to enhance seedling establishment. No seedlings were observed germinating in intact droppings during the course of this study. However, faeces produced during the wet months of autumn are likely to disintegrate quickly, although the rate has not been studied. Any nutrient pulse is likely to be very transient compared to that

provided by the dung of large herbivores, although seeds dispersed by small herbivores may also escape the negative effects of manure, such as toxicity for seedlings and low affinity for water (Malo & Suárez 1995) and severe seedling competition due to high numbers of seeds being defecated together (Traveset 1998).

Water, especially during storm surges, is not a very selective agent of seed dispersal and results often in deposition of seeds in the driftline along the dunes, that provide poor-quality microsites for salt-marsh species. Many seeds embedded in the droppings of hares and geese will undergo secondary dispersal by water. High numbers of droppings have been observed in driftlines at this site. In summary, it is not likely that small herbivores provide enough higher quality seed dispersal with respect to suitable microsite to make a important impact on seed dynamics in these marshes.

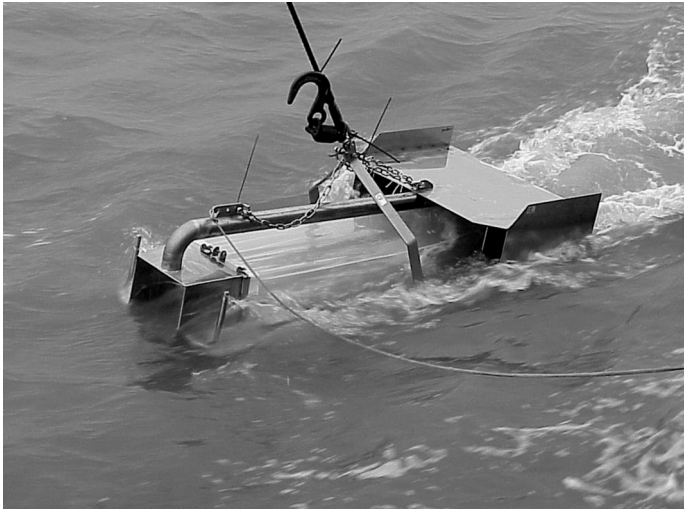
Small herbivores could still be important filters in salt-marsh assemblages if they act as agents of long-distance dispersal; that is distances greater than 100 m (Ozinga *et al.* 2004). These low-probability events have the potential for a high impact on community assembly as in the case of colonization of new habitats. A recent review on the possibilities of long-distance endozoochorous dispersal by migratory waterbirds in northern Europe (Clausen *et al.* 2002) identified some potential hurdles which led the authors to conclude that such events were likely to be rare, whereas two other reviews from the same year (Figuerola & Green 2002; Green *et al.* 2002) were more positive. However, some of hurdles identified in Clausen *et al.* (2002) may not be problematic in our system because: 1) reproductive efforts of salt-marsh plants are well-matched with long-distance movements of brent geese (mid-to-late September); 2) gut contents of birds being discarded within 300 km is well above our defined lower limit for long-distance movement (*i.e.* 100 m); and 3) migrating brent geese move between similar habitats along the Dutch Wadden Sea.

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Chapter 4

Seed dynamics linked to variability in movement of tidal water

E.R. Chang, R.M. Veeneklaas & J.P. Bakker

Summary

Community structure may be influenced by patterns of dispersed seeds (seed rain) because they contribute to the template from which plant communities develop. We explored factors influencing seed rain in a system dominated by tidal water, where direction and magnitude of water flow are difficult to predict, unlike many other hydrochorous systems where water flow is directional. We posed three main questions: 1) are patterns in seed rain linked to effects of hydrodynamic variability; 2) do these patterns in seed rain reflect distribution of seed sources and seed production; and 3) what are the implications for the assembly of tidal communities? Species compositions of vegetation, seed rain, seed production and driftlines along a chronosequence of communities were compared on the Dutch island of Schiermonnikoog. We also studied seed movement by sowing Astroturf® mats with seeds and checking for seeds remaining after a single tidal inundation. Storm surges had a significant effect on seed-rain patterns as the highest density and diversity of captured seeds were found during a stormy period. Seed rain of youngest communities was more influenced by storms than that of older communities. Patterns in seed rain generally followed similar patterns in established-plant distribution and seed production. Results suggested mostly local dispersal of seeds. However, there was some evidence of long-distance dispersal occurring during storm surges in younger communities that are regularly inundated with tidal water. The role of seed retention in constraining community development, rather than dispersal *per se*, is further examined.

Introduction

Patterns of dispersed seeds contribute to the template from which communities develop and, hence, are believed to influence community structure (Levine & Murrell 2003). In systems dominated by hydrochory (seed dispersal by water), studies have linked seed-dispersal patterns to species distribution (Orth *et al.* 1994; Rand 2000; Levine 2001; Honnay *et al.* 2001; Jansson *et al.* 2005). However, most of these studies were conducted in riparian systems where the flow of water is directional and downstream. In tidal-marsh systems, where water flow is determined by complex interactions between topography, tidal stage, wind and wave action (Davidson-Arnott *et al.* 2002), and attenuation by vegetation (Kjerfve *et al.* 1991; Yang 1998; Möller *et al.* 1999; Neumeier & Ciavola 2004), the direction and magnitude of the dispersal vector (water flow) is much more difficult to predict.

The effectiveness of tidal water as a dispersal vector may be strongly influenced by stochastic events. Extreme hydrodynamic events may have disproportionately greater effects than normal tidal regimes on patterns of seed dispersal. Storm surges have been found to have a strong effect on patterns of sedimentation in tidal-marsh habitats (Stevenson *et al.* 1988; Leonard *et al.* 1995; Roman *et al.* 1997; Bartholdy & Aagaard 2001) and sedimentation has been closely linked to seed deposition (Goodson *et al.* 2003). The role of stochastic processes, including dispersal limitation, in shaping communities relative to deterministic, local processes is currently under considerable debate (Hubbell 2001; Cottenie 2005).

In addition to the effects of the dispersal vector, the distribution and density of seed sources (adult plants) and seed production have a role in shaping patterns in seed rain (Levine & Murrell 2003). A review of the seed shadows of species dispersed by wind, ballistics, animals and no apparent mechanism concluded that most seeds seemed to disperse only a short distance from the parent plant (Willson 1993). Studies comparing seed distributions in salt marshes, as determined by seed traps (Rand 2000; Wolters *et al.* 2005) and driftlines (Bakker *et al.* 1985; Wolters & Bakker 2002), also suggested limited movement out of the parental environment. In contrast, two studies that explicitly examined movement of seeds by water action in the same tidal inlet (Koutstaal *et al.* 1987; Huiskes *et al.* 1995) suggested great potential for dispersal.

In this study, we explore the role of local dispersal, long-distance dispersal driven by episodic storm surges and seed production in determining patterns of seed rain in a tidal habitat. Three main questions were posed: 1) are patterns in seed rain linked to hydrodynamic variability; 2) do patterns in seed rain reflect distribution of seed sources and seed production; and 3) what are the implications for assembly of tidal plant communities? Hydrodynamic variability includes a comparison of the effects of storm surges versus normal tidal regime on seed dispersal,

differential exposure of communities to tidal action, movement across the elevation gradient and movement related to tidal inundation from the sea coast and creeks.

Materials and Methods

Site description

The studies were conducted on the coastal-barrier island of Schiermonnikoog, the Netherlands ($53^{\circ} 30' \text{ N}$, $6^{\circ} 10' \text{ E}$), which is extending eastward due to changing sea currents and sediment accretion (Olff *et al.* 1997). Consequently, salt marshes on the southern shore of the island form a gradient in age, resulting in a well-developed chronosequence (de Leeuw *et al.* 1993; Olff *et al.* 1997). Soils consist of a basal sandy layer and an upper layer of silty sediments (2 to 16 cm). Four plant communities in total were studied in detail along the chronosequence, each of which were characteristic of 10-, 15-, 30- and 100 year-old, low-elevation marshes. The tidal divide (ridge of high land separating opposing tidal basins) is located between the 30- and 100-year-old communities (Fig. 4.1). Because the tidal divide is the average line of zero flow velocity, it is not expected that much water would flow across it under normal circumstances.

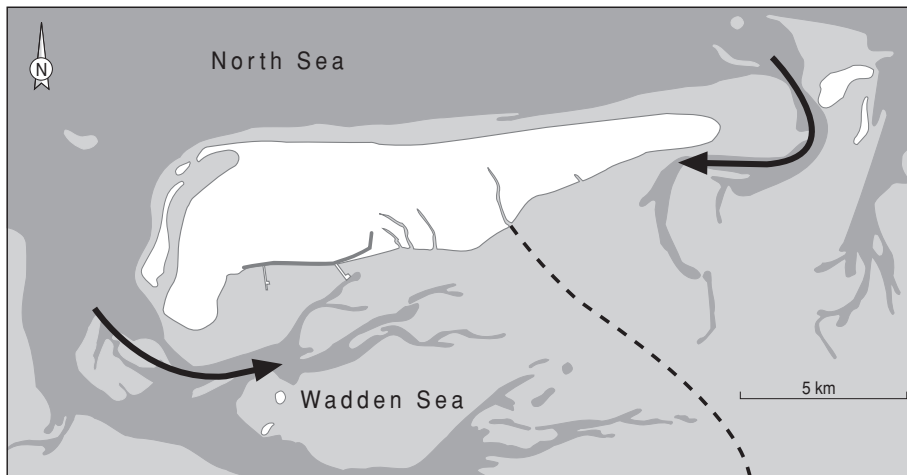


Figure 4.1 Map of Schiermonnikoog with arrows representing direction of tidal current from North Sea into the Wadden Sea. Numbers represent the age and location of communities where permanent grids were located. The dotted line represents the average tidal divide where the opposing tidal basins (entering the Wadden Sea from the west and east) meet. The tidal divide is also the line of zero current flow so that transport of water across this line is not expected under normal conditions.

Collection of vegetation, seed rain, seed production and driftline data

Vegetation data were collected from two elevational ranges in permanent grids in June 2001. The low- and high-elevational areas were situated respectively at base elevations (sandy layer) of 20 to 40 cm above MHT and 60 to 80 cm above MHT. Each low- and high-elevation area in the grid consisted of 10 columns, oriented parallel to the elevation gradient, and five rows of 1 m² sub-plots (*i.e.* 50 sub-plots in total). For each sub-plot, four species with the highest percentage cover (determined subjectively) were given dominance scores: the most dominant species received a score of 4, the next received a score of 3 and so on (modified from Tansley 1939). The dominance scores were pooled for each column, resulting in scores for 10 plots of 5 m by 1 m for each community at each of two base elevations ($n = 10$). The vegetation data from low-elevation marshes were used to characterise the communities for which seed dynamics were studied in detail, whereas the high-elevation data were used only to study seed movement across the elevational gradient.

Seed rain was estimated using seed traps made of squares of polyethylene Astroturf® (45 cm x 45 cm) (*c.f.* Wolters *et al.* 2004). The traps were fastened to the ground with pegs and a plastic bag was placed underneath each trap to keep seeds on the soil surface from adhering to the bottom of the traps. Ten seed traps were placed at least 10 m apart at each of the four communities in the close vicinity of the permanent grids at base elevations 20 to 40 cm above MHT ($n = 10$) (*i.e.* the lower sites in each marsh). They were placed in a row parallel to the coastline. The traps were set out from October to May during 2001/2002 (21 October to 7 December, 8 December to 24 January, 25 January to March 11, 12 March to 8 May) and at different locations in 2002/2003 (1 November to 19 December, 20 December to 14 February, 15 February to 31 March, 1 April to 11 May). The 2001/2002 and 2002/2003 sampling years will henceforth be referred to as 'year one' and 'year two' respectively.

After collection, the seed traps were rinsed with water over a 0.212 mm mesh sieve. The resulting sediment and seed mixtures were assessed for seed content using a modified seedling emergence technique (ter Heerdt *et al.* 1996). After exposure to a minimum of five weeks of cold stratification (6°C) in order to simulate winter conditions, the samples were transferred to a glasshouse and removed upon identification. Germination usually ceased after six weeks and samples were then left to dry for a week. The samples were then crumbled, watered and monitored for an additional two weeks for further seedling emergence.

Six randomly selected plots of 1 m² were used to measure seed production within each community. These plots also were located close to the permanent grids at low elevations. Flowering and fruiting inflorescences were counted for all species present in each plot between mid-to-late October, 2002. The average number of seeds per inflorescence was estimated by haphazardly collecting 50 fruiting

inflorescences per species at each community and counting seeds of each sample. Seed production was estimated only once because seeds of most species ripen in late September/early October and most are retained until the marshes are flooded by autumnal tides. However, a few species ripen and disperse earlier in the summer (e.g. *Armeria maritima*, *Festuca rubra*) and seed production by these species was not estimated.

Within a day after a spring tide on 13 November, 2001, ten samples of 20 cm by 20 cm were collected from the nearest driftlines (usually 60 to 100 cm above MHT) formed by each of the 15- and 100-year-old communities so that seed movement across the elevation gradient could be compared between a young and an old community. Samples were stored for three months at 6°C, air-dried for a week, broken into smaller pieces and large pieces of woody material were removed. They were then transferred to a glasshouse and processed similarly to the seed rain samples. It took almost a year for germination to cease.

Seed movement experiment

A grid of 25 Astroturf® mats (30 cm by 30 cm) were set out in five rows and columns on the low marsh (-10.9 to 16.7 cm above MHT) close to the 30-year-old community in order to compare the effects of inundation from the sea coast to inundation from overflow of creek banks on seed movement. Mats were spaced 20 m apart with one axis parallel to the Wadden Sea coast and a second axis parallel to the banks of a creek for a total of 25 mats. Therefore, mat placements ranged between 20 to 100 m from the coast of the sea or bank of the creek. Mats were fastened to the ground using stainless steel pegs and 50 marked seeds each of *Plantago maritima* and *Elytrigia atherica* were added to each mat. Textile dye was used to mark the seeds. Seeds of *E. atherica* have a higher floating capacity than those of *P. maritima* (Koutstaal *et al.* 1987). *E. atherica* possesses relatively large seeds which remain attached to bracts, whereas seeds of *P. maritima* produce a mucilaginous gel when wet. After one tidal inundation, all mats were collected, rinsed through a 0.212 mm sieve and gathered material was checked for seeds. The experiment was replicated four times in total during March, 2003. The highest level of water recorded for the first to fourth tide respectively was 4 cm, 29 cm, 21 cm and 12 cm above MHT, which indicates that most mats were fully inundated with tidal water during the last three tides.

Data analyses

Seed rain and vegetation data were analysed using multivariate methods and Monte Carlo permutation tests using the software program, CANOCO for Windows 4.52 (ter Braak & Šmilauer 1998). Data from all 29 species found in the seed rain were used simultaneously to construct an ANOVA table, partitioning all the variance explained by different sources in the model. Partial RDA was used

instead of partial CCA because we were interested in measures of absolute rather than relative abundance of species in the seed rain. The sampling design was encoded using dummy variables of 0 and 1. Seed rain data were first log10-transformed in order to improve homogeneity of variance in multivariate space. Permutation tests were conducted under the split-plot framework in CANOCO (Lepš & Šmilauer 2003). Due to an unbalanced design caused by dislodged traps, a random subset of the data was used to analyse both seasonal and successional trends in the seed rain. Five replicates and three sampling dates were used for year one. The last sampling date was not used due to paucity of captured seeds. Nine replicates and four sampling dates were used for year two. For Figures illustrating significant factors, ordinations produced by parsimonious models are shown. Similarly, analysis of inertia tables were constructed to illustrate significant factors in the vegetation. Vegetation data were not transformed and partial CCA was used because dominance is a relative measure.

Repeated-measures ANOVA was used to analyse the pooled seed-rain data and the seed movement experiment using the software program, SPSS (2003). When the assumption of sphericity was violated, we used the Greenhouse-Geisser correction for degrees of freedom and Bonferroni's procedure for multiple comparisons (Field 2000). For the seed-movement experiment, data for both species were analysed separately with two between-subjects factors (distance from sea and creek) and one within-subjects factor (tide). The interaction factor between distance from sea and distance from creek was not included in the model because of insufficient replication. However, examination of the data did not suggest a likely significant interaction between these two factors. Data for *E. atherica* were arcsine-transformed in order to meet assumptions of the ANOVA model.

Response curves of seed density (seed production and seed rain) to community age were produced for six representative species using data from both sampling years. Curves were fitted using the regression function of the software program, Sigmaplot 8.0 (Sigmaplot 2002). The simplest model (lowest number of parameters) yielding the highest model fit (coefficient of determination or R^2) was selected in order to calculate each curve.

Results

Seasonal patterns in seed rain

Twenty-nine species were recorded in the seed rain. When data for all species are pooled, all within- and between-subjects factors in a repeated-measures ANOVA model significantly influenced variance in the density of seed rain. In both years, density of captured seeds differed significantly between the sampling periods (year one: $F_{2,32} = 16.09$, $p < 0.01$; year two: $F_{1.99, 63.67} = 130.42$, $p < 0.01$). The highest

seed density was found during the third sampling period in year one (Fig. 4.2A; Tukey's multiple comparisons). A major storm occurred during this period on 26 February, 2002. In year two, there was a steady decrease in the density of captured seeds from November to May (Fig. 4.2B; Bonferroni's multiple comparisons). A major storm took place on 27 October, 2002, just before seed-rain sampling commenced for year two.

In both years, the density of captured seeds also differed significantly between communities of different ages (year one: $F_{1,16} = 242.81$, $p < 0.01$; year two: $F_{1,32} = 816.84$, $p < 0.01$). For year one, densities of seeds generally decreased with age (Fig. 4.2C; Tukey's multiple comparisons), whereas there were slightly higher seed densities in the 10- and 30-year-old communities in year two (Fig. 4.2D; Bonferroni's multiple comparisons). There was also a significant interaction factor between sampling period and community age although this effect was more significant for year one ($F_{6,32} = 12.64$, $p < 0.01$, mean square = 42 %) than year two ($F_{5.97,63.67} = 2.60$, $p = 0.03$, mean square = 1.9 %). In year one, the sharp increase in seeds captured during period three was largely due to big increases in seeds captured in the two younger communities.

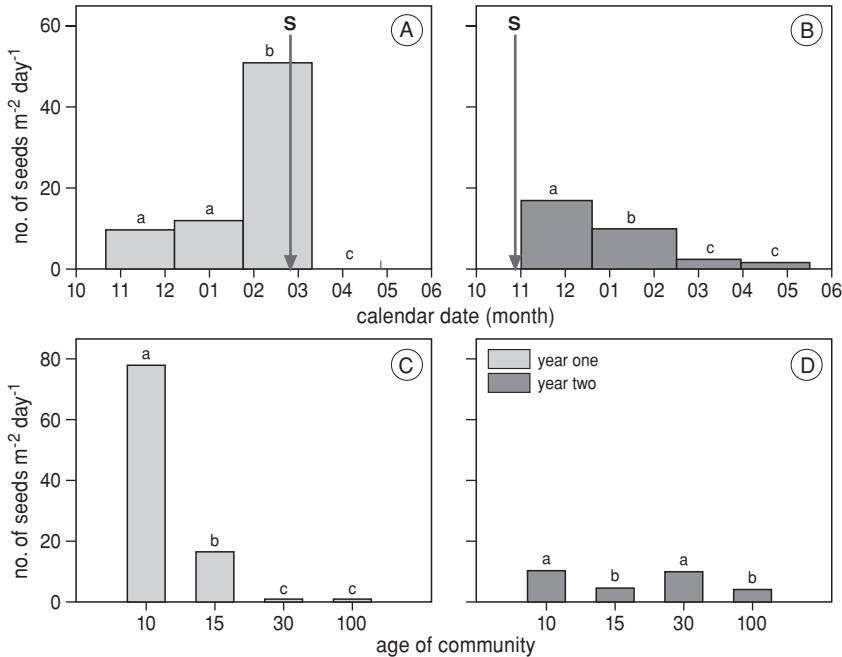


Figure 4.2 Temporal and spatial patterns in seed density captured on seed traps over two trapping seasons. Letters represent statistically different group means within each graph. The “S” represents the occurrence of major storms.

Successional patterns in seed rain

When considering multivariate data, age of the community was a highly significant factor (between-subjects) explaining 49.0 % of the variation in the seed density of different species in year one ($F = 14.88$, $p < 0.01$) and 33.8 % in year two ($F = 23.87$, $p < 0.01$). In the ordination for year one, the first RDA axis clearly separated communities based upon age, except for the two oldest communities which formed one group (Fig. 4.3A). Four groups were distinguished in the ordination for year two but the youngest community remained the most distinct, separated from the other communities along the first RDA axis (Fig. 4.3B). Salt-marsh species in the seed rain were generally associated with similar communities as in the vegetation, although these associations were stronger in year one than year two (Fig. 4.3C). For example, pioneer species such as *Salicornia europaea*, *Spergularia media* and *Suaeda maritima* were strongly associated with the youngest community (relative abundance ranges from 86 % to 98 % in year one, 76 % to 94 % of relative abundance in year two). Early- to mid-successional species such as *Aster tripolium* and *Plantago maritima* were associated with the 15-year-old community. Late-successional species such as *Festuca rubra*, *Elytrigia atherica* and *Juncus gerardi* were associated with the two oldest communities. In year two, the second, much weaker, RDA axis teased apart the three older communities and was influenced by distributions of *Atriplex prostrata* (characterised the 100-year-old community), *F. rubra* and *Seriphidium maritimum* (both characterised the 30-year-old community). The distribution of adult plants and captured seeds differed, however, for some species along the community sequence. *Glaux maritima*, for example, was most abundant as an adult plant in the 100-year-old community but was captured more often by seed traps in the 10- and 15-year-old communities.

Relationship between the vegetation, seed rain, seed production and driftline material

Of the 18 species recorded in the vegetation, only two species were not found in the seed rain (*Spergularia marina*, *Triglochin maritima*). For the seed rain, 13 out of 29 recorded species were not found in the vegetation (*Agrostis capillaris*, *Agrostis stolonifera*, *Atriplex littoralis*, *Centaureum pulchellum*, *Cerastium fontanum*, *Juncus maritimus*, *Lolium perenne*, *Odontites vernus*, *Plantago coronopus*, *Plantago lanceolata*, *Plantago major*, *Poa annua*, *Trifolium repens*). The similarity in species membership between the vegetation and seed rain ranged from intermediate to high (Sørensen similarity index: 0.54 to 0.81; Table 4.1), with the exception of the fourth sampling period when very few seeds were captured. The similarity remained generally consistent across the community sequence. Due to the different scales and sampling techniques used to measure vegetation composition and seed density in the seed rain, only qualitative comparisons could be made between the vegetation and seed rain.

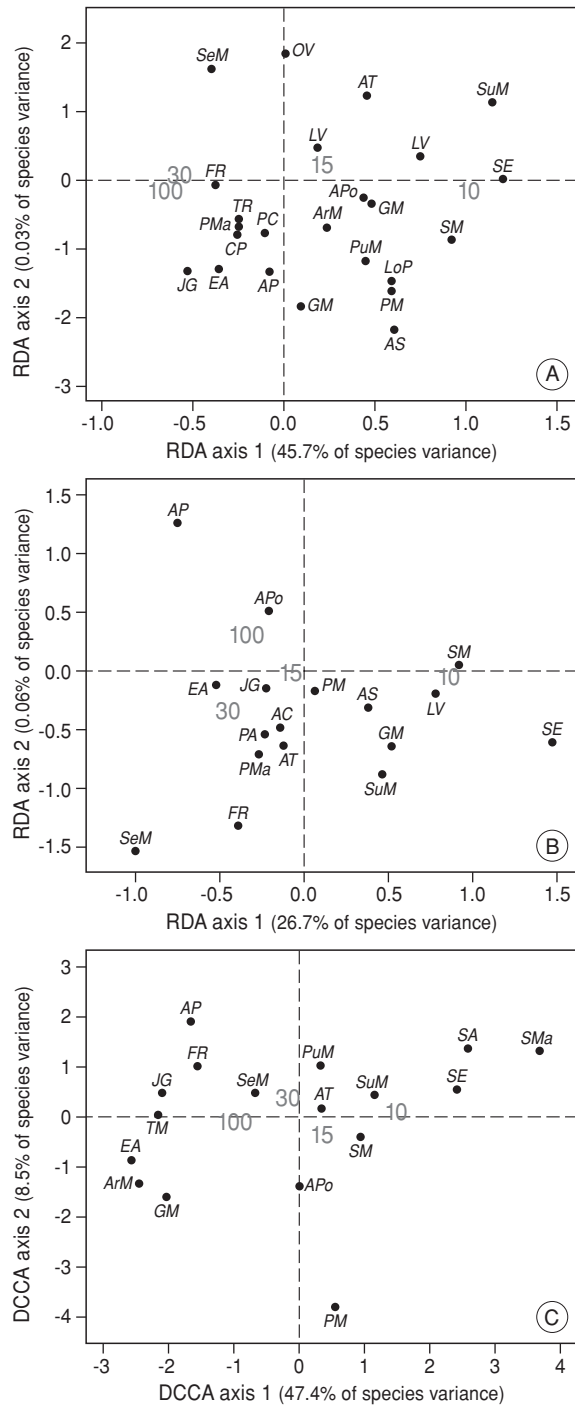


Table 4.1 Values of the Sørensen similarity index between the vegetation and seed rain collected along a community sequence.

Period	Age of community (years)			
	10	15	30	100
1. Oct. 21 to Dec. 7, 2001	0.70	0.72	0.67	0.76
2. Dec. 8, 2001 to Jan. 24, 2002	0.73	0.60	0.67	0.69
3. Jan. 25 to March 11, 2002	0.71	0.69	0.61	0.56
4. March 12 to May 8, 2002	0.25	0.13	0.13	0.38
5. Nov. 1 to Dec. 19, 2002	0.70	0.75	0.78	0.81
6. Dec. 20, 2002 to Feb. 14, 2003	0.75	0.72	0.78	0.81
7. Feb. 15 to March 31, 2003	0.70	0.61	0.78	0.69
8. April 1 to May 11, 2003	0.57	0.64	0.80	0.54

The relatively high degree of coupling between the seed rain and vegetation was supported by response curves of seed rain to seed production. Density in seeds captured along the community sequence for six representative species generally tracked changes in seeds produced (Fig. 4.4; response curves for *S. media* and *S. maritima* not shown, but were very similar to that for *S. europaea*).

When making comparisons between species distribution in the vegetation and in surface-lying seeds across the elevation gradient, there were strong differences in the 15-year-old community but not in the 100-year-old community. For the young community, the relative abundance of species typical of elevation zones (*i.e.* low marsh, mid marsh, high marsh, dune) was similar for the vegetation and seeds captured from traps on the low marsh but dissimilar for vegetation and seeds found in driftline on the high marsh (Fig. 4.5). Species typical of low marshes

Figure 4.3 (left) Plots of species and sample groups centroids illustrating main effects of year of community in multivariate (A) ANOVA of seed trap data during year one and (B) year two, and (C) analysis of inertia of vegetation data. Parsimonious models were used to produce Figures. Species abbreviations are: ArM = *Armeria maritima*, AC = *Agrostis capillaris*, AS = *Agrostis stolonifera*, AT = *Aster tripolium*, APo = *Atriplex portulacoides*, AP = *Atriplex prostrata*, CF = *Cerastium fontanum*, CP = *Centaureum pulchellum*, EA = *Elytrigia atherica*, FR = *Festuca rubra*, GM = *Glaux maritima*, JG = *Juncus gerardi*, LV = *Limonium vulgare*, LoP = *Lolium perenne*, OV = *Odontites vernus*, PO = *Poa annua*, PC = *Plantago coronopus*, PMa = *Plantago major*, PM = *Plantago maritima*, PuM = *Puccinellia maritima*, SE = *Salicornia europaea*, SeM = *Seriphidium maritimum*, SA = *Spartina anglica*, SM = *Spergularia media*, SMA = *Spergularia marina*, SuM = *Suaeda maritima*, TM = *Triglochin maritima*, TR = *Trifolium repens*. Numbers represent centroids of samples from different communities. 13 = community established in 1913, 74 = 1974, 86 = 1986, 93 = 1993.

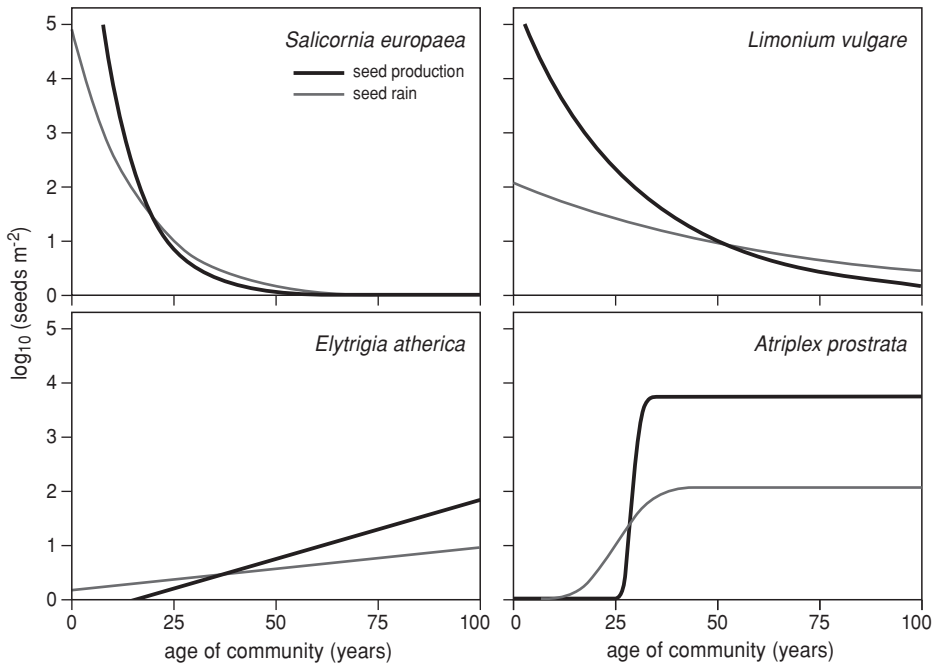


Figure 4.4 Graphs illustrating regressions between seed production, seed rain and age of community. Four representative salt-marsh species are shown. Explanation of the different curves are given in the inset key.

formed 0.4 % of the vegetation but made up 12.6 % of the driftline composition. Dune species accounted for 42.1 % of the species found in the vegetation but only 1.3 % of those found in the driftline. For the old community, there were differences in relative abundance of species groups but the shifts were much less dramatic.

Effect of tidal action by sea and creek on seed movement

Significantly more seeds of *Elytrigia atherica* ($0.75 \% \pm 0.16 \%$) were transported than of *Plantago maritima* ($0.39 \% \pm 0.14 \%$) (t-test: $t_{48} = 8.402$, $p < 0.01$). For both *P. maritima* and *E. atherica*, the distance from the sea had a significant effect on whether seeds were dispersed, whereas distance from the creek did not (Tables 4.2 & 4.3). The threshold distance for *P. maritima* was 20 m from the sea. Similar numbers of seeds sown at longer distances (40 to 100 m) were transported by tides, whereas higher numbers of seeds were transported at 20 m (Tukey's multiple comparisons). For *E. atherica*, the threshold distance was 60 m from the sea (Tukey's multiple comparisons).

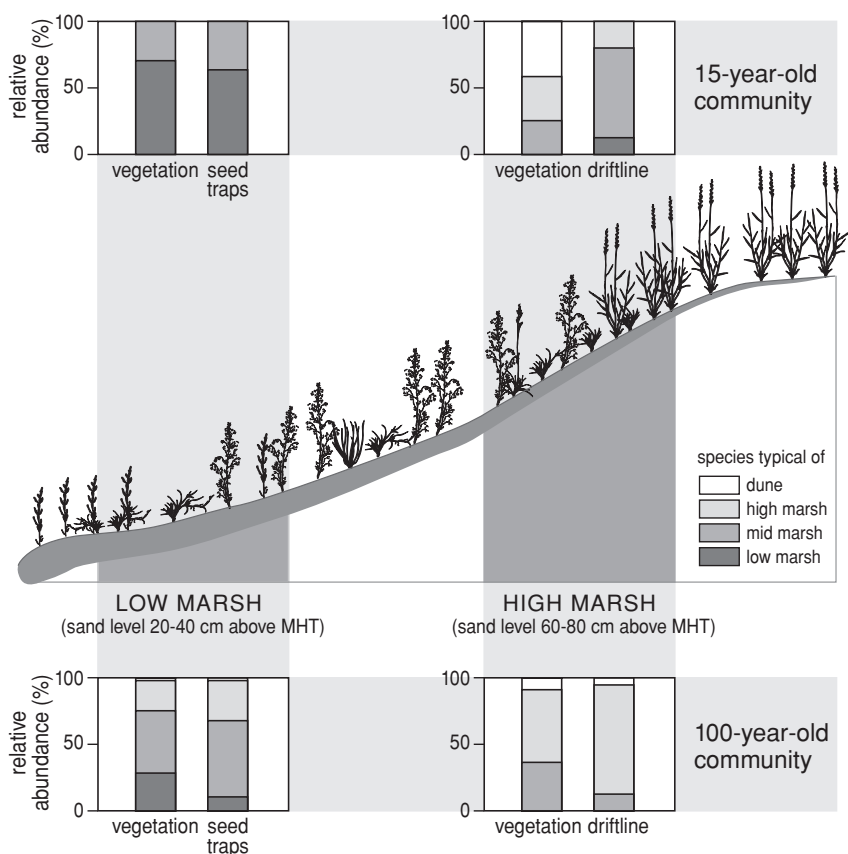


Figure 4.5 Relative abundance of species typical of different elevation zones found in vegetation and seed surveys in a factorial design with age of community (15 or 100 years-old) and elevation of marsh (high or low). Shading explained by inset key.

The effect of different tides on seed movement was also highly significant for both species (Tables 4.2 & 4.3). For both species, the first (4 cm MHT) and fourth (12 cm MHT) tides transported the fewest seeds and the values were not significantly different from each other (Bonferroni multiple comparisons). For *E. atherica*, the amount of seeds transported by the second (29 cm MHT) and third (21 cm MHT) tides was not significantly different, whereas for *P. maritima*, the highest amount of seeds was transported during the second tide followed by the third tide. There was a significant interaction between the effect of the tide and the distance from the sea coast only for *E. atherica* but it explained very little of the variance in the amount of seeds transported compared to the main effect of the tide (Table 4.3).

Table 4.2 Results of repeated-measures ANOVA for *Plantago maritima* obtained from seed movement experiment. Four different tidal cycles were sampled.

Factors	Mean squares	<i>df</i>	<i>F</i>	significance
Within-subjects				
Tide	2.036	3	37.798	< 0.01
Tide x distance from sea	0.130	12	1.906	0.06
Tide x distance from creek	0.029	12	1.446	0.18
Error	0.059	48		
Between-subjects				
Distance from sea	0.997	4	12.260	< 0.01
Distance from creek	0.045	4	2.228	0.11
Error	0.083	16		

Table 4.3 Results of repeated-measures ANOVA for *Elytrigia atherica* obtained from seed movement experiment. Four different tidal cycles were sampled.

Factors	Mean squares	<i>df</i>	<i>F</i>	significance
Within-subjects				
Tide	6.109	3	34.691	< 0.01
Tide x distance from sea	1.565	12	2.222	0.02
Tide x distance from creek	0.356	12	0.505	0.90
Error	2.817	48		
Between-subjects				
Distance from sea	3.988	4	12.078	< 0.01
Distance from creek	0.182	4	0.550	0.70
Error	1.321	16		

Discussion

Patterns in seed rain related to hydrodynamic variability

Temporal patterns in the density of seed rain are likely to be strongly influenced by storm surges, based on the storm which occurred during the sampling period in year one and the evident effects of the storm which occurred just before sampling commenced in year two. Seeds of most salt-marsh species are produced during the summer and autumn months and usually detach from adult plants by late autumn. The delayed increase in seeds captured during late winter/early spring in year one, months after primary dispersal, argues for a “real” effect of storms. This is further supported by patterns during year two, when a storm occurred early before sampling began. It can be extrapolated that the fewer seeds captured during year two and the gradual decrease over time since the period of primary dispersal was probably due to the influence of this storm.

To our knowledge, no other studies have empirically linked seed movement to extreme hydrodynamic events. However, there are studies which have explored the relationship between storms and sedimentation patterns in tidal habitats. Storm surges appear to greatly influence patterns in sedimentation, with the highest rates occurring during stormy periods in a Dutch (Dankers *et al.* 1984) and New England saltmarsh (Roman *et al.* 1997). However, rates of sediment transport and whether they result in net import or export during floods caused by storm surges can depend on season, sequence of previous import and high-energy events (Leonard *et al.* 1995; Bartholdy & Aagaard 2001), timing in relation to flood or ebb phases and wind directions (Stevenson *et al.* 1988). Depending on the floating capacity of the seed, the degree to which seed movements parallel sedimentation patterns will vary. However, a study in a riparian habitat found a strong, positive relationship between the number of captured seeds and dry weight of deposited sediment ($p < 0.001$, $R^2 = 0.686$ in Goodson *et al.* 2003).

Communities most exposed to tidal action received the highest density of seed rain in year one. Young communities in this system are most subjected to effects of hydrodynamics as attested by decreasing inundation frequency and sedimentation rates over time (Olff *et al.* 1997). Also, storm surges mostly affected the seed rain in the two younger communities and had relatively little effect on older communities. Patterns in year two, during which a storm occurred just before the sampling period, were less directly related to hydrodynamics. The highest cumulative densities of captured seeds were found in the 10- and 30-year old communities. In the 10-year-old community, the seed rain was dominated by pioneer species as in year one. However, the seed rain in the 30-year-old community was dominated by one species, *Seriphidium maritimum* (*Artemisia maritima*), which was captured in very low densities during year one (Appendix 4.2: 1.6 compared to 33.9 seeds $m^{-2} day^{-1}$ in year two).

Greater evidence for seed movement along the elevation gradient was found in the young community than in the old community. Movement induced by flood tide appeared to be more important than that caused by ebb tide as there was a net movement upwards. Seeds of low-marsh species were found in abundance on the high marsh, whereas seeds of high-marsh species were rarely found on the low marsh. This corresponds well with other studies that found a net upward movement of seeds on vegetated marsh surfaces (Bakker *et al.* 1985; Huiskes *et al.* 1995).

The relative lack of movement of seeds in the old marsh may be linked to less effective transport of seeds by creeks overflowing their banks than by direct inundation by the sea. The 100-year-old community is inundated solely by an adjacent creek whereas the younger communities are also inundated directly by the sea (Fig. 4.1) (E.R. Chang, personal observation). It may be that flow velocity of an incoming tide from the sea coast and of a creek overflowing its banks may be very different. More importantly, the narrow width of the creeks does not allow for wave formation along the axis perpendicular to the creek bank.

Patterns in seed rain related to seed source

The similarity between species absence or presence in the vegetation and seed rain was intermediate to high along the community sequence. The ordinations of the seed rain, which also take into account abundance, were similar but also exhibited differences from the ordination of seed sources (established plants) along the community sequence. Differences could possibly be attributed to interspecific differences in fecundity (annuals vs. perennials) and intraspecific annual variation in viable seed production, as well as dispersal processes. For species for which seed production was estimated, patterns in seed rain closely mirrored patterns in seed production (Fig. 4.4). Seed production was consistently important in explaining patterns for all the early-successional species (*Salicornia europaea*, *Spergularia media* and *Suaeda maritima*).

It is of note that seed-rain signatures of the two younger communities were most distinct in year one, when the majority of seed transport occurred due to a storm surge. Examination of the seed composition captured during the stormy period reveals a swamping effect by common species already present in the two younger communities (Appendix 4.1 & Appendix 4.2). However, this was also the period when the most seeds of species typical of older communities were trapped in the younger communities, suggesting that storm surges result in mostly local dispersal with a minor element of long-distance dispersal. Similar results were found in a riparian habitat with driftlines, which are formed during events of high water, containing mostly local species augmented by a small percentage of species coming from distances greater than 100 m (Skoglund 1990).

Implications for assembly of tidal communities

Evidence suggests primarily local dispersal under normal tidal regimes with possible long-distance dispersal by storm surges. Predictably, younger communities are most affected by storms because of greater exposure to tidal action and consistently high seed production by annual species, which enables them to take advantage of the dispersal vector. It may be during storm surges that species typical of older communities are able to make attempts at invading younger communities and pioneer species colonise new habitats. It may also be possible that the seed pool being transported during storms is larger than under normal tidal regimes because wind-driven transport of water across the average line of zero current (tidal divide) is likely to occur during storm surges (Koos Doekes, *Rijkswaterstaat RIKZ/ZDI*, pers. comm.). The dispersal vector (tidal water) may pick up seeds from the larger area of older communities to the west of the tidal divide as well of those from younger communities to the east (Fig. 4.1).

The important ecological issue concerning seed transport during storm surges may not be dispersal but seed entrapment. In a pilot study of seed movement on the low marsh/intertidal flat transition area below the 30-year-old community, using mass-marked release and capture techniques, results indicated that the vast majority of seeds were dispersed outside a radius of 15 m from the release point within one tidal inundation (E.R. Chang, unpublished data). Most of the captured seeds were dispersed in the direction of ebb tide, towards the sea. Huiskes *et al.* (1995) also observed a net downward transport of seeds on the mudflat in a tidal marsh in the south of the Netherlands. Once seeds reach the sea, evidence suggests that they do not easily return to the saltmarsh. A study conducted just off the coast of Schiermonnikoog, in which seeds were caught by dragging a net behind a boat, found very few seeds and species during flood tide (Wolters *et al.* 2006). In concordance, Huiskes *et al.* (1995) also observed that few seeds were imported into the marsh with flood currents whereas a significantly higher number of seeds were exported out of the marsh with ebb currents.

A scenario with high transport potential but low deposition in favourable microhabitats reconciles conflicting empirical evidence that although seeds are transported by tidal water, sometimes considerable distances (action radius of several tens of kilometres in Koutstaal *et al.* 1987), seed patterns closely follow distributions of established plants. In summary, the assembly of salt-marsh communities may at least be partly limited by dispersal, but not because seeds do not move. They just may not stop in suitable habitats.

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Appendix 4.1 Mean dominance scores for species (\pm standard error) found during vegetation surveys of permanent transects. Permanent transects were located at four stages of community development. A dominance score of 4 indicates most abundant species in a sub-plot; 3, the next most abundant species and so on. The dominance scores of a maximum number of four species was recorded for each sub-plot. $n = 10$

Species	Age of community (years)			
	10	15	30	100
Pioneer				
<i>Salicornia europaea</i>	2.74 \pm 0.09	1.00 \pm 0	0.66 \pm 0.14	0
<i>Spartina anglica</i>	0.76 \pm 0.13	0.10 \pm 0.04	0.16 \pm 0.10	0
<i>Spergularia marina</i>	0.22	0	0	0
<i>Spergularia media</i>	0.96 \pm 0.09	1.24 \pm 0.08	0.68 \pm 0.12	0.32 \pm 0.08
<i>Suaeda maritima</i>	1.22 \pm 0.08	1.00 \pm 0	0.92 \pm 0.04	0.24 \pm 0.06
Early-successional				
<i>Limonium vulgare</i>	1.16 \pm 0.13	3.72 \pm 0.07	2.08 \pm 0.20	2.58 \pm 0.09
<i>Puccinellia maritima</i>	1.02 \pm 0.06	1.00 \pm 0	1.66 \pm 0.39	0.76 \pm 0.04
Mid-successional				
<i>Aster tripolium</i>	0.18 \pm 0.05	0.98 \pm 0.02	0.90 \pm 0.33	0.04 \pm 0.04
<i>Festuca rubra</i>	0	0.52 \pm 0.14	2.28 \pm 0.46	3.18 \pm 0.18
<i>Glaux maritima</i>	0	0.24 \pm 0.10	0.04 \pm 0.03	1.14 \pm 0.05
<i>Plantago maritima</i>	0	0.94 \pm 0.03	0.10 \pm 0.04	0
<i>Seriphidium maritimum</i>	0	1.82 \pm 0.24	2.68 \pm 0.39	2.08 \pm 0.14
<i>Triglochin maritima</i>	0	0.02 \pm 0.02	0.20 \pm 0.04	0.80 \pm 0.04
Late-successional				
<i>Armeria maritima</i>	0	0.02 \pm 0.02	0	0.38 \pm 0.06
<i>Atriplex portulacoides</i>	0.38 \pm 0.11	2.34 \pm 0.24	0.98 \pm 0.28	0.86 \pm 0.04
<i>Atriplex prostrata</i>	0	0	0.60 \pm 0.14	0.68 \pm 0.06
<i>Elytrigia atherica</i>	0	0	0.04 \pm 0.03	0.86 \pm 0.05
<i>Juncus gerardi</i>	0	0	0.68 \pm 0.14	2.02 \pm 0.27

Appendix 4.2 Mean density of seeds captured by traps (seeds m⁻² day⁻¹) along a community sequence. Communities are 10, 15, 30 and 100 years-old. Traps were set during October to May of 2001/2002 and 2002/2003. Group totals are also given as percentage of seeds at a community captured during that sampling period.

Species	Sampling period 1: Oct. 21 to Dec. 7, 2001			
	Age of community (years)			
	10 (n=10)	15 (n=10)	30 (n=10)	100 (n=10)
Pioneer				
<i>Salicornia europaea</i>	17 ±5.1	0.31 ±0.12	0.091 ±0.041	0
<i>Spartina anglica</i>	0	0	0	0
<i>Spergularia media</i>	0.70 ±0.52	0.030 ±0.022	0	0.10 ±0.06
<i>Suaeda maritima</i>	2.8 ±0.70	3.0 ±1.8	0.27 ±0.13	0.02 ±0.013
Early-successional				
<i>Limonium vulgare</i>	1.1 ±0.33	0.52 ±0.13	0.17 ±0.056	0.25 ±0.09
<i>Puccinellia maritima</i>	0	0	0	0
Mid-successional				
<i>Aster tripolium</i>	0.020 ±0.013	0.081 ±0.049	0.010 ±0.010	0.010 ±0.010
<i>Festuca rubra</i>	0.010 ±0.010	0.040 ±0.031	0.33 ±0.10	0.39 ±0.13
<i>Glaux maritima</i>	0.030 ±0.015	0.020 ±0.020	0	0.091 ±0.071
<i>Plantago maritima</i>	0.020 ±0.013	0.050 ±0.034	0.010 ±0.010	0.040 ±0.022
<i>Seriphidium maritimum</i>	0.050 ±0.086	2.0 ±0.54	1.4 ±0.35	1.5 ±0.22
Late-successional				
<i>Armeria maritima</i>	0.010 ±0.010	0	0	0
<i>Atriplex portulacoides</i>	0	0.040 ±0.022	0.010 ±0.010	0
<i>Atriplex prostrata</i>	0	0.010 ±0.010	0.030 ±0.015	0.071 ±0.026
<i>Elytrigia atherica</i>	0	0	0	0.21 ±0.70
<i>Juncus gerardi</i>	0	0.010 ±0.010	0	0.54 ±0.26
Disturbed salt-marsh				
<i>Agrostis stolonifera</i>	0.33 ±0.14	0	0.040 ±0.016	0.20 ±0.046
<i>Atriplex littoralis</i>	0	0	0	0
Dune				
<i>Agrostis capillaris</i>	0	0	0	0
<i>Centaurium pulchellum</i>	0	0	0	0.010 ±0.010
<i>Cerastium fontanum</i>	0	0	0	0
<i>Lolium perenne</i>	0	0	0	0
<i>Odontites vernus</i>	0	0.010 ±0.010	0.010 ±0.010	0
<i>Plantago coronopus</i>	0	0	0	0
<i>Plantago lanceolata</i>	0	0	0	0
<i>Plantago major</i>	0	0	0	0
<i>Poa annua</i>	0	0	0	0
<i>Trifolium repens</i>	0	0	0	0
Total	22.243	6.255	2.387	3.529

Appendix 4.2 Continued

Species	Sampling period 2: Dec. 8, 2001 to Jan. 24, 2002			
	Age of community (years)			
	10 (n=10)	15 (n=10)	30 (n=10)	100 (n=10)
Pioneer				
<i>Salicornia europaea</i>	34 ± 3.3	3.3 ± 1.8	0.24 ± 0.072	0
<i>Spartina anglica</i>	0	0	0	0
<i>Spergularia media</i>	1.5 ± 0.97	0	0	0
<i>Suaeda maritima</i>	2.4 ± 0.61	1.4 ± 1.0	0.11 ± 0.039	0.010 ± 0.010
Early-successional				
<i>Limonium vulgare</i>	0.13 ± 0.044	0.062 ± 0.035	0.010 ± 0.010	0.010 ± 0.010
<i>Puccinellia maritima</i>	0	0	0	0
Mid-successional				
<i>Aster tripolium</i>	0.031 ± 0.022	0.041 ± 0.027	0.010 ± 0.010	0.021 ± 0.021
<i>Festuca rubra</i>	0	0	0.36 ± 0.094	0.051 ± 0.023
<i>Glaux maritima</i>	0.072 ± 0.031	0.072 ± 0.041	0	0.031 ± 0.016
<i>Plantago maritima</i>	0.031 ± 0.016	0	0	0.010 ± 0.010
<i>Seriphidium maritimum</i>	0.010 ± 0.010	0.021 ± 0.014	0.082 ± 0.021	0.020 ± 0.014
Late-successional				
<i>Armeria maritima</i>	0	0	0	0
<i>Atriplex portulacoides</i>	0	0	0	0
<i>Atriplex prostrata</i>	0	0	0	0.021 ± 0.014
<i>Elytrigia atherica</i>	0	0	0.010 ± 0.010	0.072 ± 0.041
<i>Juncus gerardi</i>	0	0	0.021 ± 0.014	0.17 ± 0.093
Disturbed salt-marsh				
<i>Agrostis stolonifera</i>	0.28 ± 0.10	0	0.021 ± 0.014	0.062 ± 0.031
<i>Atriplex littoralis</i>	0	0	0	0
Dune				
<i>Agrostis capillaris</i>	0	0	0	0
<i>Centaureum pulchellum</i>	0	0	0	0.010 ± 0.010
<i>Cerastium fontanum</i>	0	0	0	0
<i>Lolium perenne</i>	0	0	0	0
<i>Odontites vernus</i>	0	0.010 ± 0.010	0	0
<i>Plantago coronopus</i>	0	0	0	0
<i>Plantago lanceolata</i>	0	0	0	0
<i>Plantago major</i>	0	0	0.021 ± 0.021	0
<i>Poa annua</i>	0	0	0	0
<i>Trifolium repens</i>	0	0	0	0.010 ± 0.010
Total	38.652	4.918	0.885	0.504

Appendix 4.2 Continued

Species	Sampling period 3: Jan. 25 to March 11, 2002			
	Age of community (years)			
	10 (n=5)	15 (n=8)	30 (n=10)	100 (n=10)
Pioneer				
<i>Salicornia europaea</i>	33 ±14	11 ±2.1	0.032 ±0.023	0
<i>Spartina anglica</i>	0	0	0	0
<i>Spergularia media</i>	66 ±16	4.1 ±1.3	0	0
<i>Suaeda maritima</i>	45 ±17	13 ±4.8	0	0.011 ±0.011
Early-successional				
<i>Limonium vulgare</i>	7.7 ±1.5	3.6 ±0.98	0.097 ±0.034	0.021 ±0.014
<i>Puccinellia maritima</i>	0	0	0	0
Mid-successional				
<i>Aster tripolium</i>	0.39 ±0.31	0.23 ±0.12	0	0
<i>Festuca rubra</i>	0.47 ±0.22	0.95 ±0.53	0.52 ±0.14	0.097 ±0.044
<i>Glaux maritima</i>	0.52 ±0.19	0.39 ±0.21	0.011 ±0.011	0.043 ±0.024
<i>Plantago maritima</i>	0.56 ±0.17	0.013 ±0.013	0	0
<i>Seriphidium maritimum</i>	0.021 ±0.021	0.56 ±0.22	0	0
Late-successional				
<i>Armeria maritima</i>	0	0	0	0
<i>Atriplex portulacoides</i>	0.28 ±0.12	0.067 ±0.035	0	0
<i>Atriplex prostrata</i>	0.15 ±0.055	0.013 ±0.013	0.011 ±0.011	0.011 ±0.011
<i>Elytorgia atherica</i>	0.043 ±0.026	0.054 ±0.035	0.021 ±0.014	0.021 ±0.014
<i>Juncus gerardi</i>	0.043 ±0.026	0.35 ±0.23	0.064 ±0.036	0.086 ±0.035
Disturbed salt-marsh				
<i>Agrostis stolonifera</i>	9.9 ±3.8	0.12 ±0.043	0.032 ±0.023	0.054 ±0.033
<i>Atriplex littoralis</i>	0	0.013 ±0.013	0	0
Dune				
<i>Agrostis capillaris</i>	0	0	0	0
<i>Centaurium pulchellum</i>	0	0	0	0
<i>Cerastium fontanum</i>	0.021 ±0.021	0.013 ±0.013	0	0
<i>Lolium perenne</i>	0.34 ±0.092	0	0	0
<i>Odontites vernus</i>	0	0	0	0
<i>Plantago coronopus</i>	0.021 ±0.021	0	0.011 ±0.011	0.011 ±0.011
<i>Plantago lanceolata</i>	0	0	0	0
<i>Plantago major</i>	0	0	0	0
<i>Poa annua</i>	0	0	0	0
<i>Trifolium repens</i>	0	0	0	0
Total	167.309	35.213	0.812	0.362

Appendix 4.2 Continued

Species	Sampling period 4: March 12 to May 8, 2002			
	Age of community (years)			
	10 (n=4)	15 (n=10)	30 (n=10)	100 (n=10)
Pioneer				
<i>Salicornia europaea</i>	0	0	0	0
<i>Spartina anglica</i>	0	0	0	0
<i>Spergularia media</i>	0.043 \pm 0.043	0	0	0
<i>Suaeda maritima</i>	0.085 \pm 0.060	0	0	0
Early-successional				
<i>Limonium vulgare</i>	0	0	0	0
<i>Puccinellia maritima</i>	0	0	0	0
Mid-successional				
<i>Aster tripolium</i>	0	0	0	0
<i>Festuca rubra</i>	0	0.0085 \pm 0.0085	0.0085 \pm 0.0085	0.017 \pm 0.011
<i>Glaux maritima</i>	0	0	0	0.017 \pm 0.011
<i>Plantago maritima</i>	0	0	0	0
<i>Seriphidium maritimum</i>	0	0	0	0
Late-successional				
<i>Armeria maritima</i>	0	0	0	0
<i>Atriplex portulacoides</i>	0	0	0	0
<i>Atriplex prostrata</i>	0	0	0	0
<i>Elytrigia atherica</i>	0	0	0	0.0085 \pm 0.0085
<i>Juncus gerardi</i>	0	0	0	0.025 \pm 0.013
Disturbed salt-marsh				
<i>Agrostis stolonifera</i>	0.021 \pm 0.021	0.0085 \pm 0.0085	0	0.0085 \pm 0.0085
<i>Atriplex littoralis</i>	0	0	0	0
Dune				
<i>Agrostis capillaris</i>	0	0	0	0
<i>Centaureum pulchellum</i>	0	0	0	0
<i>Cerastium fontanum</i>	0	0	0	0
<i>Lolium perenne</i>	0	0	0	0
<i>Odontites vernus</i>	0	0	0	0
<i>Plantago coronopus</i>	0	0	0	0
<i>Plantago lanceolata</i>	0	0	0	0
<i>Plantago major</i>	0	0	0	0
<i>Poa annua</i>	0	0	0	0
<i>Trifolium repens</i>	0	0	0	0
Total	0.152	0.017	0.0087	0.076

Appendix 4.2 Continued

Species	Sampling period 5: Nov. 1 to Dec. 19, 2002			
	Age of community (years)			
	10 (n=10)	15 (n=10)	30 (n=10)	100 (n=9)
Pioneer				
<i>Salicornia europaea</i>	11 \pm 3.6	0.12 \pm 0.056	0.51 \pm 0.48	0.41 \pm 0.40
<i>Spartina anglica</i>	0	0	0	0
<i>Spergularia media</i>	0.52 \pm 0.20	0.020 \pm 0.013	0	0.022 \pm 0.022
<i>Suaeda maritima</i>	4.8 \pm 2.6	0.081 \pm 0.044	2.4 \pm 1.4	0.32 \pm 0.26
Early-successional				
<i>Limonium vulgare</i>	2.7 \pm 0.68	1.0 \pm 0.54	0.25 \pm 0.022	0.95 \pm 0.68
<i>Puccinellia maritima</i>	0	0	0	0
Mid-successional				
<i>Aster tripolium</i>	0.020 \pm 0.013	0.25 \pm 0.16	0.040 \pm 0.031	0
<i>Festuca rubra</i>	0.010 \pm 0.010	0.060 \pm 0.040	0.020 \pm 0.020	0
<i>Glaux maritima</i>	0.030 \pm 0.015	0.010 \pm 0.010	0.010 \pm 0.010	0.011 \pm 0.011
<i>Plantago maritima</i>	0.010 \pm 0.010	0.050 \pm 0.050	0	0.011 \pm 0.011
<i>Seriphidium maritimum</i>	0	10 \pm 5.5	21 \pm 3.8	5.1 \pm 3.4
Late-successional				
<i>Armeria maritima</i>	0	0	0	0
<i>Atriplex portulacoides</i>	0	0	0	0.011 \pm 0.011
<i>Atriplex prostrata</i>	0.010 \pm 0.010	0	0.55 \pm 0.38	3.6 \pm 1.6
<i>Elytrigia atherica</i>	0	0.010 \pm 0.010	0.050 \pm 0.034	0.056 \pm 0.056
<i>Juncus gerardi</i>	0	0.010 \pm 0.010	0	0.011 \pm 0.011
Disturbed salt-marsh				
<i>Agrostis stolonifera</i>	0.010 \pm 0.010	0	0	0
<i>Atriplex littoralis</i>	0	0	0	0
Dune				
<i>Agrostis capillaris</i>	0	0	0	0
<i>Centaurium pulchellum</i>	0	0	0	0
<i>Cerastium fontanum</i>	0	0	0	0
<i>Lolium perenne</i>	0	0	0	0
<i>Odontites vernus</i>	0	0	0	0
<i>Plantago coronopus</i>	0	0	0	0
<i>Plantago lanceolata</i>	0	0	0	0
<i>Plantago major</i>	0	0	0	0
<i>Poa annua</i>	0	0	0	0
<i>Trifolium repens</i>	0	0	0	0
Total	19.511	11.721	25.226	10.504

Appendix 4.2 Continued

Species	Sampling period 6: Dec. 20, 2002 to Feb. 14, 2003			
	Age of community (years)			
	10 (n=10)	15 (n=10)	30 (n=10)	100 (n=10)
Pioneer				
<i>Salicornia europaea</i>	9.4 ±2.1	0.75 ±0.081	1.2 ±1.1	0.0087 ±0.0087
<i>Spartina anglica</i>	0	0	0	0
<i>Spergularia media</i>	2.5 ±1.9	0.043 ±0.027	0	0.11 ±0.11
<i>Suaeda maritima</i>	1.4 ±0.88	0.19 ±0.053	0.82 ±0.40	0.11 ±0.043
Early-successional				
<i>Limonium vulgare</i>	2.4 ±0.26	0.32 ±0.11	0.061 ±0.037	0.46 ±0.43
<i>Puccinellia maritima</i>	0	0	0	0
Mid-successional				
<i>Aster tripolium</i>	0.44 ±0.32	0.30 ±0.17	0.49 ±0.25	0.10 ±0.077
<i>Festuca rubra</i>	0.087 ±0.039	0.026 ±0.018	0.11 ±0.067	0.026 ±0.026
<i>Glaux maritima</i>	0.97 ±0.20	0.16 ±0.065	0.63 ±0.37	0.11 ±0.10
<i>Plantago maritima</i>	0.017 ±0.012	0.035 ±0.026	0	0
<i>Seriphidium maritimum</i>	0.21 ±0.058	1.7 ±0.43	11 ±2.2	1.2 ±0.33
Late-successional				
<i>Armeria maritima</i>	0	0	0	0
<i>Atriplex portulacoides</i>	0	0	0	0
<i>Atriplex prostrata</i>	0	0.0087 ±0.0087	0.29 ±0.12	0.94 ±0.24
<i>Elytrigia atherica</i>	0.0087 ±0.0087	0.0087 ±0.0087	0.035 ±0.026	0.061 ±0.034
<i>Juncus gerardi</i>	0	0.0087 ±0.0087	0	0.0087 ±0.0087
Disturbed salt-marsh				
<i>Agrostis stolonifera</i>	0.043 ±0.019	0	0	0
<i>Atriplex littoralis</i>	0	0	0	0
Dune				
<i>Agrostis capillaris</i>	0	0	0	0
<i>Centaureum pulchellum</i>	0	0	0	0
<i>Cerastium fontanum</i>	0	0	0	0
<i>Lolium perenne</i>	0	0	0	0
<i>Odontites vernus</i>	0	0	0	0
<i>Plantago coronopus</i>	0	0	0	0
<i>Plantago lanceolata</i>	0	0	0	0
<i>Plantago major</i>	0	0	0	0
<i>Poa annua</i>	0	0	0	0
<i>Trifolium repens</i>	0	0	0	0
Total	17.544	3.543	14.468	3.110

Appendix 4.2 Continued

Species	Sampling period 7: Feb. 15 to March 31, 2003			
	Age of community (years)			
	10 (n=10)	15 (n=10)	30 (n=10)	100 (n=10)
Pioneer				
<i>Salicornia europaea</i>	4.8 ±1.1	0.088 ±0.043	0.15 ±0.13	0
<i>Spartina anglica</i>	0	0	0	0
<i>Spergularia media</i>	0.077 ±0.037	0.011 ±0.011	0.022 ±0.022	0.033 ±0.033
<i>Suaeda maritima</i>	0.33 ±0.088	0.066 ±0.029	0.36 ±0.27	0.27 ±0.23
Early-successional				
<i>Limonium vulgare</i>	0.23 ±0.083	0.14 ±0.077	0.077 ±0.029	0.022 ±0.015
<i>Puccinellia maritima</i>	0	0	0	0
Mid-successional				
<i>Aster tripolium</i>	0.088 ±0.046	0.21 ±0.12	0.14 ±0.11	0.044 ±0.024
<i>Festuca rubra</i>	0	0.011 ±0.011	0.011 ±0.011	0
<i>Glaux maritima</i>	0.011 ±0.011	0	0.033 ±0.023	0.022 ±0.022
<i>Plantago maritima</i>	0	0	0	0
<i>Seriphidium maritimum</i>	0.022 ±0.015	0.066 ±0.037	0.80 ±0.27	0.022 ±0.015
Late-successional				
<i>Armeria maritima</i>	0	0	0	0
<i>Atriplex portulacoides</i>	0	0	0	0
<i>Atriplex prostrata</i>	0	0.011 ±0.011	0.022 ±0.015	0.055 ±0.034
<i>Elytrigia atherica</i>	0	0.022 ±0.022	0.19 ±0.17	0.14 ±0.13
<i>Juncus gerardi</i>	0	0.011 ±0.011	0.011 ±0.011	0.011 ±0.011
Disturbed salt-marsh				
<i>Agrostis stolonifera</i>	0	0	0	0
<i>Atriplex littoralis</i>	0	0	0	0
Dune				
<i>Agrostis capillaris</i>	0	0	0.011 ±0.011	0
<i>Centaurium pulchellum</i>	0	0	0	0
<i>Cerastium fontanum</i>	0	0	0	0
<i>Lolium perenne</i>	0	0	0	0
<i>Odontites vernus</i>	0	0	0	0
<i>Plantago coronopus</i>	0	0	0	0
<i>Plantago lanceolata</i>	0	0	0	0
<i>Plantago major</i>	0	0	0.022 ±0.015	0
<i>Poa annua</i>	0	0	0.011 ±0.011	0.011 ±0.011
<i>Trifolium repens</i>	0	0	0	0
Total	5.574	0.636	1.866	0.636

Appendix 4.2 Continued

Species	Sampling period 8: April 1 to May 11, 2003			
	Age of community (years)			
	10 (n=10)	15 (n=10)	30 (n=10)	100 (n=10)
Pioneer				
<i>Salicornia europaea</i>	1.9 ±0.40	0.37 ±0.12	0.024 ±0.024	0.012 ±0.012
<i>Spartina anglica</i>	0	0	0	0
<i>Spergularia media</i>	0.036 ±0.026	0	0	0
<i>Suaeda maritima</i>	0.52 ±0.38	0.12 ±0.095	0.13 ±0.038	0.060 ±0.037
Early-successional				
<i>Limonium vulgare</i>	0.024 ±0.016	0.060 ±0.037	0.072 ±0.037	0
<i>Puccinellia maritima</i>	0	0	0	0
Mid-successional				
<i>Aster tripolium</i>	0	0.024 ±0.016	0.048 ±0.027	0
<i>Festuca rubra</i>	0	0.096 ±0.047	0.25 ±0.085	0
<i>Glaux maritima</i>	0.19 ±0.060	0.012 ±0.012	0.024 ±0.016	0.012 ±0.012
<i>Plantago maritima</i>	0.024 ±0.024	0	0.024 ±0.016	0
<i>Seriphidium maritimum</i>	0	0.096 ±0.035	1.1 ±0.29	0.096 ±0.050
Late-successional				
<i>Armeria maritima</i>	0	0	0	0
<i>Atriplex portulacoides</i>	0	0	0	0
<i>Atriplex prostrata</i>	0	0	0	0.024 ±0.016
<i>Elytrigia atherica</i>	0	0.012 ±0.012	0.036 ±0.018	0
<i>Juncus gerardi</i>	0.012 ±0.012	0	0.036 ±0.036	0.012 ±0.012
Disturbed salt-marsh				
<i>Agrostis stolonifera</i>	0.036 ±0.026	0.024 ±0.016	0.024 ±0.024	0
<i>Atriplex littoralis</i>	0	0	0	0
Dune				
<i>Agrostis capillaris</i>	0	0	0	0
<i>Centaureum pulchellum</i>	0	0	0	0
<i>Cerastium fontanum</i>	0	0	0	0
<i>Lolium perenne</i>	0	0	0	0
<i>Odontites vernus</i>	0	0	0	0
<i>Plantago coronopus</i>	0	0	0	0
<i>Plantago lanceolata</i>	0	0	0	0
<i>Plantago major</i>	0	0	0	0
<i>Poa annua</i>	0	0	0	0
<i>Trifolium repens</i>	0	0	0	0
Total	2.777	0.839	1.827	0.222

Appendix 4.3 Mean density of seeds collected from driftline material (seeds m⁻²) at 15- and 100-year-old communities. Fresh driftline material was sampled on Nov. 13, 2001. $n = 10$

Species	Age of community (years)	
	15	100
Low marsh		
<i>Atriplex portulacoides</i>	240 ± 58	10 ± 5.5
<i>Limonium vulgare</i>	1600 ± 340	95 ± 40
<i>Puccinellia maritima</i>	2.5 ± 2.5	0
<i>Salicornia europaea</i>	380 ± 100	2.5 ± 2.5
<i>Spartina anglica</i>	2.5 ± 2.5	0
<i>Suaeda maritima</i>	1700 ± 310	40 ± 21
Group total	3925 (12.6 %)	147.5 (0.62 %)
Mid marsh		
<i>Aster tripolium</i>	65 ± 21	15 ± 7.6
<i>Festuca rubra</i>	2400 ± 630	2600 ± 450
<i>Glaux maritima</i>	760 ± 250	110 ± 51
<i>Plantago maritima</i>	5900 ± 1200	360 ± 140
<i>Seriphidium maritimum</i>	12 000 ± 3200	62 ± 29
<i>Triglochin maritima</i>	2.5 ± 2.5	0
Group total	21 127.5 (68 %)	3147 (13.2 %)
High marsh		
<i>Atriplex prostrata</i>	2.5 ± 2.5	52 ± 16
<i>Elytrigia atherica</i>	830 ± 200	17 000 ± 7300
<i>Juncus gerardi</i>	230 ± 110	240 ± 99
<i>Agrostis stolonifera</i>	4600 ± 830	2300 ± 800
Group total	5662.5 (18.4 %)	2317 (81.6 %)
Dune		
<i>Armeria maritima</i>	2.5 ± 2.5	0
<i>Cerastium fontanum</i>	2.5 ± 2.5	20 ± 15
<i>Lolium perenne</i>	95 ± 12	12 ± 7.7
<i>Matricaria maritima</i>	2.5 ± 2.5	10 ± 5.5
<i>Odontites vernus</i>	2.5 ± 2.5	0
<i>Plantago coronopus</i>	290 ± 82	680 ± 300
<i>Plantago lanceolata</i>	0	38 ± 21
<i>Plantago major</i>	0	5 ± 3.3
<i>Poa annua</i>	0	5 ± 3.3
<i>Sagina procumbens</i>	2.5 ± 2.5	65 ± 57
<i>Trifolium repens</i>	2.5 ± 2.5	130 ± 58
Group total	400 (1.3 %)	965 (4.0 %)
Total	31 115	23 851.5



Chapter 5

Seed retention in a tidal marsh: interactions between seed morphology and environmental variables

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Summary

Patterns of seed deposition may influence community organization by forming the initial template for subsequent community development. The patterns may be easier to predict by knowing which factors make seeds stop and remain in a microsite rather than determining how far seeds are capable of travelling. We examined interactions between seed morphology, moisture conditions, vegetation structure and hydrodynamic variables and the relative role of each factor in determining seed retention based on factorial experiments. Experiments were conducted in a tidal salt marsh and in a flume facility where hydrodynamic variables could be controlled.

Moisture condition of seeds greatly influenced which factors were most important in determining seed retention, acting as a 'switch' in the system. Seed type (buoyancy) was the most significant factor when seeds were dry. In contrast, hydrodynamic effects dominated retention processes when seeds were waterlogged. Vegetation structure also influenced retention in both dry and wet conditions but less so than other factors. Results suggest that buoyancy traits appear to determine whether seeds move in the drier summer and autumn months, after initial detachment from parent plants but the intensity of wave action will determine whether waterlogged seeds stay in a microsite during the wetter months of late autumn to early spring.

Introduction

The patterns of seed dispersal, as the initial constraining factor affecting species richness, can strongly influence plant community organization (Honnay *et al.* 2001; Jansson *et al.* 2005). A recent review, however, concluded that spatial variation in seed deposition is more easily related to landscape elements that trap seeds than to the probability of dispersal distance travelled from the seed source (*i.e.* dispersal kernel) and the authors suggested that theoretical treatment of this relationship would offer new insights into community organization (Levine & Murrell 2003). In this study, we examine the processes that influence seed retention in tidal systems by identifying simple functional relationships between dispersal vectors (tidal water, wind-generated waves), trapping agents (vegetation), seed characteristics (buoyancy) and seed retention. These relationships are needed to build and test theoretical models in water-driven systems as has been done in wind-driven systems (Johnson & Fryer 1992).

Both the probability of dispersal and dispersal distance has been shown to decrease with increasing vegetation density (Watkinson 1978; Redbo-Torstensson & Telenius 1995). This is likely due to effects of the vegetation on the dispersal vector. In tidal marshes, vegetation forms important elements of landscape structure providing resistance to tidal currents (Green 2005) and orbital water movement by wind-generated waves (Möller *et al.* 1999). Tidal currents result in net movement of water particles but their velocity can be considerably dampened by the vegetation, whereas orbital water movements can more effectively dislodge particles (such as sediments or seeds) vertically but result in no net movement of water particles. The magnitudes of these effects are strongly dependent on vegetation characteristics such as shoot density and stiffness (Bouma *et al.* 2005). Understanding of seed retention in tidal systems thus requires comparison of contrasting community types under flow and wave-dominated hydrodynamic regimes.

Morphological traits of seeds, such as size, shape, presence of appendages and seed-coat properties, can influence patterns of seed distribution *per se* but also as a result of interactions with trapping agents (Peart 1984; Chambers *et al.* 1991). In systems dominated by water dispersal, seed traits enhancing dispersal may include low mass, large surface area to volume ratio, buoyant appendages, air traps and tenacious attachment to adult plant material (Praeger 1913). In contrast, traits such as mucilaginous seed coats, hygroscopic awns and collapsing pappi may enhance retention (Chambers & MacMahon 1994).

In this study, we explore the effects of morphological seed traits, vegetation structure and hydrodynamic variables on seed retention processes in a tidal marsh dominated by hydrochory by examining these processes both in the field and in a flume facility where hydrodynamic variables can be controlled. We hypothesize that seed retention will be higher in: 1) species with a trait enhancing retention

(i.e. mucilaginous seed coat) than species with a trait enhancing buoyancy (i.e. bracts) or no apparent adaptation; 2) denser vegetation compared with more open vegetation and in 3) current-dominated compared with wave-dominated environments. Interaction effects between these seed traits and environmental variables, however, are more difficult to predict than the main effects and thus form the prime objective of this study.

Methods

Field study

We conducted the field study in a back-barrier salt marsh on the Dutch island of Schiermonnikoog (53° 30' N, 6° 10' E). Five sites approximately 50 m apart were selected for the presence of three contrasting community types in close proximity (details below). Within each site, we sowed in each community type four patches (10 cm x 10 cm) with 30 dry seeds of three contrasting species (details below). We sprayed a little water on the seeds to prevent them from being blown away by the wind. Seeds were left on the marsh surface for one tidal inundation, after which turfs encompassing the patches were cut from the vegetation and searched for seeds under a magnifying glass. We analyzed one control patch for each set of four vegetation patches in order to detect presence of naturally dispersed seeds. The experiment was performed during a spring tide (8 April, 2004) when plots were inundated with 10 to 25 cm of sea water.

To test hypothesis 1, we selected 'seeds' from three salt-marsh species for their contrasting physical traits. Seeds of *Plantago maritima* (1mm x 2 mm) have a relatively short floating capacity with 50 % of seeds sinking within 0.5 to 1 hour (T_{50}) in laboratory experiments (Koutstaal *et al.* 1987) due to a seed coat that becomes mucilaginous when wetted. Seeds of *Suaeda maritima* (radius 0.5 mm) have a mid-ranging T_{50} from 2 to 30 hours (Koutstaal *et al.* 1987). Diaspores of *Elytrigia atherica* are grains encased within bracts (10 mm x 2 mm) and have the longest T_{50} ranging from 1 to 2 days (Koutstaal *et al.* 1987). The term 'seed' will be used to describe both true seeds and small, indehiscent fruits.

We compared three contrasting community types that are common in low-elevation marshes (hypothesis 2). *Spartina anglica* is a loosely tufted, tall grass with stout, inflexible stems. *Limonium vulgare* forms low rosettes with leathery, basal leaves and taller flowering stalks. *Puccinellia maritima* is a creeping grass with soft, half-prostrate stems. Plant nomenclature follows van der Meijden (1996).

Flume study

A race-track flume tank was used to establish the effect of hydrodynamic conditions (current vs. waves, hypothesis 3) on retention of three contrasting seed types

(same species as used in the field experiment, hypothesis 1) in two contrasting stand types (*Festuca rubra*, *L. vulgare*, hypothesis 2). Different saturation conditions (dry, waterlogged) were used because we expected this to have a significant effect on seed buoyancy and both conditions occur in the field. We used a flume facility to be able to repeat experiments, by having a controlled and reproducible hydrodynamic environment.

Two vegetation containers (1.0 m x 0.25 m) were placed side by side for each run in the test section of the flume where the soil could be made level with the bottom of the flume. Behind the containers, we placed a net, with an opening exactly fitted to the dimensions of the flume (mesh size ~0.5 mm), in order to catch dislodged seeds.

For the dry-seed experiment, we applied sequentially three hydrodynamic treatments: i) simulating flooding by filling the flume, ii) applying a strong unidirectional flow (40 cm/s), and iii) applying wave action (amplitude = 3.9 cm, period = 1.7 s) combined with a low unidirectional flow (20 cm/s) (wave treatment). Fifty seeds of all three species were sown approximately 20 cm downstream of the leading edge of the vegetation container. After sowing, treatment i was applied by filling the flume to a height of 30 cm with a partition placed across the flume channel so that sea-water would approach the vegetation from one direction. Very low flow velocity was generated in order to make sure that floating seeds were caught in the net. Treatments ii and iii were applied for 30 minutes each. Between treatments, we collected seeds from the net. This protocol was repeated five times for each stand type, each time with a new vegetation container.

For the waterlogged-seed experiment, 50 seeds of each of the three species were sown as in the dry-seed experiment but with the flume already filled with water to a depth of 30 cm. When all seeds had sunk and settled in the vegetation, we applied a strong-flow velocity (40 cm/s) for 30 minutes. After emptying the net of seeds, we added 50 more seeds of each of the three species and then applied wave action (amplitude = 3.9 cm, period = 1.7 s) combined with a slow-flow velocity (20 cm/s) for 30 minutes. The net was emptied and dislodged seeds were collected. This protocol was repeated five times for each stand type, each time with a new vegetation container.

In the race-track flume (circumference of ~42 m, width of 0.6 m), unidirectional flow velocity was generated through the use of a drive belt. Sinusoidal waves were generated by moving a board that moved back and forth lengthwise along the flume by means of a fly-wheel construction. A more detailed description and diagram of the flume facility at the Netherlands Institute of Ecology in Yerseke is given in Bouma *et al.* (2005).

Two species, *Festuca rubra* and *Limonium vulgare*, were grown in monoculture in containers under greenhouse conditions. We used a *F. rubra* stand instead of *P. maritima* because tillers of *F. rubra* are similar in morphology to those of *P. maritima* but

are present in much higher densities and we wished to conduct experiments with highly contrasting vegetation structures in the flume. *F. rubra* was sown to grow at a mean field density of 5600 tillers/m². Adult plants of *L. vulgare* were transplanted from the field and replanted at mean field density of 25 plants/m².

In order to relate changes in hydrodynamics to vegetation properties, we quantified the structure of the stands. We measured percentage cover values using random point quadrat measurements in all the vegetation containers. A hundred points each were recorded at soil level, 5 cm above the soil and at canopy height. We also clipped all vegetation in three areas of 10 cm x 10 cm per container for estimating biomass (g dry plant material/m²). Flow velocity measurements were taken by an Acoustic Doppler Velocimeter (ADV) (Nortek AS, Oslo, Norway) during current generation by the drive belt. The ADV measured the flow velocity in a grid of 69 cm x 22 cm at three height levels (5 cm, 11 cm and 17 cm above the soil level). The step sizes for the x (direction of current generation), y and z velocities were 3 cm, 5.5 cm and 6 cm respectively. The flow velocities along the x, y and z directions were averaged over time for each point along each axis. Because turbulence can be defined as rapid and irregular fluctuations in local velocity, we used the standard deviations (σ) of lateral-flow velocity (y-axis) and vertical-flow velocity (z-axis) within a single vegetation container as proxies for turbulence.

Data analysis

We applied ANOVA to test for effects of seed type, vegetation structure and hydrodynamic variables on seed retention using the software program, SPSS (2003). Transformations were used when necessary to adhere to assumptions of normality and homogeneity of variance but original percentage values of seed retention were used to generate figures. For the dry-seed experiment, results were not independent of each other because of the fixed order of the three sequential treatments. We nevertheless chose a fixed order because *i*) all experiments with dry seeds must start with filling the flume and *ii*) pilot studies indicated that the stronger hydrodynamics of waves removed more seeds than current velocity alone, so that cumulative plots should give accurate estimates for each treatment. Statistical analysis was not applied to assess the effect of hydrodynamic treatments in the dry-seed experiment. For the flow velocity data, spatially-explicit figures were generated by using an inverse distance squared weighted interpolation method with the Spatial Analyst module of ArcView® (ESRI 2004).

Results

Seed retention in the field study

Seed type was the most important factor in explaining seed retention in the field experiment ($F_{2,167} = 164.9$, $p < 0.01$, 84 % of mean squares (MS)). Significantly higher numbers of *P. maritima* seeds were retained followed by seeds of *S. maritima* and then *E. atherica* (Tukey's multiple comparisons), as predicted by hypothesis 1 (Fig. 5.1). There was a significant interaction effect between seed type and vegetation structure ($F_{4,167} = 13.9$, $p < 0.01$, 7.1 % of MS), which was low but still explained about the same amount of variance than the significant main effect of vegetation structure ($F_{2,167} = 14.9$, $p < 0.01$, 7.6 % of MS). Seed retention was significantly lower for seeds of *P. maritima* in stands of *S. anglica* than in other community types, whereas community type did not have an effect on the retention of *E. atherica* and *S. maritima* seeds. Spatial block was not a significant factor. The control patches captured very few seeds indicating dispersal of naturally occurring seeds into experimental patches was negligible.

Seed retention in the flume study

As in the field study, seed type was an important factor in explaining patterns in seed retention for the experiment using dry seeds ($F_{2,24} = 32.7$, $p < 0.01$, 64 % of MS). The greatest numbers of seeds of *P. maritima* were retained, followed by seeds of *S. maritima* and *E. atherica* (Tukey's multiple comparisons), as predicted by hypothesis 1 (Fig. 5.2A & 5.2B). Vegetation structure also had a significant effect on seed retention but explained less of the variance than seed type ($F_{1,24} = 17.3$,

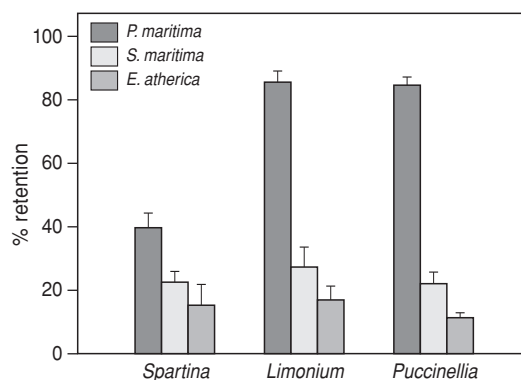


Figure 5.1 Percentage retention of sown seeds found in the field study for *Spartina anglica*, *Limonium vulgare* and *Puccinellia maritima* community types after a spring tide on 8 April, 2004 when plots were inundated with 10-25 cm of sea water. Results for seeds of *Plantago maritima*, *Suaeda maritima* and *Elytrigia atherica* are shown. Error bars represent standard errors. ($n = 5$)

$p < 0.01$, 34 % of MS). Stands of *F. rubra* retained greater numbers of seeds than those of *L. vulgare*, as predicted by hypothesis 2 (Fig. 5.2A & 5.2B). In the hydrodynamic treatments, adding a strong flow velocity resulted in the export of additional seeds that had not floated up with the ‘upcoming tide’ treatment. The wave treatment, in turn, succeeded in dislodging additional seeds that had not been transported by the velocity treatment.

When seeds were waterlogged, the hydrodynamic treatment was the most important factor in explaining patterns of seed retention ($F_{1,60} = 278.5$, $p < 0.01$, 71 % of MS). Waves dislodged more seeds than flow velocity alone, as predicted by hypothesis 3 (Fig. 5.2C & 5.2D). The vegetation structure was also a significant factor ($F_{1,60} = 74.5$, $p < 0.01$, 19 % of MS) with stands of *F. rubra* retaining more seeds than those of *L. vulgare* (Fig. 5.2C & 5.2D). In contrast to the field experiment, seed type explained the least amount of variance (2.9 % of MS), although it was still significant ($F_{2,60} = 11.6$, $p < 0.01$). More seeds of *P. maritima* and *E. atherica* were retained than seeds of *S. maritima* (Tukey’s multiple compar-

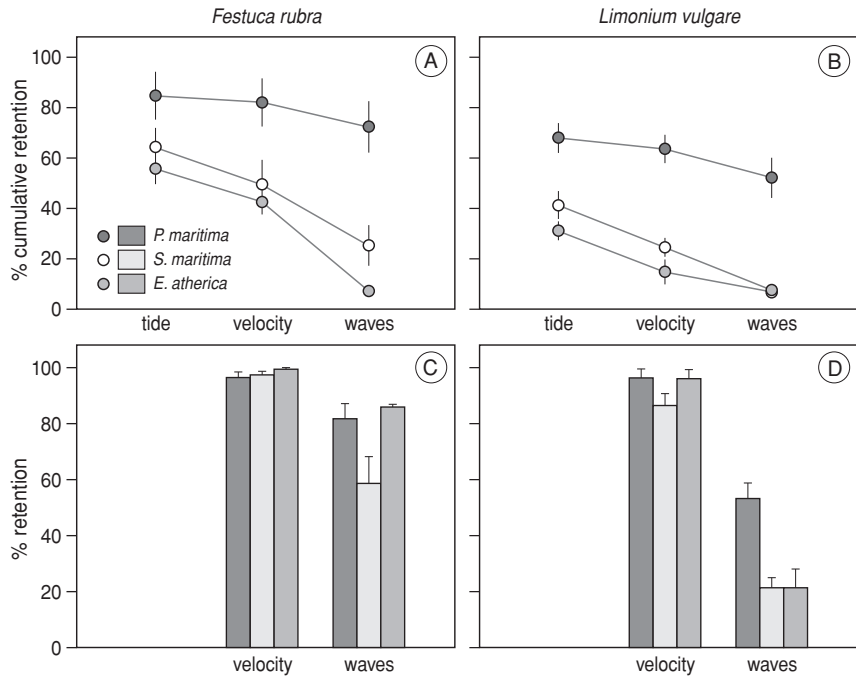


Figure 5.2 Percentage seed retention found in two stand types (*Festuca rubra*, *Limonium vulgare*) for initially dry seeds (A & B) and waterlogged seeds (C & D). Up to three hydrodynamic treatments (upcoming tide, flow velocity, waves) were applied to dislodge seeds in a flume facility. Results for seeds of *Plantago maritima*, *Suaeda maritima* and *Elytrigia atherica* are shown. Error bars represent standard errors. ($n = 5$)

isons). All first-order interactions were significant although they explained much less of the variance than the main effects except for seed type.

Effect of vegetation structure on hydrodynamics in the flume study

There were key structural differences between *F. rubra* and *L. vulgare* stands. The vertical structure of the stands was more evenly spread for *F. rubra* with much of the plant material concentrated at ground level for *L. vulgare* (Fig. 5.3A). The canopy cover of *F. rubra* (84 %) was significantly higher than that for *L. vulgare* (66 %) (t-test: $t_8 = 3.09$, $p = 0.02$). The canopy height was also generally higher for *F. rubra* with a peak at 6 cm compared to 4 cm for *L. vulgare* (Fig. 5.3B). However, biomass was significantly higher for *L. vulgare* (312 g/m²) than *F. rubra* (106 g/m²) (t-test: $t_6 = -2.81$, $p = 0.03$), indicating a more rigid structure.

When only flow velocity was generated in the flume, the mean water flow velocity at all levels above the soil (along the x-axis) was greater in *F. rubra* than in *L. vulgare* stands (Fig. 5.3C). The flow velocity at 5 cm (in the vegetation) was lower than at the other two levels (mostly above the canopy) (Fig. 5.3c). However, both mean lateral and vertical turbulence at 5 cm for *L. vulgare* stands (lateral: 3.11 σ ; vertical 1.33 σ) were greater than for the *F. rubra* stands (lateral: 0.73 σ ; vertical: 0.88 σ) (lateral: $t_{4.098} = -4.04$, $p < 0.01$, vertical: $t_8 = -5.77$, $p < 0.01$).

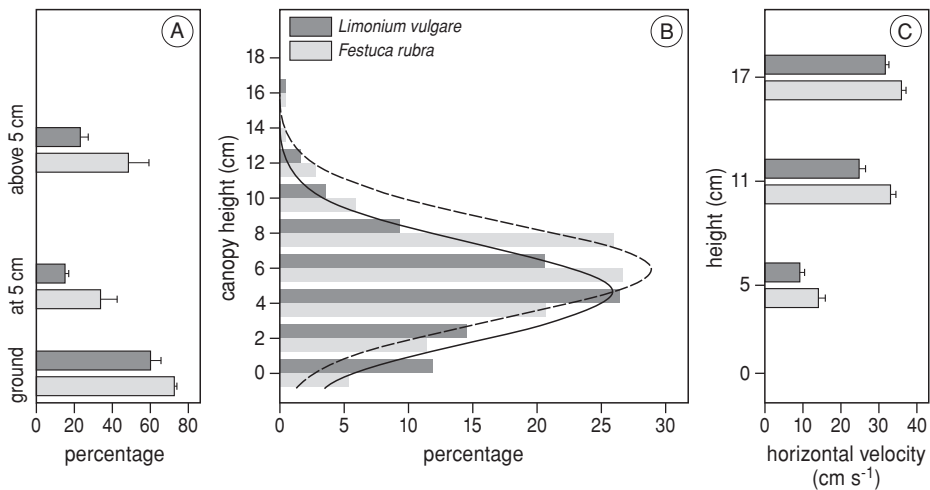


Figure 5.3 Parameters of vegetation structure and hydrodynamics at different heights: A) percentage frequency of hits for vegetation recorded with point quadrat method at ground, 5 cm above ground and above 5 cm, B) percentage frequency of canopy heights and C) measured horizontal flow velocity at 5 cm, 11 cm and 17 cm above ground. The dotted line represents the smoothed distribution in canopy height for *F. rubra*, whereas the solid line represents that for *L. vulgare*.

When examining the typical spatial distribution of velocities as demonstrated by one representative replicate each of *L. vulgare* and *F. rubra* stands, stream-wise velocity decreased with further distance into stands, although this pattern was more accentuated in *L. vulgare* than *F. rubra* (Fig. 5.4A & 5.4B). Low lateral-flow velocities were encountered at the leading edge of the vegetation containers but generally increased as water penetrated further into the *F. rubra* stand (up to 3 cm/s) (Fig. 5.4C). In contrast, pockets of high and low lateral-flow velocities were encountered throughout the *L. vulgare* stand (Fig. 5.4D). Patterns of vertical-flow velocities were similar to those found for lateral-flow velocities in both stand types (Fig. 5.4E & 5.4F).

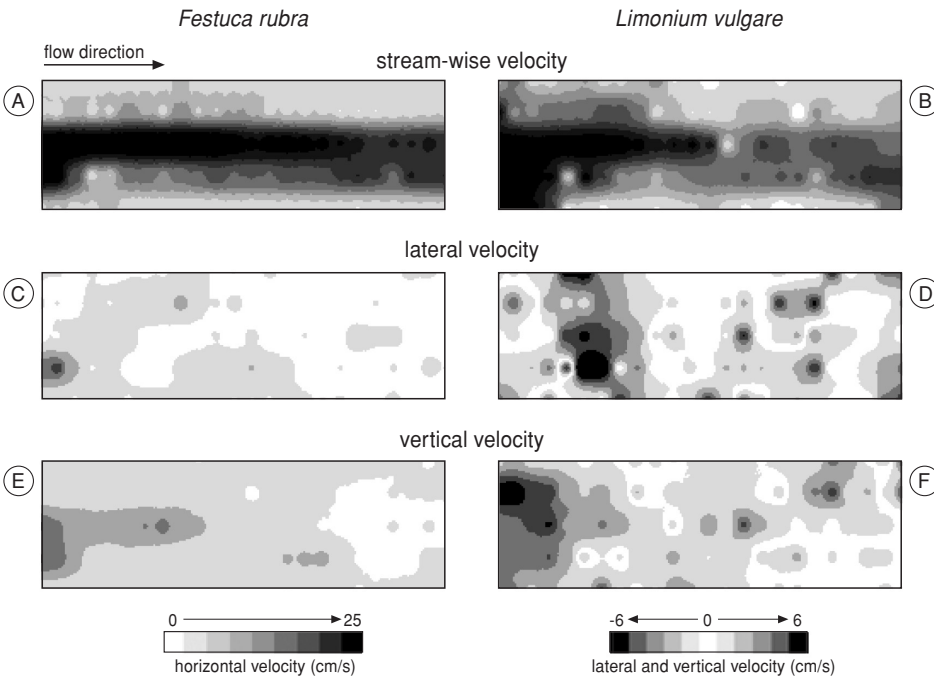


Figure 5.4 Spatial distribution of measured flow velocity in two stand types for stream-wise velocity (A & B), lateral velocity (C & D) and vertical velocity (E & F). Grey scale explained by inset legend. Note difference in scale between stream-wise velocity classes and classes for lateral and vertical velocity. The horizontal velocity legend is for A & B, and the lateral and vertical velocity legend is for C to F.

Discussion

The most important factors in predicting patterns of seed retention depend upon the moisture condition of the seeds in this study. Hydrodynamic variables are the most important determinants of retention under wet conditions. Because seeds do not float once waterlogged, wave-generated orbital water movement is necessary to dislodge and move seeds from the bottom to the water column, where they can be exported by current velocity. However, in the absence of such wave-generated orbital water movement, even high currents have a very limited ability to export waterlogged seeds.

As water currents encounter vegetation structures, current velocity decreases due to energy losses through hydrodynamic drag and generation of turbulence. For example, current velocity decreased with increasing distance from the leading edge of the bed in a flume study on *Zostera marina* beds, whereas mean turbulence intensity increased (Gambi *et al.* 1990). This transference of kinetic energy into turbulent energy was also demonstrated in our study, although this process was more marked for the more open stands of *L. vulgare* than for denser *F. rubra* stands (Fig. 5.4). As water flow passes through vegetation, turbulence intensity increases with the introduction of sparse vegetation but then decreases as stem population increases further (Nepf 1999), possibly through interactions between wakes produced behind individual stems (Green 2005). Thus seed retention was higher in the denser *F. rubra* stands compared to the more open *L. vulgare* stands that produced a higher turbulence for dry seeds. If turbulence intensity, resulting from interactions between flow velocity and vegetation resistance, is augmented by wave-generated orbital water movement, it is logical that significantly more seeds would be dislodged and exported as occurred in our waterlogged-seed experiment. The majority of hydrodynamic studies in vegetation have focussed on unidirectional flow rather than waves (see references in Bouma *et al.* 2005). However, the present study clearly demonstrates that it is necessary to include waves in order to understand transport processes (Fig. 5.2C and 5.2D), especially for all particles that have a limited floating capacity.

When seeds are dry, differences in floating ability and traits for retention become more important in explaining patterns of seed retention. In the field experiment, seed type was more important than vegetation structure in explaining patterns of seed retention. Similarly in the flume study, where differences in structure were greater between stand types, seed type was still the most important factor for the dry-seed experiment. In contrast, some minor differences were found between the distribution of small cypress seeds and more buoyant, larger tupelo fruits in a swamp but most of the patterns in distribution were explained by trapping by emergent vegetation structures (Schneider & Sharitz 1988). However, the differences in floating ability between seeds of bald cypress and tupelo (2 x) were

much less than those between *P. maritima* and the other two species in our study ($\sim 48 \times$). Retention of *P. maritima* seeds (with mucilaginous seed coats) was much higher, whereas seeds of *S. maritima* and *E. atherica* behaved similarly. If we had only used the latter two species, vegetation structure would have explained more of the retention patterns than seed type.

With respect to movement, seeds face two different challenges in this system. Firstly, they must disperse in order to colonize new areas, escape from higher mortality near con-specifics or find microsites that enhance establishment probability (Howe & Smallwood 1982). Secondly, once reaching a suitable microsite, they must stay long enough to imbibe water, germinate and establish. In our tidal system, seeds are likely driest in late summer and autumn during the period of initial detachment from parent plants. Both dispersal probability and distance would be enhanced by higher buoyancy of dry seeds and strong tidal action is not necessary to dislodge seeds as they float up even with a gentle upcoming tide (Fig. 5.2C & 5.2D).

Seeds are more likely to be waterlogged from late autumn to early spring when secondary dispersal by tidal water will redistribute seeds. Tides are generally higher and storms also occur more frequently during this period. Once waterlogged, many seeds will tend to remain at a microsite unless they are dislodged by wave action, as occurs during storms. On the salt marsh of Schiermonnikoog, the highest density and diversity of seeds captured by traps were found during a stormy period (Chapter four). After the last storm of the season, there may be some localized dispersal but many seeds will be retained at microsites, especially if located in dense vegetation, thus setting the template for seedling establishment or incorporation into the soil seed bank.

In conclusion, the same seed can have traits that enhance dispersal and retention, depending upon the moisture conditions of the environment. Thus the level of moisture can act as a type of switch in this system, determining whether seed traits or hydrodynamics, influenced by vegetation structure, will most influence patterns of seed entrapment. Further studies are needed to build empirical or mechanistic relationships between seed retention and predictor variables such as flow velocity, wave action, vegetation resistance and buoyancy. However, this study provides a way to integrate the opposing processes of dispersal and of retention into a single conceptual model on the same scale as these processes act on seeds.

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Chapter 6

The role of dispersal constraints in the assembly of salt-marsh communities: a synthesis

Introduction

In Chapter one, a conceptual framework of the dynamics of community assembly was introduced that indicated how dispersal constraints of seeds could restrict community development. The empirical studies in Chapters two to five were directed at defining the membership of community species pools present at different stages of community development and exploring more subtle considerations regarding timing and method of arrival of seeds of the different species. In the present chapter, I examine the composition and abundance of species in the seed rain and soil seed bank, as well as the established vegetation, along a sequence of communities at different stages of development in order to evaluate the potential role of dispersal constraints in influencing community structure. I also consider a case study of one species, *Elytrigia atherica*, for which molecular methods were used to reconstruct the scale of realised dispersal in the salt-marsh communities of Schiermonnikoog and integrate these results with data of proxies of dispersal used in my empirical studies. Finally, I indicate possible directions for future research on this subject.

Constraints in species composition

The species composition of salt-marsh communities is most strongly constrained by conditions that restrict establishment (E in Figure 1.5). As suggested by Keddy (2000), salinity tolerance is a very important filter in the assembly of salt-marsh communities. Dispersal filters also play a role but act together with establishment filters to constrain species richness in communities as is the case for many plant populations (Eriksson & Ehrlén 1992).

The regional species pool for salt-marsh communities in central North-Atlantic Europe contains 36 species, as defined in Wolters *et al.* (2005) (Table 6.1). A description of the compilation of this regional species pool is given in Chapter one. As communities develop, the percentage of the regional species pool present in the established vegetation rises from 22 % in the 10-year-old community to a peak of 44% in the 30-year-old community, but decreases to 36 % in the 100-year-old community.

Only three of these species (8 % of the regional species pool) are filtered out at the stage of dispersal from the regional to the local scale (A in Table 6.2). Of these species, *Spartina maritima* is very rare in the Netherlands and only occurs in the south-west of the country (Table 6.1).

Of the 33 species found in the Oosterkwelder, fourteen species (39 %) are filtered out of communities at the dispersal stage between the local and community scales (B in Table 6.2). One group of these species can be found close (tens of

metres) to the communities of interest in nearby high salt-marsh and dune communities which are at higher elevations (*Carex distans*, *Carex extensa*, *Cochlearia danica*, *Lotus corniculatus*, *Potentilla anserina*, *Puccinellia distans* and *Trifolium repens*). Despite the presence of seed sources (reproducing adult plants) within short distances (tens of metres), seeds of these species were not found in either the seed rain or soil seed bank at any of the studied communities with the exception of *Trifolium repens*. *T. repens* entered the community species pool as seed after 30 years of development but never managed to establish successfully. Species in the second group (*Bolboschoenus maritimus*, *Festuca arundinacea*, *Juncus maritimus*, *Oenanthe lachenalii*, *Ononis repens* subsp. *spinosa*, *Trifolium fragiferum*) are found within a kilometre of the 100-year-old community.

Recruitment cannot occur without seed arrival but seed arrival is no guarantee of recruitment (Nathan & Muller-Landau 2000). Almost all of the species filtered out at the stage of local dispersal are those tolerant of brackish but not saline conditions (Table 6.1). Seeds may arrive very infrequently and in very low numbers, as a result of dispersal constraints. However, these species are also unlikely to establish under the demanding conditions of a low-elevation salt-marsh, such as high salinity, wave action, loose sediments and wader/shore bird predation.

Only one species is potentially constrained at the stage of seed-bank formation (i.e. does not disperse over time) (C in Table 6.2). *Atriplex portulacoides* was present in established vegetation and produced viable seeds (40 and 286 seeds m⁻² in the 10- and 15-year-old communities respectively) but seeds were not detected in the soil seed bank. Seeds of *A. portulacoides* are relatively large and remain attached to buoyant fruits after detachment (E.R. Chang, personal observation). Due to their relatively larger size, seeds are not likely to percolate downwards through the soil unlike smaller seeds which are more likely to be buried (Peart 1984; Thompson *et al.* 1994). However, *A. portulacoides* appears to spread widely and effectively through dispersal over space. Seeds of this species were present in seed traps (up to a mean of 0.28 seeds m⁻² day⁻¹, 0.17 % relative abundance) and driftlines (from mean of 10 to 240 seeds m⁻², 0.04 % to 0.8 % relative abundance) at low relative abundance to seeds of other species (Chapter four), and were found at high relative abundance (~7 seeds per sample, 12 % relative abundance) in a net cast by a boat between the mainland and Ameland, one of the islands in the Dutch Wadden Sea (Wolters *et al.* 2006). The larger size of the seeds, while detrimental to burial processes, may enhance establishment success of seedlings due to higher resources initially provided by the endosperm (Westoby *et al.* 2002; Moles & Westoby 2004).

Only two species (5 % of the regional species pool), *Puccinellia maritima* and *Spartina anglica*, are potentially constrained by viable seed production (D in Table 6.2). These species were present along the community sequence in established vegetation but were absent (or very rarely found) in soil seed banks or in seed

Table 6.1 Species-pool membership of species capable of coexistence in salt-marsh and brackish-water plant communities at different scales. 1 = present, 0 = absent, v = established vegetation, sr = seed rain, sb = soil seed bank. Salinity tolerance of species is also shown according to a classification modified from Scherfse (1987): 1 (0-0.54 % salinity), 2 (0.55-1.08 %), 3 (1.08-1.72 %), 4 (1.72-2.9 %), 5 (2.9-4.15 %), 6 (> 4.16 %).

Regional species pool	Salinity tolerance	Local species pool	Community species pool(10-year-old community)			Community species pool (15-year-old community)			Community species pool (30-year-old community)			Community species pool (100-year-old community)		
			v	sr	sb	v	sr	sb	v	sr	sb	v	sr	sb
<i>Agrostis stolonifera</i>	3/4	1	0	1	1	0	1	1	0	1	1	0	0	1
<i>Aster tripolium</i>	5	1	1	1	1	1	1	1	1	1	1	1	0	1
<i>Atriplex portulacoides</i>	5	1	1	1	0	1	1	0	1	1	0	1	0	0
<i>Atriplex prostrata</i>	4	1	0	1	1	0	1	1	1	1	1	1	1	1
<i>Blysmus rufus</i>	3	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Bolboschoenus maritimus</i>	3/4	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Carex distans</i>	3	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Carex extensa</i>	3/4	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Centaurium pulchellum</i>	3	1	0	0	0	0	0	1	0	0	1	0	1	0
<i>Cochlearia danica</i>	2	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Elytrigia atherica</i>	3/4	1	0	1	0	0	1	1	1	1	1	1	1	1
<i>Festuca arundinacea</i>	2	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Festuca rubra</i>	4	1	0	1	1	1	1	1	1	1	1	1	1	1
<i>Glaux maritima</i>	4	1	0	1	1	1	1	1	1	1	1	1	1	1
<i>Hordeum marinum</i>		0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Juncus gerardi</i>	4	1	0	1	1	0	1	1	1	1	1	1	1	1
<i>Juncus maritimus</i>	3/4	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Limonium vulgare</i>	5	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Lotus corniculatus</i>	2	1	0	0	0	0	0	0	0	0	0	0	0	0

Table 6.1 Continued

Regional species pool	Salinity tolerance	Local species pool	Community species pool (10-year-old community)			Community species pool (15-year-old community)			Community species pool (30-year-old community)			Community species pool (100-year-old community)		
			v	sr	sb	v	sr	sb	v	sr	sb	v	sr	sb
<i>Oenanthelachenalii</i>	2	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Ononis repens</i> subsp. <i>spinosa</i>	1	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Plantago coronopus</i>	2/3	1	0	1	1	0	0	1	0	1	0	0	1	0
<i>Plantago maritima</i>	4	1	0	1	0	1	1	1	1	1	1	0	1	1
<i>Potentilla anserina</i>	3	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Puccinellia distans</i>	3/4	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Puccinellia fasciculata</i>		0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Puccinellia maritima</i>	5	1	1	1	0	1	0	0	1	0	0	1	0	0
<i>Salicornia</i> spp.	5/6	1	1	1	1	1	1	1	1	1	1	0	1	1
<i>Seriphidium maritimum</i>	4	1	0	1	0	1	1	0	1	1	0	1	0	0
<i>Spartina anglica</i>	5	1	1	0	0	1	0	0	1	0	0	0	0	0
<i>Spartina maritima</i>		0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Spergularia media</i>	5	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Suaeda maritima</i>	5/6	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Trifolium fragiferum</i>	3	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Trifolium repens</i>	2	1	0	0	0	0	0	0	0	0	1	0	1	1
<i>Triglochin maritima</i>	5	1	0	0	0	1	0	0	1	0	1	1	0	1
Total number of species (% of regional species pool)		34 (94%)	8 (22%)	16 (44%)	11 (30%)	13 (36%)	14 (39%)	14 (39%)	16 (44%)	15 (42%)	15 (42%)	13 (36%)	13 (36%)	14 (39%)

Table 6.2 Groups of species constrained at different stages of community assembly. ¹constrained only in younger communities, ²constrained only in older communities, ³constrained at both very young and very old communities, *constrained at multiple stages

A	B	C	D	E	
Dispersal from regional to local scale	Dispersal from local to community scale	Burial, survival into the soil seed bank	Seed production and seed predation/pathogens	Seed retention, germination and establishment (competition/facilitation, herbivory/pathogens, abiotic stress, disturbance)	No constraints
<i>Hordeum marinum</i>	<i>Blysmus rufus</i>	<i>Atriplex portulacoides</i>	<i>Puccinellia maritima</i>	<i>Agrostis stolonifera</i>	<i>Aster tripolium</i>
<i>Puccinellia fasciculata</i>	<i>Bolboschoenus maritimus</i>		<i>Spartina anglica</i> *	¹ <i>Atriplex prostrata</i>	<i>Limonium vulgare</i>
<i>Spartina maritima</i>	<i>Carex distans</i>			<i>Centaurium pulchellum</i>	<i>Salicornia europaea</i>
	<i>Carex extensa</i>			¹ <i>Elytrigia atherica</i>	<i>Spergularia media</i>
	<i>Cochlearia danica</i>			¹ <i>Festuca rubra</i>	<i>Suaeda maritima</i>
	<i>Festuca arundinacea</i>			¹ <i>Glaux maritima</i>	
	<i>Juncus maritimus</i>			¹ <i>Juncus gerardi</i>	
	<i>Lotus corniculatus</i>			<i>Plantago coronopus</i>	
	<i>Oenanthe lachenalii</i>			³ <i>Plantago maritima</i>	
	<i>Ononis repens</i> subsp. <i>Spinosa</i>			<i>Seriphidium maritimum</i> *	
	<i>Potentilla anserina</i>			² <i>Spartina anglica</i> *	
	<i>Puccinellia distans</i>			<i>Trifolium repens</i> *	
	<i>Trifolium fragiferum</i>			¹ <i>Triglochin maritima</i> *	
	¹ <i>Trifolium repens</i> *				

rains. Attack by herbivores or pathogens may prevent viable seed set in these species. For example, ergot fungus was found to have a detrimental effect on seed set in *Spartina anglica* (Raybould *et al.* 1998). However, given the wide distribution of these species, they appear to disperse successfully by vegetative propagation. *P. maritima* often forms large patches as a result of stoloniferous growth and *S. anglica* is strongly rhizomatous (Stace 1997). Also, larger parts of these plants may break off during storm conditions, travelling long distances and successfully establishing elsewhere. Vegetative propagules (leaves, shoots and rooted tillers) of a related species, *Puccinellia phryganodes* (Trin.) Scriber and Merr, were able to establish in sediments in a Canadian salt marsh (Chou *et al.* 1992).

Thirteen species (36 %) show evidence of being filtered out by the site conditions at one or more of the four communities along the sequence (E in Table 6.2). Of these species, four of them (*Agrostis stolonifera*, *Centaureum pulchellum*, *Plantago coronopus* and *Trifolium repens*) enter the community species pools often as seeds but never successfully establish in low-elevation salt-marsh communities. These species are tolerant of brackish, rather than saline conditions (Table 6.1). Others species are present in the community species pool as seeds but do not establish in the vegetation until the communities reach a certain stage of development. They include *Atriplex prostrata*, *Elytrigia atherica*, *Festuca rubra*, *Glaux maritima*, *Juncus gerardi* and *Seriphidium maritimum*. Establishment in younger salt-marsh communities can be constrained by stressful abiotic conditions such as high salinity for some species (Bakker *et al.* 1985). *Spartina anglica*, which appears to establish largely as a result of vegetative propagation, was not present in the oldest community. Interspecific competition within the 100-year-old community may exclude this species. *Plantago maritima*, although present in all community pools as seeds (soil seed bank, seed rain), is excluded as adult plants from both the youngest and oldest communities due to physical instability and competition respectively.

Five species (*Aster tripolium*, *Limonium vulgare*, *Salicornia europaea*, *Spergularia media* and *Suaeda maritima*) are present in all components of the community species pools along the community sequence. Two of these species are annuals, most show high fecundity and are salt-tolerant (Table 6.1). They are found most commonly in early to mid stages of salt-marsh development (Chapter two). *A. tripolium* is one of the few species which appear to be adapted to anemochory (wind dispersal) in these salt-marsh communities, and *L. vulgare* is one of the most common and abundant species, especially in middle stages of community development.

The conclusion that the composition of species in communities is most strongly constrained by establishment filters is collaborated by the results of one of the few seed-addition experiments conducted in salt-marsh communities. Seed introduction of species across habitats along a tidal elevation gradient did not result in higher rates of seedling establishment in a New England salt marsh (Rand 2000).

Patterns in seed deposition have been correlated to patterns in species distribution and diversity in many systems such as rivers (Nilsson *et al.* 1991; Nilsson *et al.* 1994; Honnay *et al.* 2001; Nilsson *et al.* 2002), swamps (Schneider & Sharitz 1988) and neotropical forests (Dalling *et al.* 2002). However, many studies which considered both seed and microsite limitation of community composition and species richness concluded that both types of filters play a role in regulation of recruitment (Eriksson & Ehrlén 1992; Tilman 1997; Zobel *et al.* 2000; Verheyen & Hermy 2001; Foster & Tilman 2003).

Species which are excluded from the community species pools often require brackish conditions (abiotic filters) in order to establish (Table 6.1). Long-distance dispersal events by these species are sufficiently rare so that seeds were not found by the methods used in this study. Unable to establish at local sites from which they could potentially invade communities at the local scale, they remain excluded from the seed rain and the soil seed bank.

Constraints in species abundance

For the species found in the community species pools, patterns of abundance in the seed rain and soil seed bank generally followed spatial patterns of established plants in the vegetation of marshes of different ages (Chapters two and four). As discussed in previous chapters, these patterns imply primarily local dispersal of propagules. However, patterns of seed rain are influenced by many factors other than dispersal *per se* including the distribution of seed sources, densities of seed sources, seed production and landscape features that trap seeds (Levine & Murrell 2003). The presence of viable seeds within the soil seed bank is influenced additionally by depth of burial and the survival rates of seeds of individual species.

The seed-production data collected for seven species (33% of all species found in the community species pools) at our site suggest that the seed rain is generally constrained by low seed production per unit area when abundance of adult plants is low (Chapter four). Past a certain threshold of adult abundance, however, the amount of seed produced becomes one to three orders of magnitude higher than that in the seed rain, suggesting that there is a high rate of net seed loss from the site that limits establishment of species. In other words, interactions between locations of the source of dispersed seeds and landscape features that trap seeds strongly influence patterns of seed rain when the abundance of adult plants is higher than a threshold value. In this thesis, the dominance scale was used as an index for adult abundance as Olff *et al.* (1997) illustrated that patterns in dominance of species generally reflect those in frequency of species, although the pattern may be amplified or dampened. For *Salicornia europaea*, this threshold was reached when adult plants attained a mean dominance value of 1 (*i.e.* they were

the fourth most abundant species found in the vegetation), whereas this threshold was reached earlier for *Atriplex prostrata* (mean dominance value of 0.6).

Seeds are highly mobile during storm surges and relatively few seeds appear to be retained on the salt-marsh surface during these events. There are two important sinks for seeds in this system: the driftline and the Wadden Sea. Due to interactions between the dispersal vector (tidal water) and landscape elements, extremely high concentrations of seeds were found in driftlines after storms (31 115 and 23 851 seeds m⁻² respectively in the 15- and 100-year-old communities), although no low-elevation salt-marsh species ever established in driftlines (Chapter four). With respect to seeds drifting out to sea, a study conducted off the coast of Schiermonnikoog indicated that few seeds and low diversity of seeds float towards the island during a flood tide, whereas many more seeds floated away from the island of Ameland during an ebb tide (Wolters *et al.* 2006). These data are supported by a study using floating and standing nets conducted in a salt marsh in the south of the Netherlands. Huiskes *et al.* (1995) observed significantly more seeds exported from a marsh by ebb flow than seeds imported to a marsh during flood tides. The fate of seeds that enter the Wadden Sea is uncertain. The vast majority are likely to perish before finding suitable habitats for establishment. However, the small minority that survives and succeeds in establishing far from their dispersal origin has important consequences for the genetic structure of populations and species composition of communities in coastal ecosystems (Cain *et al.* 2000).

In summary, the abundance of species in salt-marsh communities is influenced by processes controlling seed deposition and retention rather than those regulating dispersal *per se*. Retention rates of seeds of *Suaeda maritima* and *Elytrigia atherica* on the surface of the salt marsh during one tidal inundation were low (mean retention rates of 11 % to 27 %), whereas retention rates were much higher for *Plantago maritima* (mean retention rates of 39 % to 85 %), which has a mucilaginous seed coat (Chapter five). Many seeds appear to remain close to parent plants, reinforcing existing patterns of abundance, but some are exported by tidal water to face uncertain fates in driftlines and the sea. Seed augmentation experiments of salt-marsh communities conducted in the Netherlands (Bakker *et al.* 1985; Bakker & de Vries 1992) and north-eastern coast of the United States (Rand 2000) reported increased seedling recruitment after sowing, indicating that seed limitation affected species abundance. In a recent review, Levine & Murrell (2003) also suggest that the flooding which occurs in hydrochorous systems can export most of the seeds produced, resulting in seed limitation in these communities.

Constraints in timing of dispersal

Temporal patterns in seed dispersal at all three temporal scales (seasonal, short-term and long-term) were strongly influenced by the action of episodic storm surges (Chapter three). Storm surges resulted in greater abundance and diversity of captured seeds, more long-distance dispersal and affected younger communities more than older communities. The general quality of deposition during storm surges is not very good with many seeds being highly concentrated in driftlines or set adrift in the open water. However, the relatively few seeds that adhere to the marsh surface may receive an advantage due to the benefits of a disturbance that removes some of the competition. The distribution of species is likely enhanced, whereas the abundance of species is likely restricted by the high transport potential of storm surges.

Timing of dispersal can also be influenced by the presence of persistent seed banks in the soil through a storage effect (Belyea & Lancaster 1999). Very few species, however, formed long-term persistent soil seed banks in these salt-marsh communities (Chapter two). Artificial burial experiments predicted that seed banks of five tested species would be depleted before five years after burial (Chapter two). Despite local patterns of erosion and sedimentation in the marshes, most seeds do not survive for long periods of time and are unable to colonise communities in this manner. Perhaps it is because salt marshes are more variable and unpredictable over space than over time, due to tidal cycles, that not much effort is expended towards this strategy.

Elytrigia atherica: a case study of dispersal vs. establishment constraints

The perennial, rhizomatous grass, *Elytrigia atherica*, propagates itself through both clonal growth and sexual reproduction. It is the dominant species in this and many other salt marshes in north-western Europe in communities at mid-to-high elevations. In recent years, it has also invaded low-elevation marshes where formerly it was absent (Bockelmann 2002). I compare the data for established plants and seed dynamics presented in this thesis with information of the genetic structure of populations (Bockelmann *et al.* 2003) to gain further insights into how dispersal constraints influence the distribution and abundance of *E. atherica*.

In low-elevation communities, *E. atherica* is absent from the vegetation until the later stages of community development (Table 6.3). Its dominance was recorded in the vegetation at two different times in this study. Four years after the initial survey, it had increased its dominance in the two older stages of community development at low-elevation sites, although its dominance remained low. Seeds of

Table 6.3 Vegetation and seed data collected for *Elytrigia atherica* on Schiermonnikoog.

	Year of community establishment			
	1993	1986	1974	1913
Vegetation (dominance scale: 0 – 4)				
Sampled 1997	0	0	0	0.62 ± 0.06
Sampled 2001	0	0	0.04 ± 0.03	0.86 ± 0.05
Soil seed bank (seeds m ⁻²)				
Sampled fall 1996; upper	0	4.3 ± 4.3	8.7 ± 5.8	0
Sampled fall 1996; lower	0	0	0	4.3 ± 4.3
Sampled summer 2001; upper	0	0	0	0
Sampled summer 2001; lower	0	0	0	0
Seed germination after 2 years of burial (%)	18 ± 5.6	-	54 ± 3.2	-
Seed production in 2002 (seeds m ⁻²)	0	0	0	186
Seed rain (November to May)				
2001/2002 (seeds m ⁻²)	0.99 ± 0.66	2.0 ± 1.3	1.5 ± 0.75	15 ± 4.7
2002/2003 (seeds m ⁻²)	0.49 ± 0.49	2.5 ± 1.3	14 ± 11	14 ± 6.4
Driftline (seeds m ⁻²)	-	830 ± 200	-	17 000 ± 7300

E. atherica were missing from the soil seed bank at the youngest community stage and were present at very low densities in the other communities. Also, seeds were found in the soil only in autumn, soon after initial detachment from parent plants, indicating a transient seed bank (i.e. survives less than one year in the soil) (Thompson *et al.* 1997). However, when seeds are buried artificially, some seeds are capable of surviving at least two years in the soil (Chapter two). This suggests that burial constraints may limit amounts of viable seed in the soil.

Seed production by plants of *E. atherica* was only detected in the oldest community (100 years-old). Quantities of seeds (186 seeds m⁻²) were relatively low compared to amounts produced by annual species such as *Atriplex prostrata* (range from 172 to 7216 seeds m⁻²), *Salicornia europaea* (14 227 to 51 592 seeds m⁻²) and *Suaeda maritima* (231 to 9028 seeds m⁻²) but comparable to those produced by perennial species such as *Atriplex portulacoides* (40 to 286 seeds m⁻²), *Plantago maritima* (94 to 236 seeds m⁻²) and *Triglochin maritima* (116 seeds m⁻²). Seeds were present in the seed rain across the community sequence but they were found only at extremely low densities in the younger communities, indicating very low rates of deposition on the marsh surface away from parent plants. The abundance of seed in the seed rain increased over time but the quantity of seeds produced at the 100-year-old community (186 seeds m⁻²) was one order of magnitude higher than that found in the seed rain (15 seeds m⁻²), suggesting a high export of seeds from the system as indicated by the extremely high densities of seeds in the driftline close to the oldest community (17 000 seeds m⁻²). In the sea between the main-

land and Ameland, seeds of *E. atherica* were one of the most abundant seeds caught in nets in late autumn during an ebb tide (~40 seeds per sample), comparable to numbers of trapped seeds of very fecund annuals, such as *Salicornia europaea* and *Suaeda maritima* (Wolters *et al.* 2006). However, no seeds of *E. atherica* were captured returning to land off the coast of Schiermonnikoog. In summary, *E. atherica* produced relatively few seeds in the low marshes, most of them were exported and few were detected returning to the system on flood tides. Does this relatively high investment in long-distance dispersal pay off for this species?

At a macrogeographical scale of around 500 km, six populations sampled at six sites along the coast of Germany and the Netherlands (three populations from Schiermonnikoog) showed a very weak but significant correlation between genetic differentiation and geographic distance at distances greater than 60 km ($R^2 = 0.095$, $p_{\text{mantel}} = 0.04$, 5000 permutations) using microsatellite techniques (Bockelmann *et al.* 2003). Surprisingly, more of the variance in genetic structure could be explained by habitat (low or high marsh with a maximum geographical separation of 80 m) (61 % of variance explained by model) than by site (39 % of variance explained by model). An unpublished study conducted at the microgeographical scale on Schiermonnikoog (1500 m between a 25-year-old community and a 35-year-old community) also showed greater genetic differences *within* sites than *between* sites (Scheepens, J.F., Veeneklaas, R.M., van de Zande, L. & Bakker, J.P., University of Groningen, unpublished data). Although genetic differentiation (determined by using the same microsatellite techniques as in the first study) between the two communities was significant ($p < 0.001$), only 10 % of the variance explained by the model could be attributed to between-site differences whereas 90 % of the variance was due to within-site differences.

Both these studies indicate that gene flow (*i.e.* successful establishment by seeds) is more frequent between sites than between different habitats within a site. Parallel transplant experiments of *E. atherica* showed that resistance to herbivores (important in the low marshes) and competitive ability (important in high marshes) differs among genotypes from high- and low-elevation marshes (Bockelmann 2002). Local adaptation due to strong selection pressures along the inundation gradient has also been demonstrated for salt-marsh species such as *Salicornia europaea* (Jefferies & Gottlieb 1982; Davy & Smith 1985), *Aster tripolium* (Gray 1974), *Festuca rubra* (resistance to manganese in Singer & Havill 1985), *Armeria maritima* and *Plantago maritima* (resistance to manganese in Singer & Havill 1993).

Despite the potential hazards of long-distance dispersal, dispersal filters are less stringent than microsite filters in determining successful establishment for this species. In fact, seeds may need to move either very short distances or very large distances in order to successfully establish rather than to move intermediate distances up or down an elevation gradient with the tides within a marsh.

Assessment of conceptual model and methods

The conceptual model of community assembly introduced in Chapter one is more easily applicable to identify and explore constraints in patterns of species composition than in species abundance, due to its simplified approach to species membership (*i.e.* absent or present). Adding probability functions at each stage of the assembly process, as suggested by Zobel *et al.* (1998), and estimating the value of the functions for a particular site would allow for prediction of the abundance of different species in a community.

The hierarchical approach of the model, however, allows more precise identification of the nature and timing of constraints in the assembly of communities than binary models which only consider microsite *vs.* seed limitations. For example, seed-limited populations and communities are more likely to be constrained by the distribution and abundance of seed sources, and seed production rather than seed dispersal as argued by Levine & Murrell (2003) but a binary model would not be able to discern between these potential causes.

Methods used for investigation in this thesis included both descriptive and experimental approaches. When exploring patterns in composition of entire communities and different species pools, multivariate techniques were useful because large quantities of information could be succinctly summarised and integrated (Chapters two to four). Also, hypothesis testing facilities allowed for statistical comparison of the composition and abundance of species *within* different pools (*e.g.* vegetation, soil seed bank, seed rain) along the chronosequence and elevational gradient, and *between* different sampling periods and dispersal agents. A type of multivariate correlation, as described in Chang *et al.* (2001), would have been convenient to make comparisons between different pools (*e.g.* vegetation *vs.* seed rain). However, the dominance scale used to describe the vegetation did not provide high enough resolution to use this method.

The flume facility proved to be very useful in carrying out manipulative experiments in this subject matter. The controlled hydrodynamic environment in the flume tank can be seen as a direct analogue of wind tunnels used to help build and test models of wind dispersal (Johnson & Fryer 1992; van Dorp *et al.* 1996; Jongejans & Schippers 1999). Of the different systems of dispersal (*e.g.* hydrochory, anemochory, endozoochory, epizoochory, anthropochory), theoretical models of wind dispersal are the most advanced. With judicious use of flume tanks, similar models could be built for water-driven systems.

Directions for future research

Although most of the seeds deposited on the salt-marsh surface most likely came from nearby sources, the effect of long-distance dispersal on recent patterns of

colonisation was surprisingly strong in the late-successional dominant, *Elytrigia atherica*. I used proxies and correlations to estimate dispersal due to the difficulties in tracking the movement of 21 species. Mass marked release techniques could be useful in tracking actual dispersal (Turchin 1998) but the seeds of species in these communities are extremely small and physical markings change the floating capacity (Havik 2004). Tracking rare long-distance dispersal events can be challenging but genetic methods are proving successful as shown by the two studies on *E. atherica* discussed earlier. However, genetic studies only detect seed movement if it results in successful recruitment (Nathan & Muller-Landau 2000). A combination of ecological (surveys of natural communities, experiments), molecular and comparative ecological techniques would provide the most complete information.

Three main directions in future research are suggested by the results of this thesis in order to further evaluate the effects of dispersal constraints on the structure of salt-marsh communities and to further study possible mechanisms for constraints: studies on gene flow, seed-addition experiments and analyses of species' traits using information contained in databases (ecoinformatics). Genetic studies can be time consuming and expensive, especially if suitable microsatellite primers are unavailable for species and must be developed (Bockelmann *et al.* 2003). However, given the surprising results for *E. atherica*, studies should be conducted on the genetic population structures of other species. Species of high priority are pioneer annuals, which have very different life-history strategies than *E. atherica* and whose abundance in communities is more likely to be seed-limited (Turnbull *et al.* 2000).

Seed-addition experiments can be inherently difficult in tidal habitats where most added seeds are simply washed away. Addition of seeds at densities of 500 m⁻² and 5000 m⁻² in a salt-marsh restoration site in Tollesbury, England, resulted in no observed germination (Reading *et al.* 2002; Garbutt *et al.* 2006). In seed-addition experiments conducted by Bakker *et al.* (1985) and Bakker & de Vries (1992) on Schiermonnikoog, sites were high enough that they were not regularly inundated during the period of the study. Seed-addition experiments are necessary to reveal whether the distribution and abundance of species in salt-marsh communities are influenced by seed limitation. Also, the order of arrival in communities can be manipulated by using seed-addition experiments to order to explore whether the sequence of arrival influences the dynamics of community assembly as has been demonstrated in both theoretical and empirical studies (Drake 1990; Eriksson & Eriksson 1998).

In the conceptual model of community assembly as proposed by Keddy (2000), which was introduced in Chapter one, the filters select for or against certain *traits*. In this thesis, I did not explicitly screen species for traits and interpret the composition of species pools from this perspective. However, this final step is necessary to be able to generalise the results of this thesis to other systems. Overdispersion

of traits (traits that diverge during the assembly process) indicates strong biotic interactions that keep coexisting species from being too similar, whereas underdispersion (traits that converge) indicates strong abiotic factors that keep traits within certain limits (Weiher *et al.* 1998).

One possible effect that strong dispersal constraints could have on patterns of dispersability traits is that long-range dispersers would be more abundant in early stages of community development, whereas short-range dispersers would increase in abundance at later stages (Hovestadt *et al.* 2000). Patterns in dispersability over time (*i.e.* seed persistence) are predicted to be similar to those over space with persistent seed banks predicted for early-successional communities and transient seed banks predicted for late-successional communities (Fenner 1987). The development of widely accessible databases to integrate the information gathered from many empirical studies, such as the LEDA traitbase for the Northwest European flora (Knevel *et al.* 2003), greatly facilitates such analyses as screening traits can be extremely time-consuming. An analysis of multiple traits would allow for a more comprehensive assessment of the relative importance of different types of filters (dispersal, environmental, dispersal) during the assembly of communities.

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Summary

The presence and population size of different species in plant communities can be influenced by a number of different factors. The environmental conditions of the site where the community is located may predispose whether species are able to establish or not. The interactions between species (e.g. competition or facilitation) at a site may also determine whether species persist, spread or disappear from a community. For the past few decades, ecologists have focussed on these types of local-scale explanations for community patterns. However, species may also have to travel to a site in order to have the possibility of joining a community. Using a sequence of communities increasing in age (*i.e.* chronosequence) on a coastal Dutch island, Schiermonnikoog, as a model system, I explored how the mobility of plant species (*i.e.* dispersal constraints) can influence the composition of salt-marsh communities.

Soil seed bank generally reflects plant community

Studying the relationship between patterns in the vegetation (*i.e.* plant community) and soil seed bank (*i.e.* reserve of seeds stored in the soil) along a community sequence can predict which types of factors influence community composition (Chapter two). Three possible relationships are proposed: the similarity between the vegetation and soil seed bank is a) relatively high and does not consistently increase or decrease with age, b) decreases as communities age and c) is relatively low and does not consistently increase or decrease with age.

The Sørensen similarity index ranged between 0.47 and 0.73 with no consistent patterns along the age gradient. Multivariate analysis indicated that the most important factor in explaining species variance in the vegetation (75.1 %) and soil seed bank (61.4 %) in these communities was the age of the community. Also, the positions of species along the age gradient were similar for the vegetation and soil seed bank, indicating similar trends in abundance of species both above-and-below ground. The relationship between the vegetation and soil seed bank for the salt-marsh communities on Schiermonnikoog most closely resembled the first proposed relationship, thus indicating that seeds of many species remain close to their parent plants despite regular tidal inundations.

Small herbivores (hares and geese) less important than tidal water in dispersing seeds

Having established that limited mobility of seeds may influence communities, the effectiveness of different agents that transport seeds was compared in Chapter three. I studied how seeds move through the digestive systems of hares and geese

(endozoochory) on Schiermonnikoog by examining the contents of their droppings a) collected along the community sequence and b) after experimentally feeding them a set amount of seeds. I also trapped seeds dispersed by tidal water using Astroturf® mats.

Hares deposited more seeds of mid-successional, perennial, high-marsh species than geese, which deposited more seeds of early-successional, annual, low-marsh species. Seed survival and germination of salt-marsh species were higher after ingestion and passage through the digestive system of hares (10 % to 40 %) compared to geese (2 % to 13%). However, small herbivores dispersed two orders of magnitude fewer seeds than those dispersed by tidal water. Therefore, they are not likely to be important factors influencing community composition at this coastal island in the Netherlands.

Storms strongly affect seed movement

Results indicated that hydrochory (*i.e.* seed dispersal by water) is more effective than endozoochory (*i.e.* internal seed dispersal by animals) on Schiermonnikoog. In Chapter four, I further explored the factors influencing the movement of seeds by tidal water including timing of dispersal. Species compositions of vegetation, seed rain, seed production and driftlines along a sequence of communities were compared on Schiermonnikoog.

Storm surges had a positive significant effect on seed-rain patterns as the highest density and diversity of captured seeds were found after a stormy period. Seed rain of youngest communities was more influenced by storms than that of older communities. Results suggested mostly local dispersal of seeds during normal tides (as predicted by Chapter two). However, there was some evidence of long-distance dispersal occurring during storm surges in younger communities that are regularly inundated with tidal water. The role of seed retention in constraining community development, rather than dispersal *per se*, was further examined.

Retention of dry vs. wet seeds

The studies in hydrochory suggested that the important ecological issue concerning seed transport during storm surges may not be whether seeds move but whether they stay in suitable sites. In Chapter five, factors influencing retention of seeds were explored. I examined interactions between seed morphology (floating capacity), moisture conditions, vegetation structure and hydrodynamic variables and the relative role of each factor in determining seed retention based on factorial experiments. Experiments were conducted in a tidal salt marsh (Schiermonnikoog)

and in a flume facility where hydrodynamic variables could be controlled.

Moisture condition of seeds greatly influenced which factors were most important in determining seed retention. Floating capacity was the most significant factor when seeds were dry. In contrast, hydrodynamic effects dominated retention processes when seeds were waterlogged. Results suggest that buoyancy traits appear to determine whether seeds move in the drier summer and autumn months, after initial detachment from parent plants but the intensity of wave action will determine whether waterlogged seeds stay in a microsite during the wetter months of late autumn to early spring.

Conclusions

In short, studies conducted indicate that the distribution of species (*i.e.* presence or absence in communities) is most strongly constrained by establishment conditions at a site, whereas the abundance of species is influenced by processes controlling seed deposition and retention rather than those regulating dispersal *per se* in coastal, temperate, salt-marsh communities. The high transport potential of storm surges likely enhances distribution of species but restricts their abundance, as many seeds are washed away.

Samenvatting

De aanwezigheid en de populatiegrootte van verschillende soorten binnen plantengemeenschappen kan beïnvloed worden door verschillende factoren. De milieumomstandigheden in het gebied waar de gemeenschap voorkomt, kunnen bepalend zijn voor de kans of een soort zich wel of niet daar kan vestigen. Tevens kunnen de interacties tussen soorten (bijv. concurrentie of facilitatie) in een gebied bepalend zijn voor het voortbestaan van een soort, of deze zich kan verbreiden dan wel verdwijnt uit een gemeenschap. In de afgelopen decennia hebben ecologen zich voornamelijk gericht op het verklaren van patronen binnen een gemeenschap op een lokale schaal. Soorten hebben echter mogelijk ook een bepaalde afstand moeten afleggen naar een gebied om zich binnen een gemeenschap te vestigen. Als model-systeem heb ik gebruik gemaakt van een reeks gemeenschappen die variëren in leeftijd oplopend van jong tot oud, een zgn. chronosequentie, op het Waddeneiland Schiermonnikoog. Hiermee heb ik onderzocht hoe de mobiliteit van plantensoorten (verbreiding als beperkende factor) de samenstelling van een kweldervegetatie kan beïnvloeden.

De zaadvoorraad in de bodem is een globale afspiegeling van de aanwezige plantengemeenschap

Door de relatie tussen patronen in de vegetatie (plantengemeenschap) en de zaadvoorraad in de bodem langs een leeftijdsgradient te bestuderen kan voorspeld worden welke factoren de samenstelling van de gemeenschap kunnen beïnvloeden (Hoofdstuk 2). Er worden drie mogelijke relaties verondersteld: De overeenkomst tussen de vegetatie en de zaadvoorraad in de bodem is a) relatief groot en wordt niet consequent groter of kleiner met de leeftijd, b) wordt minder wanneer gemeenschappen ouder worden en c) is relatief laag en wordt niet consequent groter of kleiner met de leeftijd.

De Sørensen Similariteits Index varieerde tussen de waarden 0,47 en 0,73, waarbij geen consequent patroon langs de leeftijdsgradient optrad. Multivariate statistiek toonde aan dat de leeftijd van de gemeenschap de belangrijkste factor is die de soortenvariatie in de vegetatie (75,1%) en de zaadvoorraad in de bodem (61,4%) kon verklaren. Ook waren de posities van de soorten langs de leeftijdsgradient overeenkomstig in zowel de vegetatie als de zaadvoorraad, wat een indicatie is voor de parallele ontwikkeling van soortenaantallen en dichtheden zowel boven- als ondergronds. De relatie tussen de vegetatie en de zaadvoorraad in de bodem voor kweldergemeenschappen op Schiermonnikoog leek het meest op de eerst genoemde veronderstelling. Dit betekent dat de zaden van de meeste soorten dichtbij de moederplanten blijven, ondanks de regelmatige overstromingen die optreden als gevolg van de getijdenwerking.

Kleine herbivoren (hazen en ganzen) zijn minder belangrijke factoren voor zaadverbreiding dan de getijden

Nadat vastgesteld is dat de beperkte mobiliteit van zaden de samenstelling van plantengemeenschappen kan beïnvloeden, werd de effectiviteit van verschillende vectoren voor zaadverbreiding vergeleken (Hoofdstuk 3). We hebben onderzocht in hoeverre zaden het verteringskanaal van hazen en ganzen (endozoöchorie) op Schiermonnikoog overleven, door de inhoud van hun uitwerpselen te onderzoeken. Allereerst door uitwerpselen te analyseren die verzameld zijn langs een leeftijdsgradient van gemeenschappen, en ten tweede door de uitwerpselen te analyseren van dieren die in een experiment een bepaalde hoeveelheid zaden hadden gegeten. Als laatste hebben we tevens zaden, die door de getijden verbreid werden, opgevangen met Astroturf® matten in het veld.

Hazen verbreiden via hun uitwerpselen meer zaden van de meerjarige, hoge kweldersoorten uit de intermediaire stadia van de vegetatiesuccessie dan ganzen, die meer zaden van eenjarige, lage kweldersoorten uit de vroege successie stadia verbreiden. De overleving en kieming van zaad van de kweldersoorten was hoger na het passeren van het verteringskanaal van hazen (10-40%) vergeleken met de passage bij ganzen (2-13%). Kleine herbivoren echter verbreiden honderd keer zo weinig zaden als de hoeveelheid zaden die verbreid wordt als gevolg van de getijdenwerking. Daardoor lijken ze geen belangrijke factor te zijn, die de samenstelling van een plantengemeenschap op dit Waddeneiland beïnvloedt.

Stormen hebben een sterk effect op zaadverbreiding

Resultaten hebben aangetoond dat hydrochorie (door water verbreide zaden) een groter effect heeft dan endozoöchorie (interne zaadverspreiding door dieren) op Schiermonnikoog. We hebben de factoren die de verspreiding van zaden door het getij beïnvloeden verder onderzocht, inclusief de timing van de zaadverbreiding (Hoofdstuk 4).

De soortensamenstelling van de vegetatie, zaadproductie, zaadregen en het vloedmerk op verschillende plekken langs de gradiënt van plantengemeenschappen werd vergeleken.

Hevige stormen hadden een positief significant effect op zaadregenpatronen: gezien de hoogste dichtheid en diversiteit aan zaden gevonden werd tijdens stormachtige periodes. De zaadregen van de jongste plantengemeenschappen werd meer beïnvloed door stormen dan die van oudere gemeenschappen. De gevonden resultaten wijzen vooral op lokale verbreiding van zaden tijdens normale getijdenwerking (zoals voorspeld in hoofdstuk 2). Echter, er was enig bewijs dat ook lange-afstandsverbreiding voorkwam tijdens stormen in jonge gemeenschappen die regel-

matig door het getij onder water staan. Het vermogen van een plantengemeenschap om zaden vast te houden en het effect hiervan op de vegetatieontwikkeling van die gemeenschap, in tegenstelling tot zaadverbreiding *per se*, werd apart onderzocht.

Vasthouden van droge versus vochtige zaden

Uit de studie naar het belang van hydrochorie in kweldervegetaties bleek dat de belangrijkste ecologische vraag betreffende de verbreiding van zaden door water tijdens hevige stormen niet is of zaden worden verplaatst, maar juist of ze blijven op plaatsen die voor hun groei geschikt zijn. In hoofdstuk 5 werden factoren onderzocht die een rol spelen bij het vasthouden van zaden door een vegetatie. We hebben interacties tussen zaadmorfologie (drijfvermogen), vochttoestand van de zaden, vegetatiestructuur en hydrodynamische variabelen onderzocht en het relatieve belang van elk van deze factoren voor het vermogen tot vasthouden van zaden door de vegetatie door middel van experimenten. De experimenten werden uitgevoerd in het veld op de kwelder van Schiermonnikoog en in een kunstmatige waterloopkundige stroomfaciliteit, waar hydrodynamische variabelen konden worden gevarieerd.

De vochttoestand van zaden bepaalde sterk de effectiviteit van de verschillende factoren in het vasthouden van zaden. Het drijfvermogen was de belangrijkste factor als zaden droog waren. Daarentegen domineerden hydrodynamische effecten het vasthoudingsproces wanneer de zaden doordrenkt waren met water. Uit de resultaten bleek dat het drijfvermogen het proces van zaadverbreiding domineert in de drogere zomer en herfstmaanden, na het vrijkomen van de moederplanten, maar dat de intensiteit van de golfslag vervolgens bepaalt of doordrenkte zaden op een plek blijven tijdens de natte maanden van het late najaar tot het vroege voorjaar of dat ze een geschikte groeiplek alsnog verlaten.

Conclusies

Kortom, de onderzoeken tonen aan dat het voorkomen van soorten (aan- of afwezigheid in een plantengemeenschap) het sterkst bepaald wordt door vestigingsomstandigheden binnen de gemeenschap, terwijl de aantallen individuen van soorten op een plek bepaald wordt door processen die de zaadregen in de bestaande vegetatie en het vermogen van de gemeenschap om zaden vast te houden beïnvloeden. De processen die verbreiding *per se* in een gematigde kweldergemeenschap van een kustgebied reguleren blijken van ondergeschikt belang. Het grote vermogen van stormen om zaden te kunnen verbreiden lijkt het voorkomen van soorten op meer groeiplaatsen te versterken, maar tevens het aantal individuen van soorten te beperken door het wegspoelen van veel zaden uit de bronpopulaties.

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Curriculum vitae

Esther Ryumin Chang was born on the 2nd of March, 1972, in Taejun, South Korea. Her family immigrated to Canada when she was three years old. During her undergraduate studies, she served two summers as a field assistant at La Pérouse Bay Research Station in northern Manitoba, under the supervision of Dr. R.L. Jefferies. She completed her Honours B.Sc. at the University of Toronto in 1995 with a double major in English and Botany. After a year teaching English in Korea, she started her Master studies with Dr. Jefferies and completed her thesis in 1999 on the *Seed and vegetation dynamics in undamaged and degraded coastal habitats of the Hudson Bay lowlands*. Following completion of her M. Sc. degree, she lived for a year on various fishing vessels in Alaska, working as an Observer for the National Marine Fisheries Service. After winning a postgraduate scholarship from NSERC (Natural Sciences and Engineering Research Council of Canada) and an Ubbo Emmius scholarship from the University of Groningen, she moved to the Netherlands in 2001 to start her Ph.D. with Prof. dr. J.P. Bakker at the University of Groningen. In 2004, she won the prize for best oral presentation given by a student at the Seed Ecology meeting in Rhodes, Greece. She currently resides in Paterswolde with her husband, Peter Beek.

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