

Seedling establishment of the invasive clonal
grass *Elymus athericus*:
An experimental approach

Diplomarbeit von

Thies Wels

Kiel, März 2001

Mathematisch-Naturwissenschaftliche Fakultät der
Christian-Albrechts-Universität zu Kiel
Geobotanisches Institut

Contents

1	Introduction	1
2	Establishment of Transplanted Seedlings in a Low Salt Marsh Area on Schiermonnikoog	5
2.1	Methods	5
2.1.1	Study Site	5
2.1.2	Germination, Planting and Experimental Design	6
2.1.3	Soil Samples and Salinity	10
2.1.4	Elevation and Inundation	10
2.1.5	Calculation and Statistics	11
2.2	Results	11
2.2.1	Elevation, Inundation and Salinity	11
2.2.2	Germination and Transplantation	13
2.2.3	Herbivory Impact and Aboveground Competition	14
3	Seedling Establishment of Indigenous Seedlings in a Low, Young Salt Marsh	23
3.1	Methodes	23
3.2	Results	23
4	Observations on Transport of <i>Elymus athericus</i> Diaspores by Tidal Currents	26
4.1	Methods	26
4.2	Results	28
5	Discussion	30
6	Conclusion	40
7	Deutsche Zusammenfassung	42

Abstract

Elymus athericus was formally known to be restricted to high salt marsh habitats. Recently the spread into low habitats has been reported. In the present study seedling establishment of *E. athericus* in the low saltmarsh was examined. Seedlings of seeds of different populations from different habitats were grown in the greenhouse and later transplanted into a not yet by *E. athericus* invaded low salt marsh habitat of young successional stage on the Dutch Wadden Sea island Schiermonnikoog. The Influence of Herbivory and Competition were examined. Establishment success was followed by measuring fitness parameters like survival rate, ramets per plant and rhizomes per plant as well by measuring growth parameters like plant height, leaves per plant and relative growthrate. Herbivory and competition with neighbours were discovered to be the most important inhibiting factors of seedling establishment. In general, seedlings of seeds of a low habitat in an old successional stage performed lowest in the study site. Furthermore, despite the prior assumption indegenous seedlings were discovered in the area. Their development was followed analog to transplanted ones. Seedlings growing in the neighbourhood of *Limonium vulgare* were found to perform better. This was valid for transplanted as well as for indegenous seedlings. Moreover, a drift experiment with coloured *E. athericus* spikelets showed that *E. athericus* populations at the bank of creek could provide diaspores for invading low salt marsh habitats by transport with medium high tidal floods.

Chapter 1

Introduction

Biological invasion of alien plants is known to alter species composition of plant communities resulting in a loss of species diversity (eg Silvertown 1993; Frey and Lösch 1998; Meyer and Schmid 1999; Meyer and Schmid 1999). However, in the last decades a similar loss of diversity was observed by invasion of different native species (eg Soukupova 1992; Leendertse et al. 1997). One example is the spread of the clonal grass *Elymus athericus* (Poaceae, species names follow van der Meijden 1996). *E. athericus* was reported to become dominant in several high saltmarsh habitats after grazing by livestock was stopped (Bakker et al. 1993; Van Wijnen et al. 1997). On the Dutch Wadden Sea island Schiermonnikoog long term succession was followed by permanent plots over 20 years. In contrast to still grazed areas *E. athericus* became dominant in most communities after ca. 30 years of non grazing (Van Wijnen et al. 1997). Formerly the grass has been characterised as a species restricted to high salt marsh habitats (Adam 1990; Beeftink 1977). However, recently Bakker et al (1998) reported an occurrence of *E. athericus* populations also in several low salt marsh areas. On some sites as on Schiermonnikoog they even occur below mean high tide level (MHT). For the reason that *E. athericus* has been characterized as nitrophilous, increase in artificial atmospheric nitrogen ($40 \text{ kg ha}^{-1} \text{ yr}^{-1}$) was suggested as a mayor cause for the spreading success of *E. athericus* (Bakker et al. 1993). Nutrient rich conditions could favour species with a wide ecological amplitude. However, different fertilization experiments could not find an effect (Bockelmann and Neuhaus 1999). Only higher doses ($100\text{-}250 \text{ kg ha}^{-1} \text{ yr}^{-1}$) resulted in a significant increase in biomass (Van Wijnen and Bakker 1999). Another hypothesis assumes that changes in the environment could lead to rapid genetic and thus phenotypic adaptation (A.-C. Bockelmann, in progress).

The island Schiermonnikoog allows research along a chronosequenz of salt marsh succession stages. Currents moving from west to east lead to permanent accumulation of sediments and therefore extension of the island at the most easterly end. Initial salt marsh succession stages can be found in the east to about 200 year old salt marshes in the west (Bakker et al. 1998). Calm waters at the south side of the island deposit fine sediments on the sandy subsoil and thereby create a clay layer. The clay layer thickness increases with the age of the island ranging from 0 cm in the very young stages to over 60 cm in the 150 year old marshes. Furthermore, the clay layer thickness and the total N-content are positive linear related (Van Wijnen and Bakker 1997). While the oldest parts have always been grazed most parts ranging from very young to about 100 year old salt marshes were never grazed by livestock (Bakker et al. 1998). Exclosures were established in several habitats on the island after grazing was stopped or in younger stages in the beginning of the salt marsh succession to exclude large herbivores. Permanent plots in and next to exclosures allow research on the effect of herbivores on salt marsh succession.

Former investigations by A.-C. Bockelmann (in progress) indicated that *E. athericus* populations from different habitats differed in their phenotypic and genetic traits. Transplant experiments showed for example that clones and seedlings grown from seeds of different habitats differed in their ability to cope with abiotic and biotic factors. Transplanted individuals performed best in the same site they came from. Microsatellite analysis assumed that populations of high habitats differed in

their genetic structure compared to populations in the low marsh. Moreover, populations of high habitats were not clonal connected to nearby populations in the low marsh. Consequently the invasion of low salt marsh patches happened most likely by seeds. However, A.-C. Bockelmann rarely found any seedlings neither in low nor in high habitats on Schiermonnikoog, although large amounts of seeds were found in driftline material (Bakker et al. 1985)

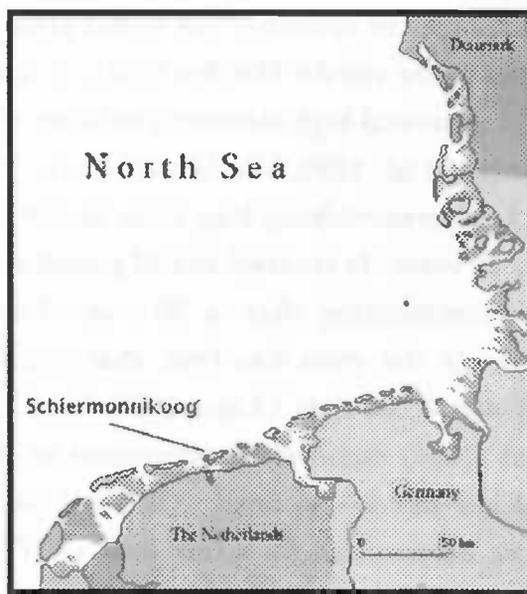


Figure 1.1: The Dutch Wadden Sea island Schiermonnikoog

and the seeds showed a high germability (Huiskes et al. 1995, A.-C. Bockelmann, in progress). *E. athericus* populations in low marshes were found from the oldest ungrazed parts to the about 30 year old saltmarsh near the dune Willemsduin. In younger marshes *E. athericus* was restricted to the high salt marsh (A.-C. Bockelmann, in progress). However, since 1998 *E. athericus* could be found in permanent plots inside exclosures in the seven year old low salt marsh in the area around exclosure T1 (see Fig. 1.1 and Fig. 4.1), while no *E. athericus* plants could be found outside the exclosures. Therefore, the occurrence of vertebrate herbivores in the area (Van Wijnen and Bakker 1997) was assumed to be one major factor inhibiting seedling establishment (A.-C. Bockelmann, in progress).

In the present research a transplant experiment was carried out to test whether *E. athericus* seedlings can establish in the young and low marsh in the area outside exclosure T1. Furthermore different origins of seeds were used to investigate for differences in their phenological traits expressed by their response to environmental factors like herbivory, competition, age and elevation of the habitat and the thereby resulting factors.

The main hypotheses were:

- Herbivores will have a negative impact on seedling establishment and performance
- Competition with neighbour plants will influence seedling establishment negative
- The different origins of seeds will result in different establishment success
- Elevation and thus inundation frequency and salinity of the soil will influence seedling establishment of *E. athericus*

During the research a first indigenous seedling was found outside the exclosures by accident. Furthermore, during the progression of the transplant experiment it turned out that at least the abiotic factors of the habitat should allow the natural establishment of *E. athericus* seedlings at the site (see section 2.2). Consequently the area was examined for indigenous seedlings. The development of these seedlings was followed through the vegetation period to compare their performance with those of the transplant experiment.

The discovery of indigenous seedlings showed that invasion must have been by seeds. As it is known that large amounts of *E. athericus* diaspores are

transported by tidal waters (Bakker et al. 1985), it is most likely that invasion occurred on this way. Strong winter floods carry diaspores mainly to high elevations of the salt marsh with a low backwards transport (Huiskes et al. 1995). Thus in the present study it was assumed that diaspores of *E. athericus* are more likely transported by medium high floods into low parts of the salt marsh. Furthermore, as medium high floods would consequently not reach high elevations with *E. athericus* populations, it was assumed that populations at the bank of creeks might supply diaspores by direct dispersal into the water. Therefore an experiment with coloured *E. athericus* spikelets was carried out to test whether diaspores of *E. athericus* populations at a creek bank could be transported into the waddensea and back into a low salt marsh within two tidal cycles.

Chapter 2

Establishment of Transplanted Seedlings in a Low Salt Marsh Area on Schiermonnikoog

2.1 Methods

2.1.1 Study Site

All experiments were carried out between March and November 2000 on the Dutch Wadden Sea island Schiermonnikoog (50°30'N, 6°10'E). An approximately 15 years old salt marsh area between creek 10 and 11 was chosen for the experiments (Fig. 2.2 and Fig. 2.1). The two creeks enclosing the approximately 300 x 100 m study area build a conspicuous successional border. East respectively west of these creeks younger respectively older successional stages can be found. While westwards creek 10 *Elymus athericus* is already present since 1975 only one individual has been found inside an enclosure easterly of creek 11 (exclosure T0) until the beginning of this study. The study area represents a successional series from mudflats over low and high salt marsh up to dunes. The experiments



Figure 2.1: The study site shows a patchy island structure. Small creeks traverse the area

were established in the low salt marsh zone, which shows a patchy island structure with differences in species composition and elevation (see Fig. 2.1). Small creeks traverse the low salt marsh leading to inundation of landwards as well as seaward parts. *E. athericus* was only present inside the permanent enclosure T1, but not outside in the experimental area.

2.1.2 Germination, Planting and Experimental Design

Seeds from *E. athericus* were collected in whole spikes from intact plants in October and November 1999. The seeds were collected at sites differing both in successional age and in habitat: An about 105-year-old high salt marsh and an about 87-year-old low salt marsh near the dune Kobbeduin. Furthermore an about 26-year-old high salt marsh and an about 7-year-old low salt marsh at the area between creek 10 and 11 close to the enclosure T1 (see Fig. 2.2 on the following page). In the following the sites will be named as "Kobbeduin" and "T1" while the four combinations of age and habitat will be named as:

YL young-low (low habitat at site T1)

YH Young-high (high habitat at site T1)

OL Old-low (low habitat at site Kobbeduin)

OH Old-high (high habitat at Kobbeduin)

At YL the spikes were collected inside the enclosure because there were no *E. athericus* plants outside. The spikes were stored in paper bags at room temperature during the winter. 300 seeds of each origin were placed into 90 mm diameter Petrie-dishes with filter paper in the beginning of March 2000. Each Petrie-dish contained 20 seeds. The paper was watered with demineralized water regularly. All dishes were placed into a germination chamber with a 12h day&night rhythm at the Biological Center of the RUG (Reijksuniversiteit Groningen). During light the temperature was regulated automatically to 17°C, while it was decreased under dark conditions to 12°C. Moisture was controlled in every Petri-dish daily and water was added if necessary. After about one week, each seedling was planted in a 50 ml plastic pot with a sand-potting soil mixture (1:2). After growing for 14 days in the greenhouse the approximately 12 cm young plants were stored for three days under cold conditions (10°C) to reduce growth. Finally all plants were transported from the Biological Center of the RUG to the island of Schiermonnikoog on 13.04.00. 150 plants of each origin were planted into the young salt marsh within the

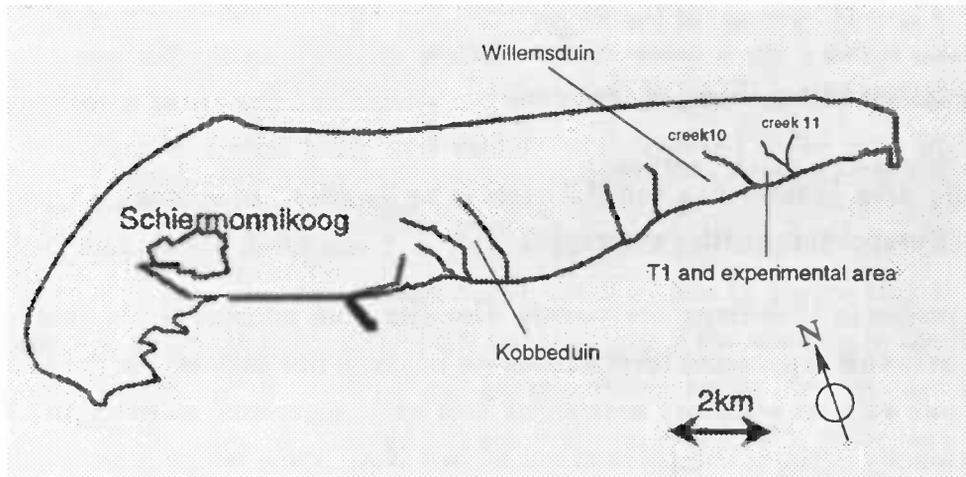


Figure 2.2: The origin of seeds and the experimental area on the Dutch Wadden Sea island Schiermonnikoog

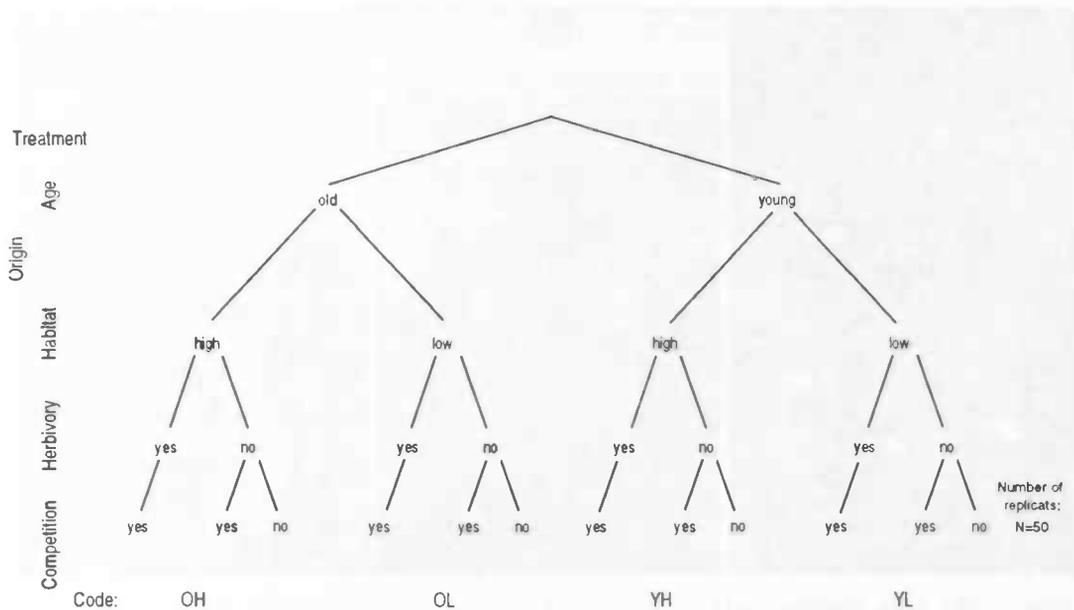


Figure 2.3: Design of the seedling establishment experiment

following four days starting on April 15th. Planting was carried out under wet soil and weather conditions at all four days.

A factorial experimental design with four factors was used (see also Fig.2.3):

- Age (old /young) of the origin
- Habitat (low /high) of the origin
- Herbivory (with /without)
- Competition (with /without)

This results in 16 different treatments. However, four possible treatments were left out in this experiment (explanation see below in this section). In the following plots without herbivory are named NoH while plots without herbivory and additionally without competition are named NoC. Plots where neither herbivores were excluded nor the competing neighbours were removed will be referred to as control-plots. The 12 different treatments were planted in 50 blocks à twelve plots, with one plot per treatment. Each plot was represented by one *E. athericus* seedling. The individual treatment position within the block was determined randomly. Small cages made out of chicken wire (15 cm high, 8 cm diameter, 2.5 cm mash width) were used for the NoH plots. All cages were fixed to the ground by wire herrings (Fig. 2.4, B.).



Figure 2.4: A: Brent geese (*Branta bernicla*) feeding in the vegetation of the experimental area (picture by J. Stahl). B: Plot with small chicken wire cage and *E. athericus* seedling. C: Control plot

In NoC plots the vegetation was removed with scissors in a 21 cm-square around the plant. Bare ground was covered with plant litter material to reduce

the impact of solar radiation. (At some plots no competing vegetation was present already under original conditions, in these cases no litter was added.) Removing vegetation and adding litter was repeated during the experiment if necessary. The possible treatment combination "without herbivory, without competition" for each of the four origins - which would mean a single plant in a bare plot without any vegetation and without a cage - was left out because the predation by geese, hares and rabbits was expected to be very high in the experimental area. Control plots were labelled and marked with plastic markers and plastic sticks (see Fig. 2.4). Cage plots got tape labels at the top of the cage. Every plot got an individual number code to ensure that it was not possible to conclude from the code to the origin of the seedling in the field. Because of extremely dry and hot weather conditions during the first days after planting, 60 ml water were added to each plant on April 22nd. After this date wet weather conditions prevailed again and no water was added anymore.

As dependant variables, the over all plant height, the number of ramets, the number of leafs and survival of *E. athericus* seedlings were measured. Plant height was measured immediately after planting. The height measurement was repeated every two weeks and from June 22nd onwards every three weeks. The last height measurement was carried out September 18th. Heights were measured from the soil surface to the longest green part of the carefully stretched plant. Because the soil surface was uneven at some plots the heights were measured to the nearest 0.5 cm only and not in millimeters. If more than one ramet occurred, the tallest ramet was chosen for the hight measurement.

Survival of transplanted seedlings was recorded weekly from April 21st to May 27th. After that the survival recording followed the height measurements frequency. The last recording of survival was carried out on October 22nd.

The number of ramets and from June 24th onwards the number of leafs per clone were recorded additionally with the heights. In the first week of December all plants were digged out, removed from the field and examined for rhizomes in the laboratory. It was recorded whether the plant had developed rhizomes or not.

The overall vegetation cover of the ground at each of the "with competition" plots was recorded at May 27th. Therefore a circle metal frame with 25 cm diameter was put on the plot (with the plant in the center) and the cover was estimated for this area to the nearest 10%. Additionally the three most dominating neighbour species were recorded on August 5th and August 6th.

2.1.3 Soil Samples and Salinity

Soil samples of approximately 1 cm diameter were taken to 5 cm depth from each plot. The sampling was carried out once under very dry and warm conditions on two days in mid June. The samples were put into plastic bags and later transferred into paper bags the same day. The paper bags were weighed with and without the individual sample and stored afterwards in the drying oven at 105°C for 24 hours. The dried samples were weighed again in order to calculate the water content of the soil. The soil was watered to the maximum water capacity. The watery soil solution was filled into polyethylene bottles and conductivity was measured with a conductivity meter (Wissenschaftlich-Technische-Werkstätten Weilheim, LF95). A calibration line was determined by measuring known salinity contents and used to calculate the salinities parts per hundred (‰) of the soilwater. Several bags became damaged in the oven and could thus not be measured anymore. For these plots no salinity data was available in the statistics.

2.1.4 Elevation and Inundation

In order to gather information of the inundation frequency for each individual plot, the elevation of each plot was surveyed with a surveyors' level to nearest 2cm (Zeiss NI III, Oberkochen, Germany) and related to Dutch Ordnance Level (NAP = *Nieuw Amsterdams Peil*, equivalent to the German *Normal Null*). Furthermore inundation was measured with a piezo-resistiv pressure sensor (DKlog200, Driesen+Kern, Bad Bramstedt, Germany) established in a small tube in a small creek close to the experimental area. The meter logged pressures every 10 minutes between April 21st and August 8th. Temperature dependent pressure deviations were corrected internally. The meter was calibrated prior to installation (max. deviation 1.25 mbar = 1.25 cm water column). To calculate Mean High Tide level (MHT) and inundation frequency (the number of inundations over a certain period of time), the water levels at high tide were used, which were analysed with the help of the Multi Trace computer program (Jensen Software Systems, Laboe, Germany). The inundation meter was taken to the laboratory two times (July 23th, August 8th). The recorded data was transferred to the laboratory computer and the battery of the inundation meter was replaced if necessary. Each time the inundation meter was brought back to the field the following day. Some data was lost, because the inundation meter had a breakdown during the measuring period after the second change. The inundation frequency of the second half of the experiment

had to be estimated by the already obtained data and the data of the official inundation meter at the harbour of Schiermonnikoog (Rijkswaterstaat 2000).

2.1.5 Calculation and Statistics

Two seedlings died already two days after planting. Consequently these were treated as a loss by planting and were not involved in the statistical analysis. Linear regression, logistic regression, Analysis of Variance (ANOVA) and Repeated Measurements ANOVA (McCullagh and Nelder 1989; Sokal and Rohlf 1995) were used to analyse the data. All data was square-root (number of ramets and leaves), log (leaf width, plant height) or arc sin (vegetation cover) transformed to achieve normality and homoscedasticity of residuals. In the case of plant height the length of each seedling at the beginning of the experiment was taken as a covariate, because differences in seedling length could influence the outcome of the experiment (see Tab. 2.1). Statistics were done with the statistic package SPSS 8.0.

The relative growthrate was calculated as $G = \frac{H_t - H_{t-1}}{H_{t-1}}$, with H_t = plant height at present measurement and H_{t-1} = plant height the previous measurement. In the following the growthrate will be expressed as growth in cm per day ($G_d = \frac{G}{t_d}$, with t_d = days between measurements).

The elevation data was divided into three classes (high, mid, low) for a better graphical presentation. Nevertheless, the ANOVA analysis were done with the log-transformed elevation data. However, only bivariate data can be used in logistic regression. Therefore, data had to be transformed in order to analyse the of measured physical factors. As the results showed, inundation frequency and elevation of plots were correlated as well as elevation and salinity were correlated. Thus inundation frequency was chosen as a representative factor. The data had to be transformed in order to calculate the influence of inundation frequency on survival. A bivariate factor was produced for the two cases: plots with 16 and more and less than 16 inundations between April 21st and August 6th. Whereas 16 is the mean number of inundations of all plots (see 2.2).

2.2 Results

2.2.1 Elevation, Inundation and Salinity

A Mean High Tide level (MHT) of 126 cm above NAP was calculated. The elevation of the plots reached from 122 cm to 151 cm above NAP. They were

thus situated between 4 cm below and 29 cm above MHT-level. According to the inundation frequency meter, plots below 132 cm above NAP (low) were inundated 32 times in average. A mean number of 74 further inundations was estimated for the time after August 6th till the end of the experiment (see section 2.1.4). Plots between 132 and 141 cm above NAP (mid) had a mean number of 11 inundations and those between 142 and 151 cm (high) a mean number of 4 inundations between April 21st and August 8th. The mean inundation frequency of all plots was 16.5 (SD = 11.3). Further inundations were estimated to 26 (mid) respectively 13 (high) after August 6th. Elevation and inundation frequencies are correlated ($R^2 = 0.952$), see Fig. 2.5).

Extreme temperatures around 28°C and high solar radiation predominated in the days before and during soil sampling. Following the salinity analysis, the mean soil salinity of all plots was 4.7 % NaCl per liter soil water, whereas low plots reached a mean salinity of 6.0 % NaCl per liter, high plots reached 4.0 %. Elevation of plots and salinity content of soil are correlate (see Fig. 2.6). A correlation was also found between salinity content and inundation frequency ($R^2 = 0.369$, d.f.=513, $F=299.5$, $p<0.0001$).

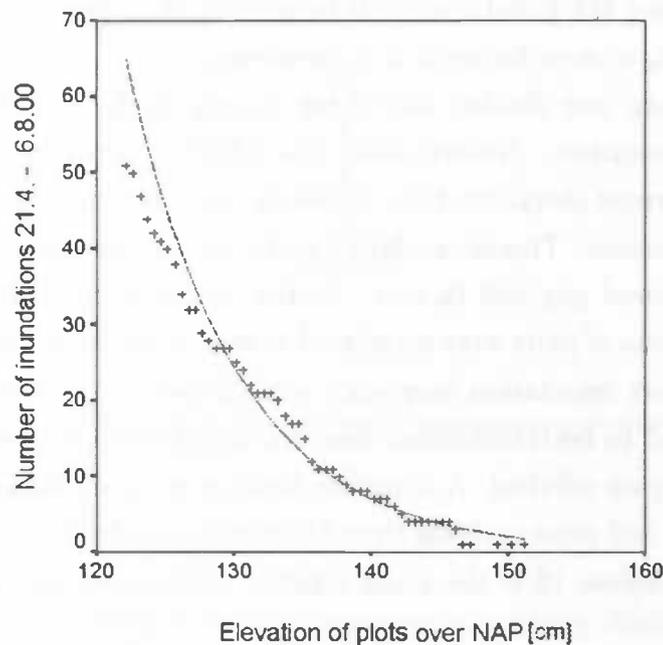


Figure 2.5: Significant Exponential Regression between inundation frequency and elevation of plots, ($R^2 = 0.952$, d.f.=594, $F=11849.6$, $p<0.001$).

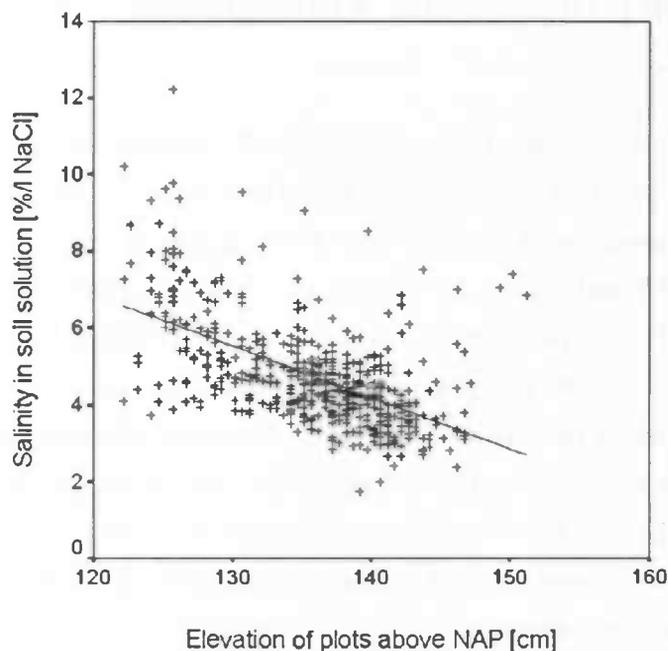


Figure 2.6: Linear Regression between elevation of the plots and the salinity content of the soil, ($R^2 = 0.318$, $d.f.=513$, $F=228.65$, $p<0.001$)

2.2.2 Germination and Transplantation

The seeds of all origins germinated well: YL: 87%, YH: 83%, OL: 86%, OH: 91%. The vegetation at the site was scarce at the start of the experiment. Most parts of the study site consisted of bare soil or plant litter material of the year before. At the moment of planting the mean plant heights of the seedlings differed depending on the origin of the seeds ($p<0.001$, see Tab. 2.1).

In the first days after the transplantation plants of all origins wilted. However, already after ten days seedlings of all origins developed new tillers or just recovered. On October 22nd, the day of the last survival census, 471 of originally 598 seedlings were alive. Moreover, in early December a high percentage of these plants were still present. However, another survival census could not be done at that time because a lot of labels were lost. 76 *E. athericus* seedlings had formed rhizomes during the seven month of the experiment.

Table 2.1: Mean plant heights per origin at the moment of planting [cm]. Seedlings of the origin OL were significant smaller ($MS=251.28$, $df=3$, $F=25,44$, $p>0.001$).

Origin	YL		YH		OL		OH		
	mean	SE	mean	SE	mean	SE	mean	SE	
	21.4.00	13.81	0.22	12.54	0.26	10.92	0.29	13.49	0.24

2.2.3 Herbivory Impact and Aboveground Competition Plant Survival

Already the first survival rate census on May 5th showed a clear herbivory impact. From 598 plants 43 died in the first three weeks. While in control plots 15,6% of the seedlings died, only 3% of the seedlings died in NoH plots ($p < 0.001$, see Fig. 2.7 and Tab. 7.2). Herbivory persisted as a strong mortality factor till the end of the experiment ($p < 0.000$). Seedlings differed in the ability to resist herbivory. Seedlings from seeds of the young marsh (T1, 7-26yr) resisted herbivory better than those from seeds of the old site (Kobbeduin, 87-106yr, significant interaction see Fig. 2.8 and Tab. 7.3). Moreover the strength of the herbivory impact did not change significantly for most seed origins over time. Only plants with seeds from OL had a conspicuously higher mortality rate within the first three weeks (see Fig. 2.11). This was not notable at plots without herbivory (see Fig. 2.10).

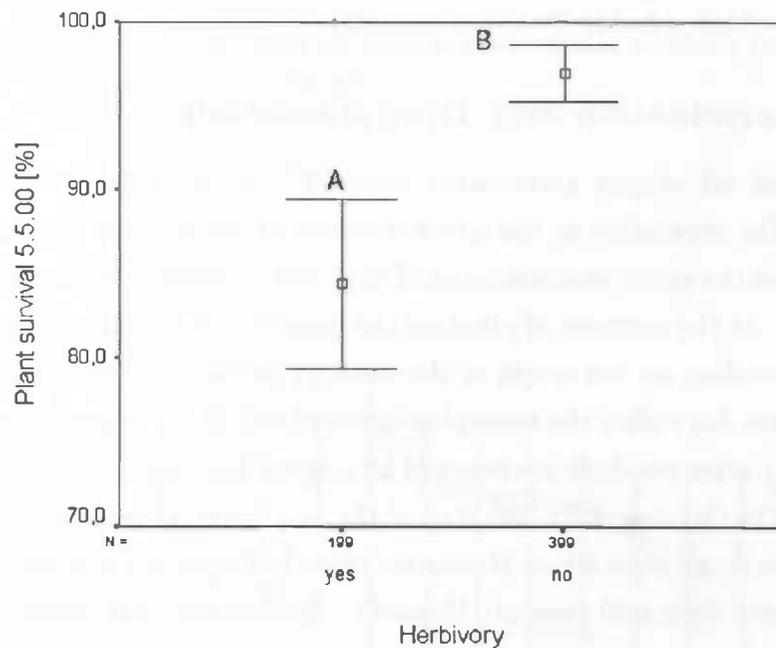


Figure 2.7: Plant survival on 5.5.00 depending on herbivory. Means with 95% confidence intervals ($df=1$, $F=0.79$, $p < 0.001$)

Furthermore the inundation frequency of the plots influenced survival. Higher mortality was found for plants in plots with more than 20 inundations between April 21st and August 6th. Nevertheless, this is only true for seedlings which were additionally influenced by herbivory (significant interaction see Tab.7.3 and Fig 2.9). Seedlings growing without competitors survived significant better than those with competitors (see Fig. 2.12). Although com-

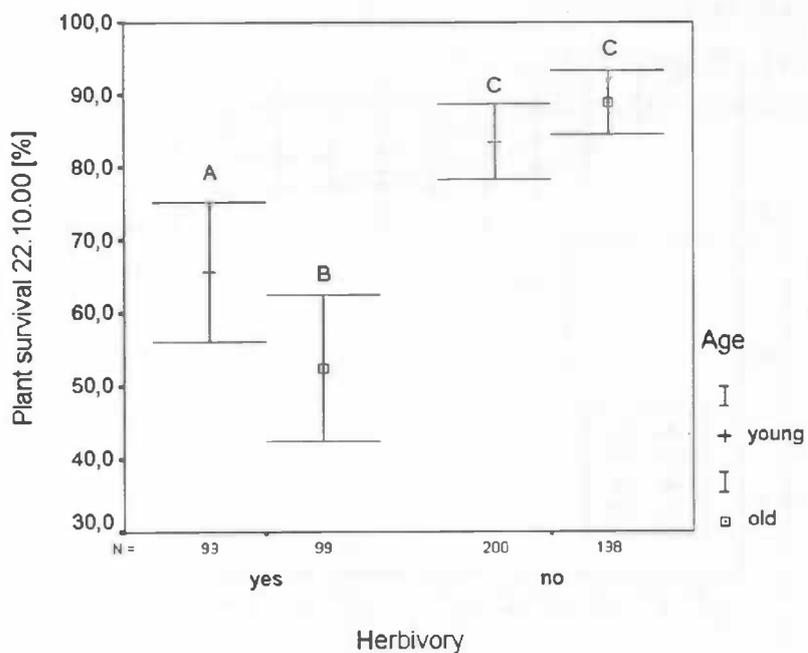


Figure 2.8: Plant survival on 22.10.00 of *E. athericus* seedlings in plots with and without herbivory depending on the age of the seeds origin. Means with with 95% confidence intervals (df=1, F=0.38, p<0.001)

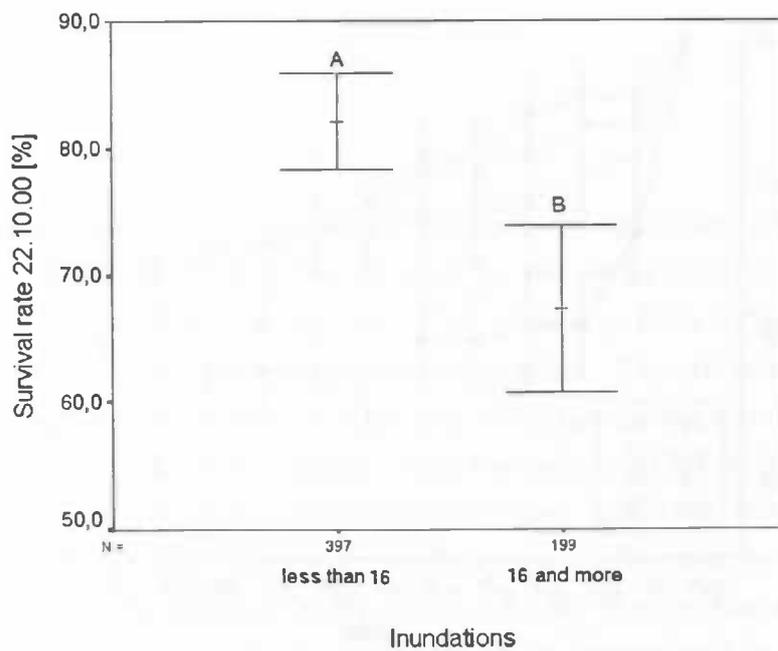


Figure 2.9: Plant survival on 22.10.00 depending on herbivory and inundation frequency between 21.4.00 and 6.8.00. Means with 95% confidence intervals (p<0.001)

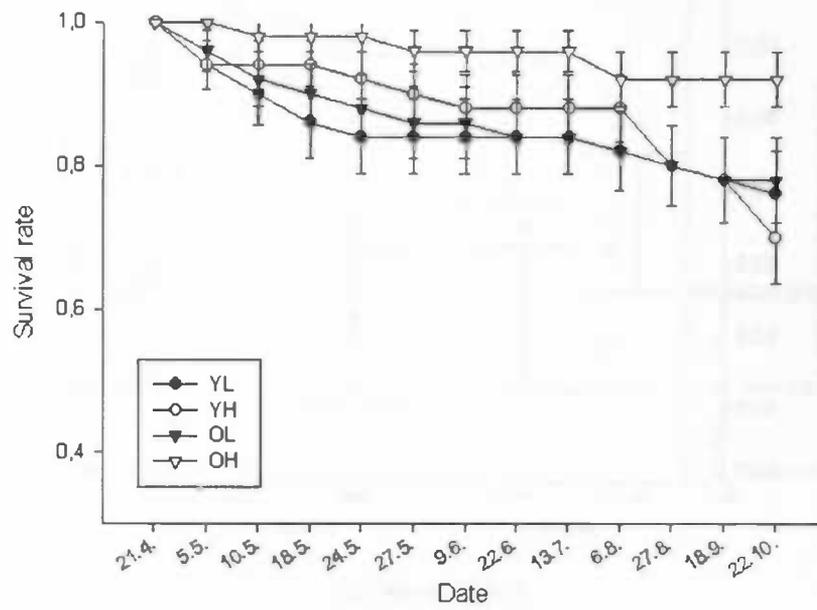


Figure 2.10: Survival rate over time of plants in plots without herbivory (with competition). Means with 95% confidence intervals

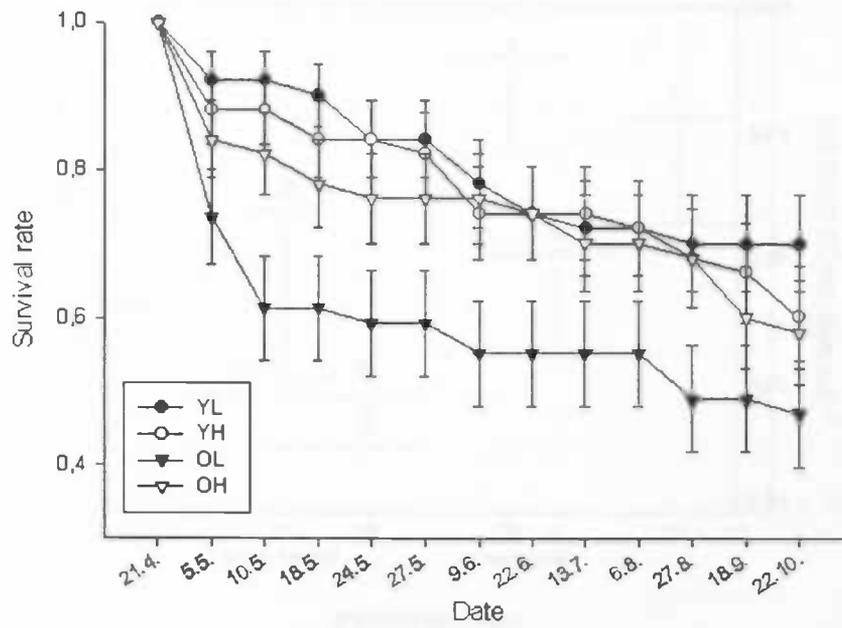


Figure 2.11: Survival rate over time of plants in plots with herbivory (with competition). Means with 95% confidence intervals

petition in general has a negative effect on plant survival, seedlings with *Limonium vulgare* as a direct neighbour plant had a higher survival chance. This context is only true for low elevations (significant interactions see Tab. 7.3 and Fig 2.13). No interaction between other neighbour plants and seedling survival was found.

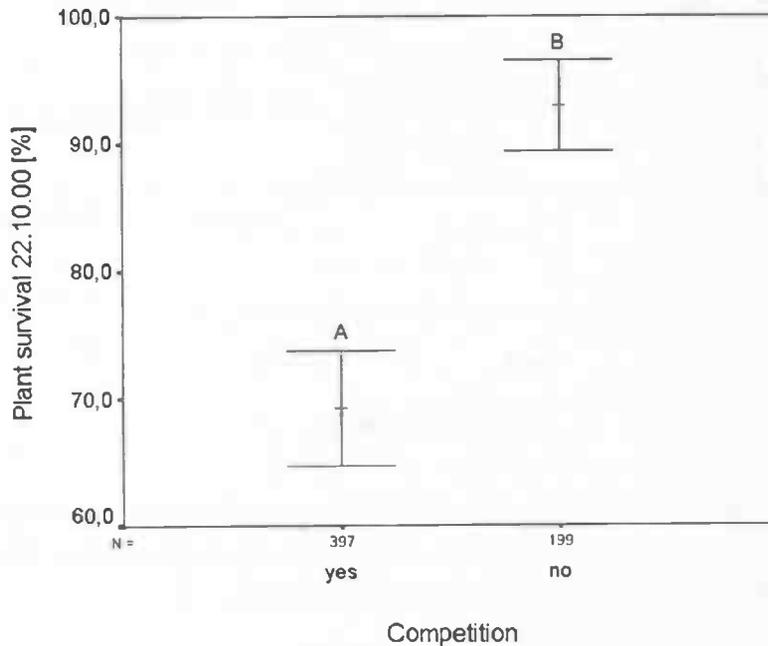


Figure 2.12: Plant survival on 22.10.00 depending on competition. Means with 95% confidence intervals ($p < 0.001$)

Number of Ramets per Plant

In contrast to the survival rate, herbivory had no significant effect on the number of ramets per plant. This is valid for the entire time as well as for the last census (see Tab. 7.4 and Tab. 7.5). Seedlings from different origins differed in the number of ramets produced per plant. The statistical analysis of the last census showed that *E. athericus* seedlings grown from seeds from the low habitat produced less ramets. This was only valid for seedlings whose parent plants came from the site Kobbeduin (see significant interactions in Tab. 7.4 and Tab. 7.5). Moreover, seedlings were influenced by competing plants in the neighbourhood. Only plants without competition showed the above mentioned habitat effect, while this effect disappeared at plots with competition and overall less ramets per plant were produced (see Tab. 7.5 and Fig. 2.14). This context is not significant for the whole time of the experiment (see Tab. 7.4).

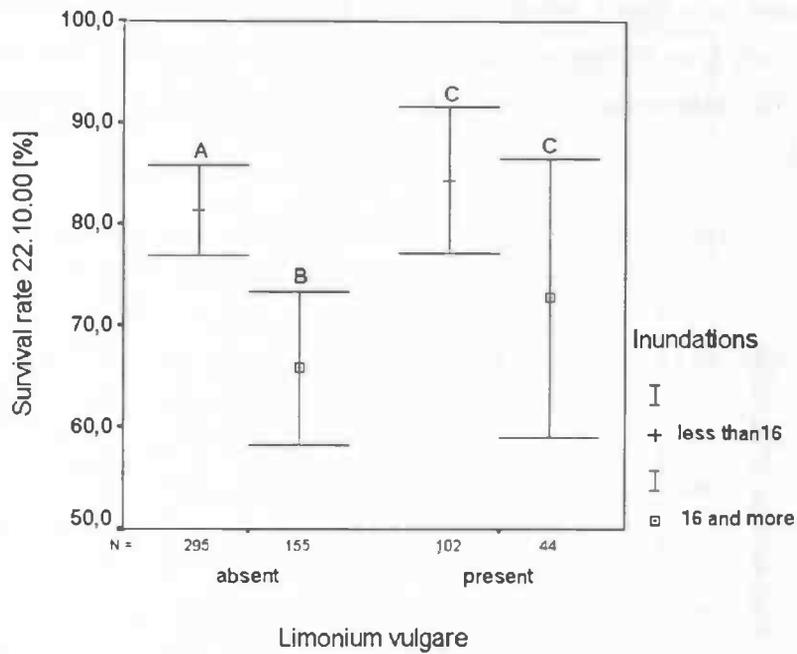


Figure 2.13: Survival rate in *E. athericus* seedlings in relation to the presence of *Limonium vulgare* in the direct neighbourhood and to the inundation frequency between 21.4.00 and 6.8.00 . Means with 95% confidence interval ($p < 0.001$).

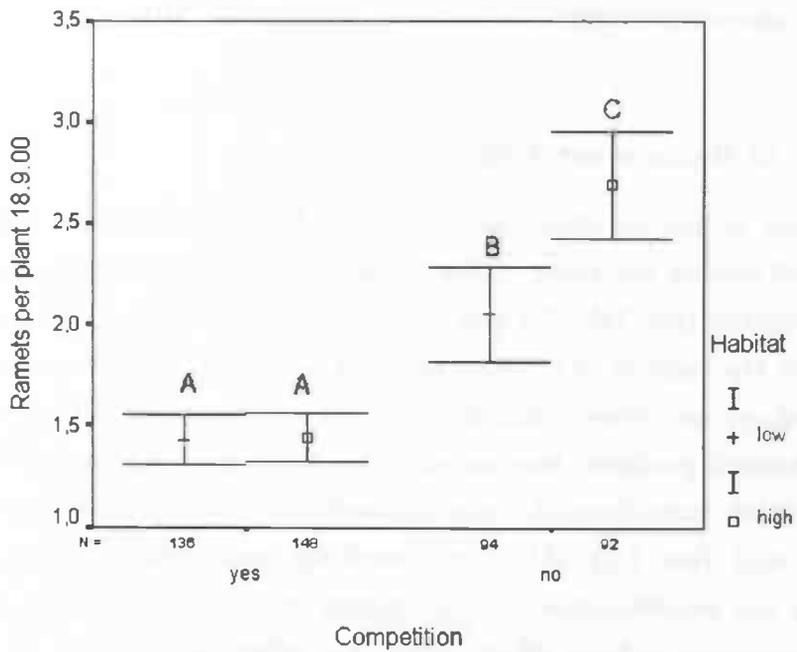


Figure 2.14: Number of ramets per plant growing of seeds of low and high habitats with and without competition. Means with 95% confidence interval ($p < 0.01$).

Number of Leafs

A similar of interaction between competition and habitat was found for the number of leafs per plant: Seedlings grown from seeds of the origin OL produced less leafs per plant in general, while this difference disappeared under the influence of aboveground competition. Herbivory also influenced the number of leafs produced per plant. Plants with herbivory developed less leafs than those which grew in the small cages. These differences appeared independently of the origin of the seeds (see Tab. 7.4, Tab. 7.5 and Fig. 2.15).

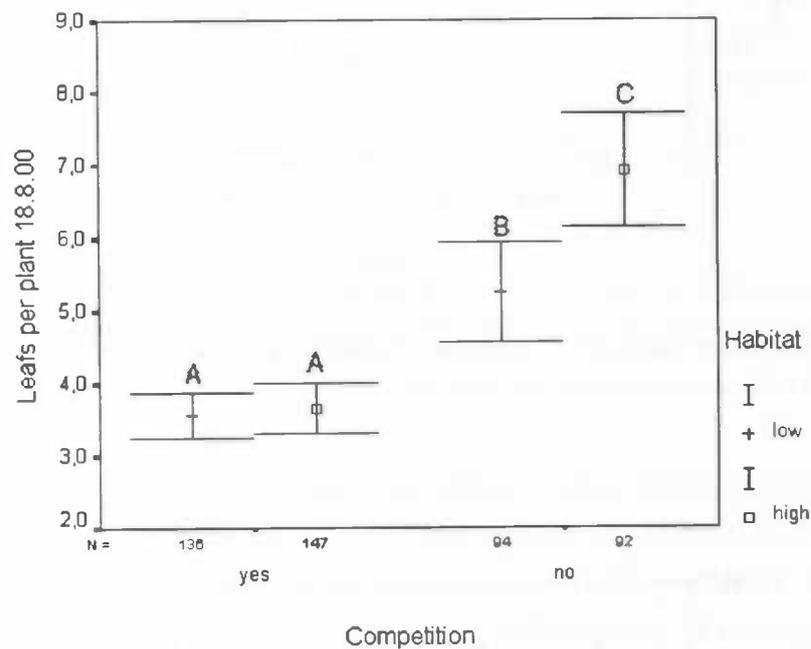


Figure 2.15: Number of leafs per seedling with and without competition depending on habitat origin of the seeds. Means with 95% confidence interval ($p < 0.01$).

Plant Height

Seedlings grown from seeds from different origins differed in plant height. Again seedlings grown from seeds of the OL habitat grew less than those of other origins (see Fig. 2.16). Furthermore, growth was significantly influenced by competition. Seedlings in plots with competition grew taller than without. The above mentioned differences between OL and the other origins disappeared in the case of competition (see Fig. 2.17). Herbivores had a significant effect on plant growth. Plants which survived herbivory pressure were reduced in plant height. They did not manage to reach the mean size of plants in cages. However, the seedlings shoot length of all origins were influenced by herbivory in the same way (see Fig. 2.18).

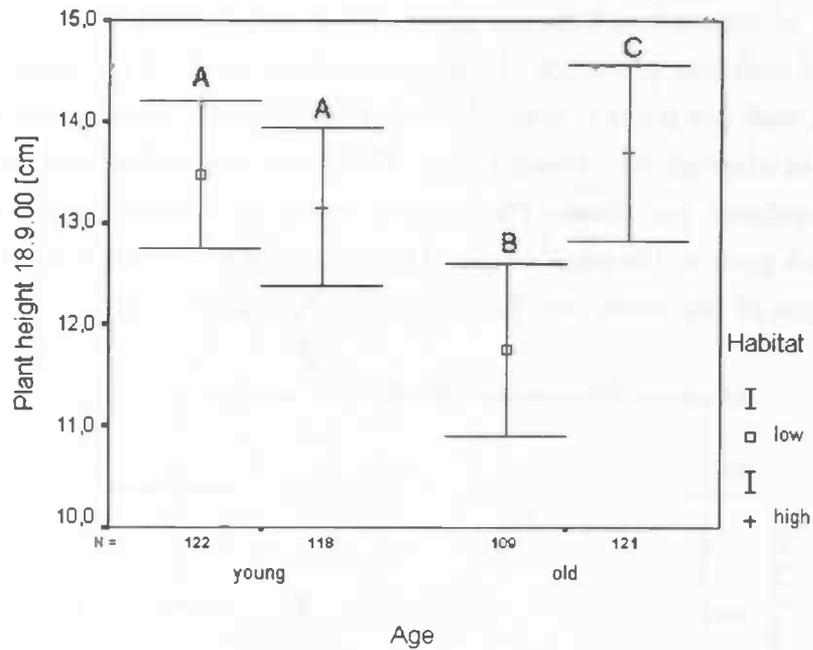


Figure 2.16: Plant height of *E. athericus* seedlings depending on the origin of the seeds. Means with 95% confidence interval ($p < 0.05$)

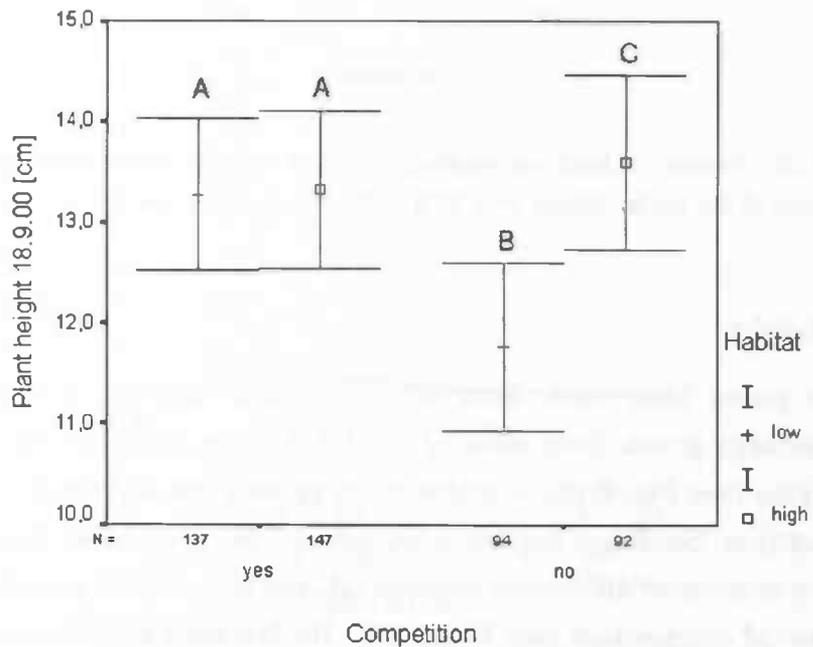


Figure 2.17: Plant height of *E. athericus* seedlings with and without competition depending on the habitat of the seeds origin. Means with 95% confidence interval ($p < 0.05$)

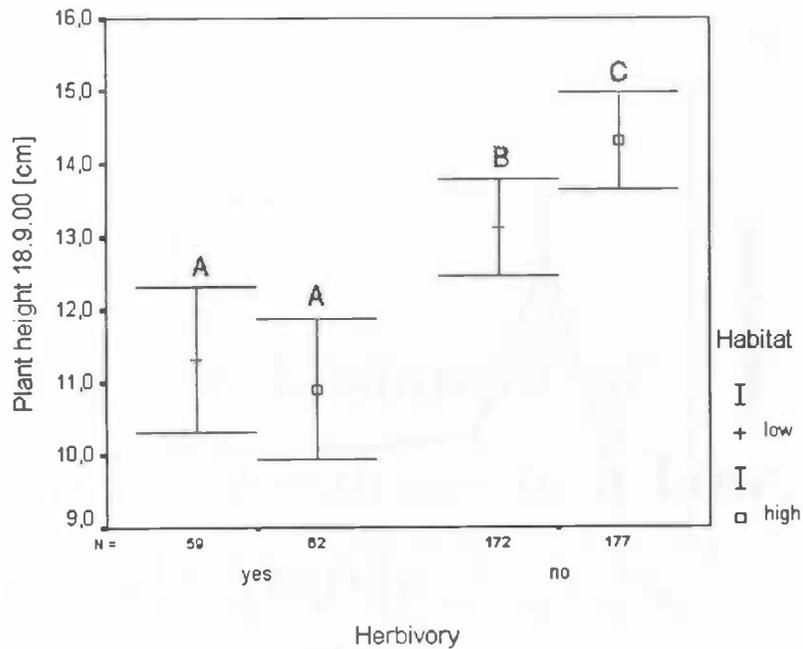


Figure 2.18: Plant height of *E. athericus* seedlings with and without herbivory depending on the habitat of the seeds origin. Means with 95% confidence interval ($p < 0.001$)

Growth Rate

Although plants growing with herbivory influence grew less tall, their relative growth rate over the whole time of the experiment was higher than of plants without herbivory influence ($MS=18.53$, $df=1$, $F=41.77$, $p < 0.001$). However, this was due to the differences in growth at the beginning of the experiment: In general the growth rate of all origins and all treatments reached its peak between planting and the end of May. Only for that period a significant different growth rate between plants in plots with herbivory and those without was found ($MS=328.44$ $df=1$, $F=44.76$, $p < 0.001$). Thereafter the growth per time decreased, remained constant till the end of the experiment and was not different between herbivory and non-herbivory plots (see Fig. 2.19 and Fig. 2.20)

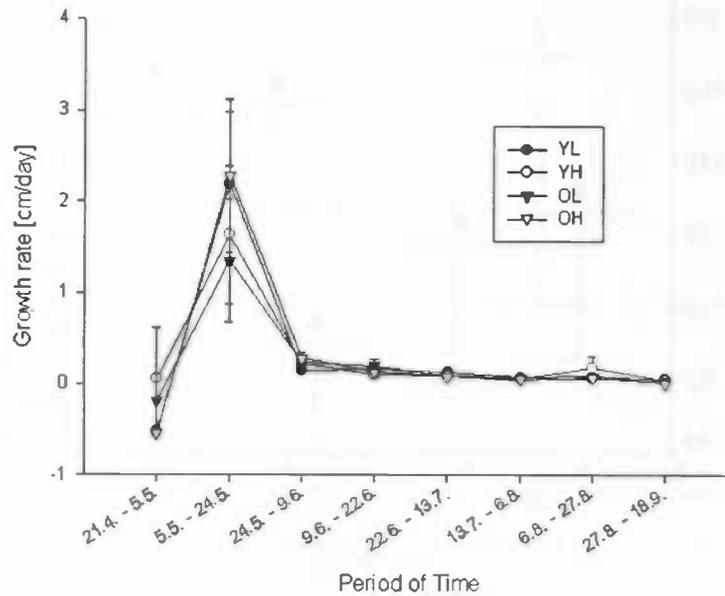


Figure 2.19: Growth rate of *E. athericus* plants in plots with herbivory and competition over the whole time of the experiment [cm/day]. Origins: YL= young-low, YH=Young-high, OL=old-low, OH=old-high. Means with S.E.

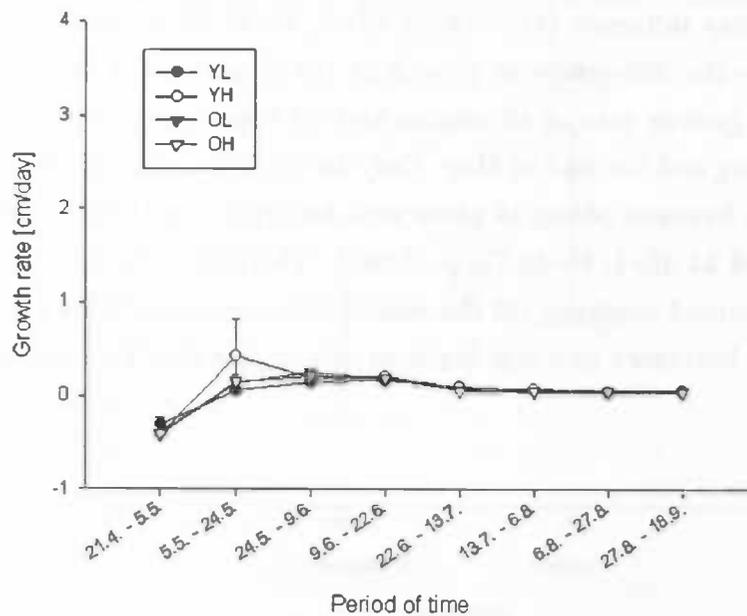


Figure 2.20: Growthrate of *E. athericus* plants in plots without herbivory (with competition) over the whole time of the experiment [cm/day]. Origins: YL= young-low, YH=Young-high, OL=old-low, OH=old-high. Means with SE.

Chapter 3

Seedling Establishment of Indigenous Seedlings in a Low, Young Salt Marsh

3.1 Methodes

Seedlings were discovered during two times a three hours search on two days in mid June. All plants were marked and followed through the vegetation period. Shoot height, number of leafs and the number of ramets were measured at all plants. All measurements and the recording of survival of these plants were repeated in the same frequency as at the experimental plots. All measurements including the elevation measurements were done as described in chapter 2.1. However, remaining plants were marked and left in the field for further research the following season.

One-Way ANOVA (Sokal and Rohlf 1995) was used to compare the data of the indigenous seedlings with those of the transplanted ones. The survival data were compared by using logistic regression (see chapter 2.1).

3.2 Results

All found seedlings were located close to the experimental plots. No adult *E. athericus* plants were present in the neighbourhood. The discovery of seedlings of *E. athericus* was quite difficult. All together 34 seedlings were found. 30 of them survived till the last census in October. The shoot length and the number of ramets per plant are significant higher for transplanted seedlings compared to the shoot lenght and the number of ramets of transplanted seedlings (see Fig. 3.1 and Fig. 3.2).

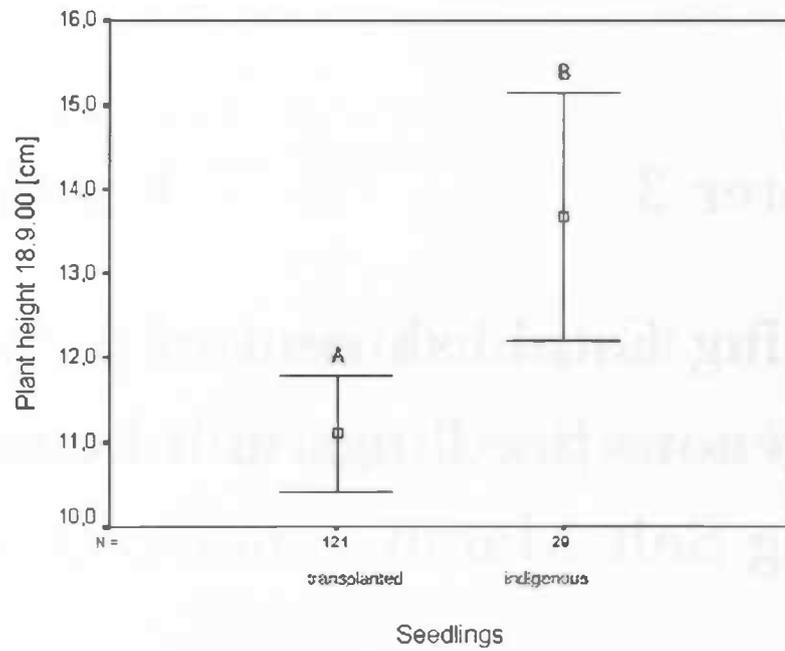


Figure 3.1: Mean shoot length of indigenous seedlings compared with control plots of transplanted seedlings. Means in cm with 95% confidence interval ($MS=0.257$, $df=1$, $F=9.568$, $p=0.002$)

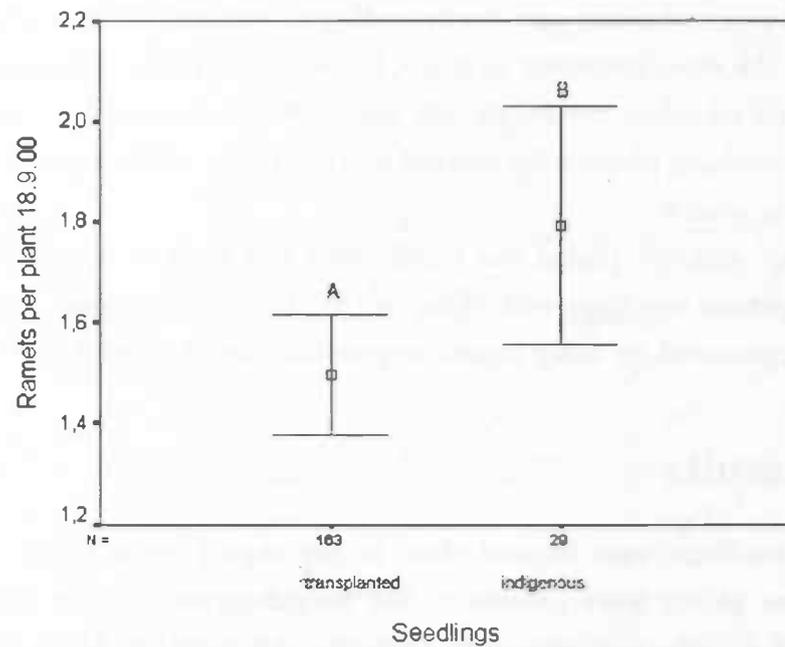


Figure 3.2: Mean number of ramets per plant of indigenous seedlings compared with control plots of transplanted seedlings. Means with 95% confidence interval ($MS=0.744$, $df=1$, $F=11.882$, $p=0.001$)

If the data from the indigenous seedlings is compared to the data of planted seedlings in NoH plots, the number of ramets of indigenous seedlings is higher ($MS=0.398$, $F=5.321$, $df=1$, $p=0.022$). Only if the indigenous seedlings are compared with planted seedlings from NoC plots, the indigenous ones have less ramets ($MS=0.709$, $F=4.79$, $df=1$, $p=0.030$) and less leafs per plant ($MS=5.708$, $F=11.21$, $df=1$, $p=0,001$).

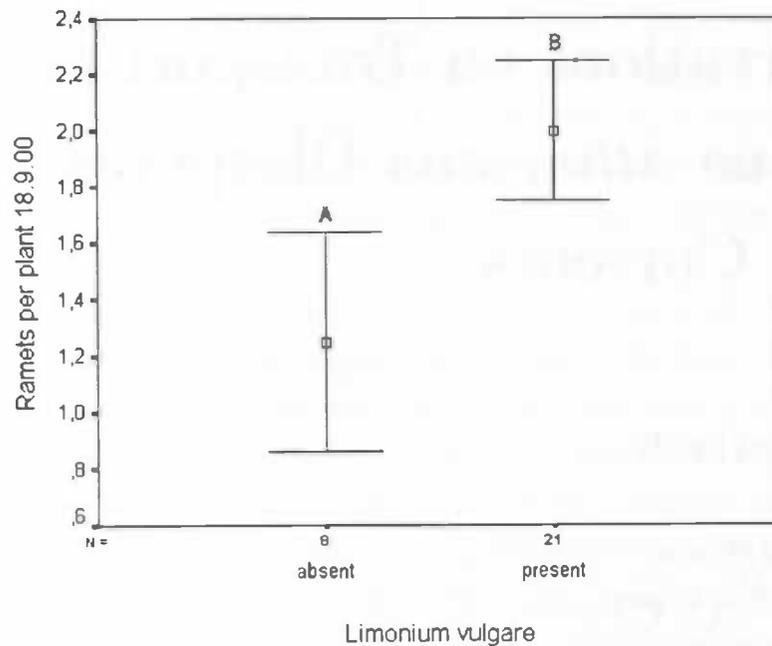


Figure 3.3: Number of ramets per plant of indigenous seedlings in presence or absence of *Limonium vulgare* as a direct neighbour ($MS=0.511$, $df=1$, $F=12.871$, $p=0.001$). Means with 95% confidence intervall

Additionally, the presence or absence of *Limonium vulgare* has an influence on the performance of indigenous seedlings. For example, the number of ramets is higher at plots with *Limonium vulgare* in the neighbourhood (see Fig. 3.3). The same relation is valid for the number of leafs ($MS=1.436$, $df=1$, $F=7.004$, $p=0,013$). However, these differences are not significant for the survival rate.

Furthermore, several adult *E. athericus* plants were found within the experimental area. Although the development of these plants was not followed through the season it was proved that none of them produced flowers or seeds within the vegetation period. Moreover even further eastwards close to enclosure T0 seedlings and adult plants were discovered. While it was difficult to discover *E. athericus* plants in the summer vegetation, later in the season additional seedlings and adult plants were found by accident more often.

Chapter 4

Observations on Transport of *Elymus athericus* Diaspores by Tidal Currents

4.1 Methods

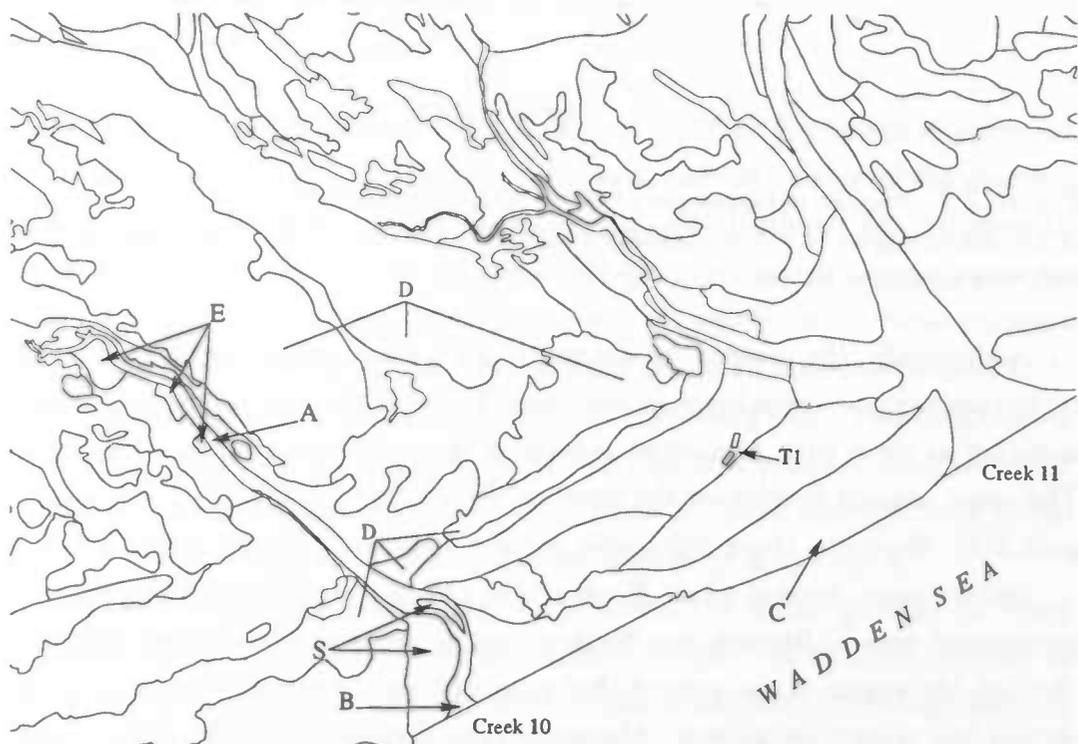


Figure 4.1: Map of the area between creek 10 and 11. A = release point at the most seaward flowering *E. athericus*-population, B = release point in the creek delta, C = release point at small creek (not shown), T1 = Enclosure, E = *E. athericus*-Populations at creek No 10, D = Dunes, S = higher elevations in the creek with *Salicornia spec.*

All drifting experiments were carried out qualitative. Creek number 10 stretches over approximately 400 meters. At point A it was approximately ten meters in wide whereas the delta was approximately 15m across. The actual water surface width depends on the tide. The creek was situated western and 200m away from the experimental area (see Fig. 4.1). A first pilot drift experiment was carried out with matches. For this purpose the heads of 800 matches were removed and the remaining wooden sticks were cut into two pieces. These 1600 approximately 2cm long artificial diaspores were thrown into creek 10. The matches were released at the creeks edge next to the most seaward *E. athericus* population (point A, Fig. 4.1 and Fig. 5.4) at the midday high tide September 27th. The floating matches were observed on their way through the creek and searched for along the creeks banks on the next day (after two tide cycles).

For the next experiments spikelets of *E. athericus* were used. *E. athericus* spikes were collected from a large population close to the field station. The spikelets were removed from the stems and put into the oven at about 250°C for 20 minutes in order to sterilize the seeds and to prevent later germination in the field. The whole amount of spikelets was divided into four samples: two times about 23000, one about 8500 and one about 8000 spikelets (estimated by weighing). The two largest fractions of 23000 were sprayed with permanent paint in two different colours. The other two samples got no colour. Due to the small supply in different paint shops only red paint and yellow fluorescent paint could be used. All spikelets were put into a plastic bag with salt water for at least one hour before the experiment to minimize strong wind effects which were observed in the match experiment (totally dry spikelets would lie on the top of the water surface, they are thus much more wind affected than wet and soaked spikelets).



Figure 4.2: The spikelets were released in the middle of the creek delta

Due to the results of the match dispersal experiment (see 4.2) the experiment with coloured spikelets was not carried out at the same spot. On midday high tide September 28th the first fraction of yellow coloured spikelets was released into the middle of the creeks delta (point B, Fig. 4.1 and Fig. 4.2) On September 30th the procedure was repeated at the same spot with the red fraction. Each time the area between creek 10 and 11 and the creek 10 were examined for the coloured spikelets the following day.

Additionally the 8500 non-coloured spikelets were released into creek 10 at point A two hours after high tide on September 30th. The diaspores were followed along their way towards the creek delta and the time needed for the approximately 300m was measured.

On October 2nd the remaining amount of seeds was used to observe how tide dispersed diaspores get caught in the vegetation when floating with the up coming tide. For this purpose the spikelets were put on the soil at the beginning of a small creek (Fig. 4.1, point C) shortly before the up coming water reached the place. Their drifting was followed till the water was not rising anymore.

4.2 Results

Wind speeds of 3-4 Beaufort predominated at the first day of the experiment (wind data follow to the Dutch radio weather broadcast). None of the matches moved more than three meters downstream at all. Within a few minutes all swam to the opposite edge of the creek and got stuck in the vegetation or by adhesive power on the bare soil. Consequently no match was movable anymore because of the low water level. During night the wind speed decreased to 1-2 Beaufort, but was as strong as before the following day. Two tidal cycles after the beginning of the experiment the furthestmost seaward matches could be found approximately 20 m away from point A. Most matches were found more upstream and even at the outermost beginning of the creek.

Similar to the experiences with the matches, the drifting of the coloured spikelets was also affected by predominating winds. All of them drifted on the water surface to the opposite edge of the creek delta, although drifting materials could be observed to move quite fast seawards in the deeper layers of the water. At the edge of the other site of the creek, a current in the opposite direction caused the spikelets to move upstream. Within ten meters the spikelets got stuck in the creek bank soil due to the low water level. After two tidal cycles no spikelets could be found directly at the creeks delta anymore.

However, some diaspores could be found widely scattered upstream up to the furthestmost point. None was found in the experimental area between creek 10 and 11.

At the third day of the experimental series wind speeds of 0-1 Beaufort predominated. All at point B released coloured spikelets could be observed to drift with the outgoing current out of the creek delta into the Wadden Sea. No diaspore moved upstream. Within half an hour the bulk of spikelets was spread in a band over 100m. The next day some spikelets could be found in the low salt marsh between creek 10 and 11. Huge parts of the low salt marsh were completely inundated but withered inflorescences of *Limonium vulgare* and vegetative parts of *Artemisia maritima* were still above water level. Several spikelets got stuck at the vegetation. Others remained in small bays with slightly higher elevation at the end of little creeks, where they were washed into by the current and got deposited when the water level decreased again (see Fig. 5.3). Finally, 50 red diaspores could be found.

The non-coloured spikelets which were released at point A swam all downstream. The big bulk got widely spread soon, but the whole band was continuously moving. After 50 minutes and approximately three hours after high tide the first 50 spikelets reached the creek delta and drifted into the Wadden Sea. Later the current strength decreased and the spikelets got dispersed at the creeks edges. The following day not more than 100 of the not coloured spikelets could still be found in the creek.

Spikelets put on the soil at point C followed the current of the small creek. A lot of them got caught in scum or drifting litter material in the tidal stream at the creeks edges. Others drifted more in the middle of the creek and were washed over the borders into the surrounding salt marsh vegetation at the endings of the creek. Here they often got caught by dead inflorescences of *Limonium vulgare* or stems of *Salicornia spec.* On this particular day, the high tide was lower than the days before. Therefore less area and only lower parts were flooded. As a result diaspores could not reach suitable sites.

Chapter 5

Discussion

The results of the transplant experiment and the discovery of indigenous seedlings and mature plants showed that *E. athericus* seedlings can establish in the low marsh of the study site. Herbivory and competition played a major role for performance and survival of the seedlings. Furthermore, the results indicate that abiotic factors like inundation frequency and salinity did only matter for plants which were stressed by herbivory. In contrast to the general negative impact of competition, *E. athericus* seedlings were facilitated by the neighbour *Limonium vulgare* in case of herbivory.

Bockelmann and Neuhaus (1999) showed that the clonal spread of mature *E. athericus* plants into low salt marsh habitats is restricted mainly by competition and not by abiotic factors. In contrast, it is commonly considered that salt marsh zonation is determined by abiotic environmental gradients (eg Ranwell 1972; Beeftink 1977). The results in the present study show that also seedling establishment of *E. athericus* in the low salt marsh is mainly determined by competition and herbivory and not by abiotic factors.

The fact that a lot of seedlings were still alive in the beginning of December leads to the assumption that permanent establishment is possible. Moreover, the development of rhizomes of some seedlings indicate that at least these might had the ability to survive during winter. In general the development of ramets can improve the survivability of clonal plants (Tschardtke 1991). More than 46% of the survived seedlings produced two or more ramets. This is quite much compared to results of A.C. Bockelmann (in progress). *E. athericus* seedlings were transplanted into different low marsh habitats on Schiermonnikoog in 1999. One year later, in March 2000, several seedlings were still alive. Moreover, the experiment showed that seedlings survived the winter although only 26% of the seedlings had produced two or more ramets. Finally the occurrence of indigenous seedlings and even adult *E. athericus* plants in

the area (see chapter 3) verifies the results and the assumption that seedling establishment is possible. Although only a relatively low amount of indigenous *E. athericus* plants was found it can be assumed that *E. athericus* populations will be part of the vegetation in the future.

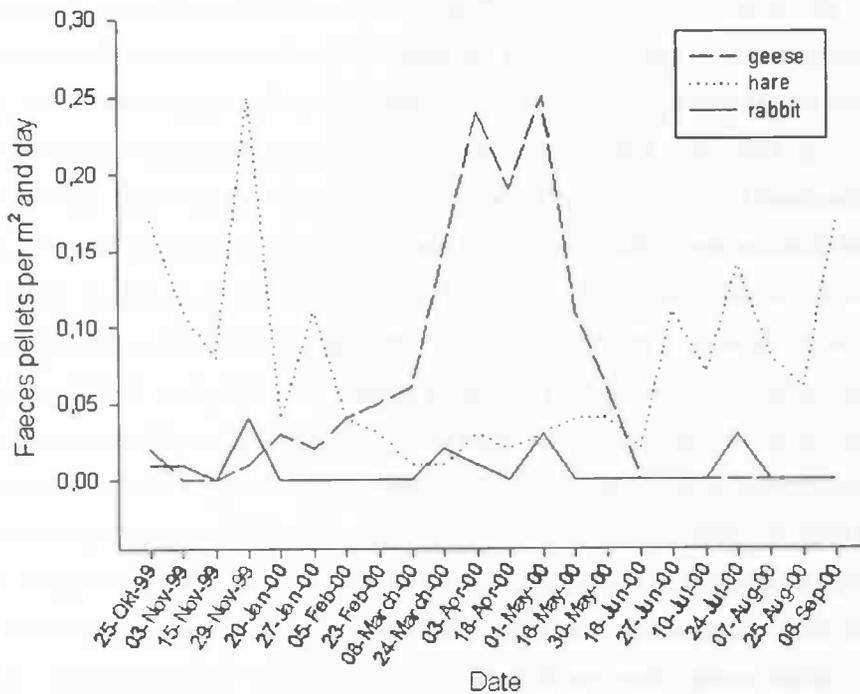


Figure 5.1: Faeces pellets frequencies of geese (*Branta bernicla*, *Branta leucopsis*), hare (*Lepus europaeus*) and rabbits (*Oryctolagus cuniculus*) in the experimental area from Oct. 1999 till Sept. 2000. Data from D.P.J. Kuijpers, unpublished.

Nevertheless, transplanted seedlings growing under similar conditions as naturally recruited plants (control plots, see 2.1.2), showed that there is a high mortality. Herbivory has been recognised earlier as a factor leading to decreased plant growth and survivability (Harper 1977). In contrast to this general opinion there is discussion on whether herbivory might be beneficial for plants in certain cases. For a critical review see eg Belsky (1986), Howe & Westley (1988). The area around T1 is a major feeding area for brent (*Branta bernicla*) and barnacle (*Branta leucopsis*) geese during spring (see Fig. 2.4, A.) After the geese have left in late May, the grazing pressure prevails. D.P.J. Kuipers (unpublished results) found by counting faeces pellets, that after the geese left the area, hares (*Lepus europaeus*) dominated during the summer. Furthermore, hares were also present in the time before the geese

arrived in January/February (see Fig. 5.1). The vegetation in the study site is thus strongly influenced by herbivores (Van Wijnen et al. 1999, D.P.J. Kuijpers, personal communication). Although it is known that geese and hares do not graze *E. athericus* as mature plants (P. Daniels personal communication) probably because of its high content of silicate acids, they can have a large impact on the plant in the early season while these permanent defence structures are not developed. Young plants could thus be well palatable for geese and hares. Even if *E. athericus* seedlings were not palatable at all it would be possible that they were killed or damaged by accident due to herbivores standing within favoured vegetation patches. Therefore, the impact of these herbivores could be responsible for the reduction of seedling survival and shoot mass as also shown by several authors for other species in different habitats (eg Myster and McCarthy 1989; Vila and Lloret 1996; Reader and Bonser 1998). Due to the results it can be assumed that there was a permanent herbivory impact by vertebrates during the whole time of the experiment. However, while in the early beginning of the experiment mortality on herbivory plots could have been a direct result of being eaten or being ripped out, mortality later in the season might have occurred more likely as a secondary repercussion of herbivory influence earlier in the season. High tissue loss by herbivory leads to overproportional decrease of fitness (Tschardt 1991). Notable damage in a young stage of the seedling could thus reduce the plants ability to cope with other stress factors like competition with neighbours or abiotic stress (Bentley and Whittaker 1979; Parker and Salzman 1985). The weakened plants could thus die due to herbivory impacts, which do not predominate at that time anymore.

The high survival of indigenous seedlings can not be compared directly to transplanted ones. The survival census of indigenous ones started in June whereas the survival census of the planted ones in late April. Thus, the observed period was not the same. However, a better performance was found for the height measurements and for number of leaves and ramets for the indigenous seedlings. These data are better comparable, because the compared values are not related to a former state of art. Nevertheless the better performance could be explained due to different preconditions: Indigenous seedlings were found after geese left the area. Seedlings that were affected but survived herbivory might have been much smaller than those that were not affected by herbivores at all, like the results with transplanted seedlings show. Probably only seedlings were found that were bigger in size because those would be easier to discover. Consequently the significant differences in height, number of

ramets and number of leafs must be seen very critical. However, the effect of *Limonium vulgare* on indigenous seedling performance was similar to the results of transplanted seedlings. On the other hand it could be assumed that the found indigenous seedlings started to germinate after the geese left the area in the end of May. Consequently the grazing pressure would have been less strong. This could also explain the better performance of indigenous seedlings compared to transplanted ones.

The overall cover and the vegetation height increased during the vegetation period (personal observation). Following N. Heuermann (personal communication) the starting point of this increase is related to the leaving of the geese in late May. A more dense vegetation leads to higher competition with neighbours which can result in a loss of fitness (Harper 1977). The results of this study show a clear influence of competition on all parameters measured on *E. athericus*. First of all, the survival rate showed the pronounced disadvantage of plants in plots with competition. Both, the number of ramets and the number of leafs, were also negative affected by competition. This is in agreement with investigations of other authors who reported a decrease in plant shoot mass in the case of competition (eg Schmid 1991; Vila and Lloret 1996; Reader and Bonser 1998; Dormann et al. 2000). However, shoot length increased significantly at plots with competition. This stretching might have been a compensational response due to reduced light availability in dense vegetation (eg Meyer & Jensen in press). Although no plant shoot mass was measured directly, it can be assumed that the decrease in numbers of leafs and ramets more than compensated this effect which led to a decreased over all shoot mass under competition at the end. For similar results with salt marsh plants see Dormann (1998). It can be concluded that competition thus had a negative effect on seedling establishment. The hypothesis that competition has a negative effect on seedling establishment of *E. athericus* in a low salt marsh must be accepted. Adult *E. athericus* plants are known to outcompete other plants very effective (eg Van Wijnen et al. 1997). Thus it can be expected that if seedlings are once established the importance of competition for their survival and general performance will decrease.

A.C. Bockelmann (2000) found evidence for an ability of rapid phenotypic adaptation of *E. athericus*. Thus, the different reactions of seedlings with respect to herbivory, might be explained by different suppositions of the sites their seeds came from. The low salt marsh at Kobbeduin was never grazed. Only in the early time of succession geese and hares might have occurred. In later successional stages and finally the dominance of *E. athericus* mature

plants, it is likely that grazing pressure disappeared completely, as can be observed along the chronosequence from east to west. Consequently, the area was not influenced by grazing approximately since approximately 30 years. In contrast, the area T1 is rather young and has been under the influence of hares and geese since development. Furthermore, the high marsh at Kobbeduin was grazed by livestock till 1958. These different influences could have led to phenotypic adaptation and thus different abilities to resist herbivory. Although a reason for the general low performance of seedlings grown from seeds of the origin OL was not found, it is proved that they reacted different. Consequently the hypothesis that the establishment success of *E. athericus* seedlings is depending on the origin of their seeds must be accepted.

The low salt marsh was inundated more often than in higher parts. The physical and abiotic condition in frequently submersed plots are more tough for plants than in higher elevations with less frequent inundation. For example the abrasive tidal water movement itself can make seedling establishment difficult (Ungar 1987; Jutila b. Erkkilä 1998). Furthermore, the frequent submersed situation leads to low substrate redox potential which is known to decrease plants performance (eg Bertness and Ellison 1987). Moreover, as also the results of this study showed, the salinity of the top soil increases with increasing inundation frequency (eg Bertness and Ellison 1987; Müller-Thomsen 1997). Several authors demonstrated that the salinity content of the soil limited the germination and establishment of seeds and growth of plants (eg Chapman 1978; Bakker et al. 1985; Bertness and Ellison 1987; Ungar 1987; Shumway and Bertness 1992). With a mean of 4.0 % soil salinities were quite high compared to those reported by others (Beefink 1977; Long and Mason 1983; Packham and Willis 1997). Beefink (1977), for example, mentioned 2.0-3.8 % for the upper 5 cm clay layer in a low marsh (19-26 cm above MHT) and 1.1-3.6 % in a medium low marsh (29-33 cm above MHT) in The Netherlands. However, the warm weather conditions and the high solar radiation during and before soil samples were taken may increased salinity. (High evaporation leads to salt accumulation at the upper soil layer (Packham and Willis 1997; Schachtschabel et al. 1998)).

The structure of salt marsh communities is an integrative product of different physical and biotical influences (Bertness and Ellison 1987; Scholten et al. 1987; Bertness 1991). In the present study the measured physical factors played a major role especially for the plants of control plots that were weakened by competition stress and herbivory stress. In the case of no herbivory impact the elevation of the plots and thus the inundation frequency

did not matter. Plants which are influenced by herbivory might be more weakened due to tissue loss and thus be more affected by physical stress like salinity and inundation (Tschardtke 1991). Consequently, if natural recruited seedlings can grow without being discovered and influenced by herbivores they can resist physical stress better. Thus, they have also in this manner a greater chance of survival. Other plants for example, could provide shelter against herbivores although they are direct competitors on the other hand. The results of chapter 2 and chapter 3 showed such a significant positive interaction between the seedlings performance and the presence of *Limonium vulgare* as a direct neighbour. *L. vulgare* can be a strong competitor. Beeftink (1985) showed



Figure 5.2: *E. athericus* seedling within a large rosette of *Limonium vulgare* A: complete rosette, B: detail of A with *E. athericus* seedling (arrow). The yellow plastic marker has a length of 7 cm.

for the Boschplaat, Terschelling, The Netherlands that *L. vulgare* outcompetes *Plantago maritima* under certain circumstances. For instance, *L. vulgare* can produce large rosettes and flowers which probably leads to a strongly reduced light availability in its neighbourhood. However, these rosettes could provide a good shelter against herbivores. A single *E. athericus* seedling might just be inconspicuous between the leaves of the rosettes (see Fig. 5.2). Moreover, geese and hares avoid *L. vulgare* (P. Daniels, N. Heuermann, D.P.J. Kuijpers

and J. Stahl, personal communication). Therefore *E. athericus* seedlings could profit from the neighbour plant also early in the vegetation period when the rosettes are not dense yet. Moreover, a dense canopy of neighbours can have an ameliorating effect on the substrate salinity. Soil patches with little or no vegetation cover are more exposed to sunlight which leads to increased evaporation and thus high soil salinities (eg Bertness 1991). Consequently neighbours can facilitate the establishment of other species as shown for example for *Juncus gerardii* by Bertness (1991). The same author cites several papers that discussed the role of facilitation for the establishment of different species in other biological and physical stressful habitats. For example Turner et al (1969) showed the importance of so called "nurse plants" for the seedling establishment of the saugaro cactus (*Carnegiea gigantea*) in a desert habitat.

However, the found effect could be an overestimation. *Limonium vulgare* prefers nutrient rich creek banks as they are of higher silt content as higher vegetation parts (Ellenberg 1996). Thus it could be that the observed higher survival of *E. athericus* seedlings was more due to higher nutrient availability than due to shading. Consequently, this question should be answered in an own study.

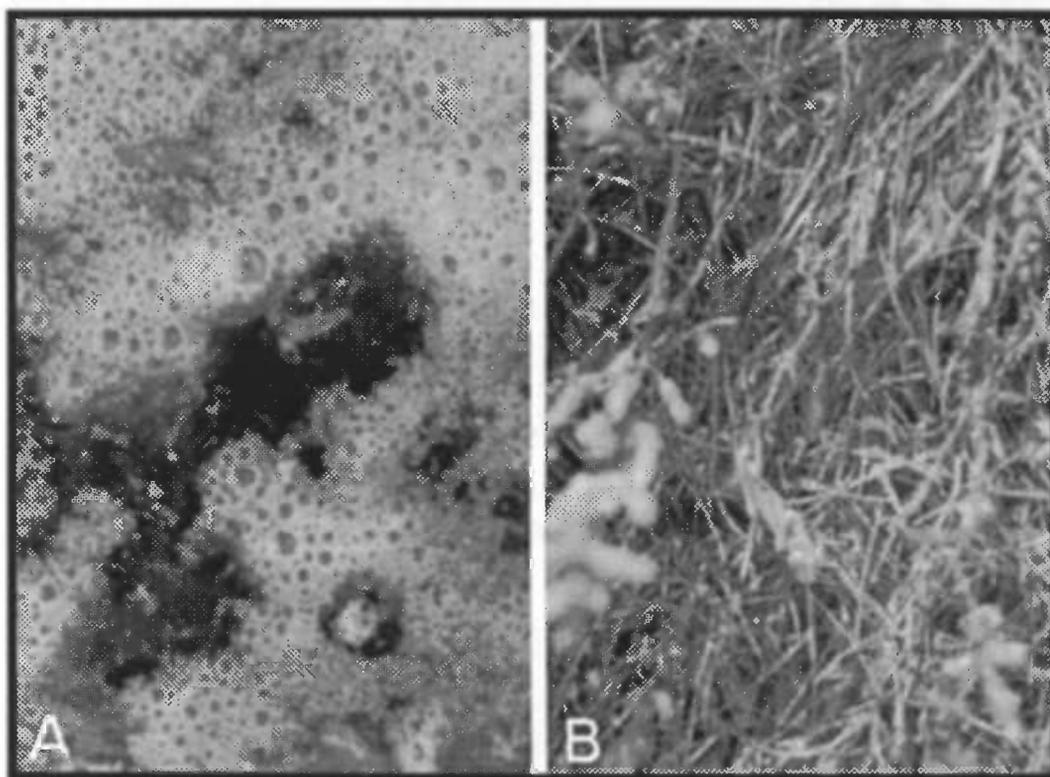


Figure 5.3: The coloured spikelets were difficult to discover. A: Two red spikelets drifting on the water surface above the salt marsh vegetation. B: One red spikelet within vegetation with similar colours

The results of the drift experiment (see 4.2) showed that a transport of diaspores of "inland" *E. athericus* populations through creeks is possible within two tidal cycles. The total amount of refund diaspores was low in comparison to the amount released into the creek. This may also be due to the colours used. Finding the red coloured spikelets was difficult because of similar colours in the vegetation (see Fig. 5.3) and could have led to an underestimation of the total amount of seeds dispersed into the study area. Although tidal water movements can carry diaspores of *E. athericus* from the salt marsh creek far out into the Wadden Sea streams, it was possible that diaspores became dispersed by currents back into the nearby area. Furthermore, under the right circumstances, it was possible that diaspores in the creek reached the open Wadden Sea within the period between high and low water. The outcome of the first experiment was not only depending on the tidal movement in the creek but also on the wind. At constant winds of 3-4 Beaufort from southwest spikelets on the uppermost layer were moved landinwards, although the main water body of the ebb stream in the creek was moving towards the Wadden Sea. The usual wind direction on the island Schiermonnikoog is southwest (Weather station of the Vrije Universiteit Amsterdam). Most creeks on the island are situated more or less in north south direction (see Fig. 1.1). This means the average wind direction does not support the transport out of the creeks. The counteracting effects of winds which might impede dispersal of water dispersed diaspores were also discussed by other authors (M. Wolters, personal communication; Koutstaal et al. 1987; Lüdecke et al. 1999). Moreover, the surface structure along the creek banks can have an impact on diaspores floating speed. For example Johansson (1993) reported for a river system that 27% of observed hydrochorous dispersed vegetative diaspores got caught at different kinds of obstacles and in curves of the stream. In the present study existing vegetation or litter at the creek banks were substantial obstacles. Moreover, due to slow water movement diaspores already got deposited on mudflats at the creek banks. In particular at the inside of curves the water streamed very slow. However, diaspores do not necessarily remain on the first spot they got trapped (Koutstaal et al. 1987; Lüdecke et al. 1999). Later tides in the present study remobilized trapped spikelets whereby these got another chance of seaward transport and dispersal into the study site. For the successful recruitment of *E. athericus* the floating capacity of diaspores is important. Koutstaal et al. (1987) reported a quite high floating capacity for *E. athericus* spikelets in salt water. After six month only 39% were sunk. However, the floating capacity for single grains was much lower with a

maximum of 12 days. Low floating capacity for *E. athericus* single grains of about 7 days was also observed in another experiment recently (J.P. Bakker, personal communication). Huiskes et al. (1995) added that 90% of floating as well as immersed *E. athericus* seeds germinated well after the six month of the experiment of Koutstaal et al. (1987).

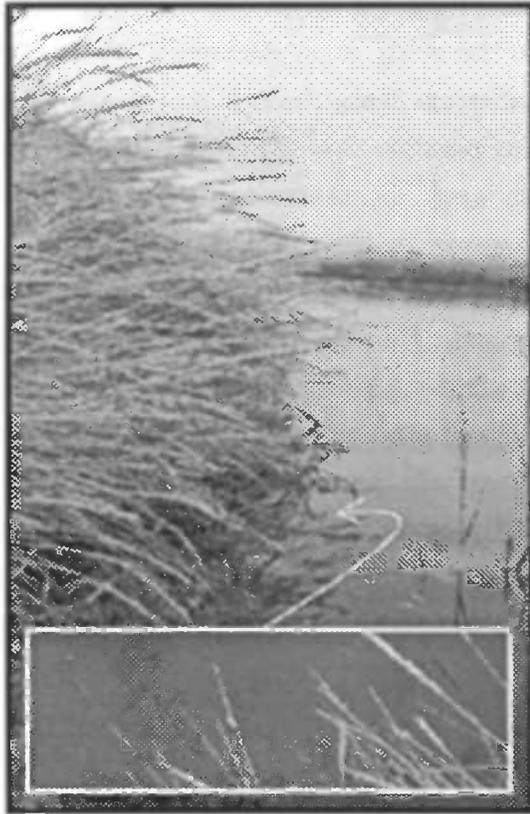


Figure 5.4: *E. athericus* population at creek bank of creek 10. Box shows undated spikelets at high tide.

Strong winter storm floods transport large amounts of diaspores of *E. athericus*, as can be seen in deposited driftline material (Bakker et al. 1985). Probably most of them are lost for recruitment because it seems very unlikely that they are transported into the low parts of the area. Flood streams carry diaspores mainly towards higher elevations in the salt marsh while relatively few floating diaspores are transported back with the ebb stream (Huiskes et al. 1995; Lüdecke et al. 1999). Consequently, driftline material carried by storm floods can be found mainly on high elevations in the saltmarsh or even higher on the foot of dunes (own observation, A.C. Bockemann and J.P. Bakker, personal communication). *E. athericus* seedlings germinate there but later die out and die (J.P. Bakker, unpublished results). Therefore, strong winter storm floods are not profitable to transport diaspores into the low marsh. From this, it seems more likely that *E. athericus* seeds were transported by moderately high spring floods into low salt marsh habitats. Although these high tides normally do not reach higher elevations where *E. athericus* populations are dominating, it is possible that diaspores become dispersed into water. *E. athericus* populations along creeks are also not necessarily flooded with every medium high spring tide as creek banks can be higher than the surrounding salt marsh (Packham and Willis 1997). However, inflorescences grown over the edge of the creek bank could disperse diaspores

even at low tide into the creek. Moreover, *E. athericus* plants can be snapped that way, that spikes are below waterlevel also beside sprigtide highwater (personal observation, see Fig. 5.4).

At moderate spring floods diaspores, as shown in section 4.2, diaspores can get trapped in the vegetation or are deposited at higher soil patches when the water level decreases again. Being trapped by vegetation might give a higher chance to establish on a certain spot. Seeds that lie on the ground without being fixed may be washed away again by the next flood (Bakker et al. 1985; Jutila b. Erkkilä 1998).

However, a site were seeds find save conditions until germination is not necessarily a suitable site for seedling establishment (Schupp 1995). Abiotic conditions of the soil can be unfavorable (Bakker et al. 1985; Shumway and Bertness 1992). For example burial under litter or wrack and abrasive tidal action can strongly inhibit seedling emerge (Goldberg and Werner 1983; Ungar 1987). Moreover, as discussed above, the moment of emergence in the season can be important. Emerging early in the season can give advantages for the competition with other emerging seedlings (Ross and Harper 1972; Ungar 1987). Additionally, early emergence might have the advantage of lower salinities in the soil. Whereas, in late spring and early summer salinities can increase due to higher evaporation and thus reduce seedling surviival (Ungar 1987). Nevertheless, late emergence can have advantages. As shown in this study herbivory impact can be higher in spring than in summer due to migrating grazers.

Chapter 6

Conclusion

The successful establishment of *E. athericus* at the study site depends on various factors: Dispersal into the area is possible through tidal waters. The question, whether this is the only way of invasion can not be cleared with this study. However, big amounts of dispersal units and a long potential floating capacity strengthen this theory. Moreover the study showed that establishment of transplanted *E. athericus* seedlings and even natural dispersed seeds is possible. Thus, the study site provides suitable sites for seeds as well as for seedlings. Herbivores have a strong negative impact on *E. athericus* seedling establishment. However, *Limonium vulgare* as a neighbour plant may support the establishment by providing shelter against herbivores or a profitable microclimate. Nevertheless, competition has a strong negative impact on the establishment. Concerning the origin of the seeds it can be assumed from the results that seeds from the site OL have the lowest chance to establish in the study site. These differences of the origin may be explained by phenotypic adaptation due to different preconditions of the sites in the past.

The high potential of adult *E. athericus* plants to invade high salt marshes and to out compete other plants has already been demonstrated well. Moreover the ability of adult plants to invade low salt marsh habitats had already been pointed out. The present study showed the high potential of seedling establishment in low salt marsh habitats. It can be concluded that seedling establishment of *E. athericus* is mainly restricted to salt marshes of young successional stage or to disturbance patches where competition is relatively low compared to marshes of old successional stage. However, small vertebrate herbivores occur mainly in young salt marshes. Herbivores keep the vegetation open and thus competitors of *E. athericus* small. Nevertheless, these herbivores influence seedling establishment negative. Thus, seedling establishment could be limited by herbivory in young salt marshes. However, as could

be shown, *E. athericus* seedlings might survive because they find shelter or germinate in the right time. Moreover, the salt marsh management can be important, as vegetations differ considerable between different management forms. Rapid phenotypic adaptations on environmental factors of a certain habitat can help *E. athericus* to invade new habitats with similar conditions. *E. athericus* has therefore a high potential to invade new habitats also by sexual recruitment, as diaspores can use tidal waters as a way for long distance dispersal.

Chapter 7

Deutsche Zusammenfassung

E. athericus ist als Salzwiesenpflanze der höheren Salzwiese bekannt. Doch in seit neuerem breitet sich die Art auch zunehmend in die untere Salzwiese aus. In der vorliegenden Arbeit wurde die Etablierung von Keimlingen in der unteren Salzwiese untersucht. Keimlinge aus Samen verschiedener Herkunft wurden im Gewächshaus vorgezogen und später in eine untere Salzwiese frühen Entwicklungsstadiums auf der Niederländischen Wattenmeer Insel Schiermonnikoog verpflanzt. In der Versuchsfläche war die Art zuvor noch nicht heimisch. Einfluss von Herbivorie und Konkurrenz wurden untersucht. Zur Ermittlung des Etablierungserfolges wurden Sprosshöhe, Anzahl der Blätter, Anzahl der Rameten regelmässig aufgenommen. Desweiteren wurde die Überlebensrate fortlaufend und das Vorhandensein von Rhizomen am Ende des Experiments kontrolliert. Herbivorie und Konkurrenz wurden als wichtigste Keimlingsetablierung beeinflussende Faktoren festgestellt. Keimlinge aus Samen einer unteren Salzwiese alten Entwicklungsstadiums etablierten sich schlechter als Keimlinge von Samen anderer Herkunft. Entgegen der ursprünglichen Annahme wurden desweiteren bereits natürlich etablierte Keimlinge gefunden. Keimlinge, sowohl verpflanzte als auch natürlich etablierte, die in Nachbarschaft von *Limonium vulgare* wuchsen, hatten eine erhöhte Etablierungschance. Desweiteren zeigte ein Drift-Experiment, dass *E. athericus* Diasporen von landinwärts gelegenen Populationen an Prielrändern durch mittelstarke Hochwasser bis in Habitate der unteren Salzwiese transportiert werden können.

Danksagungen

An dieser Stelle möchte ich all denen danken, die mit Beiträgen verschiedenster Art zu dieser Arbeit beigetragen haben. Als erstes und insbesondere sind da meine Eltern, die mich wo sie konnten unterstützten, meinen Weg zu gehen und meine Ziele zu erreichen. Weiterhin gibt es viele liebe Menschen, die ich aufzählen müsste, die mir die Natur und das Leben näher brachten, indem sie mich anregten genau hinzuschauen. Besonders sei hier Wolfhardt Schildt hervorgehoben.

Für das angenehme Studium bedanke ich mich vor allem bei Edda Meichßner, Susanne Knöpke und Uwe Simon. Für die spannenden Inhalte des Studiums sorgten besonders Prof. T. Bauer und Prof. K. Dierßen. Letztlich bleibt mir noch all jenen zu danken, die direkt an dieser Arbeit beteiligt waren:

Insbesondere Anna Christina Bockelmann, für Idee, Betreuung und vor allem Käfige falten. Prof. Jan P. Bakker, für die freundliche Aufnahme in die Arbeitsgruppe und viele wertvolle Informationen. Prof. R.L. Jeffries, für einen entscheidenden Tipp. Anne Berber de Vries und Roos Veeneklaas, für Käfige falten und Heringe biegen. Renate Mann und Nicol Heuermann für Hilfe beim Pflanzen und Käfige aufstellen. Lutz von der Heide, für Label kleben und Pflanzen ausgraben. Mara Roosjen, für Hilfe beim Pflanzen messen. StudentInnen des Vegetationsökologischen Kurses, für Hilfe beim Bodenproben nehmen. Mike Gabriel, für essentielle Hilfe beim Driftexperiment. Karen Remans, ebenfalls für das Ausgraben der Pflanzen. Kai Jensen, für angenehme Hiwi-jobs und vor allem für die Durchsicht der Arbeit und wertvolle Kommentare.

Und ganz besonders danke ich Meike Crone für ihr Verständniss für einen Biologen.

Appendix

Table 7.1: Results of elevation (cm), inundation frequency (inundations per period) and soil salinity of plots (%/l NaCl). Inundations periods: Logger = 21.4.-6.8.00, Total = 21.4.-5.12.00 (estimated, see text).

	Elevation above		Inundations		Salinity
	NAP	MHT	21.4.-6.8.00	21.4.-5.12.00	
LOW					
Mean	127.5	1.3	32.1	125	6
SD	2.6	2.6	8.0	-	1.6
MID					
Mean	137.2	11.0	11.5	38	4.4
SD	2.4	2.4	4.2	-	0.9
HIGH					
Mean	143.7	17.6	4.0	17	4.0
SD	2.1	2.1	1.3	-	1.2

Table 7.2: Results of Logistic Regression Analysis, survival census on 5.5.00.

	df	F	p
Age	1	1.884	***
Habitat	1	1.42	**
Competition	1	0.02	*
Age × Habitat × Herbivory	1	0.79	***
Constant	1	5.62	***

Table 7.3: Results of Logistic Regression Analysis, last survival census 22.10.00.

	df	F	p
Age	1	1.4	**
Competition	1	2.78	***
inundation frequency	1	1.21	***
Block	1	0.02	*
Herbivory × Limonium	1	1.21	***
Habitat × Herbivory	1	0.81	*
Age × Habitat × Herbivory	1	0.937	**
Age × Habitat × Competition	1	0.46	*
Constant	1	1.75	0.06

Table 7.4: Results of the Repeated Measurements Anova. (NS: not significant, *P<0.05, **P<0.01, ***P<0.001)

	Mean square	d.f.	F	Significance
PLANT HEIGHT				
Age	0.237	1	1.521	NS
Habitat	1.183	1	7.595	*
Herbivory	12.830	1	82.347	***
Competition	0.628	1	4.034	*
Age × Habitat	0.759	1	4.863	*
Habitat × Competition	0.448	1	2.874	NS
Block	0.318	49	2.042	***
Covariate	3.353	1	21.518	***
Error	0.156	407		
LEAFS PER PLANT				
Age	0.277	1	0.573	NS
Habitat	7.58	1	15.691	***
Herbivory	6.561	1	13.583	***
Competition	27.123	1	56.149	***
Age × Habitat	6.268	1	12.976	***
Habitat × Competition	4.523	1	9.362	**
Block	1.352	49	2.799	***
Error	0.483	409		
RAMETS PER PLANT				
Age	0.365	1	2.032	NS
Habitat	1.964	1	10.917	**
Herbivory	0.792	1	4.404	*
Competition	5.959	1	33.129	***
Age × Habitat	0.686	1	3.816	NS
Habitat × Competition	1.258	1	6.995	**
Block	0.364	49	2.026	***
Error	0.180	409		

Table 7.5: Results of Multifactorial ANOVA analysis, last census 18.9.00.

	Mean square	d.f.	F	Significance
PLANT HEIGHT				
Age	0.068	1	3.131	NS
Habitat	0.088	1	4.037	*
Herbivory	1.346	1	61.775	***
Competition	0.291	1	13.378	***
Age × Habitat	0.079	1	3.615	NS
Habitat × Competition	0.132	1	6.051	*
Block	0.053	49	2.447	***
Covariate	0.485	1	22.272	***
Error	0.022	413		
LEAFS PER PLANT				
Age	0.032	1	0.111	NS
Habitat	5.002	1	17.293	***
Herbivory	3.658	1	12.647	***
Competition	18.787	1	64.953	***
Age × Habitat	3.664	1	12.668	***
Habitat × Competition	2.593	1	8.964	**
Block	0.830	49	2.834	***
Error	0.289	413		
RAMETS PER PLANT				
Age	0.008	1	0.083	NS
Habitat	1.562	1	16.822	***
Herbivory	0.278	1	2.990	NS
Competition	7.832	1	84.360	***
Age × Habitat	1.005	1	10.828	**
Habitat × Competition	1.082	1	11.653	**
Block	0.179	49	1.930	***
Error	0.092	414		

Bibliography

- Adam 1990** ADAM, P.: *Salt marsh ecology*. Cambridge, UK : Cambridge University Press, 1990
- Bakker et al. 1985** BAKKER, J.P. ; DIJKSTRA, M. ; RUSSCHEN, P.T.: Dispersal, germination and early establishment of halophytes and glycophytes on a grazed and abandoned salt-marsh gradient. In: *New Phytologist* 101 (1985), : 291-308
- Bakker et al. 1998** BAKKER, J.P. ; ESSELINK, R. ; DIJKEMA, K.S.: Options for restauration and management of coastal salt marshes in Europe. In: *Restauration Ecology and Sustainable Development*. Cambridge, UK, 1998, : 268-322
- Bakker et al. 1993** BAKKER, J.P. ; LEEUW, J. de ; DIJKEMA, K.S. ; LEENDERTSE, P.C. ; PRINS, H.H.T. ; ROZEMA, J.: Salt marshes along the coast of The Netherlands. In: *Hydrobiologia* 265 (1993), : 73-95
- Beeftink 1985** BEEFTINK, A.: Interactions between *Limonium vulgare* and *Plantago maritima* in the *Plantagini-Limonietum* on the Boschplaat, Terschelling, The Netherlands. In: *Vegetatio* 61 (1985), : 33-44
- Beeftink 1977** BEEFTINK, W.G.: The coastal salt marshes of western and northern Europe: An ecological and physiological approach. In: *Wet Coastal Ecosystems (Ecosystems of the world)*. Amsterdam, NL, 1977, Chapter 6
- Belsky 1986** BELSKY, A.J.: Does Herbivory benefit Plants? A Review on Evidence. In: *The American Naturalist* 127 (1986), Nr. 6, : 870-892
- Bentley and Whittaker 1979** BENTLEY, S. ; WHITTAKER, J.B.: Effects of grazing by a chrysomelid beetle *Gastro viridula*, on competition between *Rumex obtusifolius* and *Rumex crispus*. In: *Journal of Ecology* (1979)

- Bertness 1991** BERTNESS, M.D.: Interspecific interactions among high marsh perennials in a New England salt marsh. In: *Ecology* 72 (1991), Nr. 1, : 125–137
- Bertness 1991** BERTNESS, M.D.: Zonation of *Spartina patens* and *Spartina alternifolia* in a New England salt marsh. In: *Ecology* 72 (1991), Nr. 1, : 138–148
- Bertness and Ellison 1987** BERTNESS, M.D. ; ELLISON, A.M.: Determinants of pattern in a New England salt marsh plant community. In: *Ecological Monographs* 57 (1987), Nr. 2, : 129–147
- Bockelmann 2001** BOCKELMANN, A.-C.: Ordinary and successful - The invasion of *Elymus athericus*. 2001. – PhD-thesis in progress
- Bockelmann and Neuhaus 1999** BOCKELMANN, A.-C. ; NEUHAUS, R.: Competitive exclusion of *Elymus athericus* from a high-stress habitat in a European salt marsh. In: *Journal of Ecology* 87 (1999), : 503–513
- Chapman 1978** CHAPMAN, V.J.: *Coastal Vegetation*. Oxford, UK, 1978
- Dormann 1998** DORMANN, C.: *The influence of herbivory, competition and nutrient availability on some salt-marsh plants*, Christian-Albrechts-Universität Kiel, Diplomarbeit, 1998
- Dormann et al. 2000** DORMANN, C.F. ; VAN DER WAL, R. ; BAKKER, J.P.: Competition and herbivory during salt marsh succession: the importance of forb growth strategy. In: *Journal of Ecology* 88 (2000), : 571–583
- Ellenberg 1996** ELLENBERG, H.: *Vegetation Europas*. 5. 1996
- Frey and Lössch 1998** FREY, W. ; LÖSCH, R.: *Lehrbuch der Geobotanik: Pflanze und Vegetation in Raum und Zeit*. Jena, D. : G.Fischer Verlag, 1998
- Goldberg and Werner 1983** GOLDBERG, D.E. ; WERNER, P.A.: The effects of size of opening vegetation and litter cover on seedling establishment of goldenrods (*Solidago* spp. In: *Oecologia* 60 (1983), : 149–155
- Harper 1977** HARPER, J.L.: *Population biology of plants*. London, UK : Academic Press, 1977

- Howe and Westley 1993** HOWE, H.F. ; WESTLEY, L.C.: *Anpassung und Ausbeutung: Wechselbeziehungen zwischen Pflanzen und Tieren*. Heidelberg FRG : Spektrum Akademischer Verlag, 1993
- Huiskes et al. 1995** HUISKES, A.H.L. ; P.M. HERMAN, B.P. K. ; BEEFTING, W.G. ; MARKUSSE, M.M. ; DE MUNCK, W.: Seed dispersal of halophytes in tidal salt marshes. In: *Journal of Ecology* (1995)
- Johansson and Nielsson 1993** JOHANSSON, M.E. ; NIELSSON, C.: hydrochory, population dynamics and distribution of the clonal aquatic plant *Ranunculus lingua*. In: *Journal of Ecology* 81 (1993), : 81–91
- Jutila b. Erkkilä 1998** JUTILA B. ERKKILÄ, H.M.: Seed banks of grazed and ungrazed Baltic seashore meadows. In: *Journal of Vegetation Science* 9 (1998), : 395–408
- Koutstaal et al. 1987** KOUTSTAAL, B.P. ; MARKUSSE, M.M. ; DE MUNCK, W.: Aspects of seed dispersal by tidal movements. In: *Vegetation between land and sea*. Dordrecht, NL : Dr W. Junk Publishers, 1987, : 226–233
- Lüdecke et al. 1999** LÜDECKE, A. ; OVERBECK, G. ; RÖDER, N.: *Experiments on seed dispersal of halophytes*. 1999. – unpublished report of: Vegetationsökologisches Praktikum II Sommer1999, TU München-Weihenstephan
- Leendertse et al. 1997** LEENDERTSE, P.C. ; ROZEN, A.J.M. ; ROZEMA, J.: Long-term changes (1953-1990) in the salt marsh vegetation at the Boschplaat on Terschelling in relation to sedimentation and flooding. In: *Plant Ecology* 132 (1997), : 49–58
- Long and Mason 1983** LONG, S.P. ; MASON, C.F.: *Saltmarsh Ecology*. Blackie, 1983
- McCullagh and Nelder 1989** MCCULLAGH, P. ; NELDER, J.A.: *Generalized Linear Models*. 2. London, UK : Chapman and Hall, 1989
- Meyer and Schmid 1999** MEYER, A.H. ; SCHMID, B.: Experimental demography of the old-field perennial *Solidago altissima*: the dynamics of the shoot population. In: *Journal of Ecology* 87 (1999), : 17–27
- Meyer and Schmid 1999** MEYER, A.H. ; SCHMID, B.: Seed dynamics and seedling establishment in the invading perennial *Solidago altissima* under different experimental treatments. In: *Journal of Ecology* (1999)

- Müller-Thomsen 1997** MÜLLER-THOMSEN, U.: Wasser-, Gas-, Salz- und Nährstoffdynamik zweier Standorte im Deichvorland Norddeutschlands (Sönke-Nissen-Koog). In: *Berichte aus dem FTZ Büsum*. 1997
- Myster and McCarthy 1989** MYSTER, R.W. ; MCCARTHY, B.C.: Effects of herbivory and competition on survival of *Caryota tomentosa* (Juglandaceae) seedlings. In: *OIKOS* (1989)
- Packham and Willis 1997** PACKHAM, J.H. ; WILLIS, A.J.: *Ecology of dunes, salt marsh and shingle*. Chapman and Hall, 1997
- Parker and Salzman 1985** PARKER, M.A. ; SALZMAN, A.G.: Herbivory exclosure and competition removal: effects on juvenile survivorship and growth in the shrub *Gutierrezia microcephala*. In: *Journal of Ecology* 73 (1985), : 903-913
- Ranwell 1972** RANWELL, D.S.: *Ecology of Salt Marshes and Sand Dunes*. London, UK : Chapman and Hall, 1972
- Reader and Bonser 1998** READER, R.J. ; BONSER, S.P.: Predicting the combined effect of herbivory and competition on a plant's shoot mass. In: *Canadian Journal of Botany* 78 (1998), : 316-320
- Rijkswaterstaat 2000** RJKSWATERSTAAT: Tide levels at the harbour of Schiermonnikoog between April and November 2000 / Rijkswaterstaat, The Netherlands. 2000. - Technical Report
- Ross and Harper 1972** ROSS, M.A. ; HARPER, J.L.: Occupation of biological space during seedling establishment. In: *Journal of Ecology* 60 (1972), : 77-88
- Schachtschabel et al. 1998** SCHACHTSCHABEL, P. ; BLUME, G. ; HARTGE, K.H. ; SCHWERTMANN, U.: *Lehrbuch der Bodenkunde*. Stuttgart : Enke Verlag, 1998
- Schmid 1991** SCHMID, B.: Konkurrenz bei Pflanzen. In: *Populationsbiologie der Pflanzen*. Basel : Birkhäuser Verlag, 1991, Chapter 13, : 201-210
- Scholten et al. 1987** SCHOLTEN, M. ; BLAAUW, P.A. ; STROETENGA, M. ; ROZEMA, J.: The impact of competitive interactions on growth and distribution of plant species in salt marshes. In: *Vegetation between land and sea*. 1987, Chapter 21, : 270-281

- Schupp 1995** SCHUPP, E.W.: Seedling conflicts, Habitat choice, and Patterns of plant recruitment. In: *American Journal of Botany* 82 (1995), Nr. 3, : 399-409
- Shumway and Bertness 1992** SHUMWAY, S.W. ; BERTNESS, M.D.: Salt stress limitation of seedling recruitment in a salt marsh plant community. In: *Oecologia* (1992)
- Silvertown 1993** SILVERTOWN, J.L.: *Introduction to Plant Population Biology*. 3rd. Oxford, UK : Blackwell Science, 1993
- Sokal and Rohlf 1995** SOKAL, R.R. ; ROHLF, F.J.: *Biometry: The Principles and Practice of Statistics in Biological Research*. 3. New York, USA : Freeman and Company, 1995
- Soukupova 1992** SOUKUPOVA, L.: *Calamagrostis canescens*: population biology of a clonal grass invading wetlands. In: *Oikos* 63 (1992), : 395-401
- Tscharntke 1991** TSCHARNTKE, T.: Die Auswirkungen der Herbivorie auf Wachstum und Konkurrenzfähigkeit von Pflanzen. In: *Populationsbiologie*. Basel : Birkhäuser Verlag, 1991, Chapter 16, : 254-280
- Turner et al. 1969** TURNER, R.M. ; ALCORN, S.M. ; OLIN, G.: Mortality of transplanted saguaro seedlings. In: *Ecology* 50 (1969), : 835-844
- Ungar 1987** UNGAR, I.A.: Population Ecology of Halophyte Seeds. In: *The Botanical Review* 53 (1987), Nr. 3, : 301-334
- Van der Meijden 1996** VAN DER MEIJDEN, R.: *Henkel's Flora van Nederland*. Groningen, NL : Wolters-Noordhof, 1996
- Van Wijnen and Bakker 1997** VAN WIJNEN, H.J. ; BAKKER, J.P.: Nitrogen accumulation and plant species replacement in three salt marsh systems in the Waddensea. In: *Journal of Coastal Conservation* 3 (1997), : 19-26
- Van Wijnen and Bakker 1999** VAN WIJNEN, H.J. ; BAKKER, J.P.: Nitrogen and phosphorus limitation in a coastal barrier salt marsh: the implications for vegetation succession. In: *Journal of Ecology* (1999), : 265-272
- Van Wijnen et al. 1997** VAN WIJNEN, H.J. ; BAKKER, J.P. ; DE VRIES, Y.: Twenty years of salt marsh succession on a Dutch coastal barrier island. In: *Journal of Coastal Conservation* 3 (1997), : 9-18

- Van Wijnen et al. 1999** VAN WIJNEN, H.J. ; VAN DER WAL, R. ; BAKKER, J.P.: The impact of herbivores on nitrogen mineralization rate: consequences for salt-marsh succession. In: *Oecologia* 118 (1999), : 225-231
- Vila and Lloret 1996** VILA, M. ; LLORET, F.: Herbivory and neighbour effects on the sprout demography of the Mediterranean shrub *Erica multiflora* (Ericaceae). In: *Acta Oecologica* (1996)