Hydrochory on the salt marsh of Schiermonnikoog

Two pilot studies

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Summary

Two pilot studies were done on the salt marsh of Schiermonnikoog.
Pilot study 1: the abundance and diversity of the seeds in creeks was determined. Floating seeds were caught with nets in two creeks at the high salt marsh.

a. The occurrence of seed transportation in the creeks on the salt marsh was ascertained. But nothing could be said on direction of transport.
b. There was no correlation between the floating capacity of the seeds and the caught seeds. This indicates a local dispersal.

Pilot study 2: the movement of seeds over salt marsh vegetation was looked at on the low salt marsh. Several potential factors on the transportation of the seeds were measured. The distance to the creek, the distance to the sea, the elevation and the height of the water level, using a known number of marked seeds on seed traps.

a. The effect of the height of the water level on the dispersal of the seeds was stronger than the effects of the distance to the creek and sea or the elevation of the location. During spring tide more seeds were transported than during neap tide.
b. Natural dispersed seeds on the seed traps were mostly of plants in the local vegetation (within 2 m).

Introduction

Salt marshes are important habitats for characteristic salt marsh plants and animals. On Salt marshes tides play an important role in the biotic and a-biotic processes, like the oxygen content and temperature of the soil and the supply of nutrients for the plants (van der Molen, 1997). On Schiermonnikoog, a Dutch barrier island in the Wadden Sea, marshes continually grow from the west to the east, because fresh sediments are deposited on the east of the island by tidal currents. New salt marsh plant communities start to grow on this freshly deposited site. The abundance and distribution patterns of these new salt marsh plant communities are strongly dependent on seed availability (Rand 2000). There have been seeds found floating in the Wadden Sea (personal communication from Chang) so it could be that seeds are deposited together with the sand, but there are many different ways for plants to have their seeds, fruits or other propagules dispersed. Propagules can be dispersed by the wind (anemochory), by animals (zoöchory), or by water (hydrochory). The size and number of plant propagules vary much. A plant can have a reproductive strategy to produce its seed output in either many small seeds or a few large ones. The size adopted by each species probably represents a compromise between the requirements for dispersal, which would favour small seeds, and the requirements for seedling establishment, which would favour large seeds (Fenner 1985). The seeds of most salt marsh species do not seem to have special adaptations for anemochory, zoöchory or hydrochory. They can have more than one dispersion mechanism (Bakker *et al.* 1996), although most tested halophyte fruits have a moderate up to a considerable floating capacity (Koutstaal *et al.* 1987, and see table 1) and it is believed that hydrochory is important for the seed distribution of salt marsh plants to other sites (Geertsema 2000, Wolters & Bakker 2002).

Hydrochory is important in coastal areas (Koutstaal *et al.* 1987, Huiskes *et al.* 1995, Wels 2001, Wolters & Bakker 2002) and is an important factor for the restoration and succession of salt marshes (Kolen & Esselink 1999, Geertsema 2000) because the sea currents can take them great distances (Koutstaal *et al.* 1987, Huiskes *et al.* 1995) so seeds dispersed by water have a good chance of getting to new sites (Geertsema 2000). Besides the tidal currents, wind is an important factor for dispersal of floating seeds and fruits. The transportation by the water can occur on the surface (floating), but also in the water column (Huiskes *et al.* 1995). Floating propagules can be carried away from a marsh by the water currents, but may return to their station of release dependent on wind direction and wind speed (Koutstaal *et al.* 1987). Yet even seeds with a moderate floating capacity may have an action radius of several tens of kilometres when the wind blows in their favour (Koutstaal *et al.* 1987). And if propagules have a low floating capacity they can't be carried for great distances by the water. But It is possible to be deposited somewhere at one high tide and being taken up again by the next tide to be transported further via "Stepping-stones" dispersal (Koutstaal *et al.* 1987). But travelling such great distances isn't the most important. The seeds must be germinable when they reach a new site. Keiffer and Ungar (1997) showed that prolonged time (> 1 year) spend in the salt water has a negative effect on the germination percentage of seeds. However, short (< 1 year) exposure to the saline environment stimulated the germination of *Salicornia europaea* and *Suaeda calceoliformis* seeds. All in all, continual genetic exchange of halophytes between isolated salt marshes is probable (Koutstaal *et al.* 1987).

Much research about floatation of seeds and the potential hydrochory has been done in the laboratory (Guppy 1906, Praeger 1913, Feekes 1936, Westhoff 1947, Koutstaal *et al.*1987) obtaining information on the floating capacities of propagules of different species (Table 1). Some researches have looked at the realised dispersal by water (Kolen & Esselink 1999, Geertsema 2000, Rand 2000). Huiskes' *et al.* (1987) researched the direction of seed or seedling movement (landward) of plant species in the salt marsh.

This research has specifically concentrated on the possibilities and actual occurrence of the transportation of seeds and other propagules in the creeks and tidal currents of the salt marsh of Schiermonnikoog. The research was divided in two pilot studies. The primary objective of the first pilot study was to catch floating seeds and determine the abundance and diversity of the seeds in the creeks. This was a descriptive research to ascertain the occurrence of seed transportation in the creeks on the salt marsh. In the second pilot study some factors that determine the movement of seeds over salt marsh vegetation were looked at. Using a known number of marked seeds we tried to get an indication of the effectiveness of the seed transportation of the tides and which factors are important for tidal transport. The hypothesis was that at locations closer to the Wadden Sea or creek the seeds would have a higher transportation percentage and that elevation might have an effect as well.

Table1: Comparison of data of various authors concerning the floating capacity of diaspores of some salt-marsh plant species.
T50, time in day(s) that it takes 50% of the seeds to sink. Ttotal, time in day(s) that it takes all seeds of a species to sink.
Superscripts stand for different diaspores used in the experiments: α = achene, ν = nut, φ = fruit, γ = grain, σ = seed

Species	Koutstaal *et al.* 1987		Geertsema, 2000		Kolen &Esselink 1999	Praeger, 1913	Guppy, 1906
	T50	Ttotal	T50	Ttotal	T50		
Aster tripolium	$2 - 4^{\alpha}$	$7 - 15^{\alpha}$	4^{α}	70^{α}	5^{σ}	5^{α}	$0 - 7^{\alpha}$
Atriplex littoralis	$0{,}003 - 0{,}007^{\nu}$	$0{,}08 - 0{,}17^{\nu}$	1^{σ}	43^{σ}			
Atriplex littoralis	$1.5 - 3^{\varphi}$	$15 - 90^{\varphi}$					
Atriplex portulacoides	45^{φ}	120^{φ}			13^{σ}		
Atriplex prostrata	$0{,}04^{\nu}$	$0{,}29^{\nu}$					
Atriplex prostrata	$0{,}27 - 2^{\varphi}$	$7 - 21^{\varphi}$	1^{σ}	43^{σ}	21^{σ}		
Elymus athericus	$1 - 2^{\gamma}$	$5 - 12^{\gamma}$	1^{γ}	$>90^{\gamma}$	$<1^{\sigma}$		
Festuca rubra	$0{,}38 - 1{,}58^{\gamma}$	$4 - 5^{\gamma}$	1^{γ}	$>90^{\gamma}$			
Glaux maritima			10^{σ}	61^{σ}			
Helianthus annuus	5^{ν}	$9 - 12^{\nu}$					
Juncus gerardi			1^{σ}	50^{σ}			
Limonium vulgare	$0{,}10^{\nu}$	$0{,}23^{\nu}$	6^{φ}	90^{φ}			
Limonium vulgare	$4 - 15^{\varphi}$	$18 - 60^{\varphi}$					
Matricaria maritima	90^{ν}	150^{ν}					$30 - 180^{\nu}$
Odontites vernus			1^{σ}	90^{σ}			
Plantago maritima	$0{,}02 - 0{,}04^{\nu}$	$0{,}29^{\nu}$	1^{σ}	40^{σ}		$0{,}0007^{\nu}$	$0 - 7^{\nu}$
Plantago maritima	$5 - 10^{\varphi}$	$14 - 21^{\varphi}$					
Potentilla anserina			1^{σ}	85^{σ}			
Puccinellia maritima	$0{,}08 - 0{,}83^{\gamma}$	$2 - 4^{\gamma}$					
Rumex crispus	$0{,}04^{\nu}$	$0{,}08 - 0{,}13^{\nu}$					
Rumex crispus	$45 - 120^{\varphi}$	240^{φ}				450^{φ}	$30 - 180^{\varphi}$
Salicornia spec.	$0{,}06 - 0{,}08^{\sigma}$	$<1^{\sigma}$	1^{σ}	26^{σ}			$0 - 7^{\sigma}$
Seriphidium maritimum			1^{σ}	18^{σ}			
Sonchus arvensis		$>150^{\alpha}$				4^{φ}	
Spartina anglica	$1.5 - 5^{\gamma}$	$4 - >60^{\gamma}$					
Spergularia maritima	$0{,}04 - 0{,}13^{\sigma}$	$0{,}21 - 0{,}29^{\sigma}$	10^{σ}	43^{σ}			
Spergularia media			35^{σ}	$>90^{\sigma}$			
Sueda maritima	$0{,}08 - 1{,}25^{\varphi}$	$7 - 14^{\varphi}$	1^{σ}	$>90^{\sigma}$	69^{σ}	2.5^{φ}	$0 - 7^{\varphi}$
Triglochin maritima	30^{φ}	180^{φ}	1^{σ}	$>90^{\sigma}$	74^{σ}	4.5^{φ}	$0 - 7^{\varphi}$

Material and Methods

Study site

The research area was Schiermonnikoog (53°30', 6°10'), one of the Friesian barrier islands in the Dutch Wadden Sea. An area of 1,650ha of the island is covered with salt marshes growing on sandy sediments stretching along elevational gradients including high and low marshes. Three zones can be distinguished: the pioneer zone, low salt marsh and the high salt marsh. The differences are in height and therefore inundation frequencies and also vegetation compositions. The mean annual inundation frequency in the low marsh was 166 per year (Bockelmann *et al.* 2002). In the high salt marsh the annual inundation frequency was 53 per year.
In the salt marsh system of Schiermonnikoog the tides come in from the Wadden Sea and through creeks that overflow when the tide is high enough. There is a mean tidal amplitude of 300 cm. With a lowest neap tide of -215 cm above N.A.P. (Dutch ordinance level) and a highest spring tide of 234 cm above N.A.P. (Rijkswaterstaat, 2001)

Test locations

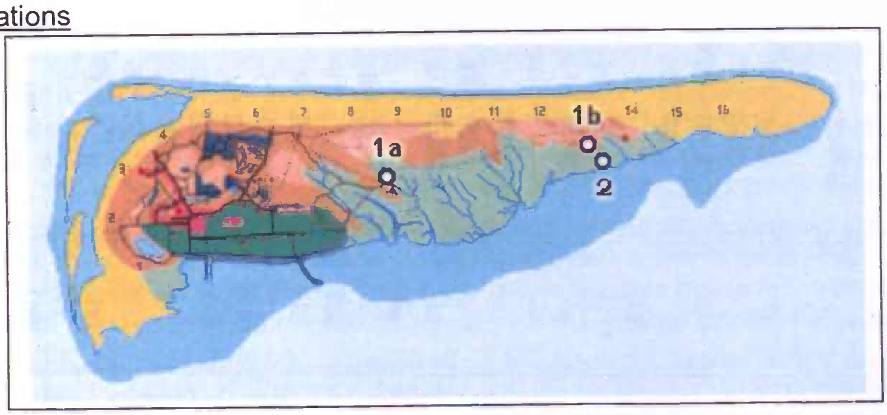

Figure 1: Chart of the island Schiermonnikoog. The test locations are indicated. 1a: creek in the old, near cattle grazed salt marsh. 1b: creek in the intermediate aged, non-cattle grazed salt marsh. 2: low salt marsh.

Two creeks were used for the pilot study on the abundance and diversity of seeds in creeks. The creek on the high salt marsh and close to the grazed part of the old salt marsh of the island Schiermonnikoog (Figure 1: 1a) was used to test the effectiveness of the nets. The part of the creek where the measurements were done was 1.9 km from the Wadden Sea. This test location was relatively narrow, about 2.50m wide, and 1.30m deep. The age of the local vegetation zone is 100 years (Walrecht 1998). Local vegetation on the ungrazed part was typical high salt marsh which included *Festuca rubra, Elymus athericus* and *Armeria maritima*.

Most of the samples for the first pilot study were taken from another creek, more to the east, in the younger, ungrazed part of the salt marsh. (Figure 1: 1b). On the location of the measurements the creek was about 3.00m and about 1.40m deep and 0.5 km from the Wadden Sea. The salt marsh vegetation zone around this creek is 25 years (Walrecht 1998). The intermediate aged salt marsh vegetation close to the creek included *Artemisia maritima*, *Sueda maritima*, *Limonium vulgare* and *Atriplex portulacoides*.

Another location was used for the pilot study on the movement of seeds over salt marsh vegetation. The set-up place for the Astro-turfs® was lower on the salt marsh, in the pioneerzone (Figure 1: 2). This area is flooded almost every high tide in winter. The sparse vegetation mostly consisted out of *Spartina anglica, Salicornia europea* and *Limonium vulgare* with a high percentage of bare soil in between.

Pilot study 1: Abundance and diversity of seeds in creeks

The presence of seeds in creeks was determined by collecting seeds with nets, on two sites with two methods over a period of a month. The first method was the standing net method. The net stood on the poles and the water was sieved as it flowed through the net (Photo 1). The nets were set up one hour before or/and after high tide (time of tides from table of RIKZ, Rijks Instituut voor Kust en Zee, Dutch institute for research on coast and sea) at the measure point. It was predicted from initial observations that during this period, the water flow would be the strongest. However the water was often lower than expected from astronomical predictions and the velocity of the water was also lower. As a result the water was observed to flow around the standing nets instead of through and the time the net was left in the water fluctuated from 15 to 55 minutes, depending on how fast the water seemed to flow. The second method, the towing net method, was an attempt to solve this problem. Two people, for 60 metres at a constant speed towed the net through the creek.

The net construction consisted of a metal frame of 50 by 50 cm and the actual net. The frame had an inner and outer frame, held together by screws. Four steel eyes attached to the outer frame allowed it to stand with two poles in the mud of the creek. The poles could also be used to drag the net through the water. The nets were made of fine material (mesh size = 240μm). The opening was 50 by 50 cm and the length was 200 cm. Velcro was used to attach it to the frame (Fig 2).

The time, height of the water level and tide were recorded. The height of the water level was measured with a height stick, tied to the net frame (Photo 1). The nets were transported back in plastic bags and rinsed with fresh water. The contents were cold-stratified (4°C in a dark room) for at least 6 weeks. All the samples were put in the greenhouse to grow on sterilised soil. Water was added daily. Germinated seeds were identified and quantified.

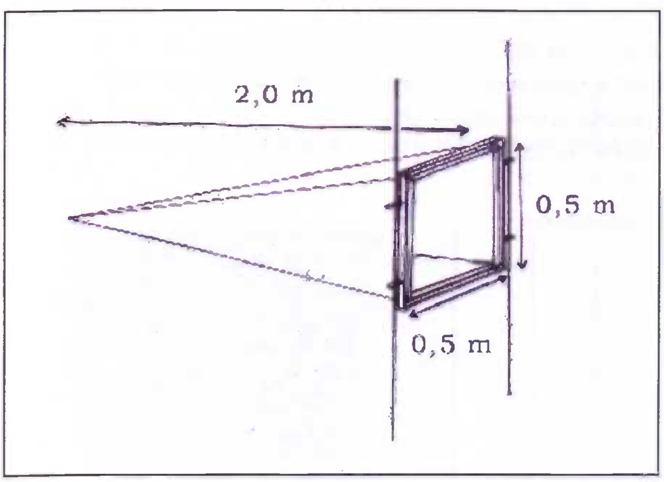

Figure 2: Standing net, also usable as dragging net, to catch propagules floating on the surface or just under.

Photo 1: Standing net at intermediate aged, cattle ungrazed salt marsh, with height measurement pole next to the right pole.

Effect of marking on floatation capacity

(preliminary research for pilot study 2)

Two marking methods were tested on two salt marsh species. The marking methods were spray paint and a textile dye. The salt marsh species were *Plantago maritima* and *Elymus athericus*. The marking effectiveness of the paint and the influence on floating capacity were tested. There were three treatments: control, dye 1 and dye 2. Each had 4 replicates of 25 seeds. The seeds were coloured 24 hours before the test. The control seeds were not marked. Dye 1 was a lacquer spray (Air Crafts, Spray enamel). Dye 2 was textile paint. When the seeds were dry they were put in cups with artificial seawater with a salinity of +/- 30.0 PSU. The artificial seawater was made with NaCl, $MgCl_2$, $CaCl_2$, Na_2SO_4 and K_2SO_4. (Appendix A). The cups were put on a shaking machine that was set at 75 shakes per minute and an amplitude of 1.5 cm. The light regime was 12 and 12 hours for day and night respectively at 16°C (Geertsema 2000). After the shaking was initiated it was checked every 30 minutes how many seeds had sunken for all the four replicates of the three treatments of the two species. After three hours it was checked which dye stayed on the best and which had the least effect on the floating capacity compared with the control replicates.

Pilot study 2: Movement of seeds over salt marsh vegetation

The movement of seeds over salt marsh vegetation was studied by means of Astro-turfs®. Four times the whole set-up was repeated, every 6^{th} tide during the period from spring tide to neap tide (±1.5 weeks). The Astro-turfs® are artificial grass mats and were cut into 30 by 30 cm squares. They were pinned to the ground with pegs. Seed traps like this (Photo 2 and 3) have been used in more researches (Wolters 2003, Wolters *et al.* 2004 in press). A grid of 5 by 5 Astro-turfs®, each 20 meter apart, was set up, going at right angles to the bank of the creek and running parallel to the Wadden Sea coast (Fig 3). The 25 Astro-turfs® were pinned to the ground in the grid at low tide with a plastic bag beneath them to exclude the seeds already on the ground from the results (Photo 2, Wolters 2003). A known number of coloured seeds was evenly distributed on each Astro-turf mat: 50 seeds of *Elymus Athericus* and 50 seeds of *Plantago maritima* (Photo 3). After inundation by one high tide the Astro-turfs® were collected and taken back in plastic bags. The next day they were rinsed with a hard stream of water and the content sieved with a 212 µm mesh. In the field, the seeds were very distinctly coloured but, in the sieve, the coats were sometimes found not attached to the *P. maritima* seeds. In these cases the bare *P. maritima* seeds were not counted as naturally dispersed.

The heights measurements of the high tides come from the official tide gauge of the RIKZ. For all the samples the remaining marked seeds were counted and removed. The remaining sediment and naturally deposited seeds were processed and put in the greenhouse similarly to the samples of the pilot study on abundance and diversity of seeds in the creek (see before).

Photo 2: Astro Turf® set out in the field

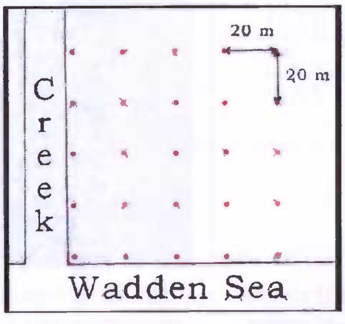

Figure 3: Experimental grid

Photo 3: Astro turf® with seeds

Several potential factors on the transportation of the seeds were measured. The distance to the creek, the distance to the sea, the elevation, the height of the high tide and the height and density of surrounding vegetation.

The statistical tests, analysis of variance (ANOVA) and multiple regression, were done separately for the two species of seed because there was a large variance in the percentages of transported seeds between the two species. *E. athericus* seeds have a significantly higher percentage of transportation than *P. maritima* seeds (paired sample t-test, $t(98) = 15.616$, $p < 0.01$) (Fig.2)

The effect of the elevation and the height of the water level were analysed using all the data, including seed traps that were not inundated. During the experiment not all the Astro-turfs® were inundated on all the days, since the height of the high tide changes during the spring tide to neap tide cycle. With respect to the possible influences of the distances from either mud flat or creek, the results of the content of the Astro-turfs® were only taken into account if they were submerged.

The statistical testing was completed using SPSS 11.5. (Univariate general linear modelling and linear regression).

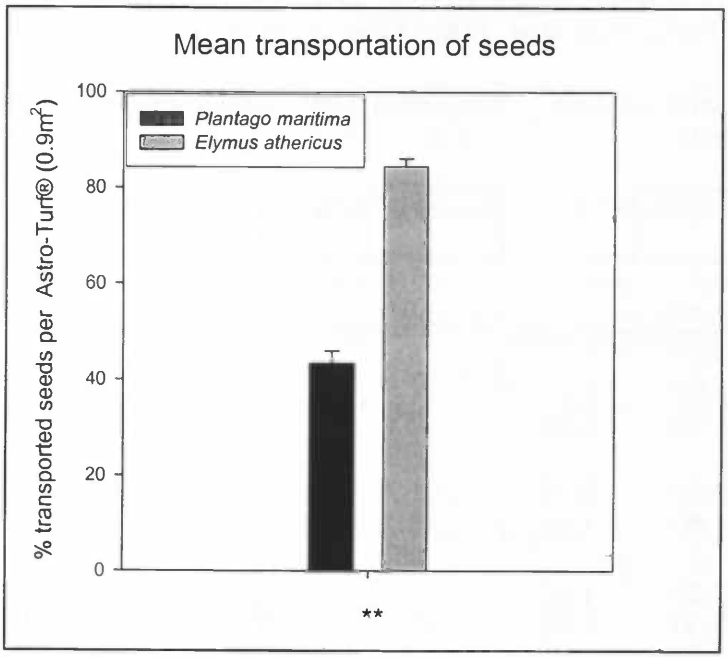

*Figure 2: Means of % transported seeds of E. athericus and P. maritima per Astro-turf® ($0.9m^2$). Using all data, N=99 Astro-turfs® per species. ** P-value < 0,01*

Results

Pilot study 1: Abundance and diversity of seeds in creeks

In table 2 the results of the trials with the nets are shown. The standing net method was used at both creeks. The highest number of species per trial for this method was found in the old and cattle grazed area (4,5 species per trial). The most species in total were also found in the creek near the grazed area (8 species in total). At the intermediate aged salt marsh site both methods were used. The towing net method yielded a much higher abundance (89,50 seeds per trial) than the standing net method (1,17 seeds per trial).

Table 2: The mean number of seeds and species of seeds, that were caught, is given for each species and for each location and method, with the standard error (s.e.). The high tide (m above N.A.P. = Dutch Ordinance Level) is given as an indication of the water movement. N = number of trials.
The floating capacity information comes from other researches ([1:] Geerstema 2000, [2:] Kolen & Esselink 1999, [3:] Koutstaal et al. 1987, [4:] Praeger 1913, [5:] Guppy 1906)

	Grazed, old salt marsh		Ungrazed, intermediate aged salt marsh				Floating capacity in literature (see also Table1)
	Standing	N=2	Standing	n=6	Towing	n=2	
Species	mean (seeds)	s.e.	mean (seeds)	s.e.	Mean (seeds)	s.e.	
Armeria maritima	0,50	0,50					no information
Elymus athericus	3,00	3,00					Days[1,2,3]
Festuca rubra	1,50	1,50			1,50	1,50	Days[1,3]
Artemisia maritima	0,50	0,50	0,67	0,42	67,50	12,50	no information
Atriplex portulacoides	1,00	1,00	0,33	0,21	6,50	2,50	Weeks[2,3]
Atriplex prostrata	2,50	1,50			3,00	1,00	Days[1,2,3]
Suaeda maritima	0,50	0,50	0,17	0,17	11,00	1,00	Weeks[1,2,3,4,5]
Salicornia europea	1,50	1,50					Hours[1,3,5]
# seeds per net	11,00	3,00	1,17	0,48	89,50	8,50	
# species per net	4,50	1,50	0,83	0,31	4,50	0,50	
high tide (m above N.A.P)	1,57	0,00	0,90	0,03	1,27	0,00	

Effect of marking method on floating capacity

(Preliminary research for pilot study 2)

The effect of the two dyes on the floating capacity of *Plantago maritima* and *Elymus athericus* seeds are shown in Figure 1. Spray paint has a positive effect on the floating capacity while textile paint has a negative effect. The textile paint adhered better to the seeds than the spray paint and both paints adhered better to *E. athericus* seeds then to *P. maritima* seeds. For the experiment with the Astro-turfs® on the salt marsh the textile paint was used, because it adhered the best. The negative effect on the floating capacity was preferred above the positive, since the latter would give an overestimation of the transport capability of water.

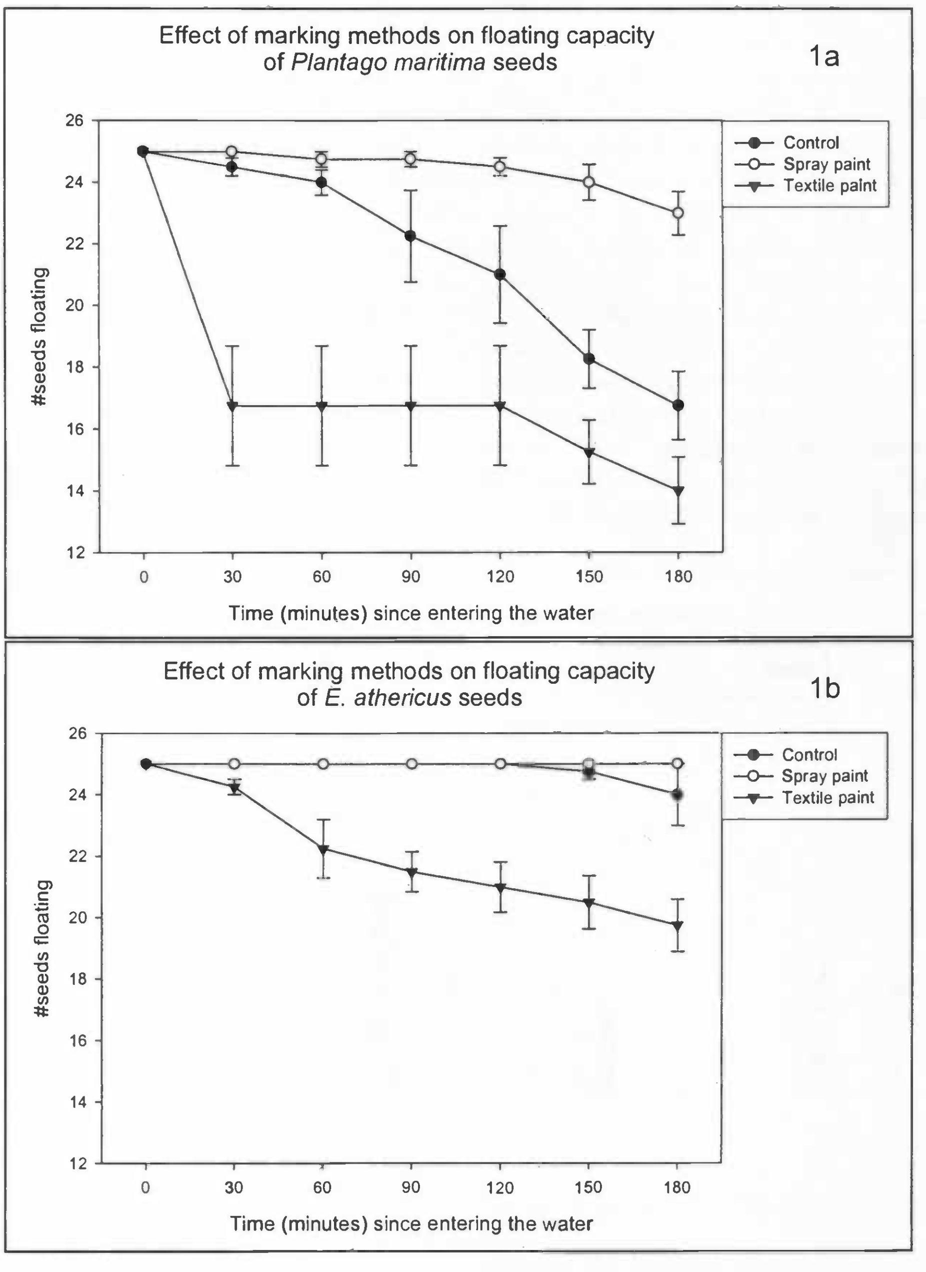

Figure 1a and b: Changes in floatation capacity of P. maritima (1a) and *E. athericus (1b) seeds when treated with two marking methods (textile and spray paint), compared with the unmarked control seeds.*

Pilot study 2: Movement of seeds over salt marsh vegetation

Single effect of variables

The height and density of the vegetation showed they did not have a significant influence on the transportation of the seeds, probably because of the high percentage of bare soil (Appendix B). The transportation of *E. athericus* seeds did not always fulfil the assumptions of the tests for ANOVA. However, this test is robust and in figure 3 there are such strong trends that the results of the ANOVA are probably trustworthy.

Out of the variables measured and tested, the water level of the high tide, had the greatest effect on the seeds of both *P. maritima* (ANOVA $F(3,8) = 18.323$, $p < 0.001$) and *E. athericus* (ANOVA $F(3,8) = 15.175$, $p < 0.001$) (Table 3). At spring tide the water level at high tide is higher and at low tide lower than at neap tide. During spring tide more seeds are being transported then during neap tide (Fig 3a).

The distance to the sea also had a significant effect on *P. maritima* (ANOVA $F(4,12) = 2.993$, $p < 0.05$) and *E. athericus* (ANOVA $F(4,12) = 3.925$, $p < 0.05$) seeds (Table 3). More seeds were transported from locations closer to the shoreline then further away (Fig 3b). However, the effect of the distance from the creek was not significant for *P. maritima* or *E. athericus* seeds (Table 3).

E. athericus seeds were less transported at the higher elevations (ANOVA $F(4,2) = 5,985$, $p < 0.001$) (Table 3 and Fig 3c). Yet, the elevation in itself was not significantly important for *P. maritima* seeds (Table 3), although there is an evident trend similar to significant trend of the *E. athericus* seeds (Fig 3c).

But when the elevation and the water level of high tide were combined to obtain the maximum water level above the seed traps, it was found that a higher maximum water column transports significantly more seeds of *P. maritima* (ANOVA $F(4,12) = 8,472948$, $p < 0.001$) and *E. athericus* (ANOVA $F(4,12) = 9,851$, $p < 0.001$) (Table 3) than a lower maximum water column (Fig 3d).

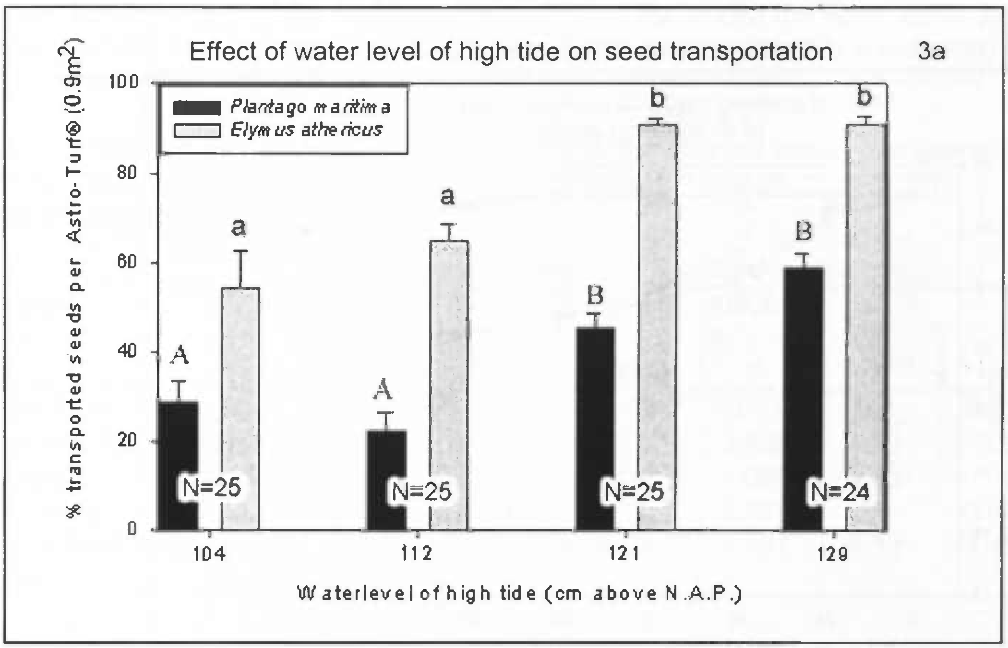

Figure 3a: The effect of water level on the seed transportation. The mean % transported seeds per Astro- turf® (0,9m^2) with s.e. against the water level of the high tide. All data was used for this graph. N = indicated sample size per species.

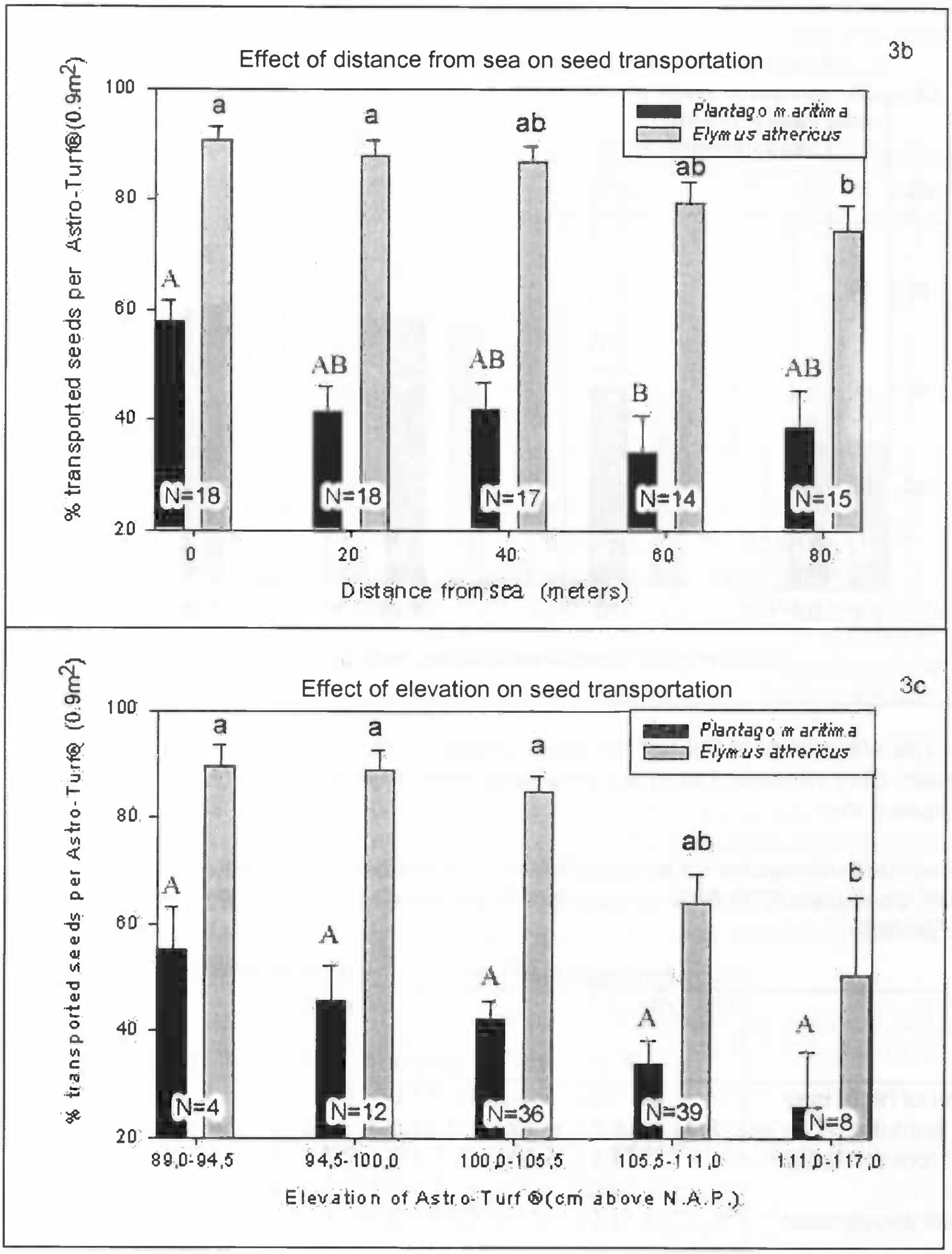

Figure 3b and c: The effects of distance from sea (b) and elevation of Astro turf® (c) on the seed transportation. For graph (b) only inundated samples were used. For graph (c) all data was used. N = indicated sample size per species.

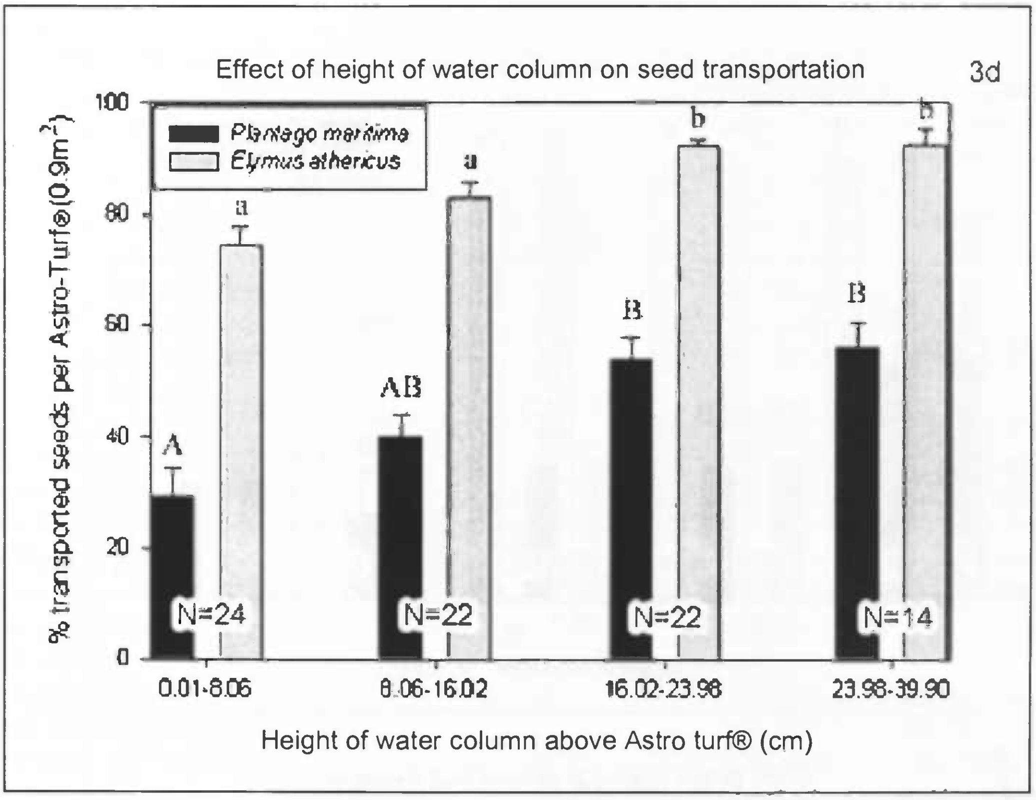

Figure 3d: The effect of the height of the water column above the Astro turf® on the seed transportation. Only inundated samples were used for this graph. N = indicated sample size per species.

*Table 3: Relation between the factors and the % transported seeds per species of seeds. GLM, univariate ANOVA. n.s. = not significant, * p<0.05, ** p<0.001. (See also figure 3)*

	Plantago maritima			*Elymus athericus*		
Factor	ANOVA			ANOVA		
	F	*df*	p-value	F	*df*	p-value
Waterlevel of high tide	18.323	3,8	1.8E-09 **	15.175	3,8	3.8E-08 **
Distance from the mud flat	2.993	4,12	0.023 *	3.925	4,12	0.0059 *
Distance from the creek	1.770	4,13	0.14	1.099	4,13	0.36
Elevation	1.959	4,2	0.11	5.985	4,2	0.00025 **
Water level above seed traps	8,472	4.12	6.1E-05 **	9,851	4.12	1.4E-05 **

Combined effect of water level and distance to sea
A multiple regression was performed for *P. maritima* to determine the dependence of the percentage of transported seeds on the distance from either creek or sea, the elevation and the water level of the high tide (see also table 3 and Fig 3 a, b and c). The data of the *E. athericus* seeds violated some of the assumptions of the test (the data is heteroscedastical and non-linear) so it was not possible to generate a regression equation for this species.

The test excludes the factors that are not contributing additional explanation to the transport of the seeds. The factors that remain have β values that give an indication of the influence on the dependent factor (% transported seeds) in a regression equation.

Regression equation:

$$P = 30{,}42 + (11{,}53 * W) - (6{,}70 * Ds)$$

P = % transported *P. maritima* seeds
W = Water level of high tide
Dm = Distance to sea

$R^2 = 0.446$

The water level of the high tide and the distance to the sea are the main factors influencing the percentage of transported seeds. The first number is the constant (30,42 %). The water level has a larger, positive effect on the percentage of transported seeds. When the water level of the high tide is higher, then a larger percentage of seeds will be transported. The distance to the sea has a smaller, negative effect. Further away from the sea, less seeds will be transported.

Deposited seeds compared with floating capacity
Although it was winter and the seed traps were in the field for only a day, still some seeds were naturally deposited. *Salicornia spp.* seeds were present in highest numbers (154 germinated seeds), although other studies indicate that it's floatation capacity is small, just a couple of hours (Geertsema 2000, Koutstaal *et al.* 1987, Praeger 1913, Guppy 1906). Not all seeds of *Suaeda maritima* germinated and seeds from *Salicornia spp.* were sometimes overlooked (see Table 4).

Table 4: Unmarked seeds found on Astro-turfs during measurements in March 2003. ([1:] Geerstema 2000, [2:] Kolen & Esselink 1999, [3:] Koutstaal et al. 1987, [4:] Praeger 1913, [5:] Guppy 1906)

Species	**Seeds** (/m2/day) Found	germinated	**Floating capacity** in Literature
Salicornia spp.	136,11	154,44	$Hours_{1,3,5}$
Sueda maritima	3,44	3,11	$Weeks_{1,2,3,4,5}$
Elymus athericus	2,33	2,33	$Days_{1,2,3}$
Limonium vulgare	1,11	1,11	$Days_{1,2,3}$
Atriplex spp.	0,11	0,11	$Days_{1,2,3}$

Discussions and conclusions

Pilot study 1: Abundance and diversity of seeds in creeks
From the collected data of the nets it can be concluded that there was a greater diversity of seeds in the creek near the older and cattle-grazed area, than at the other site at the intermediate-aged and non cattle grazed area (see Table 2). This seemed strange since the succession stage on an older salt marsh is further developed than at an intermediate-aged salt marsh and should be mostly dominated by *Elymus athericus*. But the creek lay next to a cattle-grazed area and cattle-grazed areas have a more diverse plant community than non cattle grazed areas on the old salt marsh (Bakker 1978, Bakker *et al.* 2000). An explanation for the higher diversity of seeds in the creek near the cattle grazed salt marsh could be that the creek was longer and therefore had a larger catchment basin.

At another part of the Netherlands Huiskes *et al.* (1995) caught more seeds and from plants typical of lower salt marshes in nets located at the higher salt marsh sites than the other way around, resulting in a net landward transportation of propagules. But in this study there were no surveys of the species on the creek banks, so it cannot be determined if the propagules were not locally dispersed. It was also not possible to find an indication of a difference between the number and species of propagules during flood or ebb tide, because in this study there were not enough successful measurements taken before and after high tide, because of problems with the timing of the measurements at different water levels and predicting the high tide. The tides did not correspond to the mathematically predicted tides (RIKZ), since the tides are not just dependent on the moon and sun, whose movements and effects can be calculated, but also on wind and location (Bockelmann *et al.* 2002). On Schiermonnikoog it was found by Bockelmann *et al.* (2002) that distances of 2.5-5 km between sites of the same elevation lead to differences in water levels up to 25%. There is also large friction of salt marsh vegetation that slows down overland flow during high tide across the salt marsh surface. This decreases the Mean High Water level on the more landward marshes and the highest water level is achieved at a later time (van der Molen 1997). In this study the water was often too low to take samples with the nets.

It can be reasoned that at extremely low neap tide the water does not rise above the creek banks and does not get a chance to collect seeds. But since there were no trials with the standing net at either location at both neap and spring tide, it cannot be verified if the height of the high tide had an influence on the abundance or diversity of seeds in the nets. Huiskes *et al.* (1995), however, did have enough data in his creek and concluded that the height of the tide significantly effected the abundance of propagules, if not the direction of the transportation.

For future research it is not recommended to use the standing net method as it was in this study. The seeds were moving around the nets, especially when the water velocity was low. The towing net method seemed to give better results. This method yielded the diversity of seeds, but nothing could be said of the abundance, since it is unknown how much water passed through the nets, it gave only qualitative, not quantitative data. If the creek could be partially dammed the samples would represent the actual occurring seeds more correctly. In a partially dammed creek the water would have to go through the nets with no chance of flowing around them and one could calculate the volume of water being sieved.

Pilot study 2: Movement of seeds over salt marsh vegetation

A high percentage of marked seeds was transported from the Astro-turfs® during one high tide. So water seemed to have a good potential for dispersal of seeds over the vegetation in this area. More *Elymus athericus* seeds were transported than *Plantago maritima* seeds (Fig. 2). The floating capacity of both species might cause this significant difference. According to the literature (see Table 1, Koutstaal *et al.*1987) *P. maritima* seeds stay afloat for about 0.5-1 hour, and will float maximally 7 hours. *E. athericus* seeds have a higher floating capacity, ranging from 1-2 days with a maximum of 5-12 days. Because of the marking with textile paint, the floating capacity of both species was less then natural, unmarked seeds in this study, so the percentage of natural seeds transported is probably underestimated. Bakker *et al.* (1985) reported that in open *Puccinellia maritima* vegetation, only 5% of deposited seeds of several species remained after two high tides.

It was expected that a location closer to the creek or Wadden sea would have a higher transportation of seeds and the distance to the Wadden sea was shown to be a significant effect, but the results showed that the distance to the creek did not have such an influence. On the other hand, the strongest effect on the transportation of seeds was the height of the water level (Table 3, Fig 3). During spring tide more seeds were transported than during neap tide, as was also found by Huiskes *et al.*(1995). The effect of the height of the high tide on the dispersal of the seeds was stronger than the effects of the distance to the creek and sea or the elevation of the location. This was found in a area of 80 by 80 m on the low salt marsh. Perhaps a study, that takes the whole salt marsh, low and high, into account, will find that on a larger scale other factors are more decisive.

Comparing occurring seeds with seed floating capacity

The results of neither the pilot study on abundance and diversity in creeks nor the pilot study on movement of seeds over the vegetation showed a correlation between the floating capacity of the seeds and the abundance and species of caught seeds. It was expected that seeds with a higher floating capacity would be found more in the nets (Huiskes *et al.*1995).

At the intermediate-aged salt marsh this seemed confirmed, because *Atriplex portulacoides* and *Suaeda maritima* were found in relatively high abundance (Table 2) and have a high floating capacity up to several weeks (see Table 1, Guppy 1906, Praeger, 1913, Koutstaal *et al.* 1987, Kolen & Esselink 1999, Geertsema 2000). However, at the older and cattle-grazed site, the nets caught a higher abundance of seeds with a low floating capacity (Table 2). The most abundant seeds at this creek were from *Elymus athericus, Atriplex prostrata*, and they have floating capacities of a few days (Table 1, Koutstaal 1987, Kolen & Esselink 1999, Geertsema 2000). An explanation for this contrast could be that the seeds originate from local plants, since the most abundant species at both creeks were also present in the local vegetation within 50 m (seen in the field).

Although it was not the main object of the second pilot study about movement of seeds to look at the natural occurring seeds, some observations can be made. The species that was deposited most abundantly on the seed traps was *Salicornia spp.* (Table 4), but the seeds of this species have a very low floating capacity of not more than a few hours (Table 1, Guppy 1906, Koutstaal 1987, Kolen & Esselink 1999, Geertsema 2000). Since most of the local vegetation was *Salicornia europea* (Appendix B), it is probable that these were locally deposited seeds. The other seeds that were found had floating capacities ranging from several days to several weeks, but were much less abundantly dispersed. This seems to corresponds with what Rand (2000) found in a New England salt marsh system in that dispersal appeared to be local. But the seed traps were in the field in winter/early spring, while most seeds are dispersed in autumn.

Potential of creeks

Although it was found that the creeks did carry seeds (Table 2), the distance to the creek was shown to be of no importance for the dispersal of seeds on the low salt marsh (Table 3). Huiskes *et al.* (1995) showed that there is a net landward transportation of propagules in creeks in the salt marsh, indicating that the tide could be an important vector for dispersal. Creeks could be important to bring propagules to restricted areas on the salt marsh, leaving concentrated masses of seeds in driftlines (Bakker *et al.* 1985).

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Appendix A

Protocol for salt water solution (this receipt is for 33.7 PSU, it was diluted untill it was 30.0 PSU):

	Stock code	Mw (g/mol)	Molarity (mM)	g/L	g/5L	g/10L
NaCl	N7	58.44	420	24.55	122.75	245.45
$MgCl_2*6H_2O$	M1	203.3	48.3	9.82	49.10	98.10
$CaCl_2$	C4	110.99	3.61	0.40	2.00	4.00
Na_2SO_4	N23	142.04	22.6	3.21	16.05	32.1
K_2SO_4	K26	174.27	4.88	0.85	4.25	8.5

Appendix B

Vegetation relevees at the locations of the Astro-turfs®, 4 m^2 around each measure point. The figures are percentages cover. Medium height, total vegetation cover and height above N.A.P (Dutch Ordnance Level) are also given.

	Measure point				
	1.1	1.2	1.3	1.4	1.5
Height above NAP (cm)	99.9	89.1	100.4	104.9	103.4
Total vegetation cover (%)	55	<1	33	40	1
Medium height (cm)	5	0	5	10	1
species cover (%)					
Spartina anglica	55		33	40	<1
Salicornia europea	<1	<1	<1	<1	<1
Limonium vulgaris					
Puccinellia maritima					

	2.1	2.2	2.3	2.4	2.5
Height above NAP (cm)	102.9	96.4	106.7	104.4	97.9
Total vegetation cover (%)	<1	2	3	4	1
Medium height (cm)	1	2	2	3	1
species cover (%)					
Spartina anglica	<1	1	<1	4	<1
Salicornia europea	<1	1	<1	<1	<1
Limonium vulgaris			2.5		
Puccinellia maritima					

	3.1	3.2	3.3	3.4	3.5
Height above NAP (cm)	110.1	102.4	104.9	106.4	103.9
Total vegetation cover (%)	15	2	5	5	30
Medium height (cm)	7	1	3	3	4
species cover (%)					
Spartina anglica		2	4	4	28
Salicornia europea	15		<1	1	1
Limonium vulgaris			1	<1	1
Puccinellia maritima					

	4.1	4.2	4.3	4.4	4.5
Height above NAP (cm)	116.9	106.9	106.4	105.7	105.4
Total vegetation cover (%)	20	2	7	20	25
Medium height (cm)	6	2	5	6	9
species cover (%)					
Spartina anglica		<1	5	19	24
Salicornia europea	20	2	2	1	1
Limonium vulgaris		<1	<1	<1	<1
Puccinellia maritima	<1	<1	<1	<1	<1

	Measure point				
	5.1	5.2	5.3	5.4	5.5
Height above NAP (cm)	115.1	109.4	107.1	102.9	107.1
Total vegetation cover (%)	11	5	3	2	3
Medium height (cm)	5	3	3	2	3
species cover (%)					
Spartina anglica		<1	2	<1	2
Salicornia europea	11	5	<1	2	<1
Limonium vulgaris			1	<1	1
Puccinellia maritima	<1	<1	<1	<1	