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

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Document Version
Publisher's PDF, also known as Version of record

Publication date:
2006

[Link to publication in University of Groningen/UMCG research database](#)

Seed dynamics linked to variability in movement of tidal water

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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° 30' N, 6° 10' 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.
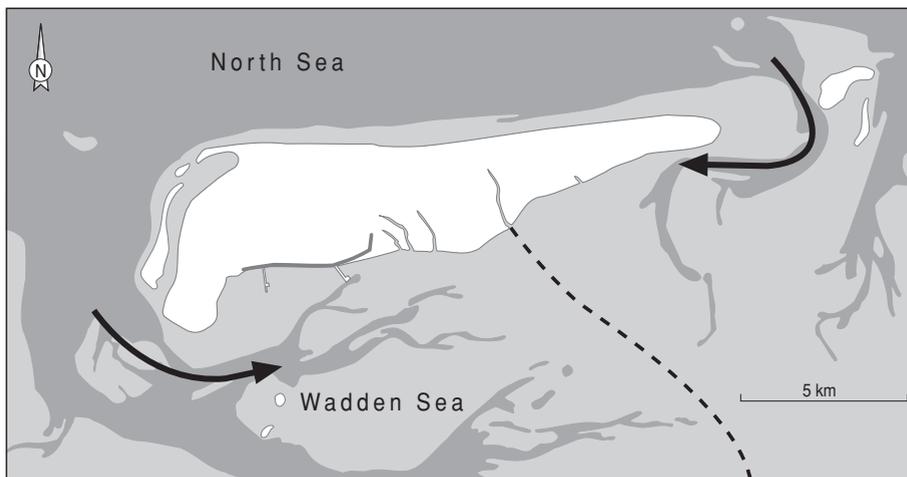

Figure 4.1 Map of Schiermonnikoog with arrows representing direction of tidal current from North Sea into the Wadden Sea. Numbers represent the age and location of communities where permanent grids were located. The dotted line represents the average tidal divide where the opposing tidal basins (entering 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.
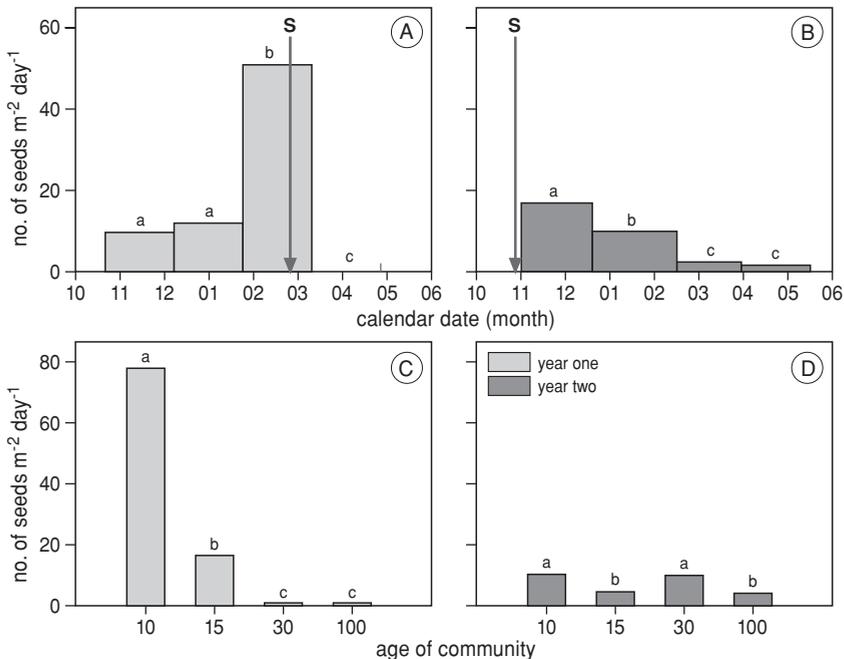

Figure 4.2 Temporal and spatial patterns in seed density captured on seed traps over two trapping seasons. Letters represent statistically different group means within each graph. The "S" represents the occurrence of major storms.

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, Centaurium 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 (Sørenson 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.
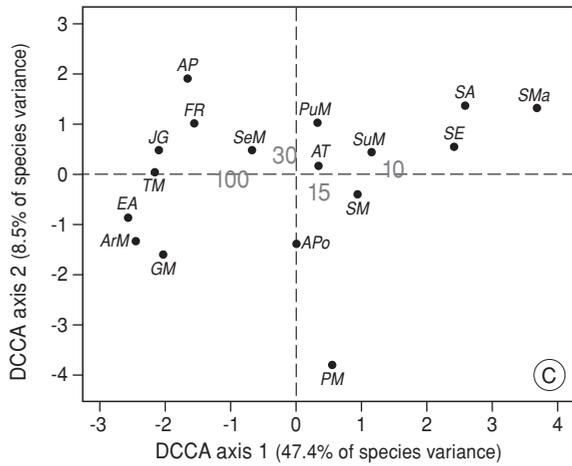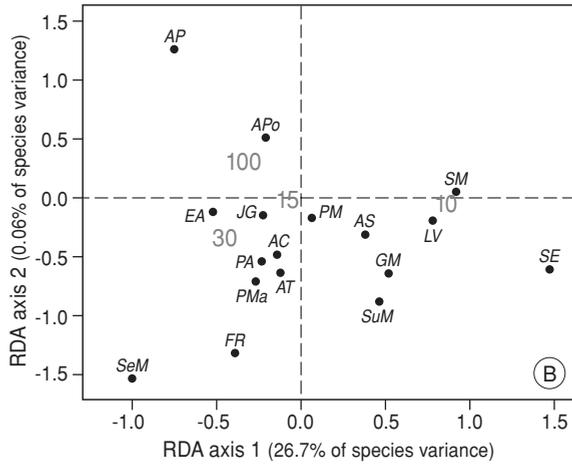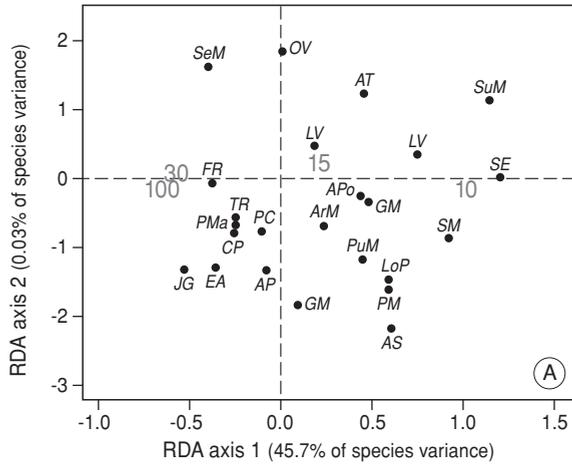
Table 4.1 Values of the Sørenson similarity index between the vegetation and seed rain collected along a community sequence.

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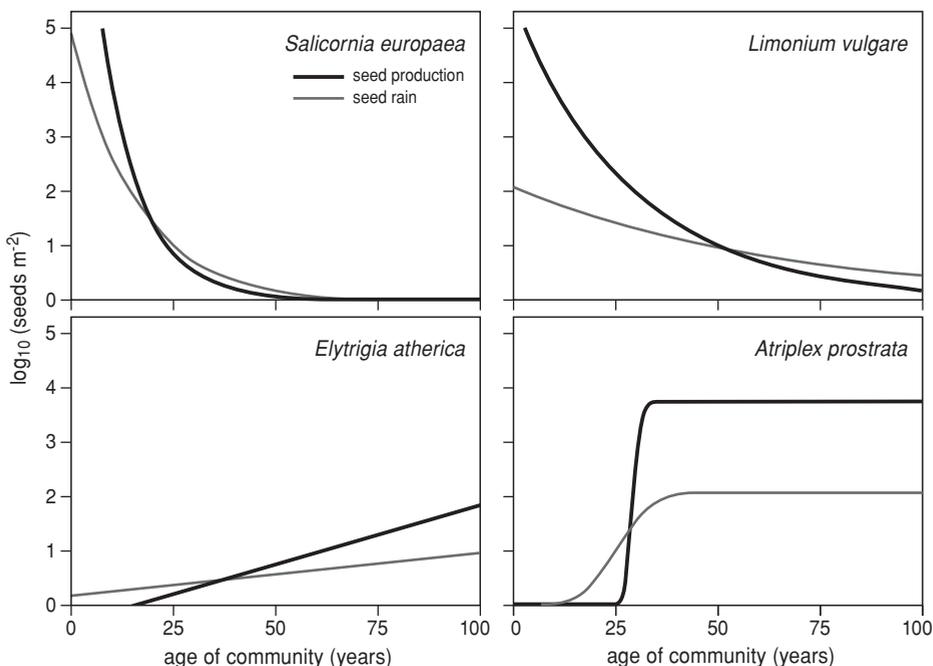
Figure 4.4 Graphs illustrating regressions between seed production, seed rain and age of community. Four representative salt-marsh species are shown. Explanation of the different curves are given in the inset key.

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 % ± 0.16 %) were transported than of *Plantago maritima* (0.39 % ± 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).
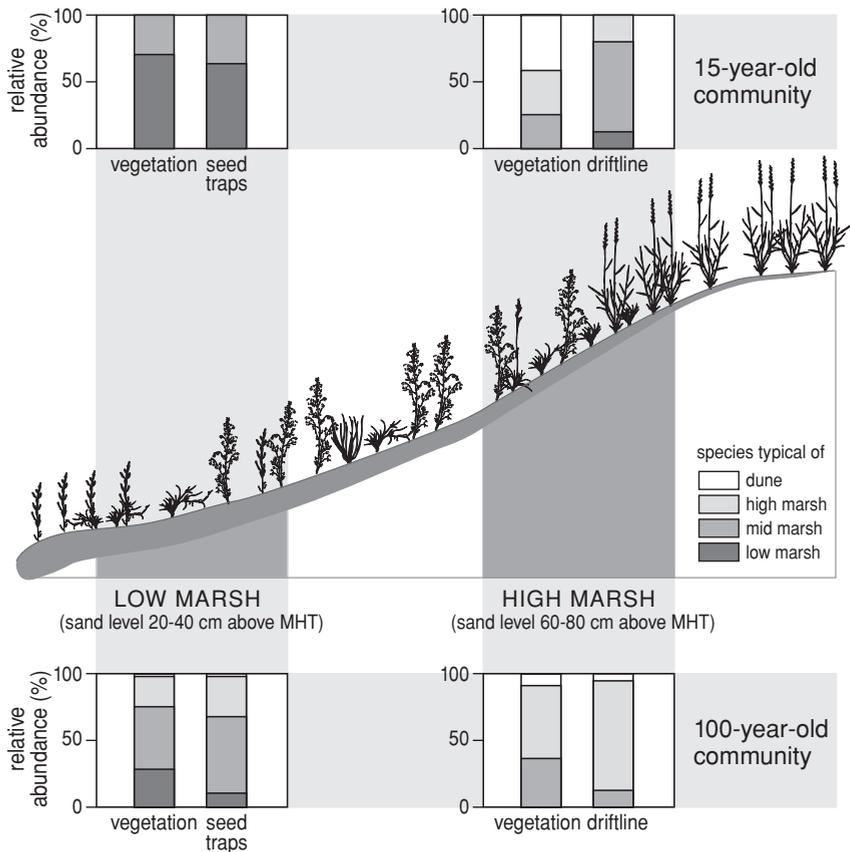
Figure 4.5 Relative abundance of species typical of different elevation zones found in vegetation and seed surveys in a factorial design with age of community (15 or 100 years-old) and elevation of marsh (high or low). Shading explained by inset key.

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	df	F	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	df	F	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.

References

Bakker, J.P., Dijkstra, M. & Russchen, P.T. (1985) Dispersal, germination and early establishment of halophytes and glycophytes on a grazed and abandoned salt-marsh gradient. *New Phytologist*, **101**, 291-308.

Bartholdy, J. & Aagaard, T. (2001) Storm surge effects on a back-barrier tidal flat of the Danish Wadden Sea. *Geo-Marine Letters*, **20**, 133-141.

Cottenie, K. (2005) Integrating environmental and spatial processes in ecological community dynamics. *Ecology Letters*, **8**, 1175-1182.

Dankers, N., Binsbergen, M., Zegers, K., Laane, R. & Vanderloeff, M.R. (1984) Transportation of water, particulate and dissolved organic and inorganic matter between a salt-marsh and the Ems-Dollard estuary, the Netherlands. *Estuarine, Coastal and Shelf Science*, **19**, 143-165.

Davidson-Arnott, R.G.D., van Proosdij, D., Ollerhead, J. & Schostak, L. (2002) Hydrodynamics and sedimentation in salt marshes: examples from a macrotidal marsh, Bay of Fundy. *Geomorphology*, **48**, 209-231.

de Leeuw, J., de Munck, W., Olff, H. & Bakker, J.P. (1993) Does zonation reflect the succession of salt-marsh vegetation? A comparison of an estuarine and a coastal bar island marsh in the Netherlands. *Acta Botanica Neerlandica*, **42**, 435-445.

Field, A. (2000) *Discovering Statistics using SPSS for Windows*. SAGE Publications, London.

Goodson, J.M., Gurnell, A.M., Angold, P.G. & Morrissey, I.P. (2003) Evidence for hydrochory and the deposition of viable seeds within winter flow-deposited sediments: the River Dove, Derbyshire, UK. *River Research and Applications*, **19**, 317-334.

Honnay, O., Verhaeghe, W. & Hermy, M. (2001) Plant community assembly along dendritic networks of small forest streams. *Ecology*, **82**, 1691-1702.

Hubbell, S.P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton.

Huiskes, A.H., Koutstaal, B.P., Herman, P.M.J., Beeftink, W.G., Markusse, M.M. & de Munck, W. (1995) Seed dispersal of halophytes in tidal salt marshes. *Journal of Ecology*, **83**, 559-567.

Jansson, R., Zinko, U., Merritt, D.M. & Nilsson, C. (2005) Hydrochory increases riparian plant species richness: a comparison between a free-flowing and a regulated river. *Journal of Ecology*, **93**, 1094-1103.

Kjerfve, B., Miranda, L.B. & Wolanski, E. (1991) Modelling water circulation in an estuary and intertidal salt marsh system. *Netherlands Journal of Sea Research*, **28**, 141-147.

Koutstaal, B.P., Markusse, M.M. & de Munck, W. (1987) Aspects of seed dispersal by tidal movement. *Vegetation between Land and Sea: Structure and Processes* (eds A.H. Huiskes, C.W.P.M. Blom, & J. Rozema), pp. 226-233. Junk, Dordrecht.

Leonard, L.A., Hine, A.C., Luther, M.E., Stumpf, R.P. & Wright, E.E. (1995) Sediment transport processes in a west-central Florida open marine marsh tidal creek: the role of tides and extra-tropical storms. *Estuarine, Coastal and Shelf Science*, **41**, 225-248.

Lepš, J. & Šmilauer, P. (2003) *Multivariate Analysis of Ecological Data using CANOCO*. Cambridge University Press, Cambridge.

Levine, J.M. (2001) Local interactions, dispersal, and native and exotic plant diversity along a California stream. *Oikos*, **95**, 397-408.

Levine, J.M. & Murrell, D.J. (2003) The community-level consequences of seed dispersal patterns. *Annual Review of Ecology, Evolution and Systematics*, **34**, 549-574.

Möller, I., Spencer, T., French, J.R., Leggett, D.J. & Dixon, M. (1999) Wave transformation over salt marshes: a field and numerical modelling study from North Norfolk, England. *Estuarine, Coastal and Shelf Science*, **49**, 411-426.

Neumeier, U. & Ciavola, P. (2004) Flow resistance and associated sedimentary processes in a *Spartina maritima* salt-marsh. *Journal of Coastal Research*, **20**, 435-447.

Olff, H., de Leeuw, J., Bakker, J.P, Platerink, R.J., van Wijnen, H.J. & de Munck, W. (1997) Vegetation succession and herbivory in a salt marsh: changes induced by sea level rise and silt deposition along an elevational gradient. *Journal of Ecology*, **85**, 799-814.

Orth, R.J., Luckenbach, M. & Moore, K.A. (1994) Seed dispersal in a marine macrophyte: implications for colonization and restoration. *Ecology*, **75**, 1927-1939.

Rand, T.A. (2000) Seed dispersal, habitat suitability and the distribution of halophytes across a salt marsh tidal gradient. *Journal of Ecology*, **88**, 608-621.

Roman, C.T., Peck, J.A., Allen, J.R., King, J.W. & Appleby, P.G. (1997) Accretion of a New England (U.S.A.) salt marsh in response to inlet migration, storms and sea-level rise. *Estuarine, Coastal and Shelf Science*, **45**, 717-727.

Sigmaplot (2002) *Sigmaplot for Windows Version 8.0*. SPSS, Chicago.

Skoglund, S.J. (1990) Seed dispersing agents in two regularly flooded river sites. *Canadian Journal of Botany*, **68**, 754-760.

SPSS (2003) *SPSS for Windows Release 12.0.1*. SPSS, Chicago.

Stevenson, J.C., Ward, L.G. & Kearney, M.S. (1988) Sediment transport and trapping in marsh systems: implications of tidal flux studies. *Marine Geology*, **80**, 37-59.

Tansley, A.G. (1939) *The British Islands and their Vegetation*. Cambridge University Press, Cambridge.

ter Braak, C.J.F. & Šmilauer, P. (1998) *CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination*. Microcomputer Power, Ithaca, U.S.A.

ter Heerdt, G.N.J., Verweij, G.L., Bekker, R.M. & Bakker, J.P. (1996) An improved method for seed-bank analysis: seedling emergence after removing the soil by sieving. *Functional Ecology*, **10**, 144-151.

Willson, M.F. (1993) Dispersal mode, seed shadows, and colonization patterns. *Vegetatio*, **107/108**, 261-280.

Wolters, M. & Bakker, J.P. (2002) Soil seed bank and driftline composition along a successional gradient on a temperate salt marsh. *Applied Vegetation Science*, **5**, 55-62.

Wolters, M., Geertsema, J.R., Chang, E.R., Veeneklaas, R.M., Carey, P.D. & Bakker, J.P. (2004) Astroturf seed traps for studying hydrochory. *Functional Ecology*, **18**, 141-147.

Wolters, M., Hogendorf, J., Willemse, M. & Bakker, J.P. (2006) Verbreiding van zaden van kwelderplanten in de Waddenzee. *De Levende Natuur*, **107**, 47-79.

Wolters, M., Garbutt, A. & Bakker, J.P. (2005) Plant colonization after managed realignment: the relative importance of diaspore dispersal. *Journal of Applied Ecology*, **42**, 770-777.

Yang, S.L. (1998) The role of *Scirpus* marsh in attenuation of hydrodynamics and retention of fine sediment in the Yangtze estuary. *Estuarine, Coastal and Shelf Science*, **47**, 227-233.

Appendix 4.1 Mean dominance scores for species (± 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				
Salicornia europaea	2.74 ±0.09	1.00 ±0	0.66 ±0.14	0
Spartina anglica	0.76 ±0.13	0.10 ±0.04	0.16 ±0.10	0
Spergularia marina	0.22	0	0	0
Spergularia media	0.96 ±0.09	1.24 ±0.08	0.68 ±0.12	0.32 ±0.08
Suaeda maritima	1.22 ±0.08	1.00 ±0	0.92 ±0.04	0.24 ±0.06
Early-successional				
Limonium vulgare	1.16 ±0.13	3.72 ±0.07	2.08 ±0.20	2.58 ±0.09
Puccinellia maritima	1.02 ±0.06	1.00 ±0	1.66 ±0.39	0.76 ±0.04
Mid-successional				
Aster tripolium	0.18 ±0.05	0.98 ±0.02	0.90 ±0.33	0.04 ±0.04
Festuca rubra	0	0.52 ±0.14	2.28 ±0.46	3.18 ±0.18
Glaux maritima	0	0.24 ±0.10	0.04 ±0.03	1.14 ±0.05
Plantago maritima	0	0.94 ±0.03	0.10 ±0.04	0
Seriphidium maritimum	0	1.82 ±0.24	2.68 ±0.39	2.08 ±0.14
Triglochin maritima	0	0.02 ±0.02	0.20 ±0.04	0.80 ±0.04
Late-successional				
Armeria maritima	0	0.02 ±0.02	0	0.38 ±0.06
Atriplex portulacoides	0.38 ±0.11	2.34 ±0.24	0.98 ±0.28	0.86 ±0.04
Atriplex prostrata	0	0	0.60 ±0.14	0.68 ±0.06
Elytrigia atherica	0	0	0.04 ±0.03	0.86 ±0.05
Juncus gerardi	0	0	0.68 ±0.14	2.02 ±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				
Salicornia europaea	17 ±5.1	0.31 ±0.12	0.091 ±0.041	0
Spartina anglica	0	0	0	0
Spergularia media	0.70 ±0.52	0.030 ±0.022	0	0.10 ±0.06
Suaeda maritima	2.8 ±0.70	3.0 ±1.8	0.27 ±0.13	0.02 ±0.013
Early-successional				
Limonium vulgare	1.1 ±0.33	0.52 ±0.13	0.17 ±0.056	0.25 ±0.09
Puccinellia maritima	0	0	0	0
Mid-successional				
Aster tripolium	0.020 ±0.013	0.081 ±0.049	0.010 ±0.010	0.010 ±0.010
Festuca rubra	0.010 ±0.010	0.040 ±0.031	0.33 ±0.10	0.39 ±0.13
Glaux maritima	0.030 ±0.015	0.020 ±0.020	0	0.091 ±0.071
Plantago maritima	0.020 ±0.013	0.050 ±0.034	0.010 ±0.010	0.040 ±0.022
Seriphidium maritimum	0.050 ±0.086	2.0 ±0.54	1.4 ±0.35	1.5 ±0.22
Late-successional				
Armeria maritima	0.010 ±0.010	0	0	0
Atriplex portulacoides	0	0.040 ±0.022	0.010 ±0.010	0
Atriplex prostrata	0	0.010 ±0.010	0.030 ±0.015	0.071 ±0.026
Elytrigia atherica	0	0	0	0.21 ±0.70
Juncus gerardi	0	0.010 ±0.010	0	0.54 ±0.26
Disturbed salt-marsh				
Agrostis stolonifera	0.33 ±0.14	0	0.040 ±0.016	0.20 ±0.046
Atriplex littoralis	0	0	0	0
Dune				
Agrostic capillaris	0	0	0	0
Centaurium pulchellum	0	0	0	0.010 ±0.010
Cerastium fontanum	0	0	0	0
Lolium perenne	0	0	0	0
Odontites vernus	0	0.010 ±0.010	0.010 ±0.010	0
Plantago coronopus	0	0	0	0
Plantago lanceolata	0	0	0	0
Plantago major	0	0	0	0
Poa annua	0	0	0	0
Trifolium repens	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				
Salicornia europaea	34 ±3.3	3.3 ±1.8	0.24 ±0.072	0
Spartina anglica	0	0	0	0
Spergularia media	1.5 ±0.97	0	0	0
Suaeda maritima	2.4 ±0.61	1.4 ±1.0	0.11 ±0.039	0.010 ±0.010
Early-successional				
Limonium vulgare	0.13 ±0.044	0.062 ±0.035	0.010 ±0.010	0.010 ±0.010
Puccinellia maritima	0	0	0	0
Mid-successional				
Aster tripolium	0.031 ±0.022	0.041 ±0.027	0.010 ±0.010	0.021 ±0.021
Festuca rubra	0	0	0.36 ±0.094	0.051 ±0.023
Glaux maritima	0.072 ±0.031	0.072 ±0.041	0	0.031 ±0.016
Plantago maritima	0.031 ±0.016	0	0	0.010 ±0.010
Seriphidium maritimum	0.010 ±0.010	0.021 ±0.014	0.082 ±0.021	0.020 ±0.014
Late-successional				
Armeria maritima	0	0	0	0
Atriplex portulacoides	0	0	0	0
Atriplex prostrata	0	0	0	0.021 ±0.014
Elytrigia atherica	0	0	0.010 ±0.010	0.072 ±0.041
Juncus gerardi	0	0	0.021 ±0.014	0.17 ±0.093
Disturbed salt-marsh				
Agrostis stolonifera	0.28 ±0.10	0	0.021 ±0.014	0.062 ±0.031
Atriplex littoralis	0	0	0	0
Dune				
Agrostic capillaris	0	0	0	0
Centaurium pulchellum	0	0	0	0.010 ±0.010
Cerastium fontanum	0	0	0	0
Lolium perenne	0	0	0	0
Odontites vernus	0	0.010 ±0.010	0	0
Plantago coronopus	0	0	0	0
Plantago lanceolata	0	0	0	0
Plantago major	0	0	0.021 ±0.021	0
Poa annua	0	0	0	0
Trifolium repens	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				
Salicornia europaea	33 ±14	11 ±2.1	0.032 ±0.023	0
Spartina anglica	0	0	0	0
Spergularia media	66 ±16	4.1 ±1.3	0	0
Suaeda maritima	45 ±17	13 ±4.8	0	0.011 ±0.011
Early-successional				
Limonium vulgare	7.7 ±1.5	3.6 ±0.98	0.097 ±0.034	0.021 ±0.014
Puccinellia maritima	0	0	0	0
Mid-successional				
Aster tripolium	0.39 ±0.31	0.23 ±0.12	0	0
Festuca rubra	0.47 ±0.22	0.95 ±0.53	0.52 ±0.14	0.097 ±0.044
Glaux maritima	0.52 ±0.19	0.39 ±0.21	0.011 ±0.011	0.043 ±0.024
Plantago maritima	0.56 ±0.17	0.013 ±0.013	0	0
Seriphidium maritimum	0.021 ±0.021	0.56 ±0.22	0	0
Late-successional				
Armeria maritima	0	0	0	0
Atriplex portulacoides	0.28 ±0.12	0.067 ±0.035	0	0
Atriplex prostrata	0.15 ±0.055	0.013 ±0.013	0.011 ±0.011	0.011 ±0.011
Elytrigia atherica	0.043 ±0.026	0.054 ±0.035	0.021 ±0.014	0.021 ±0.014
Juncus gerardi	0.043 ±0.026	0.35 ±0.23	0.064 ±0.036	0.086 ±0.035
Disturbed salt-marsh				
Agrostis stolonifera	9.9 ±3.8	0.12 ±0.043	0.032 ±0.023	0.054 ±0.033
Atriplex littoralis	0	0.013 ±0.013	0	0
Dune				
Agrostic capillaris	0	0	0	0
Centaurium pulchellum	0	0	0	0
Cerastium fontanum	0.021 ±0.021	0.013 ±0.013	0	0
Lolium perenne	0.34 ±0.092	0	0	0
Odontites vernus	0	0	0	0
Plantago coronopus	0.021 ±0.021	0	0.011 ±0.011	0.011 ±0.011
Plantago lanceolata	0	0	0	0
Plantago major	0	0	0	0
Poa annua	0	0	0	0
Trifolium repens	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				
Salicornia europaea	0	0	0	0
Spartina anglica	0	0	0	0
Spergularia media	0.043 ±0.043	0	0	0
Suaeda maritima	0.085 ±0.060	0	0	0
Early-successional				
Limonium vulgare	0	0	0	0
Puccinellia maritima	0	0	0	0
Mid-successional				
Aster tripolium	0	0	0	0
Festuca rubra	0	0.0085 ±0.0085	0.0085 ±0.0085	0.017 ±0.011
Glaux maritima	0	0	0	0.017 ±0.011
Plantago maritima	0	0	0	0
Seriphidium maritimum	0	0	0	0
Late-successional				
Armeria maritima	0	0	0	0
Atriplex portulacoides	0	0	0	0
Atriplex prostrata	0	0	0	0
Elytrigia atherica	0	0	0	0.0085 ±0.0085
Juncus gerardi	0	0	0	0.025 ±0.013
Disturbed salt-marsh				
Agrostis stolonifera	0.021 ±0.021	0.0085 ±0.0085	0	0.0085 ±0.0085
Atriplex littoralis	0	0	0	0
Dune				
Agrostic capillaris	0	0	0	0
Centaurium pulchellum	0	0	0	0
Cerastium fontanum	0	0	0	0
Lolium perenne	0	0	0	0
Odontites vernus	0	0	0	0
Plantago coronopus	0	0	0	0
Plantago lanceolata	0	0	0	0
Plantago major	0	0	0	0
Poa annua	0	0	0	0
Trifolium repens	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				
Salicornia europaea	11 ±3.6	0.12 ±0.056	0.51 ±0.48	0.41 ±0.40
Spartina anglica	0	0	0	0
Spergularia media	0.52 ±0.20	0.020 ±0.013	0	0.022 ±0.022
Suaeda maritima	4.8 ±2.6	0.081 ±0.044	2.4 ±1.4	0.32 ±0.26
Early-successional				
Limonium vulgare	2.7 ±0.68	1.0 ±0.54	0.25 ±0.022	0.95 ±0.68
Puccinellia maritima	0	0	0	0
Mid-successional				
Aster tripolium	0.020 ±0.013	0.25 ±0.16	0.040 ±0.031	0
Festuca rubra	0.010 ±0.010	0.060 ±0.040	0.020 ±0.020	0
Glaux maritima	0.030 ±0.015	0.010 ±0.010	0.010 ±0.010	0.011 ±0.011
Plantago maritima	0.010 ±0.010	0.050 ±0.050	0	0.011 ±0.011
Seriphidium maritimum	0	10 ±5.5	21 ±3.8	5.1 ±3.4
Late-successional				
Armeria maritima	0	0	0	0
Atriplex portulacoides	0	0	0	0.011 ±0.011
Atriplex prostrata	0.010 ±0.010	0	0.55 ±0.38	3.6 ±1.6
Elytrigia atherica	0	0.010 ±0.010	0.050 ±0.034	0.056 ±0.056
Juncus gerardi	0	0.010 ±0.010	0	0.011 ±0.011
Disturbed salt-marsh				
Agrostis stolonifera	0.010 ±0.010	0	0	0
Atriplex littoralis	0	0	0	0
Dune				
Agrostic capillaris	0	0	0	0
Centaurium pulchellum	0	0	0	0
Cerastium fontanum	0	0	0	0
Lolium perenne	0	0	0	0
Odontites vernus	0	0	0	0
Plantago coronopus	0	0	0	0
Plantago lanceolata	0	0	0	0
Plantago major	0	0	0	0
Poa annua	0	0	0	0
Trifolium repens	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				
Salicornia europaea	9.4 ±2.1	0.75 ±0.081	1.2 ±1.1	0.0087 ±0.0087
Spartina anglica	0	0	0	0
Spergularia media	2.5 ±1.9	0.043 ±0.027	0	0.11 ±0.11
Suaeda maritima	1.4 ±0.88	0.19 ±0.053	0.82 ±0.40	0.11 ±0.043
Early-successional				
Limonium vulgare	2.4 ±0.26	0.32 ±0.11	0.061 ±0.037	0.46 ±0.43
Puccinellia maritima	0	0	0	0
Mid-successional				
Aster tripolium	0.44 ±0.32	0.30 ±0.17	0.49 ±0.25	0.10 ±0.077
Festuca rubra	0.087 ±0.039	0.026 ±0.018	0.11 ±0.067	0.026 ±0.026
Glaux maritima	0.97 ±0.20	0.16 ±0.065	0.63 ±0.37	0.11 ±0.10
Plantago maritima	0.017 ±0.012	0.035 ±0.026	0	0
Seriphidium maritimum	0.21 ±0.058	1.7 ±0.43	11 ±2.2	1.2 ±0.33
Late-successional				
Armeria maritima	0	0	0	0
Atriplex portulacoides	0	0	0	0
Atriplex prostrata	0	0.0087 ±0.0087	0.29 ±0.12	0.94 ±0.24
Elytrigia atherica	0.0087 ±0.0087	0.0087 ±0.0087	0.035 ±0.026	0.061 ±0.034
Juncus gerardi	0	0.0087 ±0.0087	0	0.0087 ±0.0087
Disturbed salt-marsh				
Agrostis stolonifera	0.043 ±0.019	0	0	0
Atriplex littoralis	0	0	0	0
Dune				
Agrostic capillaris	0	0	0	0
Centaurium pulchellum	0	0	0	0
Cerastium fontanum	0	0	0	0
Lolium perenne	0	0	0	0
Odontites vernus	0	0	0	0
Plantago coronopus	0	0	0	0
Plantago lanceolata	0	0	0	0
Plantago major	0	0	0	0
Poa annua	0	0	0	0
Trifolium repens	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				
Salicornia europaea	4.8 ±1.1	0.088 ±0.043	0.15 ±0.13	0
Spartina anglica	0	0	0	0
Spergularia media	0.077 ±0.037	0.011 ±0.011	0.022 ±0.022	0.033 ±0.033
Suaeda maritima	0.33 ±0.088	0.066 ±0.029	0.36 ±0.27	0.27 ±0.23
Early-successional				
Limonium vulgare	0.23 ±0.083	0.14 ±0.077	0.077 ±0.029	0.022 ±0.015
Puccinellia maritima	0	0	0	0
Mid-successional				
Aster tripolium	0.088 ±0.046	0.21 ±0.12	0.14 ±0.11	0.044 ±0.024
Festuca rubra	0	0.011 ±0.011	0.011 ±0.011	0
Glaux maritima	0.011 ±0.011	0	0.033 ±0.023	0.022 ±0.022
Plantago maritima	0	0	0	0
Seriphidium maritimum	0.022 ±0.015	0.066 ±0.037	0.80 ±0.27	0.022 ±0.015
Late-successional				
Armeria maritima	0	0	0	0
Atriplex portulacoides	0	0	0	0
Atriplex prostrata	0	0.011 ±0.011	0.022 ±0.015	0.055 ±0.034
Elytrigia atherica	0	0.022 ±0.022	0.19 ±0.17	0.14 ±0.13
Juncus gerardi	0	0.011 ±0.011	0.011 ±0.011	0.011 ±0.011
Disturbed salt-marsh				
Agrostis stolonifera	0	0	0	0
Atriplex littoralis	0	0	0	0
Dune				
Agrostic capillaris	0	0	0.011 ±0.011	0
Centaurium pulchellum	0	0	0	0
Cerastium fontanum	0	0	0	0
Lolium perenne	0	0	0	0
Odontites vernus	0	0	0	0
Plantago coronopus	0	0	0	0
Plantago lanceolata	0	0	0	0
Plantago major	0	0	0.022 ±0.015	0
Poa annua	0	0	0.011 ±0.011	0.011 ±0.011
Trifolium repens	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				
Salicornia europaea	1.9 ±0.40	0.37 ±0.12	0.024 ±0.024	0.012 ±0.012
Spartina anglica	0	0	0	0
Spergularia media	0.036 ±0.026	0	0	0
Suaeda maritima	0.52 ±0.38	0.12 ±0.095	0.13 ±0.038	0.060 ±0.037
Early-successional				
Limonium vulgare	0.024 ±0.016	0.060 ±0.037	0.072 ±0.037	0
Puccinellia maritima	0	0	0	0
Mid-successional				
Aster tripolium	0	0.024 ±0.016	0.048 ±0.027	0
Festuca rubra	0	0.096 ±0.047	0.25 ±0.085	0
Glaux maritima	0.19 ±0.060	0.012 ±0.012	0.024 ±0.016	0.012 ±0.012
Plantago maritima	0.024 ±0.024	0	0.024 ±0.016	0
Seriphidium maritimum	0	0.096 ±0.035	1.1 ±0.29	0.096 ±0.050
Late-successional				
Armeria maritima	0	0	0	0
Atriplex portulacoides	0	0	0	0
Atriplex prostrata	0	0	0	0.024 ±0.016
Elytrigia atherica	0	0.012 ±0.012	0.036 ±0.018	0
Juncus gerardi	0.012 ±0.012	0	0.036 ±0.036	0.012 ±0.012
Disturbed salt-marsh				
Agrostis stolonifera	0.036 ±0.026	0.024 ±0.016	0.024 ±0.024	0
Atriplex littoralis	0	0	0	0
Dune				
Agrostic capillaris	0	0	0	0
Centaurium pulchellum	0	0	0	0
Cerastium fontanum	0	0	0	0
Lolium perenne	0	0	0	0
Odontites vernus	0	0	0	0
Plantago coronopus	0	0	0	0
Plantago lanceolata	0	0	0	0
Plantago major	0	0	0	0
Poa annua	0	0	0	0
Trifolium repens	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		
Atriplex portulacoides	240 ± 58	10 ± 5.5
Limonium vulgare	1600 ± 340	95 ± 40
Puccinellia maritima	2.5 ± 2.5	0
Salicornia europaea	380 ± 100	2.5 ± 2.5
Spartina anglica	2.5 ± 2.5	0
Suaeda maritima	1700 ± 310	40 ± 21
Group total	3925 (12.6 %)	147.5 (0.62 %)
Mid marsh		
Aster tripolium	65 ± 21	15 ± 7.6
Festuca rubra	2400 ± 630	2600 ± 450
Glaux maritima	760 ± 250	110 ± 51
Plantago maritima	5900 ± 1200	360 ± 140
Seriphidium maritimum	12 000 ± 3200	62 ± 29
Triglochin maritima	2.5 ± 2.5	0
Group total	21 127.5 (68 %)	3147 (13.2 %)
High marsh		
Atriplex prostrata	2.5 ± 2.5	52 ± 16
Elytrigia atherica	830 ± 200	17 000 ± 7300
Juncus gerardi	230 ± 110	240 ± 99
Agrostis stolonifera	4600 ± 830	2300 ± 800
Group total	5662.5 (18.4 %)	2317 (81.6 %)
Dune		
Armeria maritima	2.5 ± 2.5	0
Cerastium fontanum	2.5 ± 2.5	20 ± 15
Lolium perenne	95 ± 12	12 ± 7.7
Matricaria maritima	2.5 ± 2.5	10 ± 5.5
Odontites vernus	2.5 ± 2.5	0
Plantago coronopus	290 ± 82	680 ± 300
Plantago lanceolata	0	38 ± 21
Plantago major	0	5 ± 3.3
Poa annua	0	5 ± 3.3
Sagina procumbens	2.5 ± 2.5	65 ± 57
Trifolium repens	2.5 ± 2.5	130 ± 58
Group total	400 (1.3 %)	965 (4.0 %)
Total	31 115	23 851.5