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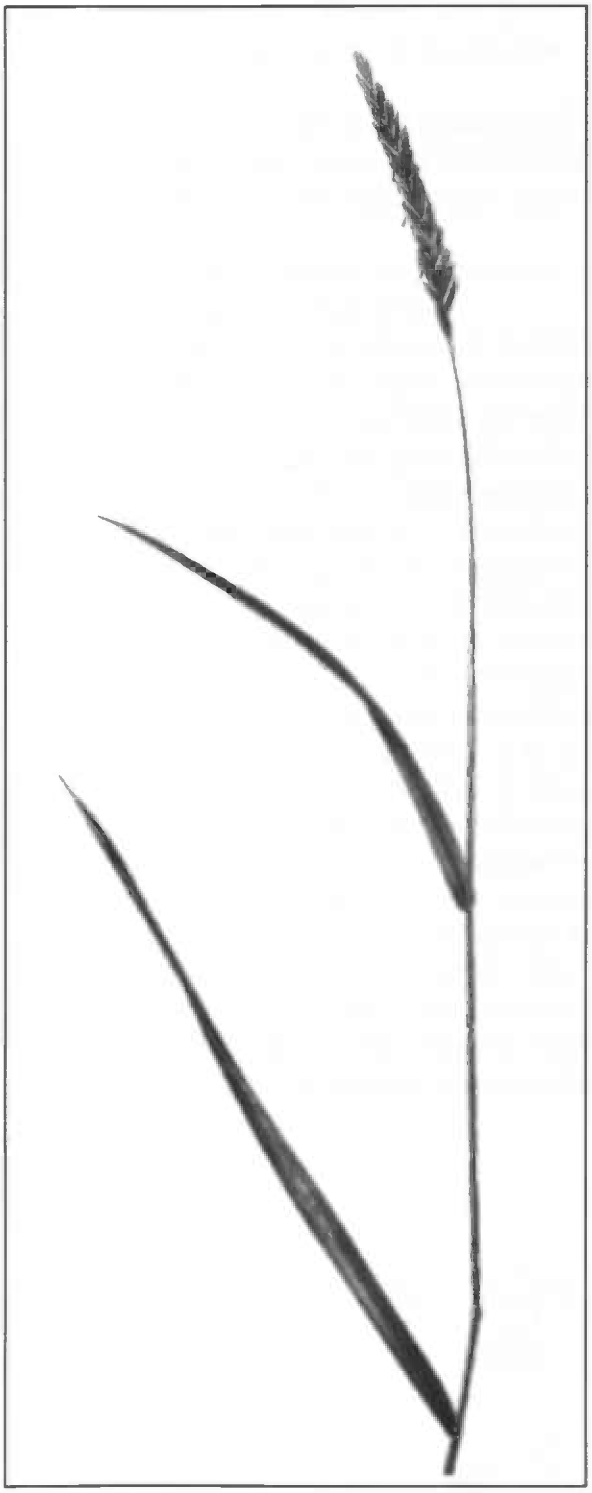

"Doctoraalverslag"
Nienke Nijhoff
March – September 2001

Plantecologie
Haren
Rijks*universiteit* Groningen
The Netherlands

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ABSTRACT

1. At Schiermonnikoog, a Dutch island in the Waddensea, a vegetation succession gradient can be observed from east to west and it features a natural productivity gradient.
2. *Elymus athericus* (a perennial grass) is a dominant species in the oldest stages of salt marsh succession on the island Schiermonnikoog, The Netherlands. It is present in low abundance at the youngest stages, but only when herbivores (especially hares) are absent.
3. Brown hare, Brent geese and Barnacle geese forage most on salt marshes with intermediate plant standing crop.
4. In the present study the effect of herbivory and competition on *Elymus* at four different stages of the salt marsh were examined. *Elymus* seedlings were transplanted in a full factorial design (control, no herbivores and/or no neighbours) A no-geese treatment was added to distinguish the effects of hares and geese.
5. Survival of *Elymus* is lowest at the youngest site, where environmental conditions are very severe (wind, seawater, low nutrient concentration).
6. Overall shoot biomass production increases with ageing of the salt marsh, very likely caused by the increasing amount of nitrogen as the salt marsh gets older.
7. Competition enormously reduces the amount of biomass produced, the maximal shoot length and the number of ramets of *Elymus* significantly. The older the salt marsh, the larger this reduction is, because competition for light increases with salt marsh-age. Plant survival is almost not influenced by competition.
8. Herbivory plays no important role on plant performance; plant biomass, number of ramets and plant height are hardly influenced by this factor. Only at the youngest salt marsh herbivores cause a large reduction in biomass. Herbivory has a small negative effect on plant survival, significant for two sites.
9. It seems there's a window of opportunity for *Elymus* to establish, which is present at the youngest salt marsh. During this period, herbivores prevent permanent establishment of seedlings. As succession proceeds other plant species hinder (further) establishment and compete with young *Elymus* plants, which may be enhanced by herbivore grazing forming a denser low vegetation.

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1. INTRODUCTION

Plant establishment, performance and survival are influenced by several factors. Abiotic ones, like temperature, moisture and light intensity have their effect. Besides these, biotic factors also influence plants. Plants can facilitate neighbouring plants or compete with them for resources, like light and nutrients. Herbivores can directly influence plants by trampling or reducing biomass. They can also have indirect effects by changing light or nutrient availability (Bakker, 1985).
Several studies show the importance of herbivory and competition from neighboring plants as environmental controls of plant survival and reproduction. (Harper, 1977; Crawley, 1990 both in Rachich & Reader 1999)

Studies in systems with a productivity gradient offer the opportunity to observe how competition changes with an increase in biomass.
Grime (1979) predicts that competition increases with an increase in biomass. Plants are namely more likely to interact and to compete for resources at sites with higher biomass.
However, Tilman (1988) states that the intensity of competition doesn't change during succession, but its nature. There will be a shift from competition for soil resources at sites where biomass is low, to competition for light at sites where biomass is high.
Several experiments are done to test if and how competition changes with increasing biomass, but they give inconsistent results (Bonser, 1995).
Biomass is also related to herbivory and the other way around. Oksanen (1981) predicts that herbivory should increase with an increase in plant productivity, because the herbivore population is large enough to support a carnivore population. The carnivores will top-down regulate the herbivores. Some researchers report an increasing herbivore-intensity with higher biomass, whereas others found the opposite (Bonser, 1995).

Van der Wal (2000b) names two main theoretical models that include both plant competition and herbivory. A) Grazing increases as productivity raises and there is a shift from plants that compete well for nutrients towards grazing-tolerators. B) As productivity increases, palatable plants will be outshaded by taller unpalatable species. Reduced competition for light and reduced grazing pressure both contribute to more biomass.
Many researchers tried to unravel the effect of competition and herbivory on plant performance (Dormann, 2000a/b; Van der Wal, 2000; Taylor, 1997; Reader, 1998; Myster, 1989; Wells, 2001; Bonser, 1995; Maron, 1997; Mulder, 1998; Shabel, 1994; Rachich, 1999). Most of them conclude that herbivory and/or competition causes has a negative effect on plant performance. Some findings also indicate independent or rather interactive effects of competition and herbivory.

In the autumns of 1995-1997 between 300-600 hares in 550 ha salt marsh were counted and the population seems to be rather stable after hunting became forbidden in 1994 (Van der Wal, 1998). Hares mainly graze on *Festuca rubra, Puccinellia maritima, Plantago maritima* and *Trichlogin maritima* (names following Van der Meijden, 1990), according to faeces analyses done by Van der Wal (2000a) and Drost (2000). They also eat species from the late successional stages, like *Elymus athericus* (only the young shoots (Dubbeld, 2000; Van de Koppel, 1996), *Artemisia maritima* and *Artriplex portulacoides.* In spring 2000, which is virtually the same as in 2001 (J. Stahl, personal comment) geese observations revealed that 4500 geese inhabited the salt marshes until the end of April and during May about 2500 Brent geese were present. Prop (1991) did visual observations and faeces analyses and concludes that geese prefer the same foodplants as hares. Geese avoid adult *Elymus athericus* plants (Van der Wal, 2000c).

With aerial photographs and topographical maps the age of the different salt marsh parts could be determined (Van der Wal, 2000c). These stages differ in species composition, vegetation biomass, height, clay layer thickness, light availability and grazing pressure (see table 1). The highest hare density can be observed on marshes of intermediate age and with intermediate level of plant standing crop. On older and younger stages, grazing pressure is lower (Drost, 2000; Kuijper, unpublished results). Geese density also peaks at these stages (Van de Koppel, 1996; Van der Wal, 2000c).
The decrease of grazing intensity at higher productivity is due to the higher abundance of tall, relatively unpalatable plant species and the accumulation of dead plant material (Van der Wal, 2000a; Olff, 1997).

The presence of herbivores has a large effect on the salt marsh vegetation. Long-term exclosures on the marshes of Schiermonnikoog have shown that hare grazing retards vegetation succession until a specific age as productivity gets to high to keep plant growth under control (Van der Wal 2000a; Kuijper, unpublished results).

Elymus athericus
One of the plants growing on the salt marsh is *Elymus athericus,* a perennial grass, with strong competitive qualities. It prefers the low-stress habitats in the higher salt marsh and can be regarded as a halophytic, nitrophilous species. Both "phalanx and "guerilla" strategy to colonize new places, have been reported (Bockelmann, 1999; Weeda, 1994). *Elymus* invests a lot in structural tissues in stems and stiff leaves. This is why older plants hard to digest for herbivores (Van de Koppel, 1996; Drost, 2000). Plant quality is low; high fiber content and low protein content is measured (Bakker, 1989). *Elymus* is considered to be a species of the late successional stages (Bockelmann, 2000; Weeda, 1994).
On Schiermonnikoog large areas in the high salt marsh are covered with *Elymus* plants (Bakker, 1989; Van Wijnen, 1997), but now it also starts to invade the lower salt marsh (Bockelmann, 1999; Bakker 1998; Olff, 1997), possibly through genetic adaptation. Also a better resistance to salt stress due to accumulation of nutrients in older marshes is named (Olff, 1997; Bockelmann, 2000). The extension in distribution of *Elymus*-species leads to considerable loss in species and community diversity (Bakker 1989, Leendertse 1995).

Study area

Schiermonnikoog (see figure 1) is an island situated in the Waddensea (53 °30'N, 6°10'E) and it gradually extends to the east due to sea currents. The island is only inundated in the south by the Waddensea and sedimentation of clayey material occurs. In this way, new salt marsh is being formed in the east of the island on the lee-side of an extensive dune system. Various stages of salt marsh development are situated next to each other; the youngest marshes are found in the east and the oldest in the west part. At the moment the age of the salt marsh ranges from 0 to 200 years old, over a distance of approximately 6 km. During the development of the salt marsh, nitrogen accumulates in the system due to the continuous sedimentation of clay on top of the sand and accumulating organic matter from decaying plant material. Therefore, the youngest successional stages have very low soil nitrogen content and support only sparse vegetation. Older stages have a large pool of nitrogen supporting a dense vegetation. This situation offers a good opportunity to study vegetation succession. Late successional species are taller and contain more fibers than those in the first stages of succession, so the successional sequence features a natural productivity gradient (Olff, 1997). Because low statue species from the young salt marsh are replaced by taller species in the final successional stages, a shift from competition for nutrients on the youngest marsh to competition for light on the older marsh occurs (Huisman 1999, Olff 1993).

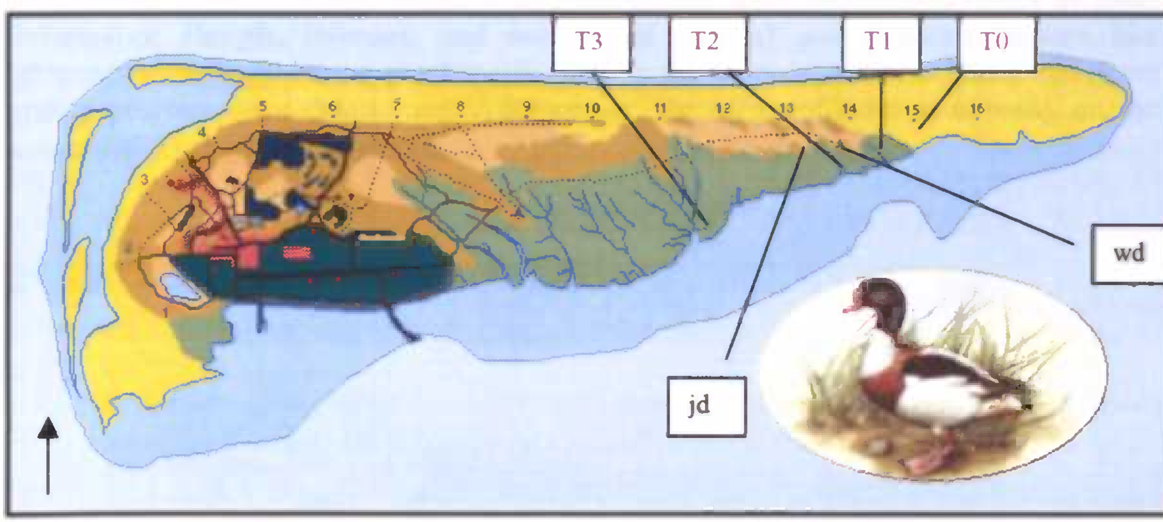


Figure 1: *Map of Schiermonnikoog (with shelduck). Study sites are indicated (T0, T1, T2 and T3) as well as Jeroensduin (jd) and Willemsduin(wd). Yellow = sand, Olive-green = the salt marsh, Light brown = dunes.*

Herbivores

The most important herbivores on the salt marsh are hares (*Lepus europeus)*; they graze on vegetation during the whole year. Barnacle geese *(Branta bernicla)* use the salt marsh in winter and early spring (until the end of April) and Brent geese *(Branta leucopsis)* are mainly present in April and May. The herbivores have almost no predators (Van de Koppel, 1996). Information on insect herbivores is lacking, but below-ground grazing by nematodes on plants of the middle high salt marsh is considered to play a very small role according to a pilot experiment (Dormann, 1998).

Experiment
As mentioned before, the marshes on Schiermonnikoog offer a good opportunity to find out how competition and herbivory influence plants, because of the productivity gradient and the different grazing intensities. The establishment of *Elymus athericus* seems to be influenced by one or both factors, since it has higher abundance in the vegetation when herbivores are excluded (Kuijper, unpublished results). On the oldest salt marsh *Elymus* has reached almost complete dominance and the principal foodplants of herbivores become overgrown by the taller *Elymus*. So, it is important to know how herbivores and neighbour plants influence the survival and production of this species.

A quite common way to reveal the effects of herbivory and competition on plants, which is used by several researchers (Dormann, 2000a/b; Van der Wal, 2000; Taylor, 1997; Reader, 1998; Myster, 1989; Wells, 2001; Bonser, 1995; Maron, 1997; Shabel, 1994; Rachich, 1999) is a full-factorial design. Mostly four treatments are used; 1) no herbivory, the plants are protected from grazing by herbivores or insects, 2) no competition, surrounding plantmaterial (above and/or below ground) is removed, 3) no herbivory and no competition, the previous treatments are combined, 4) control treatment.

A full-factorial design as described above was set up and several parameters of plant performance (length, biomass, and number of ramets) and (a)biotic factors like lightpenetration, neighboring plant species and height were determined. Hares and geese grazing pressure were determined. Additionally, the effect of time of clipping on the recovery of *Elymus* was measured.

2. *MATERIAL AND METHODS*

Main experiment

Seed of *Elymus athericus* was gathered in March 2001 between Willemsduin and Jeroensduin (see figure 1) from adult plants, where they occur in high abundance.

The seeds were sown on a 4-cm layer of potting compost and were placed in a greenhouse. The seeds received 15 hours of light per day. During the day temperature was kept at 23 ° C and 17 ° C at night. The seeds were watered twice a day. After two weeks the seeds were germinated and the plants were transplanted individually in small plastic cups (5,5 cm high and 3 cm in diameter). 3,5 weeks after sowing the plants were transported to Schiermonnikoog.

As is described in the introduction, consecutive stages of vegetation succession can be seen at Schiermonnikoog from east to west. The experiment was set up at 3 sites, which differ in age. T0 is the youngest place (1993), T1, T2 and T3 were formed in 1986, 1974 and 1964 respectively (according to Van der Wal, 2000c).

The four transects differ in many (a)biotic characteristics, which are depicted in table 1. These numbers are not exactly valid for this experiment (except from those indicated with "4" and age), but are mentioned to get an idea of the sites.

Transect	**T0**	**T1**	**T2**	**T3**
Age (year) [1]	8	15	27	37
Clay-layer thickness (cm) [2]	3.4 ± 0.08 (n = 216)	5.0 ± 0.07 (n = 200)	10.9 ± 0.10 (n = 200)	11.4 ± 0.14 (n = 200)
Base elevation (m above NAP) [2]	1.13± 0.001 (n = 216)	1.38 ± 0.003 (n = 200)	1.41 ± 0.004 (n = 200)	1.19 ± 0.002 (n = 200)
Bare soil (%) [3]	X	37	0.6	0.6
Dominant plant species [4]	*Limonium vulgare, Festuca rubra* (n = 23)	*Artemisia maritima, Limonium vulgare, Festuca rubra* (n = 86)	*Festuca rubra, Plantago maritima, Limonium vulgare* (n = 71)	*Festuca rubra, Artemisia maritima, Limonium vulgare* (n = 82)
Above ground biomass (g/m2) [3]	X	452	627	793
% live biomass [3]	X	90	76	66
Canopy height (cm) ^[4]	3,9 ± 0,2 (n = 23)	6,2 ± 0,2 (n = 86)	9,0 ± 0,3 (n = 71)	11,2 ± 0,3 (n = 82)
Light intensity at soil (%) [4]	99.6 ± 0.18 (n = 100)	96.5 ± 0.3 (n = 100)	90.2 ± 1.0 (n = 100)	79.4± 1.63 (n = 100)

1 = from Van der Wal (2000c)
2 = from Kuijper (2001; unpublished results)
3 = from Dormann (2000a/b)
4 = measured in 2001 (see fig. 3)
X = no data available

Table 1. *Site characteristics of the four successional stages. Means with standard error.*

Within one week 30 blocks with each five transplants were created at T0, T2 and T3 at similar base elevation and within existing vegetation, representative for the transect. One block consisted of 5 different treatments, arranged like a “5” on a die. Each block was 1 by 1 m and between blocks was 3 m space. The treatments were:

- No-HERB: no herbivores, a small cage (17 cm high and 8 cm in diameter), made of chicken wire was placed over the transplant.
- CONT: control, the transplant was just put into the earth.
- No-GOOS: no geese, a small cage was placed over the transplant only during the stay of the geese and was removed at 5-7 June, after the geese left the island.
- No-COMP: no competition, all aboveground biomass of neighbour plants was clipped (in a square of 20 by 20 cm) to avoid aboveground competition. Created bare ground was covered with driftline material to reduce the impact of solar radiation or wind. The borders of all plots were trenched to a depth of 20 cm with a knife, to sever rhizomes of adjacent plants. This trenching was repeated every 3 weeks.
- No-HECO: no herbivores and no competition, the same treatment was done as with COMP and with HERB.

Plants were planted with a small clump of adherent soil to prevent destruction of the fine roots. A very small bamboo stick was placed 10 cm from the CONT-transplant to find it back during measurements. All transplants were marked with a tiny plastic ring (4 mm in diameter) to distinguish them from natural *Elymus*-plants.

With this design, the effect of herbivory alone is measured by comparing *Elymus*-performance in treatment no-HECO with no-COMP. The effect of competition alone is measured by comparing no-HECO with no-HERB and the joint effect is measured by comparing no-HECO with CONT. The CONT and GOOS treatment (i.e. hare and goose grazing vs. hare grazing alone) make it possible to distinguish the effects of hares and geese. It is also possible to measure the interaction between herbivory and competition, because all combinations are present.

Transplantation took place between 13th and 21st April 2001. After one week about 68 % of the transplants at T0 were dead or seemed to be dying (and this percentage would increase with time, see figure 4a), so it was decided to set up 35 blocks at T1, where environmental conditions are less harsh. In the same week 5 extra blocks were created at T2 and T3. Every two weeks plant survival was scored and the length of the longest green sprout was measured up to the nearest mm. After transplanting the first and second leaf of most plants died. Therefore, the first datapoint is the length of the third leaf. Simultaneous with the measurements the no-COMP and no-HECO treatment were restored if necessary, i.e. removing new neighbour plants and putting driftline material around the transplant.

On 12th of May all plants received about 0.2 liter water to prevent them from dying, because the weather was very dry (25° C and no rain for already 2 weeks).

The plants were harvested between 17th and 19th July 2001. Aboveground and below ground biomass were separated. Aboveground parts were separated in leaf and stem material. All biomass samples were dried for 48 hours at 70 ° C and weighed. During harvesting, the total number of ramets per plant was counted.

Measurement at experimental plots

On 5-7 June direct neighbour plants of the no-HERB, CONT and no-GEES treatment were identified. A ring (16 cm in diameter) was placed around the *Elymus* transplant and the 3 main "neighbours" (with the highest abundance) within the ring were noted down; plant species, dead material or bare soil. The plant species are listed in table 1.

Plant height around the *Elymus* seedlings (with the same treatments) was estimated with a styrofoam disc (19 cm in diameter, 20 g) falling on a calibrated cane. The disc rests on the mean vegetation height.

On 12th of July 2001 (a half-cloudy day) light intensity at the soil was measured. Per transect 10 measurements and one calibration measurement were done between the plots of the main experiment. One measurement consisted of 10 numbers from light cells that were put one after another on a stick, which laid on the ground. A reference lightcell was held above the vegetation. Light fallen on the reference cell was taken as 100 % and the numbers the measurement-cells gave, were converted to percentages of light penetration compared to the reference cell.

Grazing pressure

Dropping density is commonly regarded as a proper estimate for goose grazing pressure (Olff, 1997; Owen, 1971) and the actual number of hares (Langbein, 1999).

To determine dropping density 20 dropping plots of 4 m^2 were established at the four transects, near to the experimental plots (see also Drost, 2000; Kuijper, unpublished results). They were marked with a small bamboostick (20 cm high), to which hares are not extra attracted (Kuijper, unpublished results). Immediately after positioning, these plots were cleared from geese and hare droppings. The plots were checked for droppings of those herbivores every week in April and May and every two weeks in June and July. During dropping counts a rope of 1,13 m. was used, to get a circle of 4 m^2 with the stick as the centre. On 2nd of June the experimental plots were inundated by seawater and droppings were washed away, so the next count was not valid. Dropping numbers were transformed to droppings per day per m^2.

Besides, while measuring plant height (see main experiment), signs of grazing were recorded.

Clipping experiment

To discover if plant recovery is influenced by the moment of grazing during the season, a small experiment was set up at the field station at Schiermonnikoog. 75 seedlings (8 days old) were planted individually in small plastic cups (5,5 cm high and 3 cm in diameter) and divided in 5 groups. They were watered when necessary. Plant height was measured when the experiment started on 24th of May. There were no differences in the initial values of plant height (one way ANOVA; $F_{4,7} = 0.7$, $P = 0,6$).

Group 1 was artificially grazed (this means, clipped with scissors) after one week, group 2 after two weeks, etc. Group 5 was never clipped. Plants were clipped 2 mm above soil surface. Clipped biomass samples were dried for 48 hours at 70 ° C and weighed. Six weeks after the experiment started, all aboveground plant material was harvested, dried and weighed.

Statistical analyses.

Blocks 1 – 30 of the main experiment were used to gather plant performance data and to determine survival all 35 blocks were used. The data of shoot biomass, (neighbour) plant height, number of ramets and the clipping experiment were analysed with a one way-ANOVA and a Tukey-test, so treatments and transects could be compared.
Logistic regression was used to analyse survival.

3. *RESULTS*

Grazing pressure

Goose- and haredroppings were counted at T3, T2, T1 and sometimes at T0. In figure 2 dropping density per day per m^2 is shown. It is clear that in April and the first week of May, most goosedroppings are found. In May less goosedroppings were found in the plots. After 31st of May no more goosedroppings are counted. Geese seem to prefer T2 to graze on, especially in April. Geese seem to graze in same numbers at T1 and T3. Later on the difference in dropping densities between these transects is almost gone. At T0 geese almost never forage; dropping counts are very low. The same pattern in goosedropping densities was found in 2000 (D. Kuijper, unpublished results).
The number of haredroppings per day per m^2 fluctuates more as is shown in figure 2b. The numbers drop at T3, T2 and T1 from half May. It is very clear that hares also prefer to graze at the vegetation at T2. T3 and T1 are less favourite, and almost no hares graze at T0. In 2000 T2 also had the highest grazing pressure and T3, T1 and T0 had lower, but about the same numbers (D. Kuijper, unpublished results). This means that hares do graze at T0, which can not really be concluded from above-mentioned results.

During the experiment signs of grazing at the transplants were recorded, except with the harvest. The percentage of (partly) grazed transplants per transect and treatment are given in table 2. At T3 and T2 grazing was low at control-transplants. The no-COMP treatment is more grazed than its matching control treatment, although this is not really true for T0.

Transect	**T3**		**T2**		**T1**		**T0**	
	Cont	**no-comp**	**cont**	**no-comp**	**cont**	**no-comp**	**cont**	**no-comp**
2-May	0	14	0	3	31	33	X	X
9-May	0	21	23	0	14	17	18	20
17-May	0	10	4	12	7	13	X	X
30-May	0	0	0	4	11	3	25	25
14-Jun	0	4	0	11	0	0	X	X
3-Jul	0	0	0	25	0	0	0	0

Table 2: *Percentages of grazed transplants over time (X = no data).*

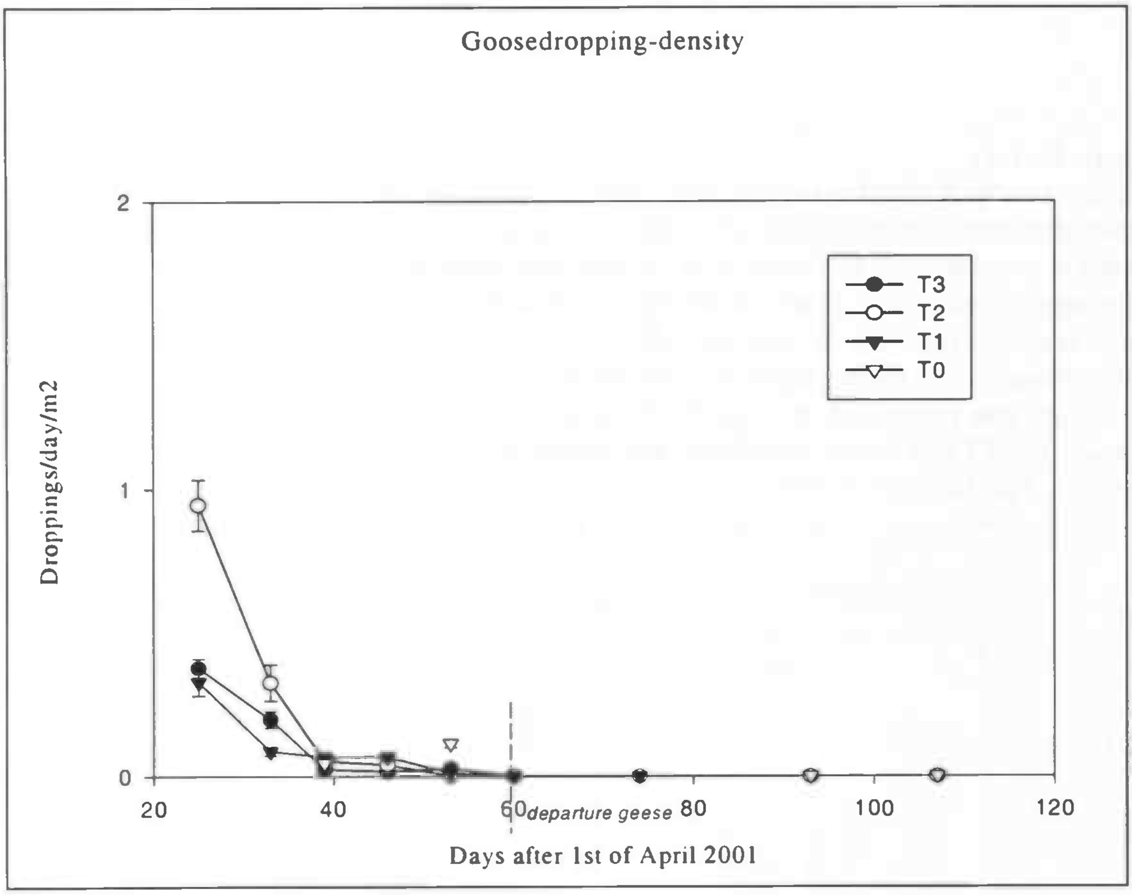
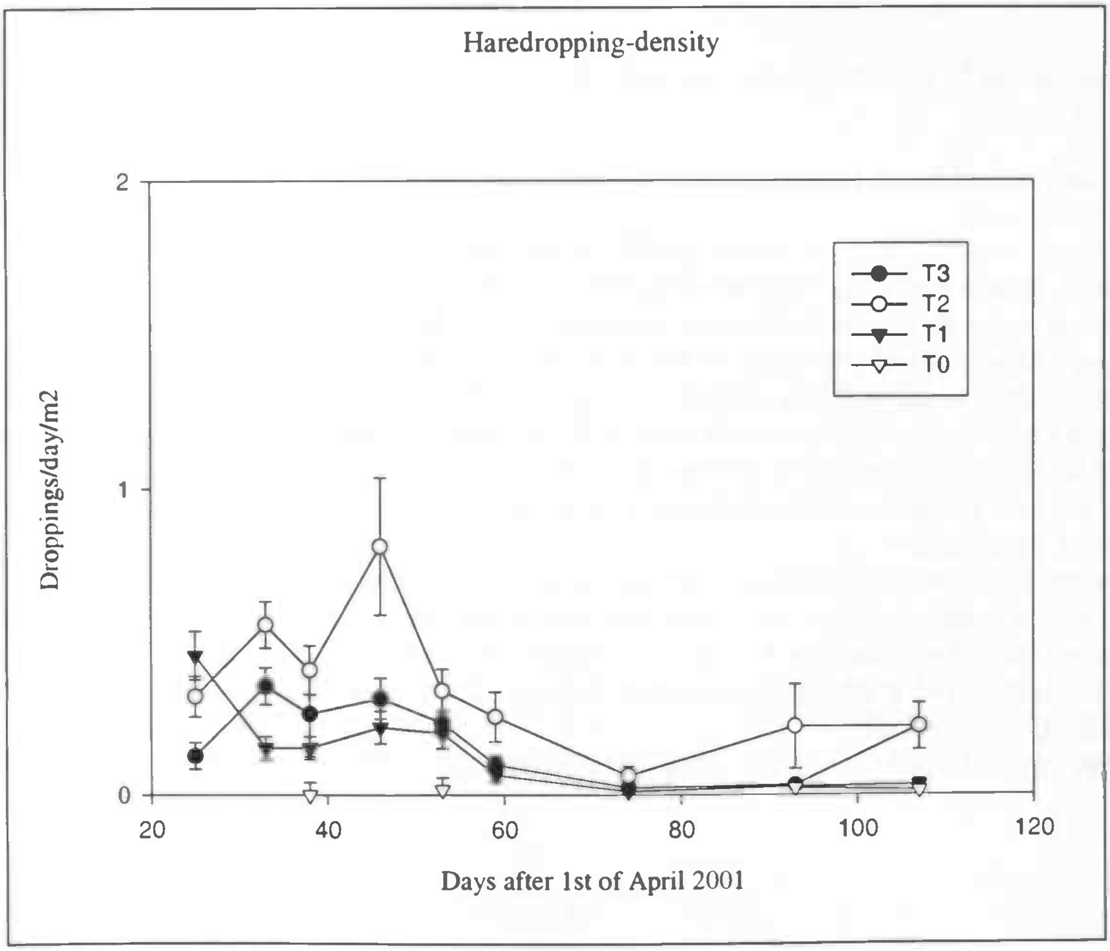


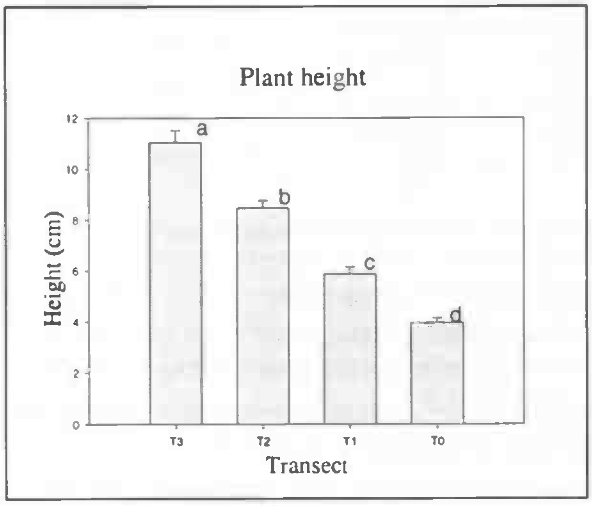
Figure 2a and b: Goose- and haredropping densities for all transects, counted during the experimental period. Geese departure is indicated with a dashed line.



Abiotic factors

In table 1 several abiotic factors, that play a role at the experimental sites, are listed. During this experiment height of neighbouring plants and light intensity at the earth surface was measured. In figure 3a it is clear that plant height increases with age of the salt marsh. Surrounding plants at T0 are smallest and plant height increases to T3. All transects differ significantly (one way-ANOVA; F_{262}: 94.69, *P*: 0.000).

Light intensity was measured to say something about light competition. The percentage of sunlight that penetrates through the canopy increases from T3 to T0. The differences between T3, T2 and T0 are significant and between T1 and T0 almost (figure 3b;one-way ANOVA; F_{39}: 34.40, *P*: 0.000).



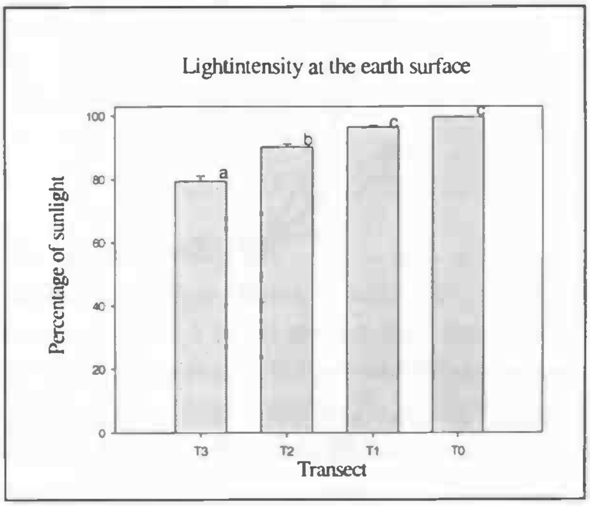


Figure 3a and b: Plant height and light intensity at the surface at the experimental sites measured for all transect.

Parameters of plant performance

Plant survival

In figure 4 (a-d) plant survival is given. Overall survival was highest at T1. There's no almost difference in survival between the treatments. At T2 survival was intermediate. Also at this site the no-herbivores treatments show best survival, and also the control group. About half of the plants in the no-COMP treatment died. Plants at T3 also show high survival rates, with the exception of no-COMP. Most plants died at T0 and there the whole no-COMP treatment didn't survive. Treatments without herbivores (no-HERB and no-HECO) had highest survival rates at all sites.

At T0 and T3 herbivores significantly lower survival (*P* = 0.05 and 0.04) and at T2 almost significant.

Competition is not a significant mortality factor for each transect.

All plants were inundated on 2 June with salt water due to extremely high tide (1.75 m above Mean High Tide) for 4 - 6 hours. After the inundation (day 63) many plants died in all treatments and at all transects (except T1), especially the no-COMP treatments decline drastically in number.

After day 70 (8^{th} of June) most living plants stayed alive until the end of the experiment.

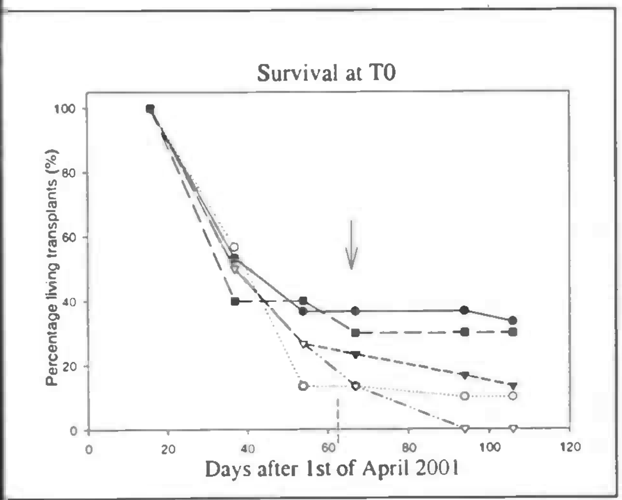


Figure 4a

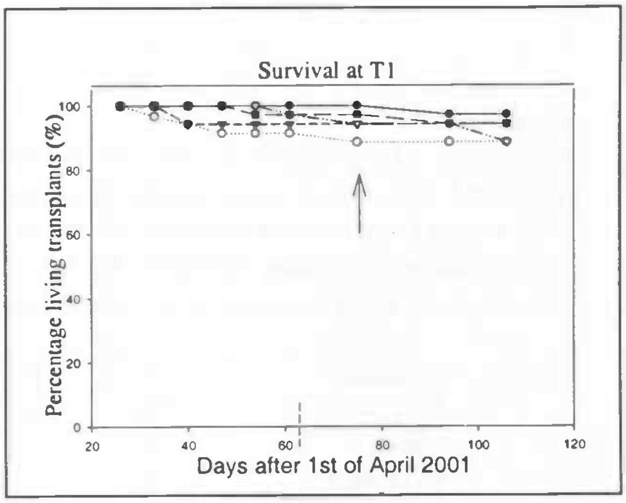


Figure 4b

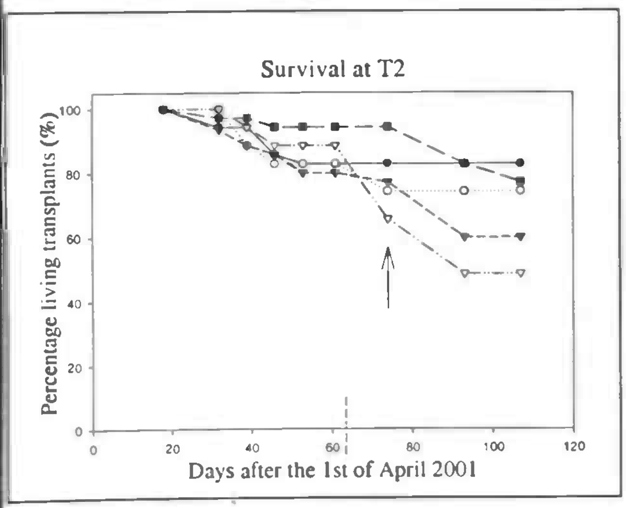


Figure 4c

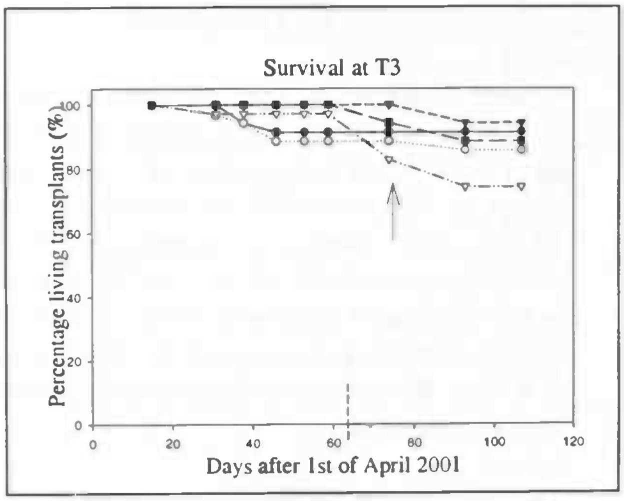


Figure 4d

Figure 4a, b, c and d: *Percentages of seedling survival during the experiment at T1, T2 and T3 for all treatments (▼ no herbivores ○ control. ● no geese ▽ no competition, ■ no herbivores and no competition). The inundation is indicated with a dashed line on the x-axe and removal of the goose cages with an arrow.*

Plant height

Right after planting (T1 en T2) or one week later (T3 and T0) total plant height was measured. The mean plant height (± standard deviation) was 120 mm ± 24.0 and there were neither differences in initial plant height between transects nor between treatments in one transect (one way ANOVA, F_{572}: 1.366, *P*: 0,137).

In table 3 the final sizes (n) of all experimental groups are presented (out of 30 blocks).

Transect	**T0**	**T1**	**T2**	**T3**
no-HERB	10	29	24	27
CONT	3	27	22	25
no-GOOS	4	29	17	28
no-COMP	0	26	14	22
no-HECO	9	28	22	27

***Table3*: Group sizes of all treatments at harvest.**

Group sizes of the treatments at T0 are too small to do serious statistics with.

During the experiment plant growth was followed. Figure 5 (a-d) shows that transplants differ remarkably (and all significant, one way- ANOVA; F_{392}: 80.0, *P*: 0.000) in sprout length between transects. At T3 they always have the longest sprouts, in all treatments, although the no-HECO treatment at T2 catches up in the end. At T0 plants stay very small.

Around Aprilday 60 (30th of May) differences between treatments per transect become visible, except for T1 (only after day 100, which is 9th of July). Between Aprilday 60 and 80 (19th of June) a stagnation or even a decline can be seen at all transects in the sprout length for the no-COMP treatment. The five treatments show about the same pattern at T3, T2 and T1 during the experiment. There's never a significant difference between the treatments no-HERB, CONT, no-GOOS and no-COMP in sprout length, but transplants in the no-HECO treatment differ significant from those. At T1 the differences between these four treatments seem to be smallest and they become larger at T2 and are maximal at T3. At T0 there is no significant difference between the no-HERB, no-GOOS and no-HECO treatment.

Above ground biomass

The results of the total above ground biomass measurements are depicted in figure 6. The amount of produced biomass during the experiment is highest at T3. This site differs significantly from the others ($F_{394} = 8.25$, $P = 0.00$), whereas these don't differ from each other. All sites show the same pattern. The no-HERB, CONT and no-GOOS treatments produce fewest biomass and they do not differ significantly in biomass within one transect (signs for significance are in the graph). The treatments without neighbour plants (no-COMP and no-HECO) produced significantly more biomass, except for T0, and partly T3 and T1. No-HECO plants always have more biomass than no-COMP (which is not so clear for T0).

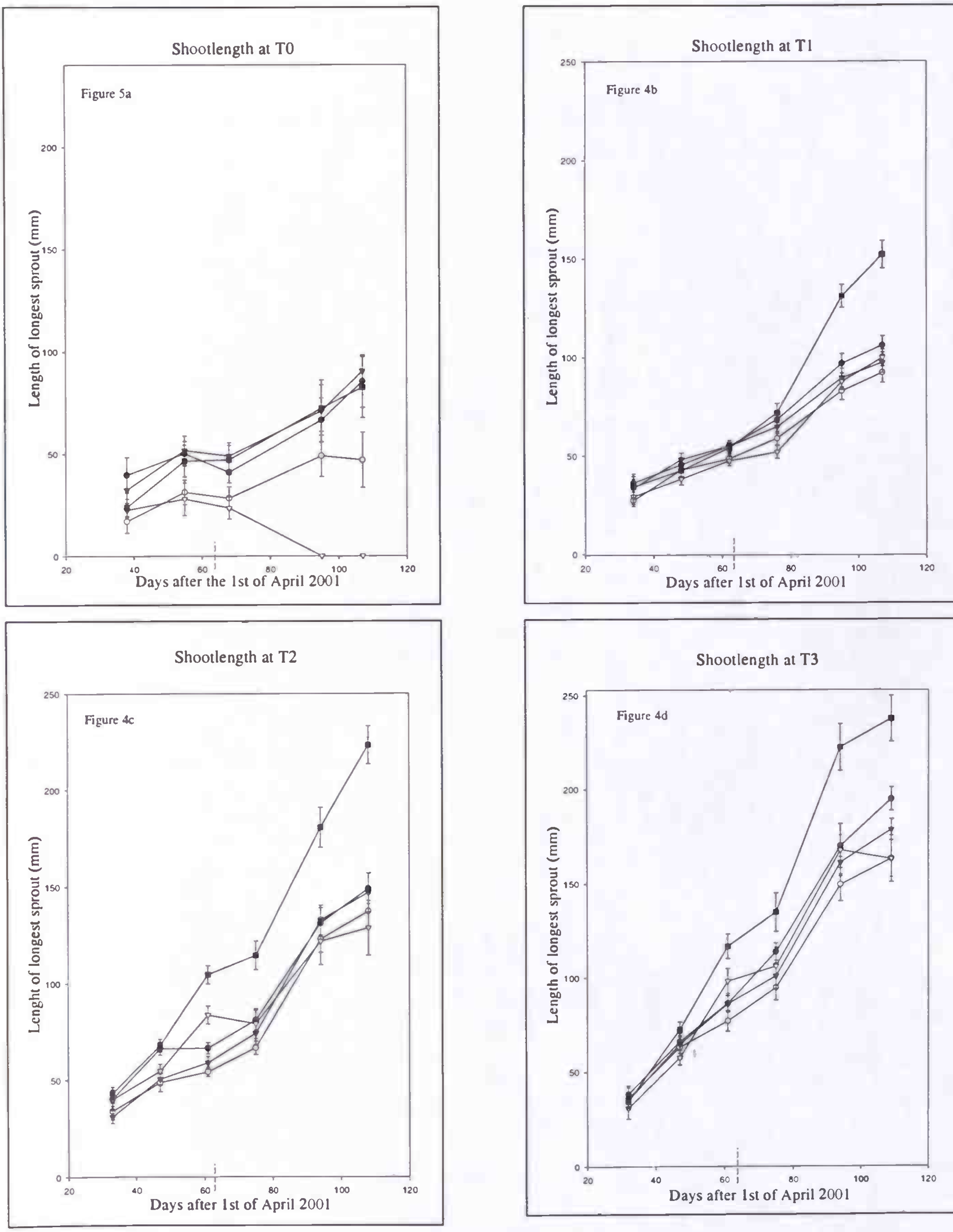


Figure 5 a, b, c, and d: *Shoot length measured during the experimental period at every transect for all treatments (▼ no herbivores ○ control. ● no geese ▽ no competition, ■ no herbivores and no competition). Inundation is depicted with a dashed line in the x-axe.*

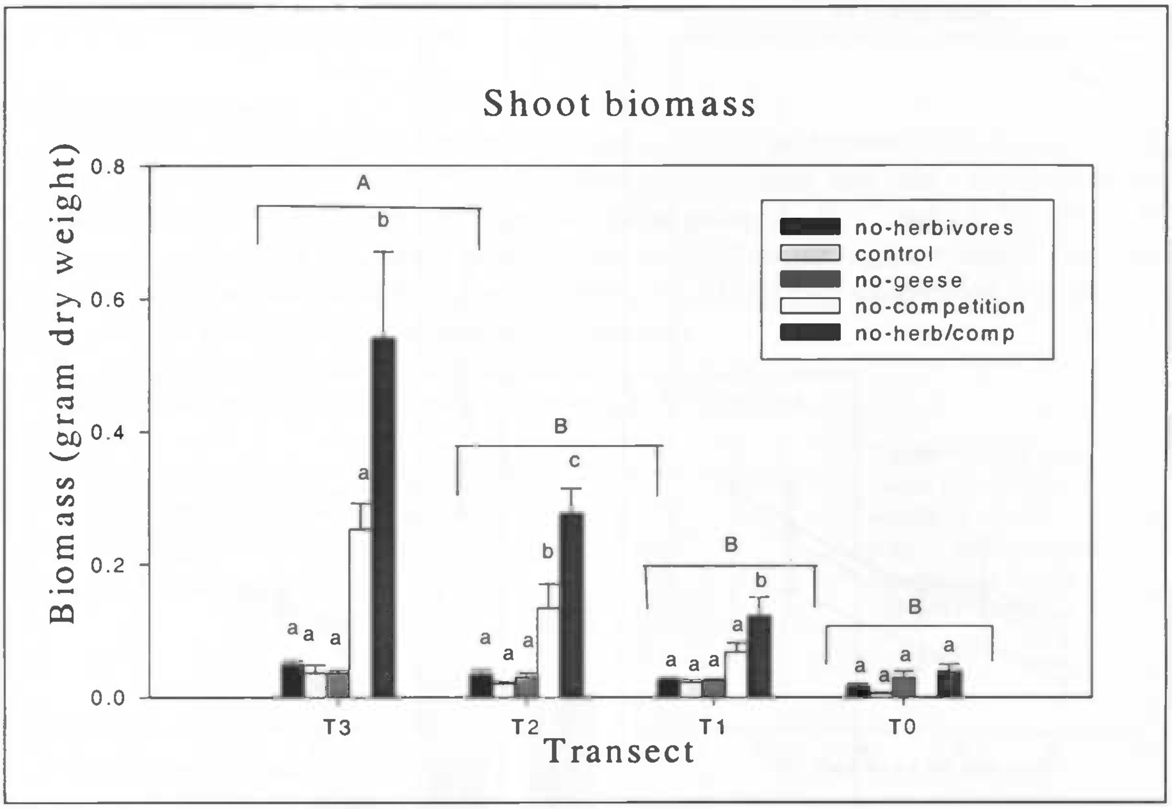


Figure 6: *Total amount of above ground produced biomass at every transects for all treatments. Differences between and within transects are indicated with letters.*

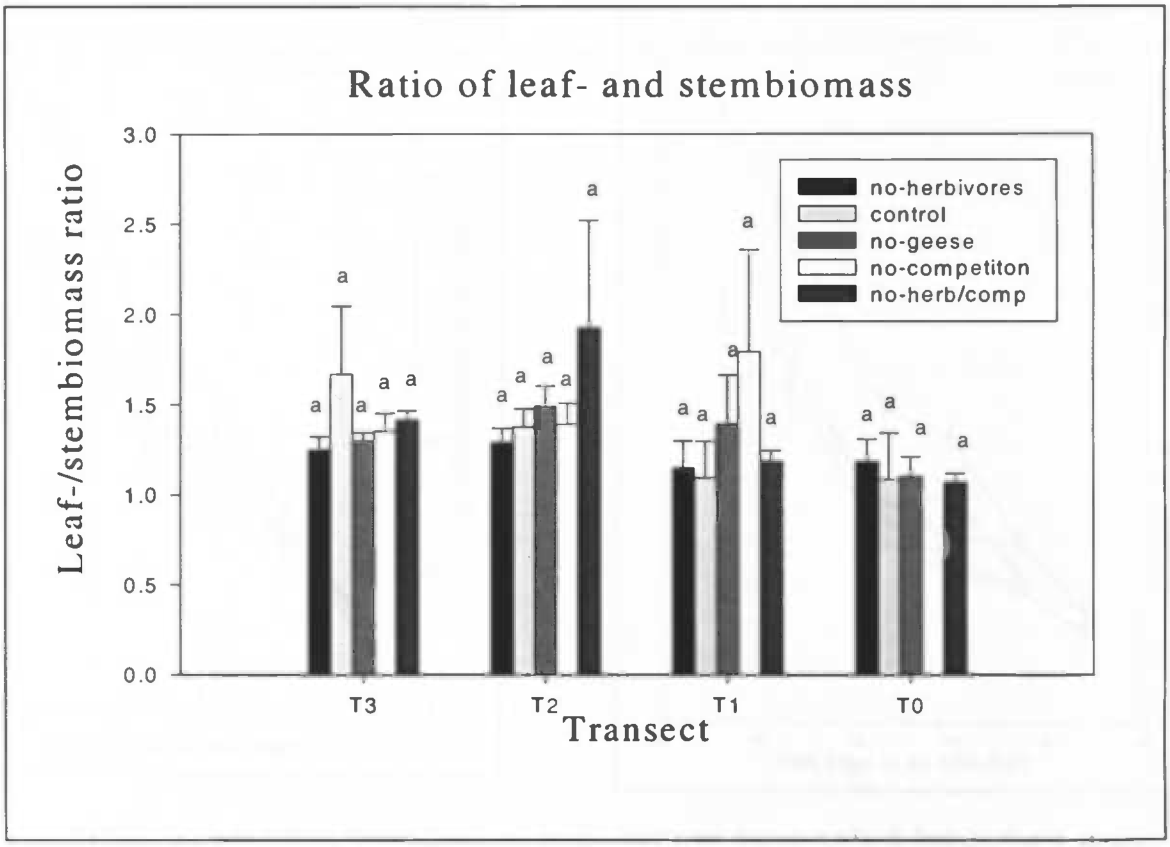


Figure 7: *Ratio between leaf and stem biomass at every transect and for all treatments.*

It is possible that competition and/or herbivory influences the allocation pattern of a plant. The ratio between produced leaf and stem biomass gives and indication about possible change in allocation pattern and is given in figure 7. Almost all treatments at the four sites have the same leaf/stem-biomass ratio and there are no significant differences between or within transects.

Number of ramets

Figure 8 shows the total number of ramets per plant. The number of ramets produced increases significant with age; most ramets were produced at T3 (significance is given in the graph). Each transect shows the same pattern, except for T0. Plants with neighbours produced about one ramet. Plants without neighbours in contrast always produced significantly more ramets (except at T0).

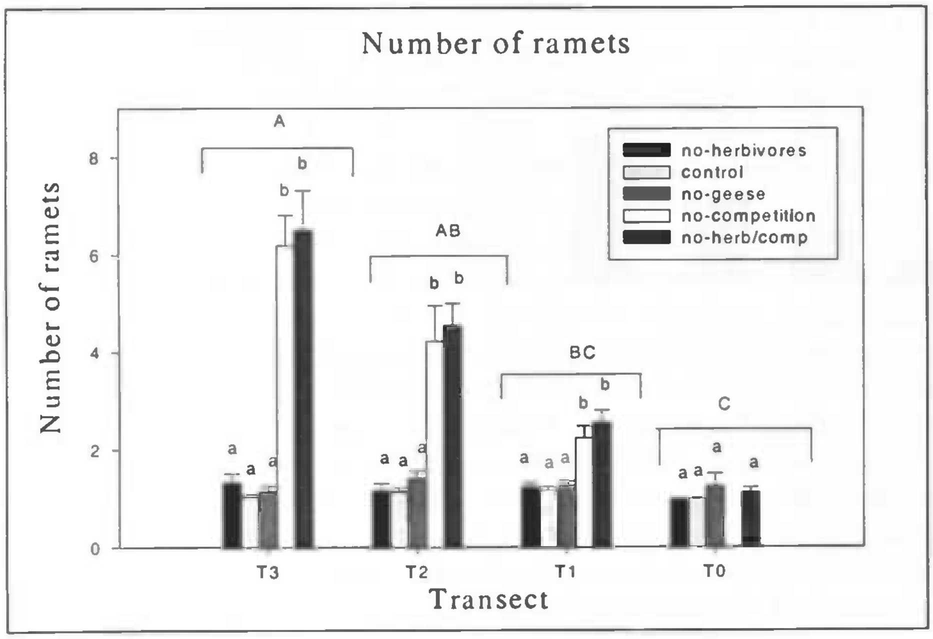


Figure 8: *Mean number of ramets produced per transplant for every transect and all treatments (significance is indicated with letters).*

Clipping experiment

Figure 9 shows that the four treatments that were clipped at different age, produced the same amount of biomass during the experiment, i.e. before and after clipping taken together. There's no significant difference between group A, B, C and D. Treatment E (the control group, that was never clipped) has a significantly higher biomass than the clipped groups (one-way ANOVA; $F_{73} = 10.960$, $P = 0.000$) The subdivision in produced biomass before and after clipping is shown in the bars.

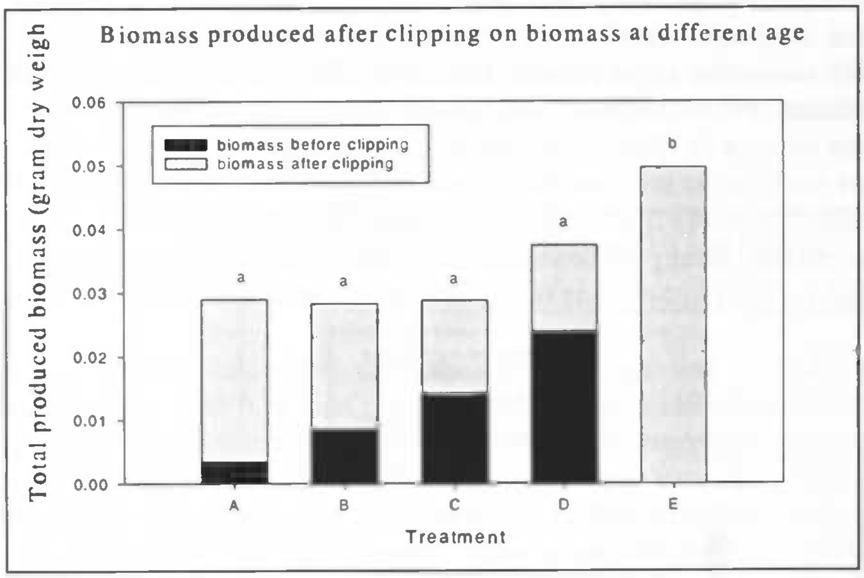


Figure 9: *Total produced biomass by seedlings after clipping at different ages. Significance is indicated with letters.*

4. DISCUSSION AND CONCLUSIONS

Productivity and survival

As is already mentioned in the introduction the salt marshes on Schiermonnikoog represent a productivity gradient. The highest nitrogen concentrations are found on the oldest salt marshes (Olff, 1997, Van Wijnen, 1998). This phenomenon is also clearly visible in the results of the current experiment. Produced above ground biomass is lowest at T0 and increases with age. The production of ramets is also dependent on the nitrogen availability, as the number of ramets increases with age. So, the differences in biomass can almost totally be explained by the differences in the number of produced ramets. Plant length from the no-HECO treatment is significantly higher for all transects, which also is very likely caused by the highest nitrogen amount.
The effect of nitrogen content on biomass and ramets is overruled by competition. The trend for these parameters to increase with successional age is only seen in the treatments without competition. Dormann (2000), who did a similar experiment on Schiermonnikoog with other species, also reports this phenomenon.

Survival of the transplants shows a different pattern. T1 has highest survival rates, closely followed by T3. T2 is intermediate and the most severe site for transplants to grow is T0. The outcome may seem a bit curious, but one can see two optima at T3 and T1 in survival percentage and T2 as minimum in between. At T3 plants may survive better due to high nitrogen amounts. At T1 facilitative effects of neighbours (i.e. protection to environmental conditions like wind or solar radiation) and low competition cause higher survival (Van der Wal, 2000b). Both these factors are present to a lesser extent at T2; facilitating plants become each other's competitor, because less light is available. Besides, highest herbivore density occurs at this site. So, survival is lower.
T0 is the first stage of a succession range and abiotic conditions are expected to be most extreme. Plant density is lower and the lack of sheltering by neighbours make it hard to survive (Van der Wal, 2000b). Besides, *Elymus* is known to be susceptible for high stress habitats with low nutrient concentration (Bockelmann, 1999), so this site is not very suitable for *Elymus* to grow.

Competition

Competition is a strong negative factor in the production of biomass. Surrounding plants reduce the amount of biomass *Elymus* seedlings produce.
At T3, T2 and T1 plants without neighbours produce significantly more biomass, even 6 (no-COMP) or 12 (no-HECO) times more than the control plants at T2 and T3 and 3 or 6 times more at T1. Biomass at no-COMP is only significant at T2, but P is 0.051 at T1. Treatments do not differ in biomass at T0.
Vila (1996), Reader (1998), Bonser (1995), Dormann (2000a), Van der Wal, (2000b), Ellison (1987), Taylor (1997) and Mulder (1995) also report this reduction in biomass with competition, but Myster (1989) and Taylor (1997) mention no effect.
Removal of neighbour plants did not influence the ratio between leaf- and stem biomass. It would be expected that plants facing light competition would invest more in stem tissue, but all plants at all sites have the same allocation pattern.

As soon as competition is absent, *Elymus* seedlings start to expand and produce 2, 4 or even 6 times more ramets (resp. T1, T2 and T3). Surrounding plants hinder the spread of *Elymus* transplants. In 2000 transplants at T1 showed the same pattern in number of ramets (Wells, 2001). At T0 no differences in number of ramets are measured and light intensity at the surface is high, so competition for light doesn't seem to play an important role at that site (see also Huisman, 1999; Olff, 1993).

Plants with neither neighbours nor herbivory grew significantly higher, which is not the case for only no-neighbours. The latter treatment turned out to be not perfectly designed (see below), but it is clear that competition has a negative effect on plant height. A similar experiment at T1 in 2000 had the same result (Wells, 2001), but Maron (1997) reports a decline in shoot length with this treatment.
Elymus seedlings didn't really have higher survival rates when not surrounded by other plants; so competition is not really a strong mortality factor for *Elymus* seedlings. In 2000 Experiments with other plant species neighbour plants reduce survival (Maron, 1997; Dorman, 2000b; Rachich, 1999; Van der Wal, 2000b; Ellison, 1987).

Light intensity decreases significantly with age and average plant height increases significantly, which is also observed by Huisman (1999) and Olff (1993). So, it is very likely that competition for light is more and more important factor as the marshes become older. In fact, the reduction in biomass and length caused by competition is largest at the oldest site (T3). It's a pity that the whole COMP-treatment died at T0, but it still seems that competition for light doesn't play an important role at T0. Because of the low nitrogen concentration at young stages (Olff, 1997), competition for this source is expected to be highest there.
So, Tilman's theory (1988) can be cautiously applied on the productivity gradient on Schiermonnikoog; this means that at T0 competition for nutrients is most important and competition for light becomes prominent with increasing age (and productivity). However, the effect of competition for nutrient could not be detected with the design used for this experiment, which only eliminated competition for light.

It is quite common to remove neighbours in competition experiments (Aarssen, 1990), but Campbell (1991) questions this method. Roots of removed neighbours are usually not (completely) gone and will decompose. This results in an increase in below ground nutrient concentration, especially at sites with low fertility and low biomass. Consequently, the increase in target plant growth due to neighbour removal may be greater at sites with low biomass, due to differential nutrient release from decaying roots. However, in this experiment, the increase in growth (i.e. biomass) is highest at the most fertile site with highest biomass (T3) and declines with decreasing fertility and biomass. So, rectifying for differential nutrient release among sites would only make the difference in response to neighbour removal between high and low biomass larger.

Herbivory

The highest goosedropping densities occur in April and the first week of May. In these weeks the number of geese present on the marshes is highest (J. Stahl, personal comment). In May less goosedroppings grazing signs are found. This can be explained by the departure of the Barnacle geese, which mainly graze on *Festuca rubra*. The remaining Brent geese rather eat Puccinellia maritima on the lower salt marsh. After 31st of May, dropping density has dropped to zero. This perfectly correlates with data obtained from goose observations on the salt marshes. According to those data, the Brent geese left the island between 27 and 29 May (C. Rothkegel, personal comment).
Also numbers of hare droppings decreases from half May. A possible explanation is that the vegetation is getting less palatable. It is not known where they graze instead (D. Kuijper, personal comment).

In general, grazing pressure is highest at T2 and continues longest, according to dropping counts and percentages of grazing signs. T1 and T3 are equal in grazing pressure. Herbivory is most present at intermediate level of plant standing crop. This is consistent with previous studies (Van de Koppel, 1996; Drost, 2000; Kuijper, unpublished results). As table 2 shows many transplants at T0 showed grazing signs, whereas dropping densities suggest that herbivores are almost absent at this site. Presumably, the small number of herbivores present is responsible for all the grazing. Plant density is very low at T0, so the chance for a plant of being grazed is higher.
Oksanen's (1981) theory, which says that herbivory intensity increases with increasing productivity, is not supported with the results from the current experiment.

Herbivory has almost no effect on the amount of produced biomass, although hares and geese are present at the experimental sites and transplants are grazed. The differences in biomass between no-HERB, CONT and no-GOOS are not big and not significant within each single transect. Only some other investigations also name no effect of herbivory (Vila, 1996; Dormann, 2000a; Taylor, 1997), but most other researches actually mention a decrease in biomass with the presence of herbivores (Dormann, 2000a; Bonser, 1995; Myster, 1989; Van der Wal, 2000b; Reader, 1998; Mulder, 1998; Taylor, 1997). The different treatments do not differ significant in ratio between leaf- and stem biomass. It would be expected that plants that are grazed would be richer in stem biomass, because especially the leaves are eaten, but all plants at all sites have the same allocation pattern.

Herbivory also doesn't influence the number of produced ramets, because the transplants of the no-HERB, CONT and no-GOOS treatment almost always consist of one ramet, regardless of the site. This also occurred in 2000 at T1 (Wells, 2001). Plant height is also not effected by herbivores, although the seedlings were certainly grazed. This is different from the experiment in 2000 at T1, when herbivory reduced plant height significantly (Wells, 2001).The seedlings used for that experiment were marked with plastic sticks and plastic markers, which could have made them more visible for grazing herbivores.

The amount of removed biomass by herbivores was not recorded during the experiment. It is very likely that this amount was very small and therefore not visible as a significant

difference. Besides, many control plants were never grazed (probably due to protection by neighbours) and thus performed the same as no-herbivore plants.
However, survival is effected by herbivory. Survival rates of treatments without herbivores are always higher than with, although the difference is not big. At T0, this negative effect is largest. It is very possible that herbivory is a strong mortality factor there, enhanced by the severe abiotic conditions. Wells (2001) did a more or less similar experiment in 2000, at T1, and reports that herbivory was a strong mortality factor. The same is also concluded for other species (Myster, 1989; Maron, 1997; Ellison, 1987; Van der Wal, 2000b; Rachich, 1999). Only Dormann (2000b) mentions no effect.

The no-hares and geese (i.e. no-HERB) and the no-GOOS treatment do not differ in biomass and plant height, but there are some differences in survival. At T3, T2 and T0, the number of living no-GOOS transplants declines, when they become exposed to hare grazing (day 75). It is unlikely this is caused by hares, because the number of control plants (which are also exposed to hare grazing) stays constant. The results don't make it really possible to draw conclusions about the differences between hares and geese grazing. They both must be responsible for the grazing of the transplants during the experiment, because droppings from hares as well as geese are found.

Van der Wal (2000b) mentions that competitive interactions among plants may change, when herbivores are excluded. In this experiment, the exclosure (i.e. cage) was very small, so the effect on competition with neighbour plants can be regarded as nearly nil. Herbivores were still able to graze on the direct neighbours of the transplants.

The clipping experiment was done to test if a herbivore peak during the first weeks of the experiment would have a more negative effect on the young *Elymus* transplants, than later in the season, when the plants are more grown. If seedlings are clipped very early (one week after transplantation) they will produce the same amount of biomass during 7 weeks as seedlings that are clipped after 4 weeks. This suggests that it doesn't matter at what age the *Elymus* seedlings are clipped. The control group produced significantly more biomass during the experiment. So, clipping still has a negative effect on growth and reduces the production of biomass. The same conclusion was drawn from a greenhouse experiment with *Elymus* (Dubbeld, 2000).
The seedlings grew under far better conditions than the ones on the salt marshes (potting compost, enough water, and almost no competition), but the outcome of the experiment may still be applied in the field. Transplants did survive grazing in the field (personal observation) and the clipping experiment shows that it is very likely that time of grazing had no large effect. The difference between grazed (CONT) and not grazed (no-HERB) is very small and non-significant, in contrast to the clipping experiment. This might be due to the way plants were clipped (2 mm above soil level), which might have made the differences larger.

Interaction

Many studies report about the effects of competition and herbivory individually as well as together (Reader, 1998; Dormann, 2000a; Ellison, 1987; Maron, 1997; Taylor, 1987; Myster, 1989; Rachich, 1999). These researchers did neighbour removal and herbivore exclosure experiments at the same time, but only some of them considered a possible interactive effect on biomass of both factors.

Bonser (1995) and Rachich (1999) divide interactive effects in two groups; a) independent, herbivores (or neighbours) would reduce the biomass by the same amount regardless of whether neighbours (or herbivores) are present and b) interactive, the absence of herbivores (or neighbours) enhances or diminishes the effect of competition (or herbivory). Independent effects are found in the studies done by Maron (1997), Dormann (2000a), Taylor (1987), Myster (1989) and Reader (1998).

Interactions between competition and herbivory (positive or negative) are reported by Dormann (2000a), Vila (1996), Rachich (1999) and Van der Wal (2000b).

The difference in biomass between no-HERB and CONT is caused by grazing, which has to be the same relative difference between no-HECO and no-COMP, if an interaction between herbivory and competition is absent. Actually, the latter difference is always bigger. This could be an indication for an interactive effect, e.g. the no-COMP treatment is relatively more grazed than a control plant (which in fact is true, table 2), because of the absence of facilitative effects of neighbours (e.g. *Elymus* performs better with *Limonium vulgare* as neighbour (Wells, 2001). However, others state that experimental removal of neighbours simultaneously reduces food available to herbivores, so less grazing and maybe better performance (Van der Wal, 2000b).

A more plausible explanation for this difference is that the no-COMP treatment didn't function as well as planned. Survival rates of this treatment are always lowest at every experimental site. Besides only no-COMP transplants show a stagnation or even a decline in plant height after day 63 (inundation) which is also observed by Wells (2001) at T1 in 2000. Apparently, the no-COMP treatment was more exposed to severe abiotic factors (see also Rachich, 1999) like higher temperatures and draught (sometimes the driftline material was blown away by the wind) or salt stress (caused by the inundation). However, competition is still eliminated, because the no-COMP and no-HECO transplants don't differ in the number of ramets. Obviously, this parameter is less susceptible to the harder conditions.

The results of this treatment are less useful and unfortunately, real calculations to reveal a possible interactive effect of competition and herbivory in this experiment, could not be done, due to no-COMP design.

Indices

The Relative Competition Index (RCI) and the Relative Competition-Herbivory Index (RCHI) are calculated for each transect as described in Dormann (2000a) and are given in table 4. Unfortunately, it is not possible to calculate Herbivore Interaction Indices (RHI), because of the less useful COMP-treatment. From the differences between RCHI's and RCI's a "RHI" is calculated, which assumes no interactive effect between herbivory and competition.

Transect	T0	T1	T2	T3
a. RCI	0.585	0.786	0.876	0.909
b. RCHI	0.851	0.812	0.924	0.932
"RHI" (b-a)	0.226	0.026	0.048	0.021

Table 4: *The relative competition index, relative competition-herbivory index and the relative herbivory index (calculated from the two former ones). RCI = (no-HECO – no-HERB)/ HECO*
RCHI = (no-HECO – CONT)/ HECO; numbers of biomass are used.

The RCI (RHI) shows to what extent the reduction in biomass is caused by competition (herbivory). At all transects competition has a stronger negative influence than herbivory. The numbers in the table show that the reduction caused by competition becomes larger with ageing of the marsh. This indicates that competition for light is more and more important with progressing succession, which was concluded before.
The largest reduction in biomass (although not significant) caused by herbivores occurs at T0, herbivore density is lowest there. Those few herbivores graze on the few edible plants that occur at T0 and the negative effect of grazing on plants is enhanced by harsh abiotic conditions. That's why grazing at T0 causes such a large reduction.
The reduction at T2 is about twice as high at T3 and T1. This perfectly coincides with dropping counts, that also demonstrated that herbivores prefer to graze at marshes of intermediate age.

Ecology on salt marshes

As is already briefly mentioned in the introduction long term exclosures are present on the salt marshes. In 1993 transects T1-T5 were established and in 1994 transect T0. Primary succession at these sites was estimated to have progressed for different time periods. At each transect four large exclosures were placed, two at the low marsh and two on the high marsh, to investigate the effect of herbivores on the vegetation. Each exclosure consists of a part not accessible to geese and hare (full-exclosure) and the other part not to geese (goose-exclosure).
Van der Wal (2000a) and Kuijper (unpublished results) conclude that the abundance of late successional species is higher inside the full-exclosure at young salt marsh stages. The vegetation in the control treatment and in the geese free treatment do not differ. So hare grazing effectively slows down succession.

Since 1999 *Elymus* is reported to occur inside the exclosure at T0 in low abundance. Outside the exclosure *Elymus* isn't found (D. Kuijper, personal comment). As T0 is a very young salt marsh, one would expect an increasing abundance of *Elymus* in the exclosures with age, because of rapid clonal spreading during succession and increasing

nutrient levels over time (Weeda, 1994). This does not happen. In fact, at T1 and T2, less adult *Elymus*-plants than expected are present. At T3, *Elymus* starts to take over and at T5 (100 year) it is almost the only species present (personal observation D. Kuijper).
It seems a window of opportunity for *Elymus*-seeds to establish is present at a certain time on the youngest salt marsh. This window has passed when neighbour plant density increases a little later in succession and this prevents the establishment of *Elymus*.
During the presence of this window of opportunity, herbivores have a negative impact on establishment. They reduce survival and biomass to a reasonably high extent. These negative effects of herbivores during the presence of the window and of competition by other species thereafter, lead to the very low abundance of *Elymus* outside the exclosures.
Besides this direct negative impact by herbivores (i.e. grazing on very young seedlings) as this experiment demonstrated, herbivores may also prevent seedling establishment at the older stages (from T1) in an indirect way (Myster, 1989). They may change the vegetation to such an extent, that a dense *Festuca rubra* vegetation is formed.
This explains why in T2 almost no *Elymus* can be found inside the exclosure. Before herbivores were artificially excluded, this dense *Festuca* vegetation had already developed and after construction of the exclosures, it was hard for *Elymus*-seed to germinate and establish inside it. Also at T3 *Elymus* has an enormous potential to grow there, but existing neighbouring plants prevent this growing.
Adult *Elymus* plants are known to outcompete other plants very effective (Van Wijnen, 1997; Weeda, 1994), so it is expected that, once well established, the negative effect of competition will decrease en dense *Elymus* swards will be formed. Indeed this is happening at the oldest salt marshes on Schiermonnikoog (Van Wijnen, 1997).

Conclusions and future research
So, in general competition has a remarkable negative effect on biomass produced by *Elymus athericus* seedlings. The stronger competition for light is, the higher the reduction in biomass. Herbivory also reduces biomass, to a much smaller extent. This reduction is largest at the site T0, where even a small impact of herbivores has large effects. At T2 herbivore density is highest. Herbivory and competition have the same effects with other aspects of plant performance, like number of ramets and plant height.
Both competition and herbivory are mortality factors for *Elymus* seedlings, but survival is more influenced by herbivores than by competition.

To test the indirect effects of herbivore grazing during the "window of opportunity", this experiment has to be repeated, certainly at T0. There, a higher number of transplants is necessary, so that enough plants survive and better statistical analyses can be done.
To discover possible indirect effects of grazing, an extra treatment is needed; a larger piece of vegetation, completely exclosed, in which a seedling is planted (see Dormann, 2000b). In this way herbivores are not able to change the surrounding vegetation. Obviously, this is an experiment that has to be done at several stages of the salt marsh and for some years successively

5. *ACKNOWLEDGMENTS*

Without some people this research would have been far more difficult or even impossible to do. I would like to thank Dries Kuijper for his friendly supervising, a lot of help in the field (which made the days pass much faster), transport of the *Elymus*-seedlings and my bike to Schiermonnikoog and use of his computer.
Further, Marlies van der Welle, Conny Rothkegel, Sem de Rooij en Mirjam Hospers; thanks for you help and cosiness in the field, Marlies Kubbinga for the same in the lab, Daan Bos for his useful comments on earlier versions of this report and Simon Verhulst for his help with statistical analyses.
And a last thank-you for the people in "De Herdershut" on Schiermonnikoog, which made my stay pleasant.

6. REFERENCES

Aarssen, L.W. and Epp, G.A., 1990, *Neighbour manipulations in natural vegetation; a review*, Journal of vegetation Science 1, p. 13-30

Bakker, J.P., 1989, *Nature management by grazing and cutting*, Geobotanie 14, Kluwers Academische Publicaties, Dordrecht, The Netherlands

Bakker, J.P., Esselink, P., Van der Waal, R. and Dijkema, K.S., 1998, *Options for restoration and management of coastal salt marshes in Europe*, in: Restoration ecology and sustainable development (ed. K. Urbanska), Cambridge University Press, Cambridge, UK, p. 286-322

Bakker, J.P., 1985, *The impact of grazing on plant communities, plant populations and soil conditions on salt marshes,* Vegetatio, 62, p. 391-398

Bockelmann, A.C., 2000, *The invasion of* Elymus athericus*; an ecological and evolutionary approach*, Introductory essays in funcional ecology, CEES, Haren, The Netherlands

Bockelmann, A.C. and Neuheus, R., 1999, Competitive exclusion of *Elymus athericus* from a high stress habitat in a European salt marsh, *Journal of ecology 87, p. 503-513*

Bonser, S.P. and Reader, R.J., 1995, *Plant competition and herbivory in relation to vegetation biomass*, Ecology 76 (7), p. 2176-2183

Campbell, B.D., Grime, J.P., Mackey, J.M.L. and Jalili, A., 1991, *The quest for a mechanistic understanding of resource competition in plant communities; the role of experiments,* Functional ecology 5, p. 241-253

Dormann, C. and Van der Wal, R., 1998, *Salt-marsh nematodes do not live up their reputation as regulators of plant performance*, PhD Thesis R. van der Wal, Rijksuniversiteit Groningen, Groningen, The Netherlands, p. 59-66

Dormann, C.F. and Bakker, J.P., 2000b, *The impact of herbivory and competition on flowering and survival during saltmarsh succession*, Plant Biology 2, 68-76

Dormann, C.F., Van der Wal, R. and Bakker, J.P., 2000a, *Competition and herbivory during salt marsh succession: the importance of forb growth strategy*, Journal of Ecology 88, p. 571-583

Drost, A., 2000, *The relationship between vegetation succession and cattle grazing with the occurence of Hares on the salt marsh*, MSc thesis, Rijksuniversiteit Groningen, Groningen, The Netherlands

Dubbeld, J., 2000, *Het effect van stikstof, knippen en competitie op de groei van* Elymus athericus *en* Festuca rubra, MSc thesis, Rijksuniversiteit Groningen, Groningen, The Netherlands

Grime, J.P., 1979, *Plant strategies and vegetation processes*, John Wiley & Sons, London, UK

Huisman, J., Grover, J.P., Van der Wal, R. and Van Andel, J., 1999, *Competition for light, plant species replacement, and herbivore abundance along productivity gradients*, in: Herbivores: Between plants and predators (eds. H.Olff, V.K. Brown and R.H. Drent), Blackwell Science, Oxford, UK, p. 239-269

Langbein, J., Hutchings, M.R., Harris, S., Stoate, C., Tapper, S.C. and Wray, S., 1999, *Techniques for assessing the abundance of Brown Hares (*Lepus europeus*)*, Mammal Review, 29, p. 93-116

Leendertse, P.C., 1995, *Impact of nutrients and heavy metals on salt marsh vegetation in the Waddensea*, PhD Thesis, University of Amsterdam, Amsterdam, The Netherlands

Maron, J.L., 1997, *Interspecific competition and insect herbivory reduce bush lupine* (Lupinus arboreus) *seedling survival*, Oecologia 110, p. 284-290

Mulder, C.P.H. and Ruess, R.W., 1998, *Effects of herbivory on arrowgrass: interactions between geese, neighbouring plants and abiotic factors*, Ecological Monographs 68 (2), p. 275-293

Myster, R.W. and McCarthy, B.C., 1989, *Effects of herbivory and competition on survival of* Carya tomentosa *(Juglandaceae) seedlings*, Oikos 56, p. 145-148

Oksanen, L., Fretwell S.D., Arruda, J. and Niemelä, P., 1981, *Exploitation ecosystems in gradients of primary productivity*, American Naturalist 188, p. 240-261

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

Olff, H., Huisman, J. and Van Tooren, B.F., 1993, *Species dynamics and nutrient accumulation during early primary succession in coastal sand dunes*, Journal of Ecology 81, p. 693-706

Prop, J. and Deerenberg, C., 1991, *Spring staging in Brent Geese* Branta bernicla*: feeding constraints and the impact of diet on the accumulation of body reserves*, Oecologia 87, p. 19-28

Rachich, J. and Reader, R., 1999, *Interactive effects of herbivory and competition on blue vervain* (Verbena hastata L.: *Verbenaceae)*, Wetlands 19, p. 156-161

Reader, R.J. and Bonser, S.P., 1998, *Predicting the combined effect of herbivory and competition on a plant's shoot mass*, Canadian Journal of Botany 76, p. 316-320

Shabel, A.B. and Peart, D.R., 1994, *Effects of competition, herbivory and substrate disturbance on growth and size structure in pin cherry* (Prunus pensylvanica L.) *seedlings*, Oecologia 98, p. 150-158

Taylor, K.L., Grace, J.B. and Marx, B.D., 1997, *The effects of herbivory on neighbour interactions along a coastal marsh gradient*, American Journal of Botany 84, p. 709-715

Van de Koppel, J., Huisman, J., Van der Wal, R. and Olff, H., 1996, *Patterns of herbivory along a productivity gradient: an empirical and theoretical investigation*, Ecology 7(3), p. 736-745

Van der Meijden, R., Weeda, E.J., Holverda, W.J. and Hovenkamp, P.H., 1990, *Flora van Nederland*, 21st ed., Wolters-Noordhoff, Groningen, The Netherlands

Van der Wal, R., 1998, *Herbivores and vegetation succession*, PhD Thesis, Rijksuniversiteit Groningen, Groningen, The Netherlands, p. 3-7

Van der Wal, R., Egas, M., Van der Veen, A. and Bakker, J., 2000b, *Effects of resource competition and herbivory on plant performance along a natural productivity gradient*, Journal of Ecology 88, p. 317-330

Van der Wal, R., Van Wijnen, H., Van Wieren, S., Beucher, O. and Bos, D., 2000a, *On facilitation between herbivores; how Brent geese profit from brown hares*, Ecology 81 (4), p. 969-980

Van der Wal, R., Van Lieshout, S., Bos, D. and Drent, R., 2000c, *Are spring staging brent geese evicted by vegetation succession?*, Ecography 23(1), p. 60-69

Van Wijnen, H.J., Bakker, J.P. and De Vries, Y., 1997, *Twenty years of salt-marsh succession on the coastal barrier islands of Schiermonnikoog (The Netherlands)*, Journal of coastal conservation 3, p. 9-18

Van Wijnen, H.J., Van der Wal, R. and Bakker, J., 1999, *The impact of herbivores on nitrogen mineralisation rate: consequences for salt-marsh succession*, Oecologia 118, p. 225-231

Vila, M. and Lloret, 1996, F., *Herbivory and neighbour effects on the sprout demography of the Mediterranean shrub* Erica multiflora *(Ericaceae)*, Acta Oecologia 1146-609, p. 127-137

Weeda, E.J., Westra, R., Westra, Ch. and Westra, T., 1994, *Nederlandse Oecologische Flora*, part V, IVN, Amsterdam, The Netherlands

Wells, T., 2001, *Seedling establishment of the invasive clonal grass* Elymus athericus*; an experimental approach*, MSc-thesis, Christian-Albrechts-Universität, Kiel, Germany