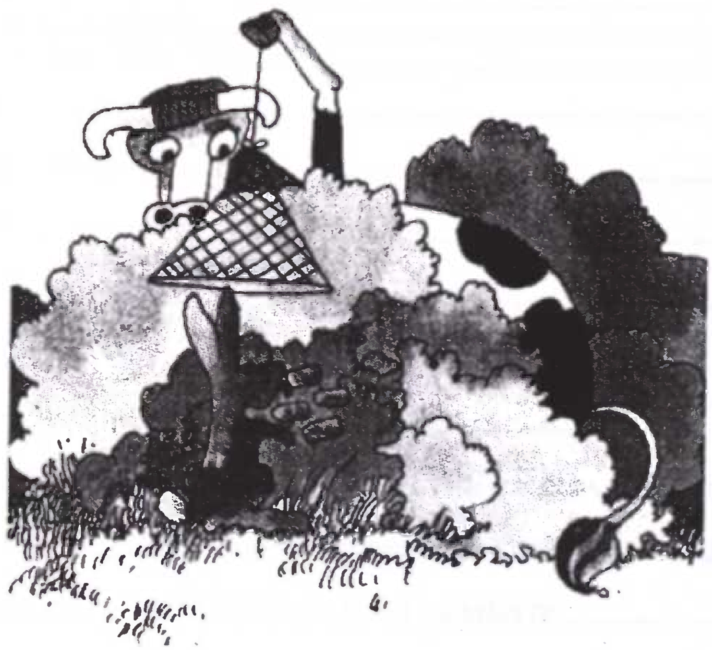
The relationship between vegetation succession and cattle grazing with the occurrence of Hares on the salt marsh



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May 2000

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Abstract

In this study the density of Brown Hares (*Lepus europaeus*) was compared on salt marsh of different ages on Schiermonnikoog. The question was if Hares are evicted by vegetation succession as well as geese are. The differences in Hare density was tried to be explained by differences in vegetation composition and canopy height. To obtain a measure of the Hare density, droppings were counted on all transects. Vegetation relevées were taken and the canopy height was measured to describe the transects. The Hare density was most influenced by the amount of *Elymus athericus* and *Festuca rubra* on the salt marsh. A clear relation between canopy height and Hare densities could not be found. Dropping analysis were performed to establish the diet of the Hares on the different transects. *Festuca rubra* appeared to be the most favoured food plant on all transects with on average 75% of the diet. On the old salt marsh the fraction of *Festuca rubra* was lowest. In these parts the Hares are forced to eat more *Elymus athericus* which is of poor quality. The Hare density showed a peak at the salt marsh of intermediate age. On these transects the fraction of *Festuca rubra* in the vegetation was high and there were some parts with a higher vegetation where the Hares could find shelter. On these transects the fraction of *Festuca rubra* in the diet was the highest. After this peak on the intermediate successional stage the numbers dropped.

Another factor studied was the effect of cattle grazing. Cows seem to facilitate for Hares by reducing the canopy height and making the favoured food plants of the Hares accessible again. In the cattle grazed parts the numbers of Hares were higher as on the ungrazed parts of the same age.

It seems Hares are evicted by vegetation succession as well as geese are.

1 Introduction

The succession of a salt marsh starts with bare, intertidal flats. When dunes are formed close to the mudflat, the mudflat is less exposed to inundation and turbulent water (Olff *et al.* 1997). Hence dissolved clay particles start to sink to the bottom and sedimentation starts. The first plants that start to grow on this thin clay layer are plants that have a high salt tolerance, such as *Salicornia sp.* and *Suaeda maritima.* These parts are still frequently flooded and a lot of sedimentation takes place. Because of this the salt marsh increases in height and the layer of clay gets thicker. This results in a higher nutrient availability. On these early successional stages favourite food plants for Brown Hares (*Lepus europaeus*) and geese (*Branta sp.*) occur, such as *Festuca rubra*, *Puccinellia maritima*, *Plantago maritima* and *Triglochin maritima*. In these stages competition for nutrients is probably the most important factor for determining what plant becomes dominant (van Wijnen & Bakker 1997; Huisman *et al.* 1997). When the salt marsh grows older accumulation of sedimentation takes place and more nutrients become available. Because of this a shift takes place in competition for nutrients to competition for light (Huisman *et al.* 1997; Tilman 1985). Species that become dominant later in the succession are mostly species that invest much in structural tissues and thus grow taller. These species will outshade the shorter species, mainly the attractive food plants, that were dominant when nutrients were limiting. On the high salt marsh *Elymus athericus* gets dominant. Only 7% of the incident light intensity penetrates through the *Elymus* canopy (Huisman *et al.* 1997). *Festuca* will be outshaded by the *Elymus* and will disappear. On the low salt marsh *Atriplex portulacoides* gets dominant.

Small herbivores are able to influence succession but are also influenced by succession themselves. Hares seem to retard succession of the salt marsh vegetation. In a study of van der Wal it has been shown that sites that were grazed by Hares, a later successional species like *Atriplex portulacoides*, reaches dominance about 25 years later when compared to ungrazed sites (van der Wal *et al.* 1998a). Hares seem to do this by keeping the vegetation short and cutting the taller unfavoured species. Especially in winter they eat species from the late successional stages, like *Elymus athericus*, *Atriplex portulacoides* and *Artemisia maritima*. However they can not prevent these species from establishing and at a certain moment succession takes over again, probably because of an increased nutrient availability, and the favoured short *Festuca rubra*-vegetation will eventually be replaced by a high, not preferred *Elymus athericus*-vegetation. *Elymus athericus* invests much in structural tissues in stems and their stiff leaves, making it unpalatable for herbivores. Small herbivores have a preference for plant species that are dominant in an intermediate succession stage, for geese they are *Puccinellia maritima, Festuca rubra and Plantago maritima* (van der Wal *et al.* 2000). Geese selectively pick their favourite feeding plants, which are plants, that are dominant early in the succession. Because of this they are not able to retard the succession. The island of Schiermonnikoog extends eastward, hence new salt marsh develops at the eastern point including young successional stages. The core feeding areas of Brent Geese (*Branta bernicla*) shifted eastward over the years. But the size of their feeding area didn't change. This indicates that geese are evicted by plant succession and have to change their feeding areas to stay in a favoured area (van der Wal *et al.* 2000). As Hares are able to retard succession, they facilitate for geese by keeping their favourite feeding areas longer available.

In this study the distribution of Brown Hares over a successional gradient has been investigated. The causes behind the observed pattern were tried to be explained. The question is whether Hares are also evicted by vegetation succession.
Another factor that is looked upon in this study is the influence of large herbivores on the Hare distribution. Big herbivores have a great ability of reducing the canopy height by reducing the abundance of high structure plants (Olff *et al.* 1997). Because of this, shorter vegetation with more favoured plant species is created. So cows might facilitate for Hares by creating more favoured vegetation. Olff *et al.* (1997) showed that cows do facilitate for geese by eating the higher *Elymus* vegetation and making the favoured food plants available again. Facilitation between herbivores is found before (see van der Wal *et al.* (1998a) for a review) but this could not be proven in other cases (de Boer & Prins 1990). It is expected that Hares prefer a short vegetation for grazing but also need tall vegetation for shelter or cover. Extensive cattle grazing creates patchy vegetation with short swards and higher patches. Intensive cattle grazing creates homogeneous short vegetation without much tall vegetation. It is expected that Hares have a preference for a more patchy vegetation so a higher Hare density is expected on the extensively grazed parts.

2 Material and methods

2.1 The study site

The study was performed on the "Oosterkwelder", a salt marsh in the east of the island of Schiermonnikoog (53°30'N, 6°10'E) in the Dutch Wadden Sea (figure 1). Because this island is gradually moving eastward, new salt marsh is being formed. A result of this is a successional gradient running from east to west (figure 2, Walrecht *et al.* (1998)). The eastern part of the salt marsh is just being formed and has an age of 0 years and the oldest part in the west is almost 200 years of age.

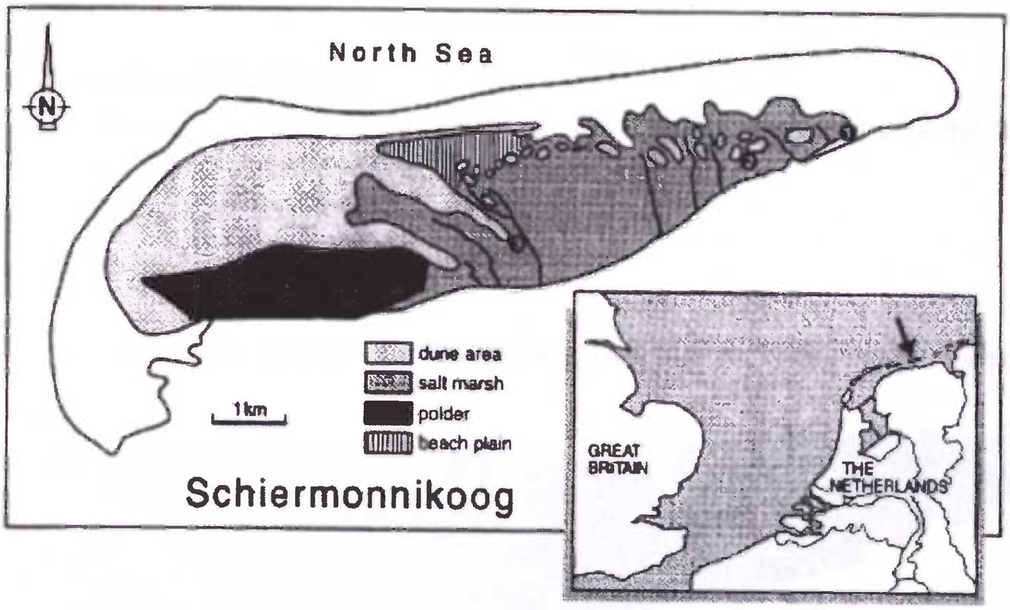

figure 1: The Wadden Sea island Schiermonnikoog

The oldest part is cattle grazed in summer. A grazing gradient is formed opposite to the successional gradient as most cows are seen close to the drinking places that are placed in the west (Verweij 1999). Another factor that influences this grazing gradient is the year that the salt marsh was first grazed. The western part of the grazed area has always been grazed (OBK), the middle part has been grazed since 1972 (NBK) and the eastern part has been grazed since 1989 (TBK).

Nine transects were established on the salt marsh (see table 1). All transects were established at similar height above Mean High Tide (MTH) and run all from the foot of a dune to the beginning of the pioneerzone. This means that they are all different in length, but they all consist of 20 plots were recordings took place. From this point on the transects that are placed on salt marsh that are of 7, 15, 25, 35, 65 and 100 years of age will be referred to as T0, T1, T2, T3, T4 and T5 respectively. The transects on the grazed salt marsh will be referred to as TBK, NBK and OBK which are 100, 150 and 175 years of age, respectively.

table 1: the transects

Transect	age (yr.)	Cattle grazing since:	length (m)
T0	7	ungrazed	80
T1	15	ungrazed	110
T2	25	ungrazed	240
T3	35	ungrazed	233
T4	65	ungrazed	100
T5	100	ungrazed	155
TBK	100	1989	236
NBK	150	1972	220
OBK	175	1850	240

2.2 The measurements

The fieldwork was performed in the autumn of 1999. On all transects the following measurements were carried out:

- dropping counts,
- vegetation relevées,
- canopy height measurements.

Furthermore on the transects T2, T3, T5 and NBK diet analyses were performed.

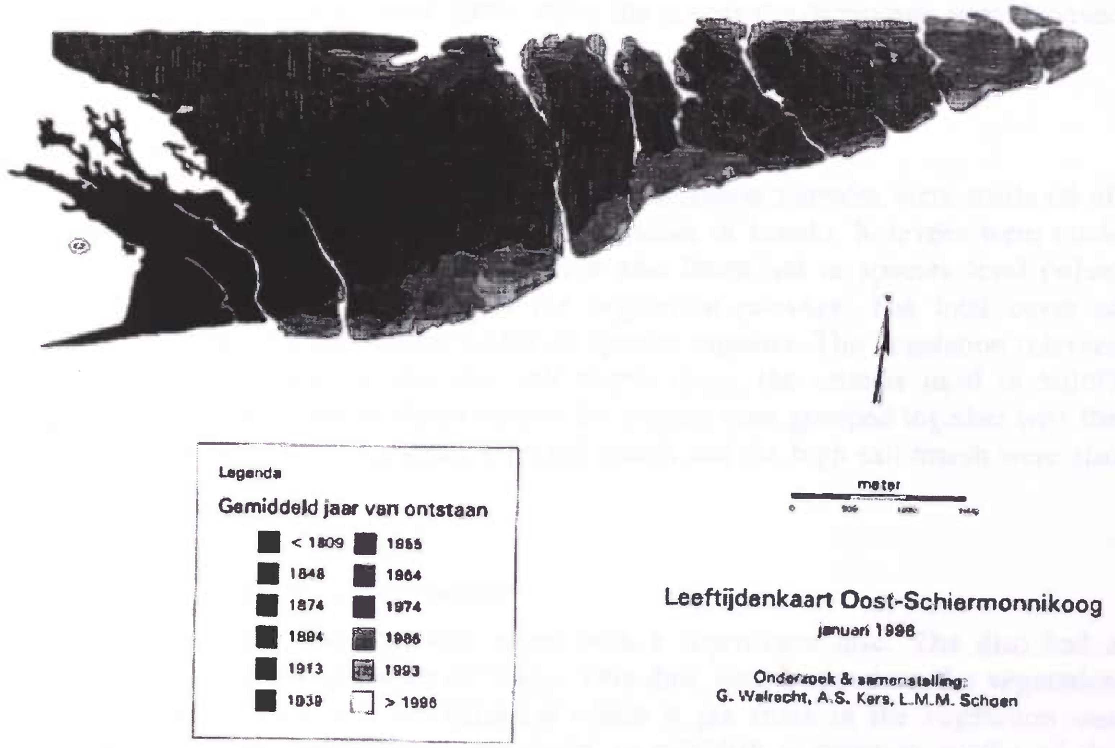

figure 2: map of the Oosterkwelder, Schiermonnikoog with years of start development salt marsh.

2.2.1 Dropping counts

Dropping counts give a good indication of the grazing intensity of the Hares in an area (Daniels 2000). The numbers of droppings per plot are closely related to the Hare density estimated with other methods. This method was chosen because it gives a quick view on the use of the salt marsh of the Hares. Difficulties with this method are discussed in Langbein *et al.* (1999). The main difficulties mentioned in that study are the "findability" of the droppings and the decay rate of the droppings. As the vegetation did not differ much along the different transects, the chances of finding droppings were assumed to be equal on all transects. As the counts were performed just before a spring tide, the decay rate is assumed to be fairly low and the same on all transects. Langbein *et al.* (1999) state that Hare droppings become unrecognisable after 34.0 ±1.32 days, which is much longer then the average of 11 days between the dropping counts in this study. Droppings were divided in Hare or Rabbit (*Oryctolagus cuniculus*) droppings based on size and structure. A blind test with Hare and Rabbit droppings showed that around 80% of the droppings were identified correctly as Hare or Rabbit (pers. obs.).

Four dropping counts were performed to get the distribution of the Hares along the different transects. These counts were performed once every 11,75 (9-14) days on the 25th of October and the 3rd, 15th and 29th of November. All counts took 2 days. It was tried to count in similar weather conditions and always just before a spring tide. Droppings were counted with a wire of 1.13m, which makes a circle with a surface of 4m^2. The middle point of the circle was placed 1.13m away from the pole that marked the plot to prevent a possible effect of the poles on the Hares. Previous studies indicated a small problem of Hares being attracted by the poles and drop more close to the poles (Baarspul and Kunst 2000). After the counts the droppings were removed from the plots.

2.2.2 Vegetation relevées

In the beginning of the study period (October) vegetation relevées were made on all plots on all transects according to the decimal scale of Londo. Relevées were made on a square of 1m x 1m. Dead plants were also identified to species level (when possible) because of the late date of the vegetation relevées. The total cover of standing dead material was estimated for all species together. The vegetation relevées were categorised into high and low salt marsh using the criteria used in Salt97 (appendix 1). To make the analyses easyier the pioneerzone grouped together with the low salt marsh and the intermedeate high salt marsh and the high salt marsh were also grouped together.

2.2.3 Canopy height measurement

Canopy height measurements were taken with a Styrofoam disc. The disc had a weight of 60.55g and a diameter of 30cm. This disk was dropped on the vegetation along a calibrated stick and the height at which it got stuck in the vegetation was measured. This was done once every meter to establish a structure profile of the transects. The height measurements were also taken in October 1999.

2.2.4 Structure transects

On the moderately grazed salt marsh (NBK) 5 short transects were established, running from the edge of a patch with a very high *Elymus* cover to an open area dominated by *Festuca* or other short grasses. These transects had a length of 12m. and had 5 plots along it, with a distance of 3m. between them. All five transects were placed in homogeneous stands. The transects were counted only twice due to limited time and bad weather. Droppings on these transects were counted to see if there was a preference of Hares for feeding places close to parts with taller vegetation, in which the Hares could find shelter.

2.2.5 Diet analyses

Since Hares do not have a really efficient digestion, many of the cell wall structures are preserved. The size and shape of the epidermis as well as the position of specific characters as stomata and hairs are still intact. As combinations of those characters are specific for plant species, identification of these cells was possible. In this way it was possible to assess the diet of Hares by examining the droppings of the Hares.

Droppings that were used for those analyses were collected during each dropping count on four transects, T2, T3, T5 and the NBK, in total 4 samples per transect. It was tried to collect around 20 droppings per count per transect, spread out over the entire transect. This is to avoid a too big influence of a certain vegetation type. Sometimes it proved not possible to collect droppings over the complete transect because there were often no droppings found on the lower salt marsh. In that case droppings were only collected on the high salt marsh.

After collection the droppings were dried for 48 hours in a stove at 70°C.

A reference collection with several important salt-marsh species was used before the real analyses to learn the species that could occur in the diet. There was also a good picture collection and a key available (van Lieshout *et al.* 1996).

A method of analysing the droppings was used as described in (De Jong *et al.* 1995; De Jong 1997). Homogenised samples were made from all droppings collected during one count on one transect. Of each sample 1½ grams (dry weight) was ground in a kitchen blender to homogenise the sample. After this the sample was sieved through a bacterial sieve to flush away too small particles. This sample was kept in 70% alcohol until the start of the microscopic analyses.

For the microscopic analyses microscopic slides were made by taking a random sample from a Petri dish and spreading it on an object glass. Ten plant fragments in two transects were identified per slide. Steward (1967) shows that diet analyses on basis of surface area give a better idea of the diet than counts of plant fragments as the fragments fall apart in pieces of different sizes. The fragments were identified by an 80x magnification. The fragments were identified to species level and the size was measured with an ocular micrometer. When identification to species level was not possible the fragment was placed in one of the rest categories unknown monocot, unknown dycot or unknown plant. Per sample 100 fragments were identified. Beyond this sample size the proportion per species levells out (van Lieshout *et al.* 1996). Species were only measured and identified when they were (partially) in the transect.

3 Results

3.1 The dropping counts

Four dropping counts were preformed. The numbers on T0 are fairly low and then the numbers increase to a peak at T2 (figure 3). Later in the succession the number of droppings decreases again. With cattle grazing (TBK, NBK and OBK) the numbers increase again, without a significant difference between them.

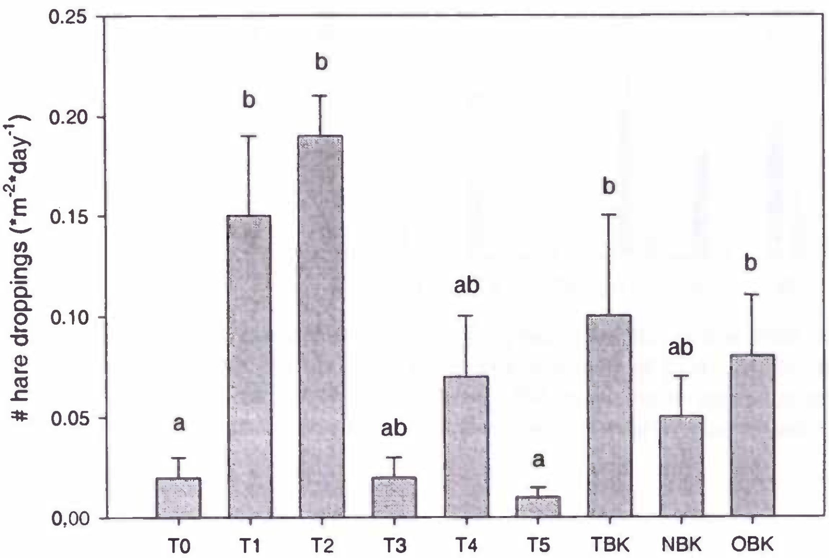

figure 3: number of Hare droppings over the transects. Significant differences are indicated with different letters ($p < 0.05$).

The results were tested non-parametrically because they were not normally distributed There was a significant difference between the transects for the droppings (Kruskal-Wallis test: χ^2 =38.623, df. = 8, $P < 0.001$). After this test the non-parametric multiple comparison Nemenyi's test was performed to look which transects differed. The significant differences are given in figure 3.

This means the Hare density is significantly lower on T0, then increases to a peak on T1 and T2. After T2 it decreases again to a significant lower value on T5. And with cattle grazing the numbers are significantly higher. There is a significant difference between the ungrazed T5 and the grazed TBK. As both transects have the same age and are just 50m. apart the only difference is the cattle grazing. The difference between those transects has to be explained by this factor.

Because the density of the most favoured food plants was the highest on the high saltmarsh, it was expected that Hares showed a preference for the high salt marsh. There was a significant difference in use by Hares of the high and the low salt marsh (Mann-Whitney U-test: Z = -6.915, $P < 0.001$; figure 4). Almost all droppings were found on the high salt marsh. During the period of counting the number of goose droppings were more or less equal on all transects. Rabbit droppings were only found on the highest plots and didn't differ much among the transects. These effects were assumed not to have an effect on the Hare density.

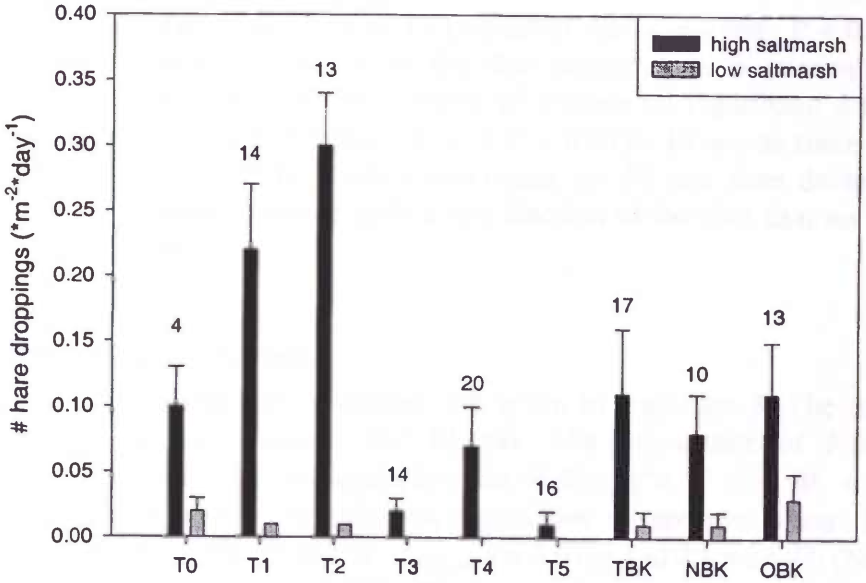

figure 4: the number of Hare droppings on the salt marsh, high and low salt marsh separated. The number of plots on the high salt marsh are given. A significant difference between the number of droppings on the high and the low salt marsh was found ($p < 0.001$).

3.2 *The diet*

Diet analyses was performed on the transects T2, T3, T5 and NBK. This was done for droppings collected during all dropping counts. The most preferred food plant on all transects is *Festuca rubra*, with an overall average of 75.4% ± 5.19 (figure 5, appendix 2). Over all the dropping analyses only 2.55% ± 0.45 was not identified and 0.02% ± 0.02 was placed in the category unknown dicot and 5.02% ± 1.47 in the category unknown monocot.

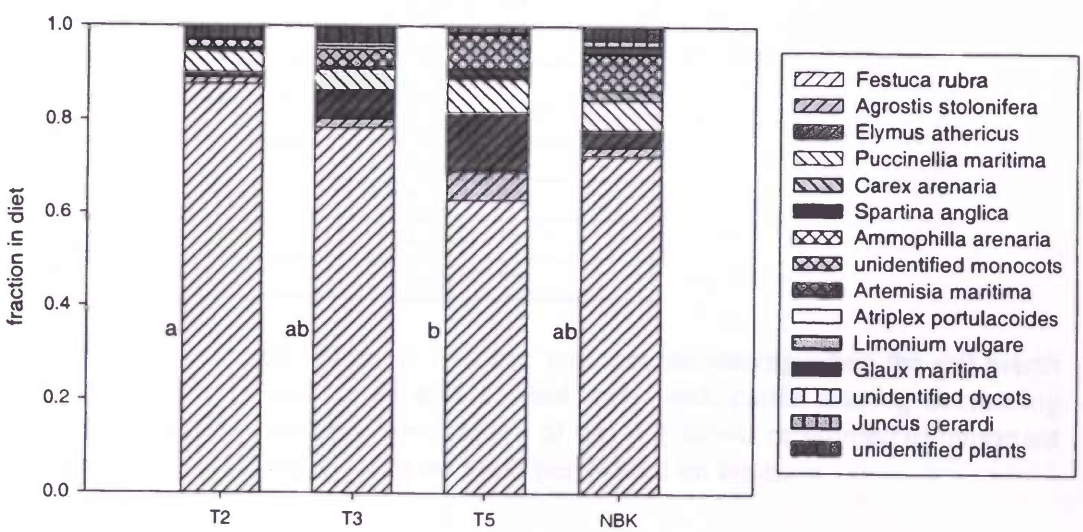

figure 5: the diet of Hares on the different transects. Differences are indicated with different letters.

A significant difference was found between the fraction of *Festuca* in the diets between different transects (Kruskal-Wallis: χ^2= 9.419, df. = 3, P = 0.24). The only transects that differed were T2 and T5 (Nemenyi test: q = 4.096, P < 0.05, $q_{0.05,\infty,4}$ = 3.633). The fraction of *Festuca* in the diet decreases to a minimum on T5 and increases again on NBK. For the fraction of *Elymus* no significant differences were found (Kruskal-Wallis: χ^2 = 6.993, df. = 3, P = 0.072). However there is a trend that *Elymus* increases in the diet with a maximum on T5 and then decreases again on NBK. The other plants formed such a low fraction of the diet that no analyses were performed on them.

3.3 *The vegetation relevées*

The results of the vegetation relevées are given in appendix 3. The most important plants for Hares are *Festuca* and *Elymus*. The abundance of *Festuca* differed significantly between the transects (Kruskal-Wallis: χ^2= 21.554, df. = 8, P = 0.006) (figure 6). The transects that showed significant differences where TBK with T0 (Nemenyi test: q = 5.246, P < 0.01, $q_{0.01,\infty,9}$ = 5.078) and T1 with T0 (Nemenyi test: q = 4.632, P < 0.05, $q_{0.01,\infty,9}$ = 4.387). This means that the amount of Festuca available on T0 is less then on T1 and TBK.

For *Elymus athericus* differences between the transects were found, too (Kruskal-Wallis: χ^2= 56.415, df. = 8, P < 0.001). Significant differences between transects are given in table 2.

table 2: significant differences in fraction *Elymus athericus* in the vegetation found with the Nemenyi's test ($q_{0.05,\infty,9}$ = 4.387, $q_{0.01,\infty,9}$ = 5.078, $q_{0.001,\infty,9}$ = 5.903; * = P < 0.05, ** = P < 0.01, *** = P < 0.001).

Transects with sign. differences	q-value
T0 – T5	5.289 **
T1 – T4	4.635 *
T1 – T5	5,611 **
T2 – T5	4.840 *
T3 – T4	4.929 *
T3 – T5	5.905 ***
T3 – TBK	4.650 *
NBK – T5	5.133 **
OBK – T4	4.658 *
OBK – T5	5.635 **

This means the fraction of Elymus is first low and then increasing when the salt marsh grows older to a maximum at T4 and T5 and then, with cattle grazing decreasing again. The other plants formed a low fraction of the vegetation or seemed unimportant for the Hares and no statistical analyses were performed on them.

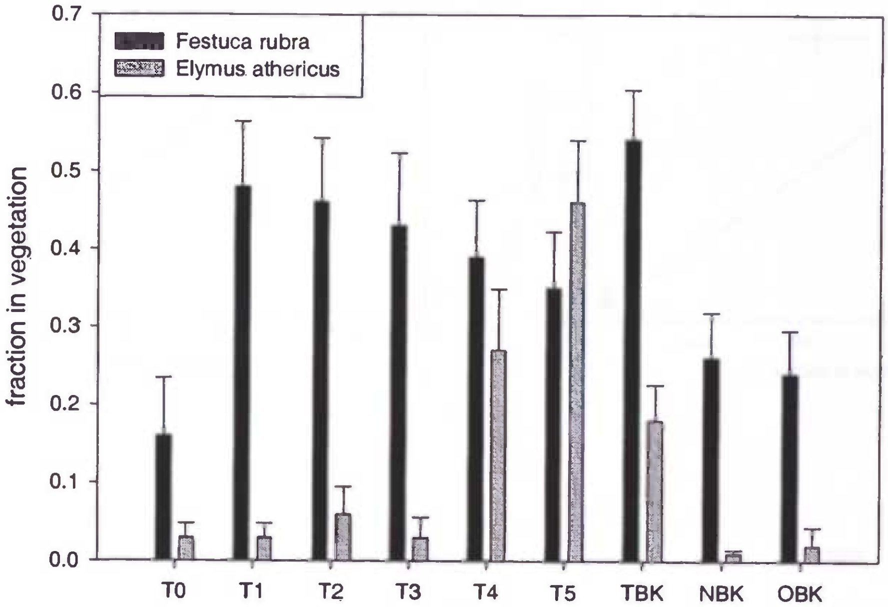

figure 6: the change of *Festuca rubra* and *Elymus athericus* in the vegetation along the transects.

3.4 Selection of food plants

Graphs were made with the fraction of a plant species in the vegetation on the x-axis and the fraction of the same species in the diet on the y-axis (figure 7). This was done per transect. A plant species was classified as preferred when the species was above the y = x line and two 2 * S.E. in both directions did not overlap with the y = x line. A plant species was classified as non-preferred when the species was below the y = x line and two 2 * S.E. in both directions did not overlap with the y = x line. A plant was classified randomly taken when 2 * S.E. in at least one direction did overlap with the y = x line or the fraction in the vegetation was less then 0.05.
On all transects *Festuca* was strongly selected. On T5, where *Elymus* was most abundant in the diet it was still non-preferred. On the other transects *Elymus* formed such a small part of the vegetation that it was classified as randomly taken.
All other plants had too low fractions to be selected.

3.5 The canopy height

Most droppings were found on the plots with a canopy height of between 6 cm. and 20 cm. (figure 8). At these heights the amount of *Elymus* in the vegetation was low and the amount of *Festuca* high. The low numbers of droppings and the high amount of *Elymus* at a height of 15 cm are caused by lying *Elymus* on the old salt marsh. The canopy height on the transects was analysed with a boxplot (figure 9). For crosscuts through the canopy see appendix 4. The transects T1, T2 and T3 do not differ much from each other. On those transects the vegetation is fairly low, but with enough spreading to taller stands to give the Hares possibilities for shelter. On the TBK there is more low vegetation than on the

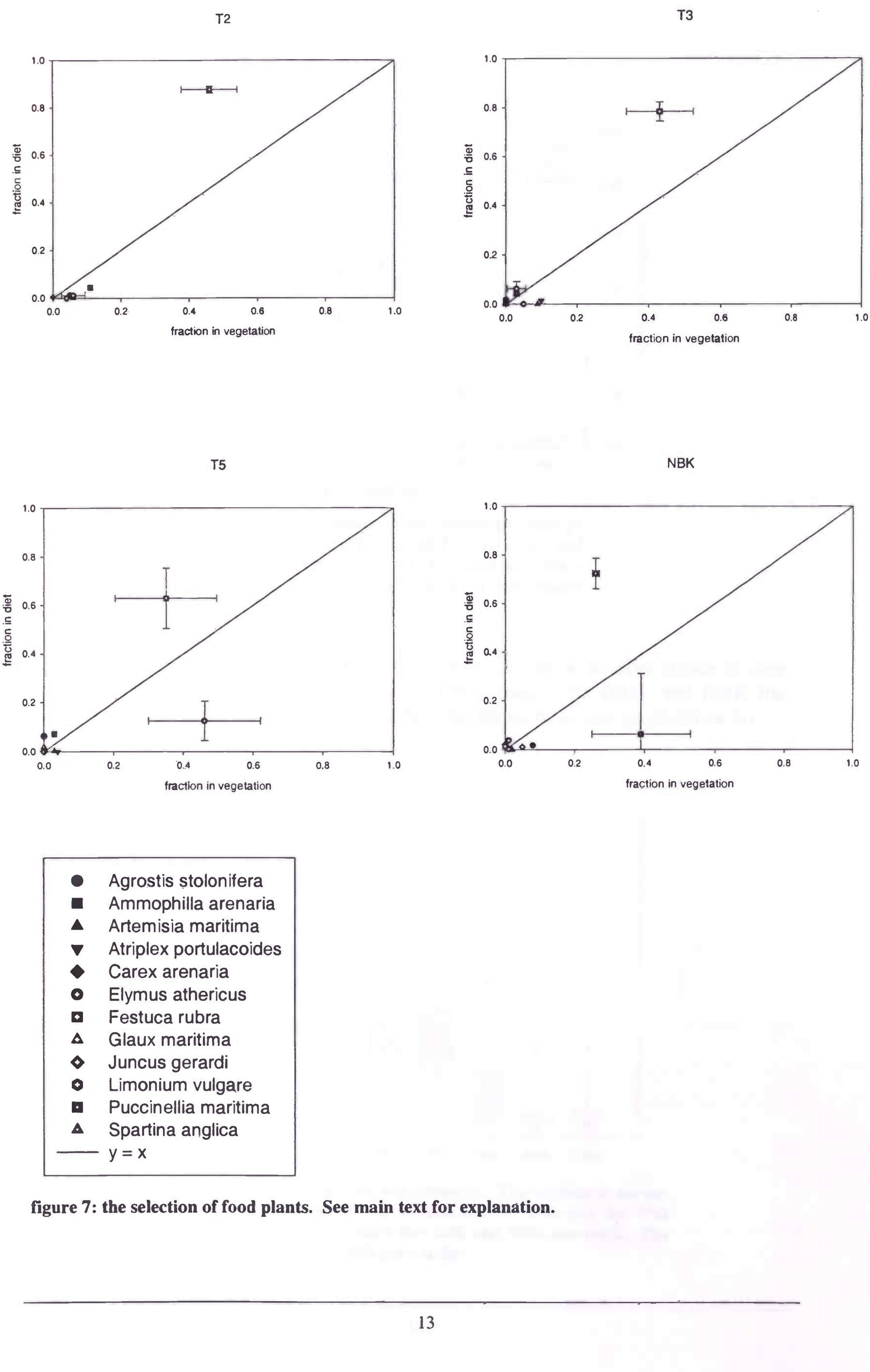

figure 7: the selection of food plants. See main text for explanation.

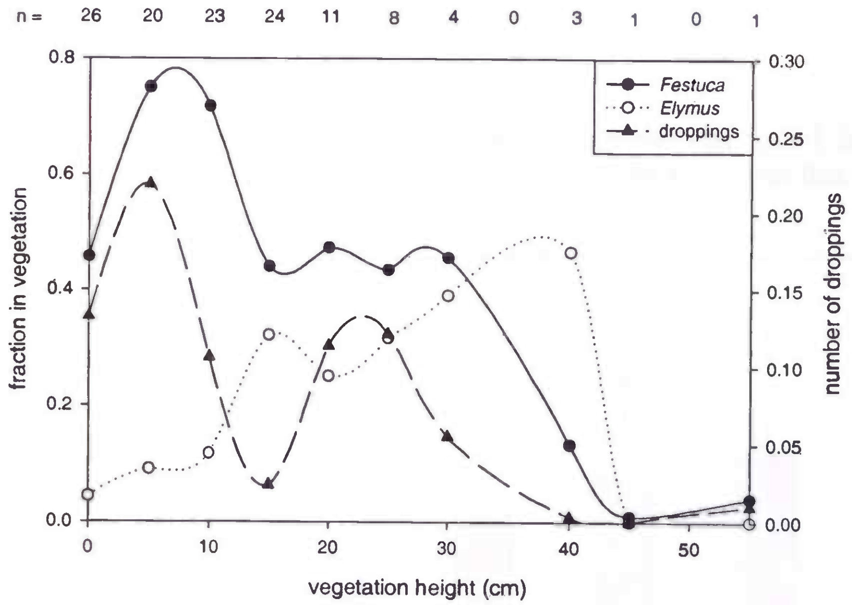

figure 8: The average number of droppings per canopy height. Also shown are the fraction of *Festuca rubra* and *Elymus athericus* per canopy height. The numbers above the graph indicate the number of plots with that canopy height.

three previous mentioned transects, but there is much variation to taller stands so they have also possibilities for shelter there. On the transects T0, NBK and OBK the vegetation is lower with less spreading, so here the Hares have less possibilities for

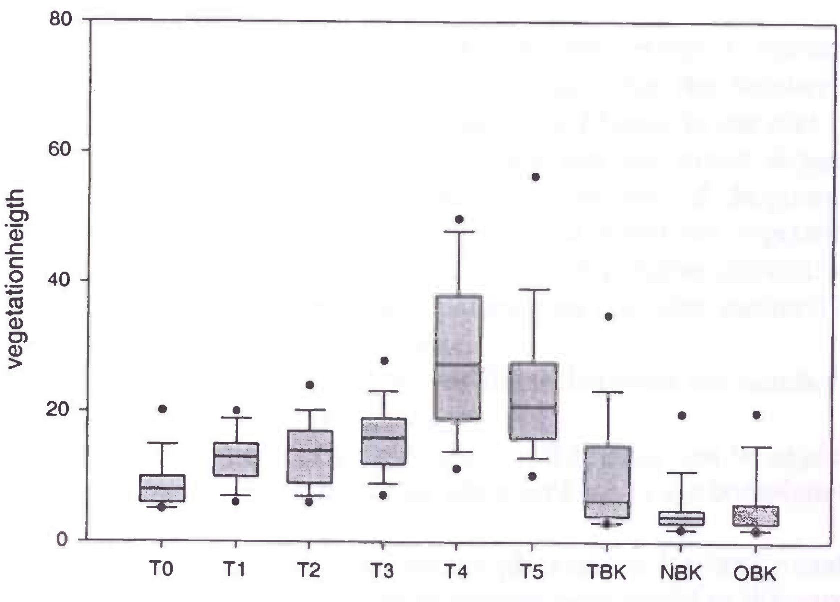

figure 9: the canopy height on the transects. The median is shown. The upper and lower bound of the box are the 25th and the 75th percentile. The error bars show the 10th and 90th percentile. The dots show the 5th and the 95th percentile.

shelter. On T4 and T5 there is a great variance but there is only very little short vegetation that Hares need for feeding.

3.6 *The structure transects*

On the short structure plots no significant difference was found between the plots (figure 10). So no effects of distance to cover could be shown on this small scale.

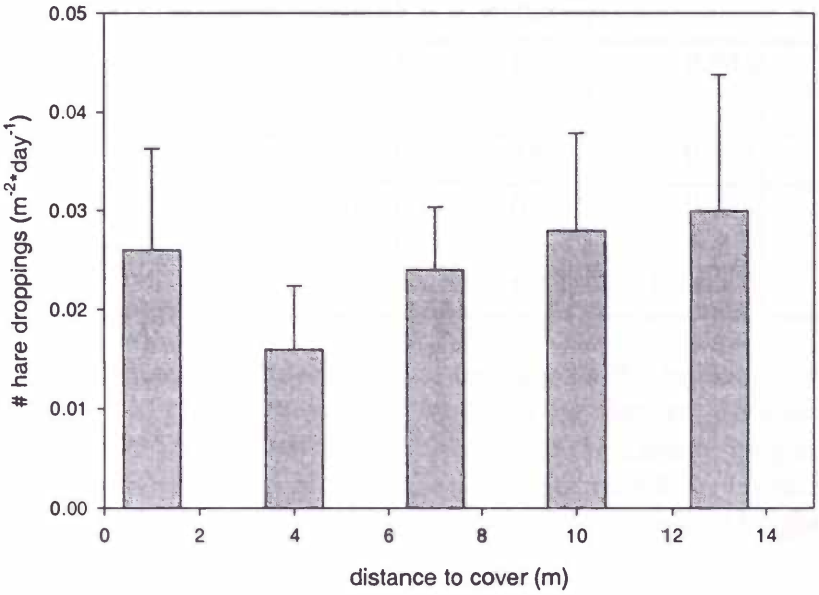

figure 10: the average number of droppings on the five structure transects.

3.7 *Relations between measurements*

To test for relations between the different measurements, Spearman's correlations were calculated. This was done on all transects for the number of droppings, the canopy height and the fraction of *Festuca* and *Elymus* in the diet. This was done for all plots as well for the plots of the high and low salt marsh separated. A significant negative correlation was found between the number of droppings and the canopy height in all plots (table 3). This indicates that when the vegetation gets higher the plots are less used by the Hares. The significant positive correlation between canopy height and the fraction *Elymus* in the vegetation indicates indirectly that *Elymus* is an important factor for the canopy height.

A significant positive correlation was found between the number of droppings and the fraction of *Festuca* in the vegetation.

The positive correlation between *Festuca* and *Elymus* can be explained because both are species of the high salt marsh so when looking to the complete transects they will occur together.

Correlations were also calculated for the plots on the low salt marsh separately (table 4). On the low salt marsh only few droppings were found so the correlations will be of less importance. Also on the low salt marsh the number of droppings was strongly correlated with the fraction of *Festuca* in the vegetation. The fraction of *Festuca* in the vegetation and the fraction of *Elymus* in the vegetation were also correlated. This can be explained because both plants are typical

table 3: Spearman's correlations for the whole transects between the canopy height, the number of Hare droppings and the fraction of *Festuca rubra* and *Elymus athericus* in the vegetation. n = 180, ** = P < 0.01, *** = P < 0.001.

		Hare droppings	Canopy height	Fraction *Festuca rubra* in vegetation
Canopy height	Correlation coefficient	-0.250	-	-
	Sig. (2-tailed)	0.001**		
Fraction *Festuca rubra* in vegetation	Correlation coefficient	0.618	-0.044	-
	Sig. (2-tailed)	0.000***	0.554	
Fraction *Elymus athericus* in vegetation	Correlation coefficient	0.020	0.272	0.238
	Sig. (2-tailed)	0.792	0.000***	0.001**

for the high salt marsh so they can occur together on the higher parts of the low salt marsh, but only very little *Elymus* was found on the plots on the low salt marsh. The fraction of *Elymus* was negatively correlated with the canopy height on the low salt marsh. This can be explained because there was just very little *Elymus* on the low salt marsh and other plants are of greater importance for the canopy height on the low salt marsh.

table 4: Spearman's correlations for the low salt marsh between the canopy height, the number of Hare droppings and the fraction of *Festuca rubra* and *Elymus athericus* in the vegetation. n = 59, * = P < 0.05, ** = P < 0.01.

		Hare droppings	Canopy height	Fraction of *Festuca rubra* in the vegetation
Canopy height	Correlation coefficient	-0.148	-	-
	Sig. (2-tailed)	0.263		
Fraction of *Festuca rubra* in the vegetation	Correlation coefficient	0.360	-0.189	-
	Sig. (2-tailed)	0.005**	0.152	
Fraction of *Elymus athericus* in the vegetation	Correlation coefficient	0.222	-0.271	0.408
	Sig. (2-tailed)	0.090	0.038*	0.001**

Strong negative correlations were found between the number of Hare droppings and the canopy height and between the number of Hare droppings and the fraction of *Elymus* in the vegetation at the high saltmarsh (table 5). Because the canopy height and the fraction of *Elymus* in the vegetation are positively correlated these previous two correlations indicate more or less the same. A positive correlation was found between the number of Hare droppings and the fraction of *Festuca* in the vegetation.

table 5: Spearman's correlations for the high salt marsh between the canopy height, the number of Hare droppings and the fraction of *Festuca rubra* and *Elymus athericus* in the vegetation. n = 121, * = P < 0.05, ** = P < 0.01, *** = P < 0.001.

		Hare droppings	Canopy height	Fraction of *Festuca rubra* in the vegetation
Canopy height	Correlation coefficient	-0.404	-	-
	Sig. (2-tailed)	0.000***		
Fraction of *Festuca rubra* in the vegetation	Correlation coefficient	0.363	-0.181	-
	Sig. (2-tailed)	0.000***	0.047*	
Fraction of *Elymus athericus* in the vegetation	Correlation coefficient	-0.342	0.332	-0.251
	Sig. (2-tailed)	0.000***	0.000***	0.006**

The negative correlations between canopy height and the fraction of *Festuca* in the vegetation and the correlation between the fraction of *Elymus* in the vegetation and the fraction of *Festuca* in the vegetation indicate the same because the canopy height and the fraction of *Elymus* are correlated.
Because the fraction of *Elymus* in the vegetation and the canopy height are correlated it can be concluded that *Elymus* is an important factor for the canopy height.
A stepwise forward selection multiple regression was performed to see how the number of droppings could be explained by the fraction of *Elymus* and *Festuca* in the vegetation and the canopy height (table 6 and table 7).

table 6: Multiple regression coefficients

Dependent variable: droppings	Unstandardized coefficients		T	Sig.
	B	Std. Error		
(Constant)	0.164	0.136	1.212	0.228
Elymus in vegetation	-0.163	0.047	-3.475	0.001
Festuca in vegetation	0.165	0.055	2.997	0.003

table 7: ANOVA table for the multiple regression

	Sum of Squares	df	Mean Square	F	Sig.
Regression	1.399	2	0.699	13.544	0.000
Residual	6.093	118	0.051		
Total	7.492	120			

Addition of the canopy height did not result in a better model (t = -1.965, P = 0.052).
The regression model that explains most variance was:

*Number of Hare droppings = 0.164 – 0.163 * fraction Elymus in vegetation + 0.165 * fraction Festuca in vegetation.*

This model had a r^2 of 0.173. A residual analysis showed that not all variation was explained and that probably another (missing) factor should be added for a better model.

4 Discussion

Droppings were counted to get an estimate of the Hare density and habitat use of Hares. Dropping counts give a good indication of the actual number of Hares in a certain area (Langbein *et al.* 1999). Daniels (2000) showed that on a smaller scale dropping density on a plot was correlated with grazing intensity. This means that dropping density is a good measure of the habitat use of Hares and they don't have special places for droppings (latrines) like Rabbits.

Figure 8 shows that Hares have a preference for vegetation between 5 cm and 22 cm of height. The low numbers around 15 cm can be explained by a higher abundance of *Elymus athericus* on those plots and a lower abundance of *Festuca rubra.* In these plots with a low canopy height the *Elymus* is mainly flattened by flooding or wind. This category would normally have a higher canopy height. When those plots with a high *Elymus* cover were excluded, the number of droppings increased again.

Higher canopy heights are mainly caused by *Elymus athericus* and are not favoured by Hares. An experiment showed that Brent Geese (*Branta bernicla*) have a preference for short vegetation, too (Summers & Critchly 1990; van der Wal 1998b). Summers & Critchly (1990) also showed that short, grazed *Festuca* has a higher nitrogen content than longer, ungrazed *Festuca.* This indicates a higher quality of *Festuca* at shorter vegetation. On the salt marsh of Schiermonnikoog geese had a higher intake on shorter vegetation than on taller vegetation (van der Wal *et al.* 1998b). Concluding it can be said that the high Hare density on the intermediate salt marsh can be explained by two factors: the *Elymus athericus* can hinder Hares when they are searching for their favourite food plants, the absence of *Elymus* on the young salt marsh makes this area more attractive. Another factor can be that the quality and biomass production of *Festuca* is higher on these younger sites because they are much more intensively used by both hare and gees. Geese come back to feed on the same site every four days (Prins *et al.* 1996). In an experiment where *Plantago maritima* (which is an important food plant for geese) was clipped it was shown that the production of biomass showed an optimum when clipping was preformed once every four days. This shows that geese can increase the amount of available food by feeding on the same spots on a regular basis.

The numbers of Hare increased when the salt marsh grows older to a maximum around salt marsh of 25 years of age. Simultaneously an increase in the most important food plant, *Festuca rubra* occurred. On the very young salt marsh almost no *Festuca* was available so the Hares have no possibilities for feeding. An important reason for the increase in *Festuca* on the transects is probably the increase in amount of the total salt marsh and with that also the amount of high salt marsh. The total area of salt marsh increases because the island becomes wider to the west. The vegetation on the high salt marsh is very similar on the young and intermediate transects (T0 – T3).

When the salt marsh grows older the Hare density decreases again. The decrease on T3 is unexpected because the vegetation composition and height looks very similar to the vegetation on T1 and T2. There is no clear explanation for this. A possible explanation is that the Herring Gull (*Larus argentatus*) and Lesser Black-backed Gull (*Larus (fuscus) graelsii*) colony higher on the salt marsh (and above the transect) attract all Hares in the area. Bazely *et al.* (1990) showed that gull-colonies seem to have a positive influence on the occurrence of geese. Areas occupied by gulls in spring were very attractive as feeding sites for geese, probably because of the very nutrient-rich plants that are growing there. Although higher numbers of Hares were seen in the area of the gull-colony (pers. obs.) no data were collected.

On the older transects *Elymus* became the dominant plant species and covered the *Festuca*. In contrast to the model used by Huisman *et al.* (1997), the total cover of *Festuca* on these transects is not much lower than on the younger transects but it is completely covered by Elymus and the Festuca grows much taller on the older transects. Van der Wal *et al.* (1998b) showed that intake rates for geese drop at higher standing crops. The nitrogen content of *Festuca* is also lower at higher standing crops (Summers & Critchly 1990). Concluding it can be said that the lower numbers of Hares on the older salt marsh can be explained by two factors: the high *Elymus* cover that makes the *Festuca* inaccessible, and the lower quality of the *Festuca* itself.

The few Hares present on those transects were found on patches with a high cover of *Festuca* and a low cover of *Elymus*. On these transects they strongly concentrated on the *Festuca* patches without *Elymus*. But very few of such patches were found on those transects.

The findings in this study are confim a study of van der Koppel *et al.* (1996). In that study simular dropping counts were preformed, but on shorter transects. This study also showed a preference for salt marsh of intermediate age.

On TBK the Hare density was significantly higher than on T5. As both transects are close together they are about the same age. The only factor that can explain this difference is the cattle grazing on TBK. This cattle grazing results in a (not significant) higher amount of *Festuca* and a (not significant) lower *Elymus* cover on TBK. On the more intensively grazed NBK and OBK the fraction of *Elymus* differed significantly from T5. The canopy height decreased strongly on TBK. The NBK and OBK also had higher numbers of Hares then on T5. This indicates that cows facilitate for Hares by reducing the canopy height and making the food recourses accessible again. No significant differences were found in Hare numbers between the grazed transects. This indicates that the patchyness of the vegetation does not play not such an important role. Another indication for this, on a smaller scale, is that no pattern was found in the short structure plots.

Festuca rubra was the most favoured food plant on all transects. The amount of *Festuca* in the diet decreased and the amount of *Elymus* in the diet increased towards the older transects. It looks like that Hares are forced to eat more *Elymus* while there is enough *Festuca* present. *Festuca* has a much higher protein content than *Elymus*, respectively 24% and 12% in May (Olff *et al.* 1997). This indicates that *Festuca* has a much higher quality than *Elymus*. The diet of the Hares on the older salt marsh, where they are forced to eat more *Elymus* is thus of a lower quality.

On the cattle grazed salt marsh the amount of *Festuca* increased and the amount of *Elymus* decreased again.

Concluding can be said that Hares seem to be evicted by succession as well as geese. Because of an increase in nutrients tall, unpalatable species like *Elymus* outcompete favoured foodplants like *Festuca rubra*. Possibly the quality of the *Festuca* decreases as well. On the older salt marsh the diet of Hares is of worse quality as on the younger salt marsh. This study gave proof that cows also facilitate for Hares because the numbers of Hares increased with cattle grazing and the diet quality improvd again.

In a future study it would be good to measure the quality of the different plant species on the different transects on the salt marsh and to make an estimate of the fitness differences of the Hares on the different transects. It would also be good to get year round data on the Hare distribution to look for time patterns.

5 Acknowledgements

First of all I would like to thank my supervisor, Dries Kuijper. Without his help this report would only be half of what it is today. I would also like to thank Maarten Loonen for his help with the analysis and the whole Plant-Animal interaction group for the useful comments. I would also give a big thanks to Christine de Jong who helped with the dropping analysis, without her the diet of hares would probably consists only of *Festuca*. Finally I would like to thank my fellow inhabitants of the Herdershut, Dries, Petra and Conni. Thanks for the pleasant time and the nice discussions. Without you the time would have been much more boring.

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7 Appendix 1: the criteria of Salt97

Below are the criteria of the program Salt97, with which the division in high, intermedeate high and low salt marsh and pioneerzone was made.

Pionierzone
groupB > 0 & groupB => totcov-groupB & Pucci mar < 25

Low salt marsh
groupC > groupF

Intermedeate high salt marsh
groupB + groupC + groupD + groupF - Festu rub - Agro sto > groupK

High salt marsh
groupK + groupL > 0 & groupK + groepL ⇒ groupD + groupF - Festu rub - Agro sto

Species in different groups
Names based on: Heukels 20[nd] edition.

GroepB
Salic eur
Salic dol
Salic bra
Spart ang

GroepC
Pucci mar
Halim por
Cochl ang
Halim ped

GroepD
Aster tri
Sperl mar
Trigl mar
Limon vul
Plant mar
Parap str

GroepF
Artem mar
Armer mar
Juncu ger
Festu rub
Agros sto
Glaux mar
Carex dis

GroepK
Elymu rep
Leont aut
Poten ans
Rumex cri
Trifo fra
Odont v-s
Lotus ten
Loliu per
Trifo rep
Tarax off
Plant maj
Poa tri
Poa pra
Ranun rep
Horde sec
Festu aru
Eleoc p-u
Daucu car
Arrhe ela
Alope pra
Dacty glo
Senec jac
Galiu apa
Urtic dio
Calys sep
Tussi far
Medic lup
Minua hyb
Erige can
Epilo hir
Aspar off
Epilo par
Lotus cor
Juncu art
Leont sax
Juncu alp
Schoe nig

GroepL
Centm pul
Cirsi arv
Cirsi vul
Sonch arv
Matri mar
Achil mil
Polyn avi
Senec vul
Rumex obt
Capse bur
Lycop eur
Vicia lut
Bromu hor
Poa ann
Arcti tom
Ceras sem
Belli per
Plant lan
Ceras fon
Trifo pra
Alope gen
Agros cap
Cochl off
Leymu are
Ammop are
Sedum acr
Centm lit

Appendix 2: The diet of Hares

The diet of Hares. The first four tables give the fractions of the plants found in the diets per dropping count per transect. The last table gives the average diet over the whole period, first per transect and then the overall average.

25-Oct				
Species	T2	T3	T5	NBK
Festuca rubra	0.911	0.762	0.604	0.816
Agrostis stolonifera	0.032	0.028	0.095	0.004
Elymus athericus	0.008	0.146	0.180	0.040
Puccinellia maritima	0.011	0.000	0.038	0.008
Carex arenaria	0.000	0.000	0.000	0.007
Spartina anglica	0.000	0.000	0.000	0.000
Ammophila arenaria	0.000	0.000	0.000	0.000
Unknown monocot	0.000	0.018	0.050	0.082
Artemisia maritima	0.007	0.000	0.016	0.000
Atriplex portolacoides	0.012	0.047	0.000	0.000
Limonium vulgare	0.000	0.000	0.000	0.013
Glaux maritima	0.000	0.000	0.000	0.000
Unknown dicot	0.000	0.000	0.000	0.004
Juncus gerardi	0.000	0.000	0.000	0.000
Unknown plant	0.020	0.000	0.016	0.026

03-Nov				
Species	T2	T3	T5	NBK
Festuca rubra	0.840	0.900	0.811	0.678
Agrostis stolonifera	0.009	0.010	0.042	0.008
Elymus athericus	0.027	0.014	0.020	0.053
Puccinellia maritima	0.042	0.003	0.062	0.031
Carex arenaria	0.000	0.000	0.000	0.079
Spartina anglica	0.022	0.000	0.000	0.000
Ammophila arenaria	0.000	0.000	0.000	0.000
Unknown monocot	0.020	0.021	0.040	0.050
Artemisia maritima	0.000	0.000	0.000	0.000
Atriplex portolacoides	0.000	0.006	0.000	0.000
Limonium vulgare	0.000	0.006	0.000	0.000
Glaux maritima	0.000	0.000	0.000	0.000
Unknown dicot	0.000	0.000	0.000	0.000
Juncus gerardi	0.000	0.000	0.000	0.047
Unknown plant	0.040	0.042	0.025	0.053

15-Nov				
Species	T2	T3	T5	NBK
Festuca rubra	0.873	0.752	0.532	0.692
Agrostis stolonifera	0.000	0.006	0.045	0.044
Elymus athericus	0.003	0.048	0.196	0.054
Puccinellia maritima	0.069	0.055	0.109	0.082
Carex arenaria	0.000	0.000	0.006	0.000
Spartina anglica	0.000	0.000	0.000	0.000
Ammophila arenaria	0.000	0.000	0.000	0.000
Unknown monocot	0.011	0.043	0.111	0.125
Artemisia maritima	0.000	0.000	0.000	0.000
Atriplex portolacoides	0.000	0.000	0.000	0.000
Limonium vulgare	0.000	0.000	0.000	0.000
Glaux maritima	0.000	0.000	0.000	0.000
Unknown dicot	0.000	0.000	0.000	0.000
Juncus gerardi	0.000	0.000	0.000	0.000
Unknown plant	0.045	0.096	0.000	0.002

29-Nov				
Species	T2	T3	T5	NBK
Festuca rubra	0.883	0.722	0.570	0.712
Agrostis stolonifera	0.010	0.031	0.069	0.015
Elymus athericus	0.011	0.045	0.105	0.005
Puccinellia maritima	0.060	0.115	0.078	0.131
Carex arenaria	0.000	0.000	0.006	0.000
Spartina anglica	0.004	0.002	0.075	0.000
Ammophila arenaria	0.000	0.014	0.000	0.000
Unknown monocot	0.029	0.067	0.087	0.050
Artemisia maritima	0.000	0.000	0.000	0.000
Atriplex portolacoides	0.000	0.004	0.000	0.000
Limonium vulgare	0.000	0.000	0.000	0.000
Glaux maritima	0.000	0.000	0.000	0.057
Unknown dicot	0.000	0.000	0.000	0.000
Juncus gerardi	0.000	0.000	0.000	0.000
Unknown plant	0.002	0.000	0.010	0.030

Average per transect	T2	T3	T5	NBK	average
Festuca rubra	0.877	0.784	0.629	0.724	0.754
Agrostis stolonifera	0.013	0.018	0.063	0.018	0.028
Elymus athericus	0.012	0.063	0.125	0.038	0.060
Puccinellia maritima	0.045	0.043	0.072	0.063	0.056
Carex arenaria	0.000	0.000	0.003	0.021	0.006
Spartina anglica	0.007	0.001	0.019	0.000	0.006
Ammophila arenaria	0.000	0.004	0.000	0.000	0.001
Unknown monocot	0.015	0.037	0.072	0.077	0.050
Artemisia maritima	0.002	0.000	0.004	0.000	0.001
Atriplex portulacoides	0.003	0.014	0.000	0.000	0.004
Limonium vulgare	0.000	0.001	0.000	0.003	0.001
Glaux maritima	0.000	0.000	0.000	0.014	0.004
Unknown dicot	0.000	0.000	0.000	0.001	0.000
Juncus gerardi	0.000	0.000	0.000	0.012	0.003
Unknown plant	0.027	0.034	0.013	0.028	0.025

Appendix 3: the vegetation relevées

Listed are all species seen on high and low saltmarsh together, with their cover.

species	T0	T1	T2	T3	T4	T5	TBK	NBK	OBK
cover	0.77	0.80	0.95	0.90	0.93	0.90	0.94	0.89	0.96
bare soil/litter	0.23	0.20	0.05	0.10	0.07	0.10	0.06	0.11	0.04
standing dead	0.19	0.08	0.03	0.07	0.23	0.08	0.05	0.03	0.09
mosses	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
Agrostis capillaris	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
Agrostis stolonifera	0.00	0.00	0.05	0.00	0.00	0.00	0.08	0.08	0.05
Armeria maritima	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.03
Artemisia maritima	0.00	0.05	0.06	0.09	0.02	0.03	0.08	0.02	0.02
Aster tripolium	0.02	0.01	0.00	0.06	0.01	0.01	0.00	0.01	0.00
Atriplex portulacoides	0.02	0.00	0.00	0.10	0.00	0.04	0.01	0.00	0.00
Atriplex prostata	0.00	0.00	0.00	0.00	0.18	0.02	0.00	0.00	0.00
Carex arenaria	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Carex extensa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cerastium arvense	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cerastium fontanum	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Elymus athericus	0.03	0.03	0.06	0.03	0.27	0.46	0.18	0.01	0.02
Elymus repens	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Festuca rubra	0.16	0.48	0.46	0.43	0.39	0.35	0.54	0.26	0.24
Galium verum	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Glaux maritima	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Juncus gerardi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.01
Juncus maritimus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Leontodon autumnalis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Limonium vulgare	0.04	0.10	0.04	0.05	0.06	0.00	0.03	0.01	0.06
Lotus corniculatus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Plantago coronopus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Plantago lanceolata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Plantago maritima	0.00	0.01	0.01	0.00	0.00	0.00	0.01	0.01	0.00
Poa pratensis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.19
Potentilla anserina	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Puccinellia maritima	0.31	0.10	0.11	0.03	0.00	0.03	0.07	0.39	0.22
Rumex acetosella	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sagina maritima	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Salicornia spp.	0.16	0.06	0.07	0.07	0.00	0.01	0.03	0.00	0.02
Sedum acre	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Spartina anglica	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Spergularia maritima	0.03	0.02	0.00	0.00	0.03	0.00	0.01	0.02	0.00
Stellaria graminea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Stellaria media	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00
Suaeda maritima	0.00	0.00	0.10	0.09	0.00	0.11	0.00	0.00	0.00
Trifolium repens	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.03	0.04
Triglochin maritima	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00

Appendix 3a: vegetationrelevées on the high salt marsh

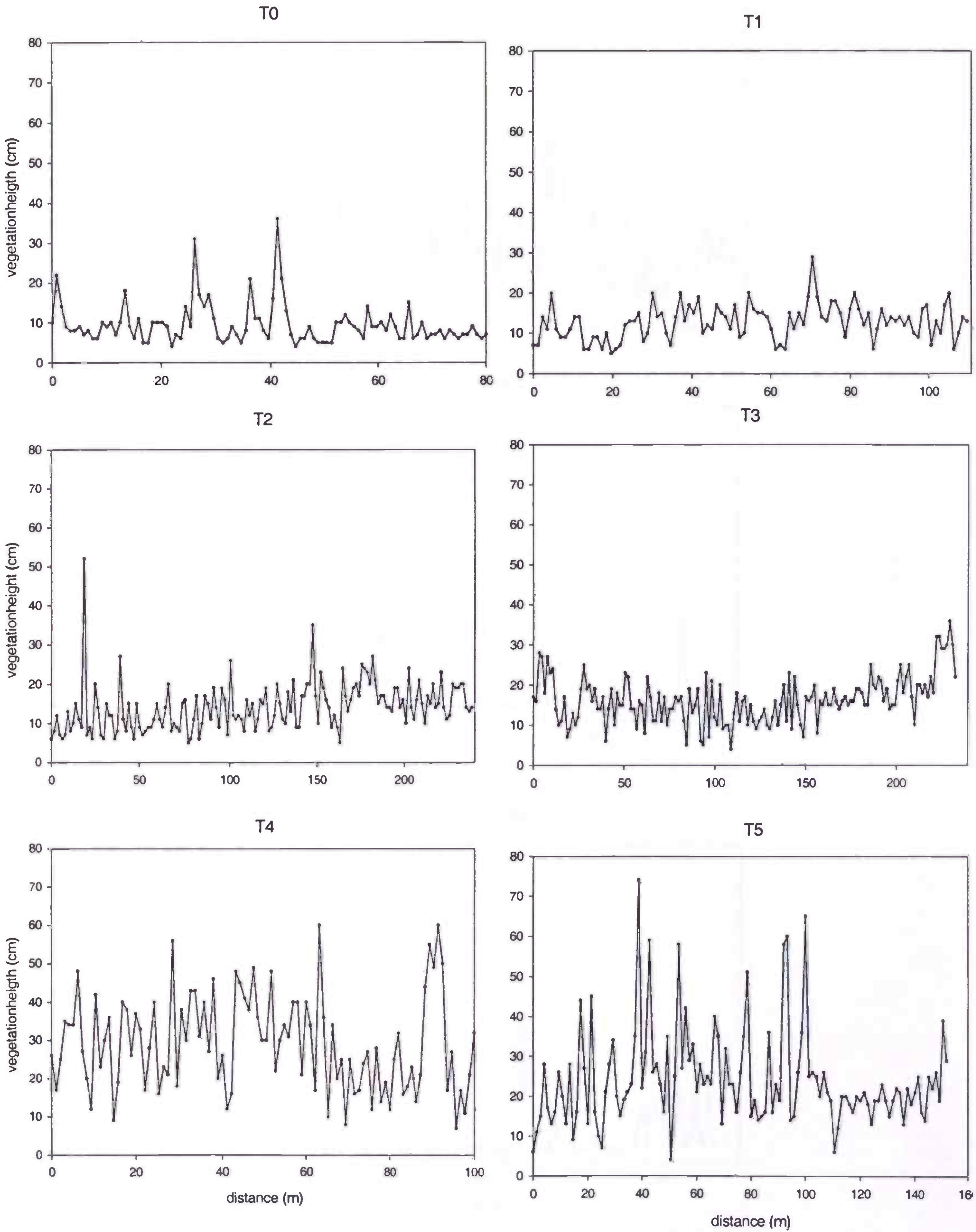
soorten	T0	T1	T2	T3	T4	T5	TBK	NBK	OBK
cover	0.98	0.89	0.97	0.90	0.93	0.91	0.95	0.96	0.98
bare soil/litter	0.03	0.11	0.03	0.10	0.07	0.09	0.05	0.04	0.02
standing dead	0.09	0.05	0.03	0.07	0.23	0.07	0.02	0.03	0.06
mosses	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04
Agrostis capilaris	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.02
Agrostis stolonifera	0.00	0.00	0.08	0.00	0.00	0.00	0.10	0.16	0.07
Armeria maritima	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.01	0.05
Artemisia maritima	0.01	0.06	0.09	0.11	0.02	0.00	0.04	0.02	0.00
Aster tripolium	0.00	0.01	0.00	0.07	0.01	0.00	0.00	0.00	0.00
Atriplex portulacoides	0.01	0.00	0.00	0.04	0.00	0.01	0.00	0.00	0.00
Atriplex prostata	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00
Atriplex litoralis	0.00	0.00	0.00	0.00	0.18	0.00	0.00	0.00	0.00
Carex arenaria	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
Carex extensa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cedum acre	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cerastium arvense	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cerastium fontanum	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Elymus athericus	0.14	0.04	0.09	0.04	0.27	0.58	0.21	0.02	0.04
Elymus repens	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
Festuca rubra	0.80	0.69	0.70	0.61	0.39	0.44	0.64	0.44	0.35
Galium verum	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Glaux maritima	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Juncus gerardi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.00
Juncus maritimus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Leontodon autumnalis	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Limonium vulgare	0.01	0.09	0.02	0.02	0.06	0.01	0.01	0.01	0.00
Lotus corniculatus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Plantago coronopus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Plantago lanceolata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Plantago maritima	0.01	0.01	0.01	0.00	0.00	0.00	0.01	0.01	0.00
Poa pratensis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.29
Potentilla anserina	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Puccinellia maritima	0.00	0.02	0.00	0.01	0.00	0.00	0.02	0.14	0.03
Rumex acetosella	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sagina maritima	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Salicornia spp./Suaeda maritima	0.01	0.02	0.01	0.05	0.00	0.00	0.00	0.00	0.00
Spergularia maritima	0.00	0.01	0.00	0.00	0.03	0.00	0.01	0.00	0.00
Stellaria gramminea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Stellaria media	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00
Trifolium repens	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.06	0.06
Triglochin maritima	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

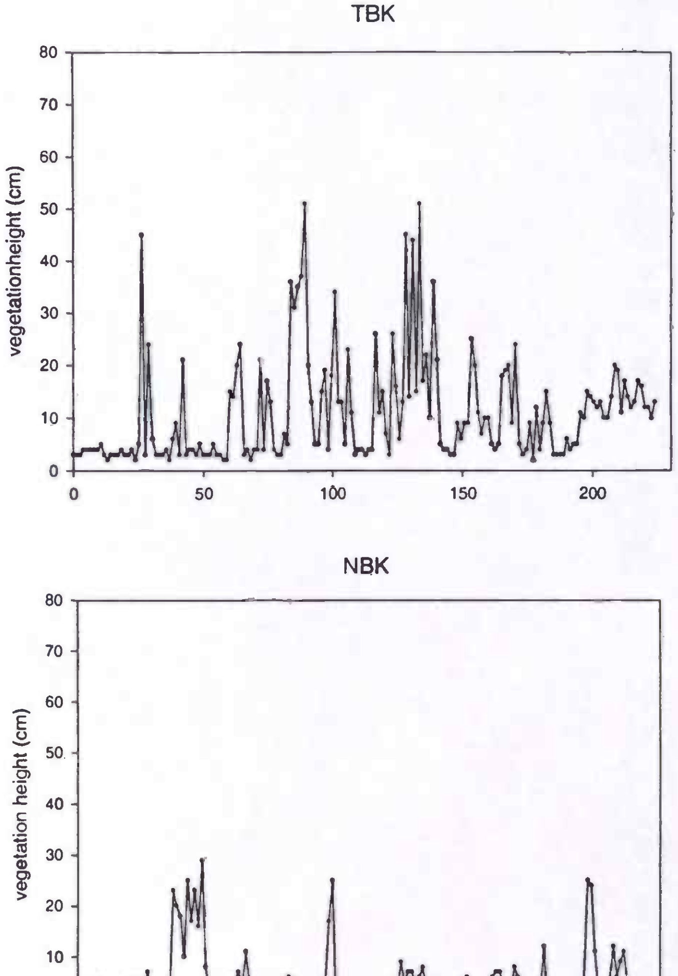
Appendix 3b: Vegetation relevées on the low salt marsh

soorten	T0	T1	T2	T3	T4*	T5	TBK	NBK	OBK
cover	0.72	0.59	0.90	0.85		0.85	0.87	0.82	0.92
bare soil/litter	0.28	0.41	0.10	0.15		0.16	0.13	0.19	0.08
standing dead	0.21	0.16	0.04	0.07		0.11	0.20	0.03	0.14
mosses	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00
Agrostis stolonifera	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00
Armeria maritima	0.00	0.00	0.00	0.00		0.10	0.00	0.00	0.00
Artemisia maritima	0.00	0.00	0.00	0.02		0.00	0.30	0.01	0.06
Aster tripolium	0.02	0.01	0.00	0.06		0.03	0.01	0.01	0.00
Atriplex portulacoides	0.02	0.00	0.01	0.24		0.18	0.05	0.00	0.00
Atriplex prostata	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00
Cerastium fontanum	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00
Elymus athericus	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00
Festuca rubra	0.00	0.01	0.01	0.01		0.00	0.00	0.08	0.03
Glaux maritima	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00
Juncus gerardi	0.00	0.00	0.00	0.00		0.00	0.00	0.04	0.03
Juncus maritimus	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.02
Limonium vulgare	0.05	0.13	0.09	0.11		0.00	0.13	0.02	0.16
Plantago coronopus	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00
Plantago maritima	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00
Puccinellia maritima	0.39	0.30	0.31	0.07		0.16	0.33	0.64	0.56
Salicornia spp./Suaeda maritima	0.20	0.14	0.47	0.38		0.59	0.17	0.00	0.07
Sedum acre	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00
Spartina anglica	0.03	0.01	0.00	0.00		0.00	0.00	0.00	0.00
Spergularia maritima	0.04	0.07	0.00	0.01		0.00	0.00	0.03	0.01
Triglochin maritima	0.00	0.00	0.04	0.00		0.00	0.00	0.00	0.00

* On T4 no low saltmarsh was found.

Appendix 4: the canopy height measurements




TBK
vegetationheight (cm)
0
10
20
30
40
50
60
70
80
0
50
100
150
200
NBK
vegetation height (cm)
0
10
20
30
40
50
60
70
80
0
50
100
150
200
OBK
vegetationheight (cm)
0
10
20
30
40
50
60
70
80
0
50
100
150
200
distance (m)