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

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Chapter 5

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

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Summary

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

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

Introduction

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

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

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

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

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

Methods

Field study

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

To test hypothesis 1, we selected 'seeds' from three salt-marsh species for their contrasting physical traits. Seeds of *Plantago maritima* (1mm x 2 mm) have a relatively short floating capacity with 50 % of seeds sinking within 0.5 to 1 hour (T₅₀) in laboratory experiments (Koutstaal *et al.* 1987) due to a seed coat that becomes mucilaginous when wetted. Seeds of *Suaeda maritima* (radius 0.5 mm) have a mid-ranging T₅₀ from 2 to 30 hours (Koutstaal *et al.* 1987). Diaspores of *Elytrigia atherica* are grains encased within bracts (10 mm x 2 mm) and have the longest T₅₀ ranging from 1 to 2 days (Koutstaal *et al.* 1987). The term 'seed' will be used to describe both true seeds and small, indehiscent fruits.

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

Flume study

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

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

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

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

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

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

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

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

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

Data analysis

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

Results

Seed retention in the field study

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

Seed retention in the flume study

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

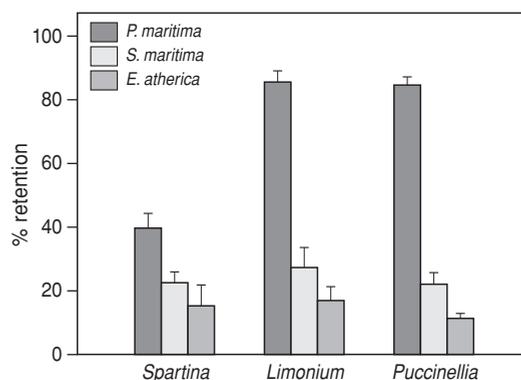


Figure 5.1 Percentage retention of sown seeds found in the field study for *Spartina anglica*, *Limonium vulgare* and *Puccinellia maritima* community types after a spring tide on 8 April, 2004 when plots were inundated with 10-25 cm of sea water. Results for seeds of *Plantago maritima*, *Suaeda maritima*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

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

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

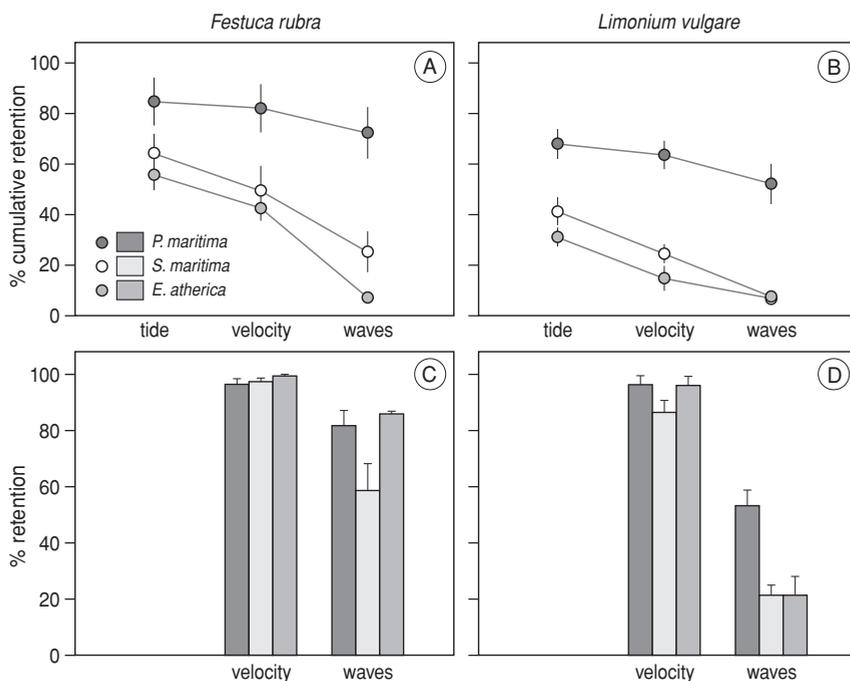


Figure 5.2 Percentage seed retention found in two stand types (*Festuca rubra*, *Limonium vulgare*) for initially dry seeds (A & B) and waterlogged seeds (C & D). Up to three hydrodynamic treatments (upcoming tide, flow velocity, waves) were applied to dislodge seeds in a flume facility. Results for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

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

Effect of vegetation structure on hydrodynamics in the flume study

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

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

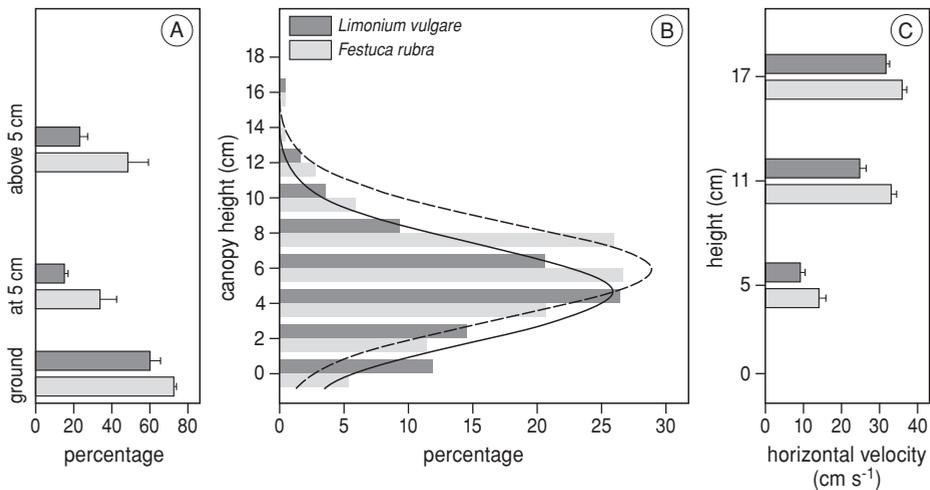


Figure 5.3 Parameters of vegetation structure and hydrodynamics at different heights: A) percentage frequency of hits for vegetation recorded with point quadrat method at ground, 5 cm above ground and above 5 cm, B) percentage frequency of canopy heights and C) measured horizontal flow velocity at 5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

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

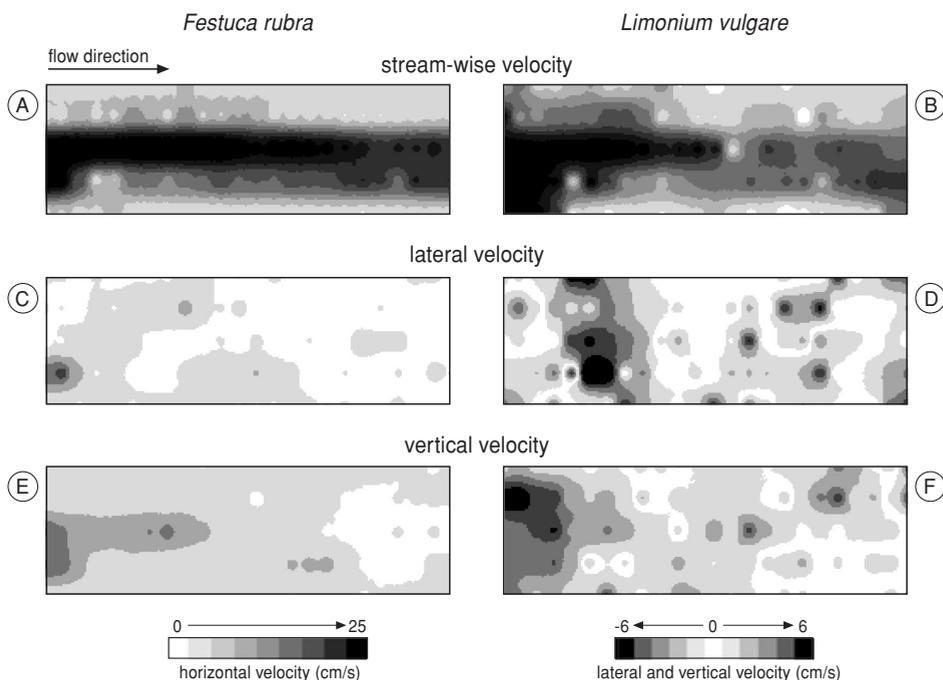


Figure 5.4 Spatial distribution of measured flow velocity in two stand types for stream-wise velocity (A & B), lateral velocity (C & D) and vertical velocity (E & F). Grey scale explained by inset legend. Note difference in scale between stream-wise velocity classes and classes for lateral and vertical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

Discussion

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

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

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

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

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

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

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

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