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

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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 Scherfose (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 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	
<i>Agrostis stolonifera</i>	3/4	0	1	1	0	1	1	0	0	0	1
<i>Aster tripolium</i>	5	1	1	1	1	1	1	1	1	0	1
<i>Atriplex portulacoides</i>	5	1	1	0	1	1	0	1	1	0	0
<i>Atriplex prostrata</i>	4	0	1	1	0	1	1	1	1	1	1
<i>Blysmus rufus</i>	3	0	0	0	0	0	0	0	0	0	0
<i>Bolboschoenus maritimus</i>	3/4	0	0	0	0	0	0	0	0	0	0
<i>Carex distans</i>	3	0	0	0	0	0	0	0	0	0	0
<i>Carex extensa</i>	3/4	0	0	0	0	0	0	0	0	0	0
<i>Centaurium pulchellum</i>	3	0	0	0	0	0	1	0	0	1	0
<i>Cochlearia danica</i>	2	0	0	0	0	0	0	0	0	0	0
<i>Elytrigia atherica</i>	3/4	0	1	0	0	1	1	1	1	1	1
<i>Festuca arundinacea</i>	2	0	0	0	0	0	0	0	0	0	0
<i>Festuca rubra</i>	4	0	1	1	1	1	1	1	1	1	1
<i>Glaux maritima</i>	4	0	1	1	1	1	1	1	1	1	1
<i>Hordeum marinum</i>	0	0	0	0	0	0	0	0	0	0	0
<i>Juncus gerardi</i>	4	0	1	1	0	1	1	1	1	1	1
<i>Juncus maritimus</i>	3/4	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
<i>Lotus corniculatus</i>	2	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>Oenanthe lachenalii</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	0	0	1	1
<i>Triglochin maritima</i>	5	1	0	0	0	1	0	0	1	0	1	0	1	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 and incorporation 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>	<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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