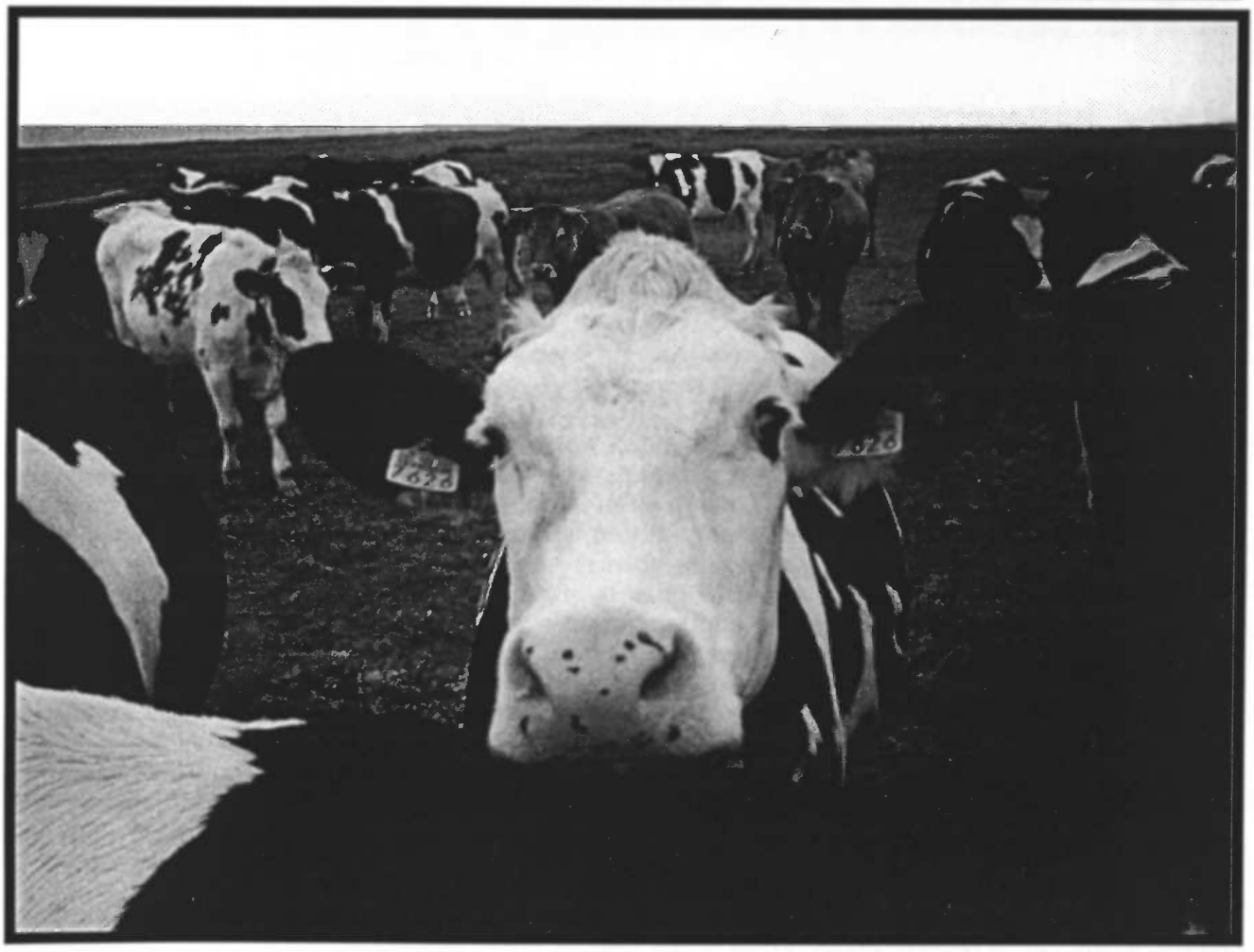
Effects of cattle grazing on food patch choice of brown hares on the salt marsh of Schiermonnikoog



Peter Beek
Supervised by Dries Kuijpers
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1. Abstract

Nitrogen input by clay sedimentation has been shown to be the driving force behind plant species replacement in the Wadden sea salt-marsh system. Old successional stages are dominated by the superior light competitor, *Elymus athericus*, and suitable grazing sites for the brown hare (*Lepus europaeus*) dissappear. Consequently hare densities increase with age of the salt marsh, but seem to increase again at salt-marsh areas which are grazed by cattle. This study discusses the effects of cattle grazing on hare grazing on the grazed salt marshes of Schiermonnikoog, one of the barrier islands in the Dutch Wadden Sea.

The effects of cattle grazing on the vegetation and subsequent on hare feeding patch choice in short-term and long-term will be discussed. Short-term effects are defined as within a season and are monitored by measuring quality and biomass. Long-term effects accumulate over multiple years and can be seen in influences on succession. In the short term cattle grazing is predicted to decrease the biomass of *Festuca rubra*, which has been shown to be the hares preffered forage. However, cattle grazing is also expected to increase the quality of *Festuca rubra*. These two effects can be termed as direct competition and facilitation, respectively. In the long term, cattle grazing is predicted to increase the availability of *Festuca rubra*, by decreasing abundance of light's shading, dominant plant, *Elymus athericus*. This long-term effect can be described as indirect facilitation.

Diet analyses were performed on hare faeces, collected from grazed and ungrazed salt marsh areas, and, taken together with vegetation measurements, showed that hares actively select for *Festuca rubra* both in presence and absence of cattle grazing.
An experiment manipulating forage quality and biomass was set up, in order to find the preference hares have when choosing their grazing site. Manipulations of quality and biomass were intended to mimick the effects of cattle grazing within a season, i.e. short-term effects of cattle grazing. Neither quality nor biomass manipulations of *Festuca rubra* caused the hares to show significant preference, neither in the early growing season, nor later in the season.

Long term effects on the vegetation by cattle grazing were studied by using exclosed areas. There was one exclosure that had been excluded from grazing for 4 years and five exclosures which had been excluded from grazing for 30 years. After 4 years of excluding cattle, a higher biomass and a taller vegetation was found and the composition of the vegetation was changed. Later successional species were abundant in the ungrazed area, which indicates that cattle grazing impedes plant species replacement and thus retards vegetation succession. Furthermore *Festuca rubra* was equally abundant inside and outside the exclosure. Hares did not show a clear preference for the grazed or the ungrazed areas.
Areas which had been excluded from cattle grazing for 30 years, characterised by old successional stages, exhibited very little to no hare grazing. The abundance of *Elymus athericus* appeared to be the most important factor which deters hares. Extremely low hare grazing intensity was found in vegetation with more than 30% of *Elymus athericus* coverage and the highest dropping densities were found on sites where *Elymus athericus* was lacking.
Abundance of *Festuca rubra* cannot explain the hare grazing density results. Therefore it seems that the hypothesis discussing the indirect facilitative effect of cattle grazing on hare grazing, concerning the availability reduction of *Festuca rubra* due to shading by the strong competitor *Elymus athericus*, must be discarded. Another possible hypothesis is that structural plants, such as *Elymus athericus*, may effect hare grazing density.

2. Contents

3.Introduction

3.1 Salt-marsh development, vegetation succession and grazing

Salt marsh development in a temperate region occurs when sand bars along the mainland coast develop into sand barriers (due to sand trapping by *Elymus farctus* and *Ammophila arenaria*). This protects the inward sea from high turbulence, which creates a system where sedimentation can take place. The sedimentation rate is low at the foot of the sanddunes, due to lower inundation frequency and is low close to the sea because of high water movement (wave-turbulence). Sedimentation is therefore highest at intermediate elevational positions on the young salt marsh (Olff et al. 1997). Nitrogen has been shown to be the limiting nutrient for plant growth in the Wadden Sea salt marshes (Kiehl et al. 1997) and it is accumulation of nitrogen by means of clay sedimentation which appeared to be the main factor causing species replacement (Olff et al. 1992).
Vegetation succession starts with pioneer species such as *Salicornia europaea* and the following plant species proceed in the vegetation in chronological successional stages: *Puccinellia maritima*, *Plantago maritima*, *Triglochin maritima*, *Festuca rubra*, *Artemisia maritima*, *Atriplex portulacoides*, *Elymus athericus* (Bakker et al. 1997).
Plant species replacement during succession on lower parts of the salt-marshes appears to be faster probably due to higher rate of clay-sedimentation (Olff 1992). At the lowest salt-marsh sites, *Atriplex portulacoides* will become dominant and *Elymus athericus* will become dominant in the higher salt-marshes after 60-100 years of succession. At least 7 cm of clay seems to be the prerequisite for this plant to become dominant (van Wijnen 1999). There is a shift from competition for nutrients towards competition for light. Therefore taller species replace smaller species (Olff 1992).

Vegetation succession, accompanied by nutrient accumulation, is generally associated with increasing abundance of superior light competitors, such as the relatively tall species, *Elymus athericus*. A high investment in structural tissues is an important trait enabling this species to attain dominance under productive conditions. However, these tissues are generally low in nutrients, especially nitrogen, and difficult to digest, which reduces the quality of tall plants as a food source for herbivores. Furthermore, tall rhizomateous grasses like *Elymus athericus* withdraw nutrients efficiently from senescing leaves, so that large quantities of standing dead material of low forage quality are left in the autumn. In the subsequent spring, these dead leaves can comprise up to 50% of the above-ground biomass. Bigger herbivores with a lower requirement for high-quality forage May be able to utilize such late successional species and May remove tall, productive, relatively unpalatable species (Olff et al. 1997). Herbivorous species that reduce the abundance of a competitively dominant plant species can act as 'keystone' species and increase diversity by releasing other species from competition (Paine 1966; Harper 1969; Crawley 1983; Pacala & Crawley 1992).

In situations of top-down control, strong reduction of dominant light competitors by herbivores yields a plant community with abundant high quality plants in which multiple herbivores have additive effects and increased plant diversity (van der Koppel et al. 1996). A single herbivore species can either accelerate or retard succession. Herbivore grazing can accelerate plant species replacement by grazing preferentially on weaker competitors. Herbivore grazing can retard plant species replacement or succession by grazing on the stronger competitor. In the situation of more than 1 herbivore, herbivore effects are compensatory when herbivore species consume different plant species and are additive when they consume the same plants. (Ritchie et al. 1999)

Facilitation can be direct or indirect (Figure 3.1). In case of direct facilitation, herbivorous species 1 affects herbivorous species 2 by modifying a shared food resource. Indirect facilitative effects can occur when two herbivorous species utilize different but competiting food plants (Vandermeer 1980, Dethier & Duggins 1984)

An example of facilitation in a salt marsh system is the effect of hare grazing, which has been shown to retard succession for 25 years by grazing on *Atriplex portulacoides* and thereby enables large areas of *Puccinellia maritima*, the favourite foodplant of the Brent Geese, to subsist (van der Wal, 1998). This is an example of indirect facilitation. Another example is sheep grazing which

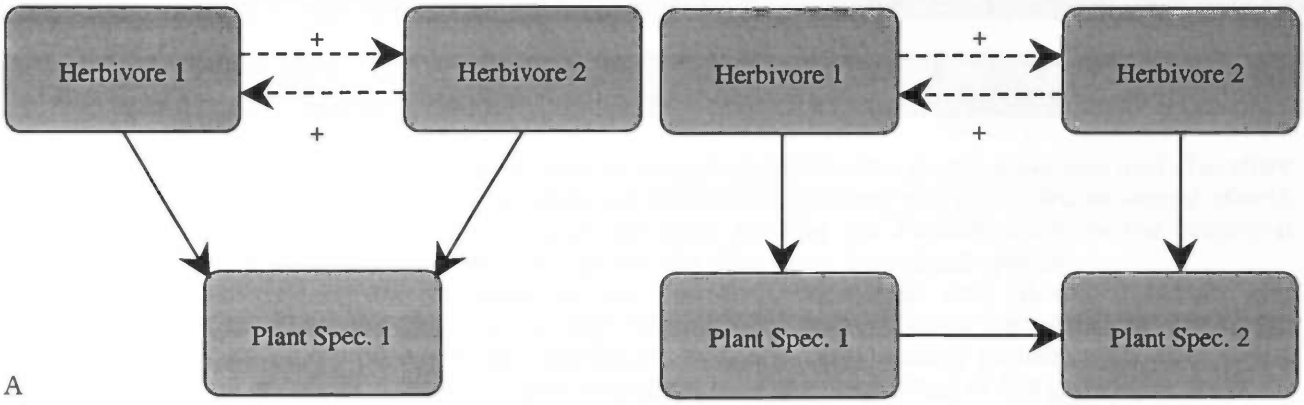

Figure 3.1: A simplified scheme of direct facilitation via a shared food resource (A) and indirect facilitation via two different food plants competing with each other (B). Indicated are two plant species (1 and 2) and the two herbivorous consumers (1 and 2). Solid arrows show direct negative effects, while dashed arrows show positive, facilitative effects.

facilitates for grazing by Brent Geese, both within the season (short term) and over years (long term), which is an example of direct facilitation (Bos 2002).

A potential interaction between cattle and hares on the salt marsh of Schiermonnikoog was detected after unpublished results by Kuijper (University of Groningen). He showed a decrease in the numbers of hares as the salt marsh gets older. However, more hares could be observed as soon as cattle grazing occurs (Figure 3.2).

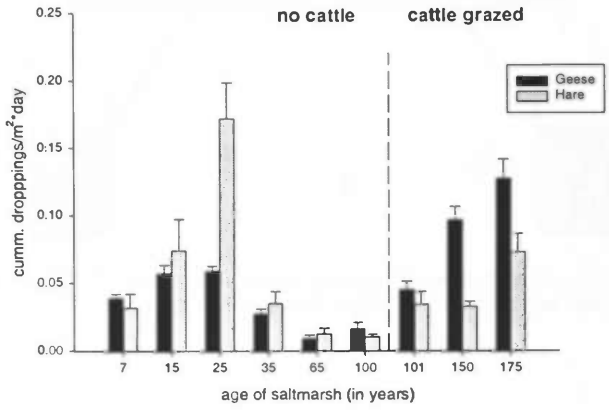

Figure 3.2: Cumulative number of droppings per year (1999-2000) of Geese and Hare in relation to the age of the salt marsh on Schiermonnikoog. The older marshes are cattle grazed (unpublished results Kuijper)

This could indicate that cattle grazing facilitates hare grazing on the older salt marshes and therefore in this research the relationship between cattle and hares on the salt-marsh of the island of Schiermonnikoog will be explored.

3.2 Research question

Research question:

- How do effects of cattle grazing on the vegetation influence hare feeding patch choice?

Subquestions:

- What are short-term (seasonal) effects of cattle grazing on the vegetation in terms of changes in quality and quantity?
- What preference do hares show for these changes?
- What are long term (multiple years) effects of cattle-grazing on the vegetation?
- How do these effects influence hare feeding patch choice?

3.3 Hypotheses

3.3.1 Short-term (seasonal) effects by cattle grazing: Hare feeding preference for quality or biomass

Short term effects will be defined here as effects occuring within the growing season and therefore will be termed as seasonal effects. It is expected that cattle-grazing will have two seasonal effects on the vegetation, which might be important for hare grazing. As *Festuca rubra* is the principal foodplant (van der Wal 1999), the focus will be on the effects on this plant species.
Cattle-grazing will reduce the biomass of the standing vegetation and therefore reduce the biomass of *Festuca rubra*, resulting in a competitive relationship between the cows and the hares (Figure 3.3.A). This might be especially important in places and during periods with little living vegetation such as on lower sites of the salt-marsh or near the beginning of the growing season.
However cattle-grazing might also be of advantage for the hares. By grazing the vegetation and, therefore also *Festuca rubra*, a drop in nitrogen content in the leaf tips might be prevented, comparable to the facilitative effects of grazing barnacle geese in early spring on grazing of brent geese later in the spring (Ydenberg & Prins 1981). This would be a relationship of direct facilitation (Figure 3.3.B)

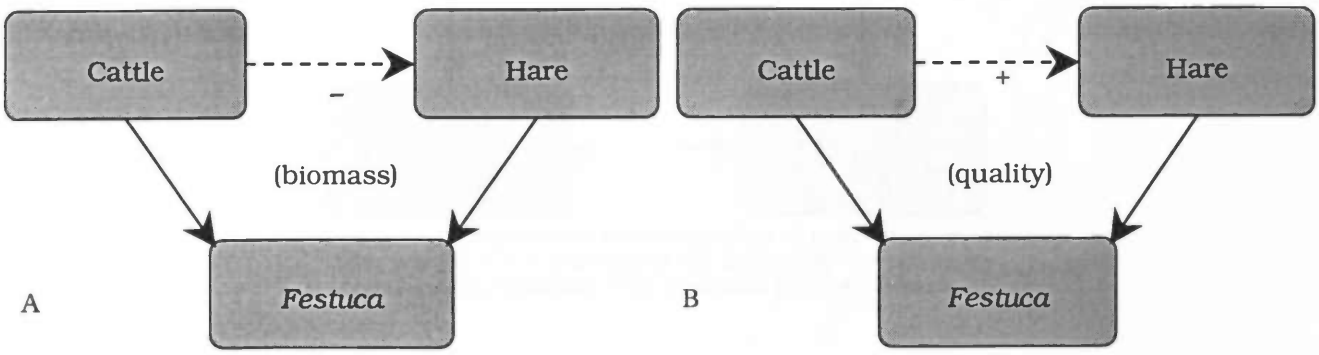

Figure 3.3: Hypothetical effects of cattle grazing on hare grazing, by effecting *Festuca rubra*, a shared food source. A. Competitive effect (-) by decreasing the biomass of *Festuca rubra*. B. Facilitative effect (+) by increasing the quality of *Festuca rubra*.

Therefore preference of hares for quality or biomass was tested and performed two times to look at differences in preference during the season. It is thought that earlier in the season, when the vegetation is comparably low in biomass, hares might choose to graze in areas which carry relatively more vegetation. Later in the season when there's plenty of biomass and the standing vegetation loses its freshness and the nitrogen drop in the leaf tips takes place, hares might search for vegetation with higher nitrogen levels. These would be the cattle-grazed areas according to the hypothesis.

3.3.2 Long term (multiple years) effects of cattle grazing on hare grazing

Long-term effects will be defined here as effects occurring over multiple years to decades and, because these effects are expressed in directional changes in the vegetation, they can be termed as successional changes.
As stated before, during undisturbed succession on the higher marsh, *Elymus athericus* will thrive and thus will outcompete every other plant species, including *Festuca rubra*. However cattle can retard species replacement during succession by reducing the abundance of competitively dominant plant species, in this case *Elymus athericus*, which might ensure the availability of *Festuca rubra*. Hares might profit from this effect, which opens doors for an indirect facilitative effect of cattle-grazing on hare grazing (Figure 3.4)

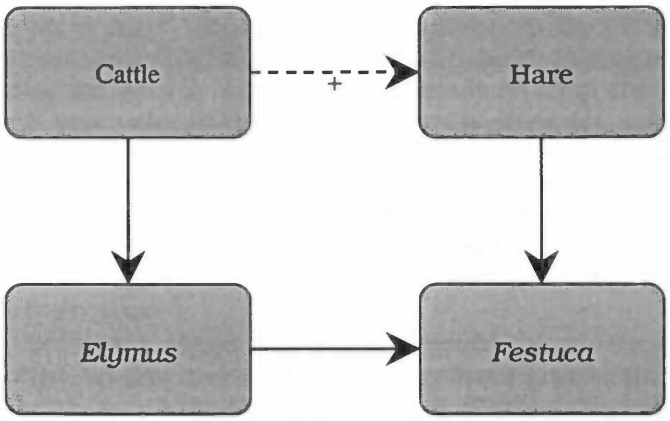

Figure 3.4: Hypothetical facilitative effect of cattle grazing on hare grazing due to increase of the availability *Festuca rubra* by reducing the biomass of the dominant *Elymus athericus*.

4 Methods

Firstly there will be a short description of the area where this project was carried out and why the choice was made to use this specific area.
Secondly basic analysis, measuring and recording methods used for this research will be discussed in order to avoid repetition. Discussed are faeces analyses, vegetation composition, food plant quality, biomass, vegetation heights, sproutlengths, and finally hare dropping counts. In general the decision was made to use at least 6 replicates during each sampling procedure to ensure sufficient power.
Finally there will be a description of which, when and how these methods have been applied to the different experiments and field sites within the study area.

4.1 Research area

The research area was on the eastern salt marsh of the island of Schiermonnikoog (53°30'N, 6°10'E), which is one of the 5 main islands along the northern Dutch coast in the Wadden Sea (Figure 4.1). Long-term research is performed here on the development of the salt marsh because the island is growing eastward with a distinctive age gradient from the oldest salt marsh in the western part, which is 200 years old, to the youngest part in the east.
The oldest parts of the salt-marsh on the island of Schiermonnikoog are grazed by cattle and cover an area of 415 hectares . It is grazed from the beginning of May until the end of October by approximately 200 young cows. The area is divided in three parts:

- OBK, which stands for Oud Beweide Kwelder (Old Grazed Salt marsh), is the area between the dyke, which separates the embanked pasture area and the salt marsh, and the first creek. This area has always been grazed.
- NBK, which stands for Nieuw Beweide Kwelder (Newly Grazed Salt marsh), is the area in between the first and the second creek. This area has been grazed since 1972.
- TBK, which stands for Toekomstige Beweide Kwelder (Future Grazed Salt marsh), is the area in between the second creek and the third creek. Grazing in this area has started only in 1989. (Verweij 1999)

This research project will focus on the NBK. When grazing was started in 1972, relatively small areas were fenced to prevent cattle-grazing. These exclosures were set up to monitor the development of the vegetation in the presence and absence of cattle-grazing (Bakker 1989). In figure 4.1, these exclosures are indicated by I-V. Another exclosure was erected by Bos in 1998, which will be reffered to as the D-exclosure.

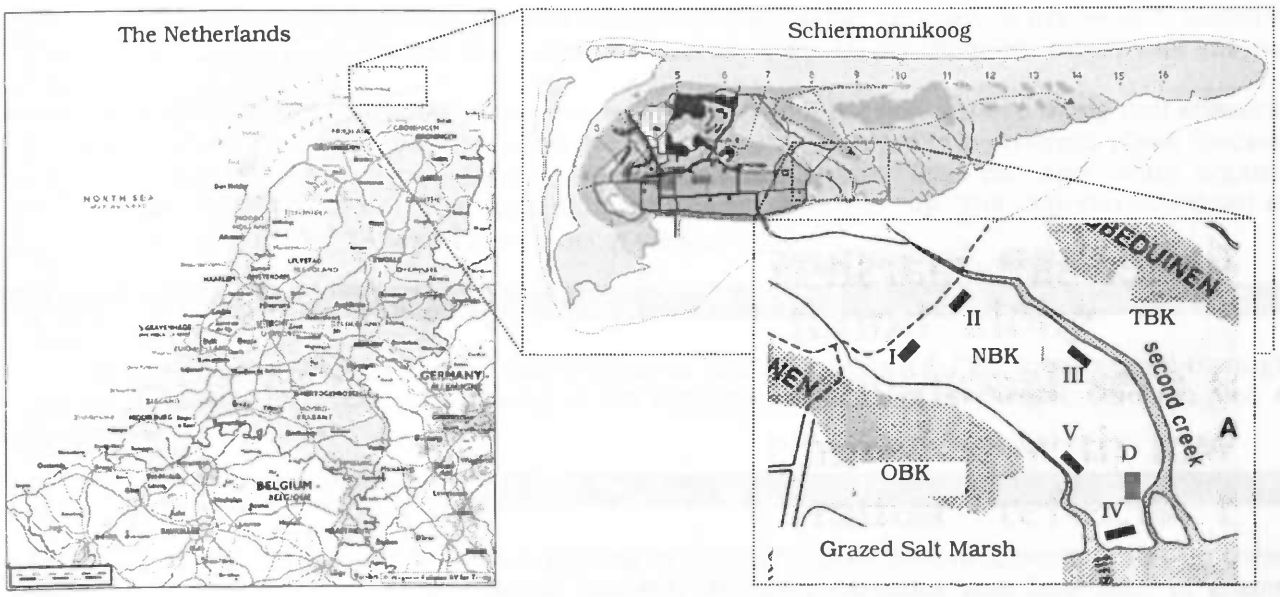

Figure 4.1: The salt marsh on the island of Schiermonnikoog, the most eastern of the 5 main barrier islands along the northern coast of the Netherlands. Three grazed areas: OBK, NBK and TBK. Shown on the NBK: D-exclosure (4 years) and exclosure I-V (30 years). See text for further information.

4.2 Analytic, measuring and recording methods

4.2.1 Faeces analyses

Faeces of hares contains a lot of undigested material which makes it possible to recognize the plant species that hares consume. Plant species can be identified by characteristics of epidermal fragments such as size, form and position of cells and stomata, the structure of the edge of the leaf and the presence of hairs or thorns. Reference material composed of pictures, microscopic slides of epidermal cells of fresh plant material and a key (van Lieshout 1995; see Appendix 1) were used in this technique.
To ensure sufficient sample material, each sample had to contain at least 5 hare droppings. Preserving the sample material before analysis was done by drying the faeces in a stove at 70°C for 24 hours. After crushing and wetting the faeces, material was taken and spreaded as uniformly as possible on a microscope slide.
Microscope slides were made of 10 subsamples, each taken randomly from each sample. From each subsample, 10 plant fragments were identified. To account for differences in fragmentation size, the surface area was determined (Steward 1967). In this way, the percentage of occurrence of each plant species in the hare's faeces could be calculated.

4.2.2 Vegetation composition

Vegetation composition recordings were done on 2 by 2 metres squares. The presence of each plant species and the area each plant species covered were recorded using the Londo scale (Londo 1976).

4.2.3 Food plant quality

As it has been described in several studies, *Festuca rubra* is the main plant species consumed by hares (van der Wal, 1999). Therefore the decision was made to use this monocotyledonous species for quality analysis and the percentage of nitrogen as a rough measure of protein content was measured. In the field, the tips of *Festuca rubra* leaves were collected and dried in the dry stove at 70°C for 24 hours. In the laboratory the dried material was pulverised and the analysis was performed by the laboratory assistant.

4.2.4 Biomass

To find out how much of each food plant is present and available in terms of dry weight, biomass samples were taken. Each sample consisted of a turf of 10 by 10 centimetres, which was cut out of the soil.
In the laboratory all organic material was cut off at the level of the soil surface using nail scissors. The dead material was separated from the living material and sorted into different plant species. In general, samples were sorted into 5 categories: dead organic material and living organic material from *Festuca rubra*, 2 other dominant species and a rest group. The material was dried in a drying stove at 70°C for 24 hours before being weighed.

4.2.5 Vegetation heights

The height of the standing vegetation was measured using a calibrated PVC tube pierced through a Styrofoam disc, which rested on the top of the vegetation indicating the height. On each plot, 6 measurements were taken.

4.2.6 Hare dropping counts

A good indication of the amount of hare grazing is the amount of hare droppings found on these sites. A good correlation has been found between dropping densities and frequency of grazed shoots by Daniels (2000).
One of the conditions for correct results was that the dropping counts had to be carried out within certain time limits to prevent decomposition. Personal observations in the field showed that during persistently wet conditions, hare droppings would perish after 2 weeks, but dry conditions

could conserve hare droppings almost up to 2 months, if not longer. Therefore the decision was made to carry out dropping counts every week.
Another condition is that all counted hare droppings had to be removed from the fixed plots to prevent double-counting the next time.
Furthermore there has been some discussion about the reliability of the method in case the plots would be marked by sticks. These are thought of functioning as an attractive restroom for the hares. However unpublished experiments have shown that this only occurs in case the used sticks protrude fairly distinctly above the vegetation. In this research, attempts have been made to use sticks as low as possible to prevent these effects.

4.3 Selection and avoidance of food plant species by hares in grazed and ungrazed areas

4.3.1 Faeces analyses

Faeces material was collected from the NBK (representing grazed area) and from the nearby area between the 3rd and 4th creek because usage of faeces material from the old cattle-exclosures would give an incorrect representation of ungrazed areas. As faeces production takes at least a couple of hours after consumption of the concerning plant material and that the surface of the cattle exclosed areas is extremely small compared to the rest of the grazed area, the probability of analysing faeces which contain plant material actually consumed inside the cattle-exclosures would be minimal.
From both grazed and ungrazed areas, 6 samples of hare faeces were collected.

4.3.2 Vegetation composition

From both grazed and ungrazed areas, 6 sites were chosen randomly, but linked to the sites from the diet analysis samples and from each site, 6 vegetation composition records were made.

4.3.3 Diet selection

By combining the percentage of a plant species presence in the diet with the presence in the vegetation in grazed and ungrazed areas, it is possible to find out what plant species hares select for, which plant species they avoid and to compare this among grazed and ungrazed areas.
Selection occurs when the concerned plant species is found significantly more in the diet than it is present in the vegetation, while avoidance occurs when the plant species supply in the vegetation is significantly larger than the percentage found in the diet. A neutral valuation occurs when presence in the vegetation has the same value as the presence in the diet.
In graphical terms, in a diagram with the percentage of a plant species presence in the vegetation on the x-axis and the percentage of a plant species presence in the diet on the y-axis, every plant species found above the line x=y will indicate selection, every plant species found under this line will indicate avoidance and every plant species found on this line will indicate indifference.

4.3.4 Quality of *Festuca rubra*

From both grazed and ungrazed areas, 6 samples of *Festuca rubra* were taken for quality measurements on the same sites as the hare faeces had been collected and the vegetation composition had been recorded.

4.4 Short-term (seasonal) effects by cattle grazing: Hare feeding preference for quality or biomass

In order to find the preference hares might show in the process of choosing their grazing site, an experiment was set up to manipulate biomass and quality of the vegetation. To find out if there would be a seasonal effect on possible preference, the experiment was repeated later in the season (Session I and Session II)
The experiment was set up in a *Festuca rubra* vegetation type, as this grass species has been shown to be the hare's favourite food plant.
Both sessions consisted of a row of 24 plots, each plot represented by a square of 4 square metres (Figure 4.2). In both sessions, 4 different treatments were spread randomly among the plots. These 4 treatments were:

- C = Control
- F = Fertilized
- M = Mown
- F+M = Fertilized + Mown

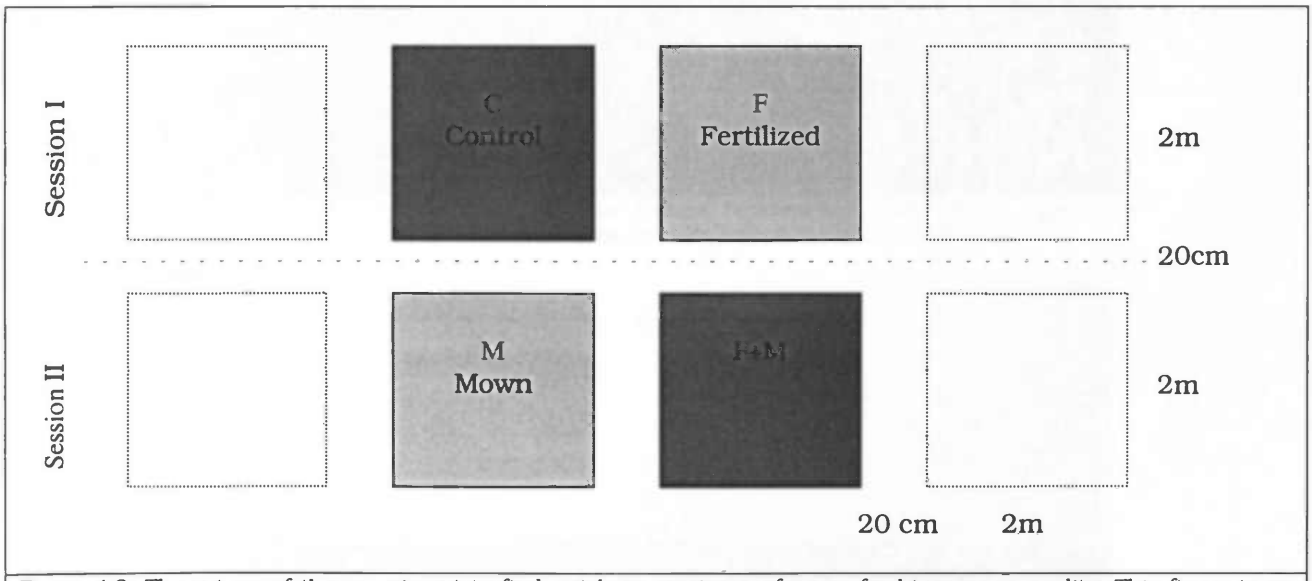

Figure 4.2: The set up of the experiment to find out hare grazing preference for biomass or quality. This figure is an indication of how the plots were set up in the field and it does not show all 24 plots. See text for further explanation.

Fertilisation using 12.5 gN/m^2 with nitrogen-based commercial fertiliser ($CaCO_3 \cdot NH_4NO_3$, 27%, concentration 125 Kg N ha^{-1}) was performed twice, for both sessions at the same time. First fertilisation took place on April 25 and the second on May 20.
Mowing was performed approximately 1 to 1.5 weeks before opening of each session. For session I, mowing was performed during the period of May 16 and May 22. Unfortunately due to problems with the cutting device, mowing session II was performed on June 25, using manual shears.
The experimental site was continuously exclosed from cows by electric fence and temporarily exclosed from hares by chickenwire fencing until each of the sessions opened.
The first session was opened to grazing on May 29, 2002 and the second session was opened on July 4, 2002.
Before the opening of each session to grazing, several initial measurements and samples were taken on the local vegetation of each individual plot: quality samples of *Festuca rubra* and biomass samples were taken and analysed, vegetation heights were measured and vegetation composition was recorded. Dropping counts were done every week during a period of 4 weeks after opening each session. Figure 4.3 and 4.4 show the experimental plots in the field.

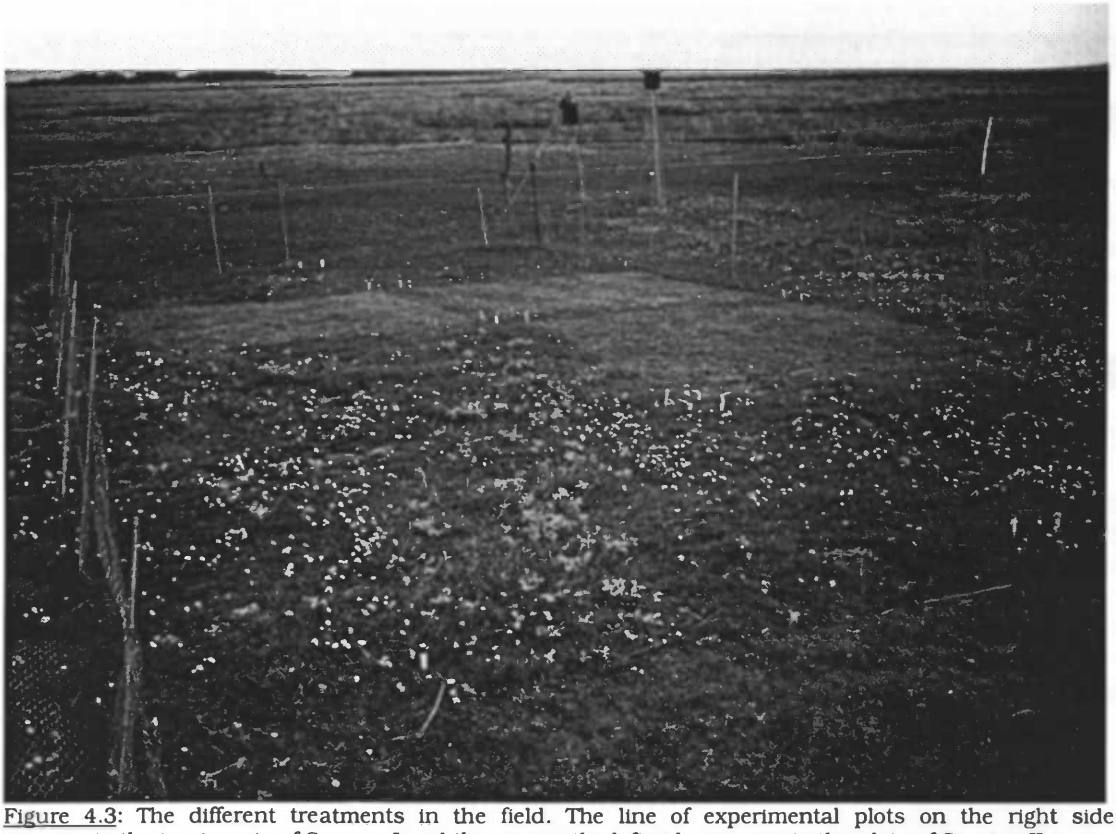

Figure 4.3: The different treatments in the field. The line of experimental plots on the right side represents the treatments of Session I and the row on the left side represents the plots of Session II.

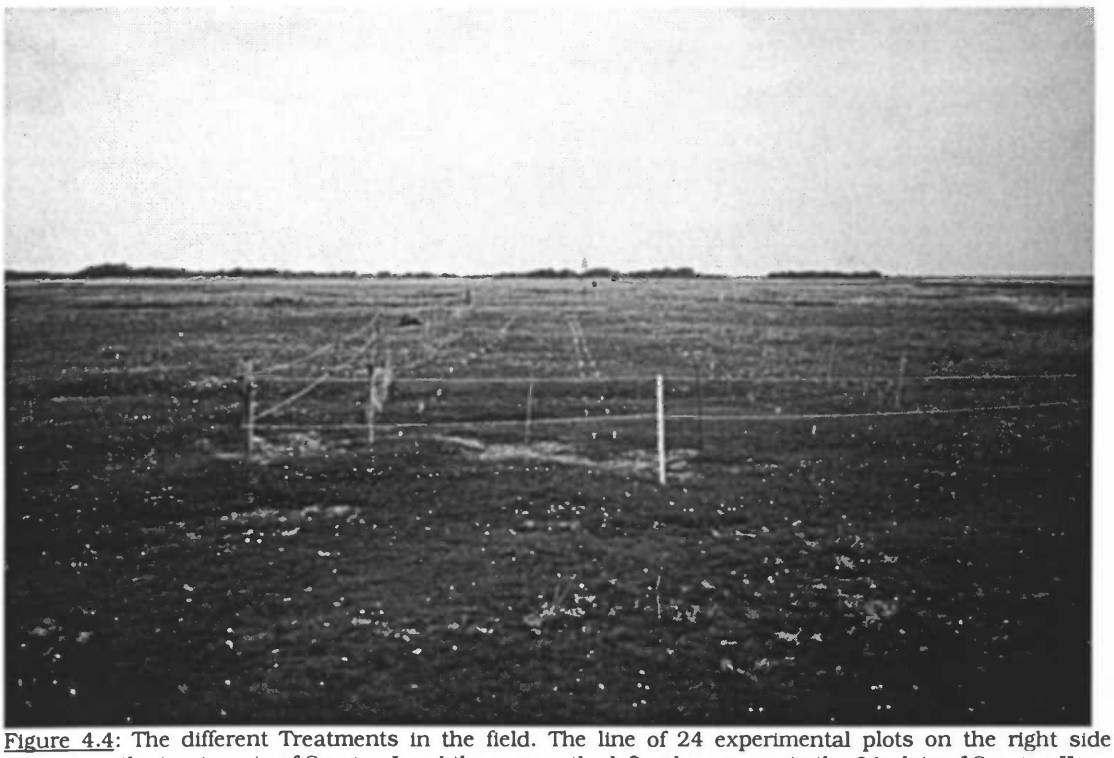

Figure 4.4: The different Treatments in the field. The line of 24 experimental plots on the right side represents the treatments of Session I and the row on the left side represents the 24 plots of Session II.

4.5 Long term (multiple years) effects: Cattle-exclosures and hare grazing

4.5.1 The D-exclosure: Cattle-grazing excluded for 4 years

The exclosure is fenced off by electric fence to keep out cattle but is set up in such a way that hares can move in and out freely. Dropping counts were performed on equally spaced 6 permanent plots inside and on 6 permanent plots outside the exclosure during the period between April 11 and August 1, 2002. The quality of *Festuca rubra*, the biomass of the vegetation, the height of the vegetation and the composition of the vegetation were measured.

4.5.2 The old exclosures: Cattle-grazing excluded for 30 years

The old exclosures, which were built in 1972, are fenced off by barbed wire and electric fencing but hares can move in and out freely (Figure 4.5).
Dropping counts were performed on 6 fixed plots inside and on 6 fixed plots outside the exclosures during the period between May 15 and August 1, 2002. The fixed plots were set up arbitrarily in relation to present vegetion structures, though systematically, in order to facilitate finding them again.
The height and the composition of the vegetation was measured in all the plots inside and outside the exclosures. As no significant amounts of *Festuca rubra* were found inside the exclosures, it was decided not to perform any quality or biomass analyses inside and outside the old exclosures.

Figure 4.5: Long term exclosure number V on the NBK. Cattle grazing occurs outside the exclosure.

5 Results

5.1 Selection and avoidance of food plant species by hares in grazed and ungrazed areas.

No significant differences in the amount of *Festuca rubra* in the diet were detected between the cattle-grazed areas and ungrazed areas (Figure 5.1; df=10, F=0.772, P=0.449). *Elymus athericus* increased significantly in the diet of the hares in the ungrazed areas (df=10, F=3.388, P=0.035) contrary to *Puccinellia maritima*, which was significantly higher in grazed areas than in ungrazed areas (df=10, F=1.708, P=0.019). There were no significant differences found between the grazed and ungrazed areas in the presence of *Juncus gerardii* (df=10, F=0.088, P=0.421) or the dicotyledonous plant species (df=10, F=1.375, P=0.496). Dicotyledonous species found in the faeces included *Plantage maritima* and *Aster tripolium*.

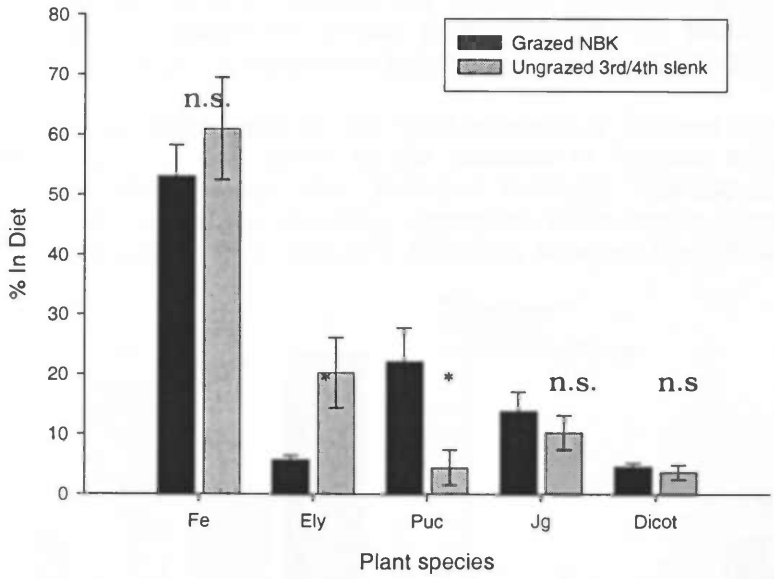

Figure 5.1: Percentage of food plant species present in the diet of hares in grazed and ungrazed areas. Fe: *Festuca rubra*; Ely: *Elymus athericus*; Puc: *Puccinellia maritima*; Jg: *Juncus gerardii*; Dicot: Dicotyledonous species. * and ** indicate significant differences (P<0.05 and P<0.01 resp.) using independent samples T-test.

The vegetation in the grazed and ungrazed areas was recorded and the cover was plotted against the percentage in diet in order to determine the selectivity behaviour of the hares for certain food plant species (Figure 5.2). Although 53.1% and 61.0% of the analysed hare faeces collected in grazed areas and ungrazed areas, respectively, is represented by *Festuca rubra*, the percentages of *Festuca rubra* found in the vegetation are considerably lower (18.1% and 20.1% respectively). This indicates selective behaviour by the hares for *Festuca rubra*. Hares tend to avoid *Elymus athericus* and *Juncus gerardii*. Hares seem to be neutral about *Puccinellia maritima*.

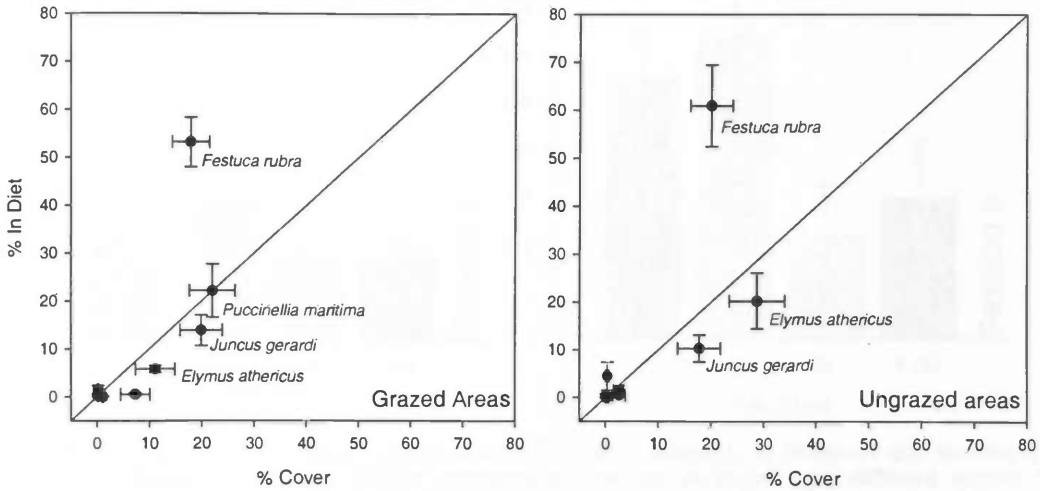

Figure 5.2: Comparison of the percentage of different food plant species presence in the local vegetation with the presence in the diet of hares in grazed and ungrazed areas. Bars represent standard errors.

The position of the plots in relation to the line y=x determines selective, avoidance or neutral grazing behaviour by the hares towards different food plant species. By a rule of thumb selectivity or avoidance was considered significant if, in graphical terms, the distance between the concerning plot and the line y=x is at least two standard errors. This cannot be tested statistically.

5.2 Short-term (seasonal) effects by cattle grazing: Hare feeding preference for quality or biomass

The effects of the different treatments on the quality of *Festuca rubra* are shown in Figure 5.3. Addition of nitrogen causes a significant increase in quality of the *Festuca rubra* plants in Session I, expressed as the percentage of nitrogen representing total protein content (Figure 5.3; df=1, F=122.379, P=0.000). A significant increase in nitrogen content of *Festuca rubra* by mowing was also found (df=1, F=9.064, P=0.007). Addition of nitrogen causes a highly significant increase in quality of the *Festuca rubra* plants in Session II (df=1, F=15.717, P=0.001). A highly significant increase in nitrogen content of *Festuca rubra* by mowing was found (df=1, F=63.454, P=0.000).

The effects of the different treatments on the total biomass of *Festuca rubra* are shown in Figure 5.4. No significant difference was found in the biomass of *Festuca rubra* among the different treatments in Session I (Fertilisation: df=1, F=0.416, P=0.526; Mowing: df=1, F=3.147, P=0.091). Concerning the total biomass of the standing vegetation there was a significant treatment effect: (graph not shown; Fertilisation: df=1, F=5.784, P=0.026; Mowing: df=1, F=23.097, P=0.000).

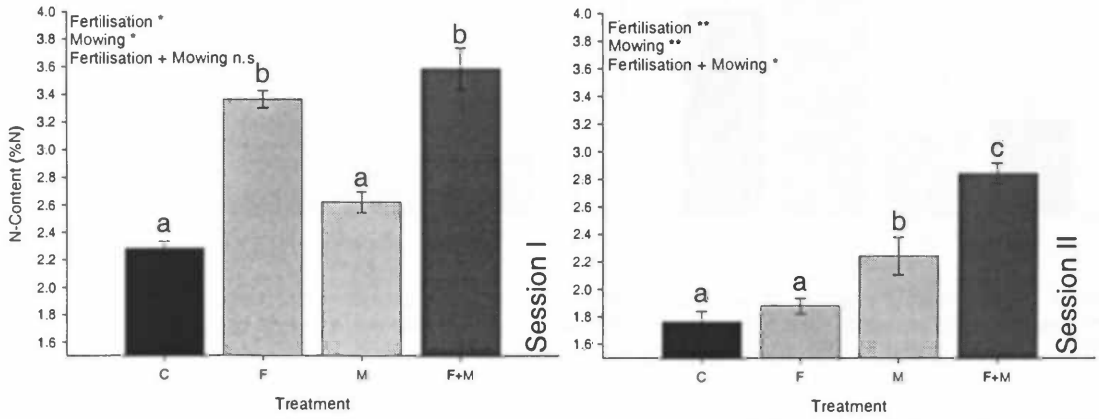

Figure 5.3: Quality of *Festuca rubra*, expressed as percentage nitrogen, for the different treatments in Session I and Session II. Significant differences (P<0.05) using the Tukey's multiple comparisons test are indicated with different letters; * indicates significant effects (P<0.05) and n.s. stands for non-significant effects using ANOVA. C: Control; F: Fertilisation; M: Mowing; F+M: Fertilisation + Mowing.

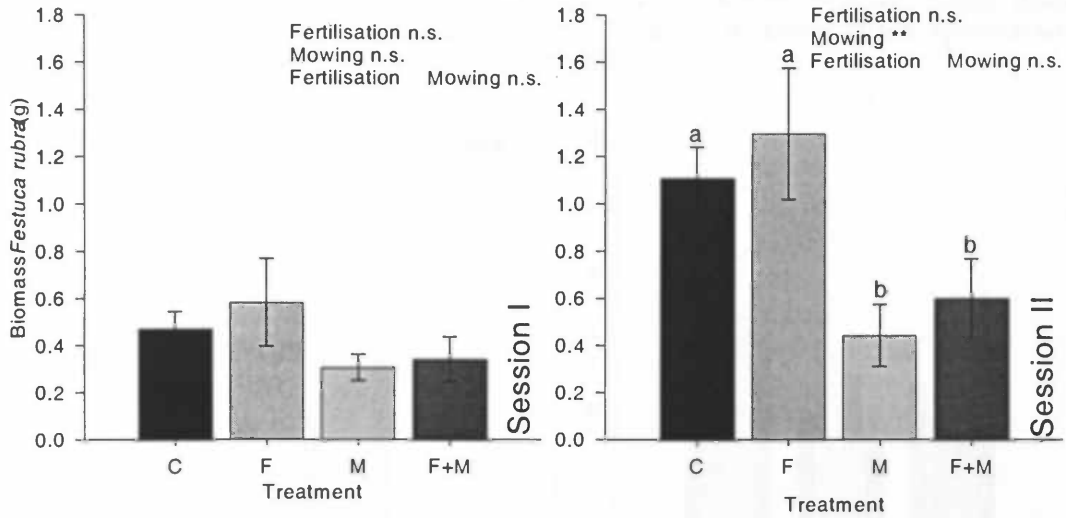

Figure 5.4: Total biomass of *Festuca rubra* in grams for the different treatments in Session I and Session II. Significant differences (P<0.05) using the Tukey's multiple comparisons test are indicated with different letters; ** indicates significant effects (P<0.01) and n.s. stands for non-significant effects using ANOVA. C: Control; F: Fertilisation; M: Mowing; F+M: Fertilisation + Mowing.

The biomass of *Festuca rubra* later in the season (Session II) had considerably increased. A significant decrease due to mowing later in the season was found (df=1, F=13.437, P=0.002). No significant increase could be ascribed to fertilisation (df=1, F=0.855, P=0.366). Again there were significant treatment effects on the total biomass of the standing vegetation: fertilisation caused an increase and mowing caused a decrease of total biomass (graph not shown; Fertilisation: df=1, F=27.1311, P=0.000; Mowing: df=1, F=113.680, P=0.000).

Figure 5.5 shows the effects of the different treatments on the height of the vegetation. As expected, mowing reduced the height of the vegetation significantly (Session I: df=1, F=25.730, P=0.000; Session II: df=1, F=180.217, P=0.000). Relatively early in the season (Session I), the vegetation in the mown plots was between 3.5-4.8 cm high and in the unmown plots 2.7-2.9 cm high. The vegetation on the mown plots later in the season (Session II) was 10.3-14.8 cm and in the unmown plots 4.2-4.8 cm high. Fertilisation caused the vegetation on the fertilised plots to be significant higher than the unfertilised plots in both sessions (Session I: df=1, F=7.165, P=0.14; Session II: df=1, F=18.820, P=0.000). Tiller lengths measurements showed the same pattern but are not shown here.

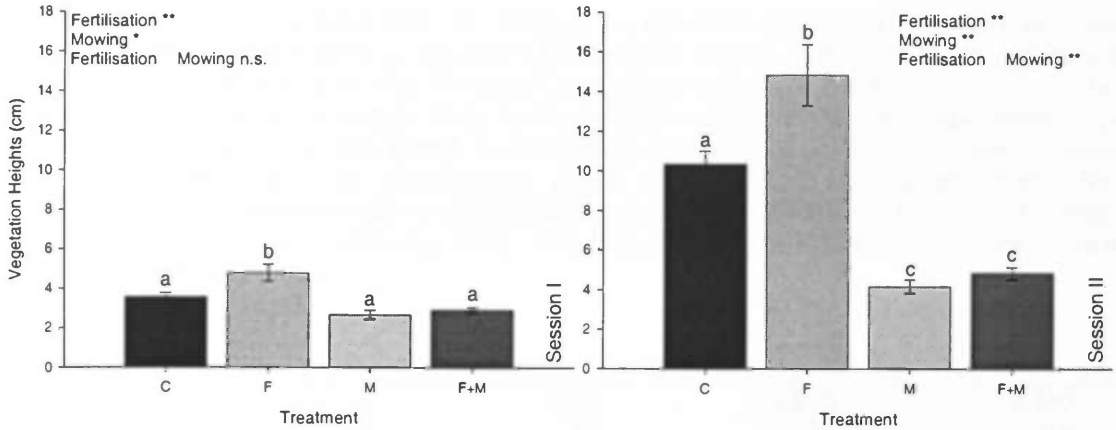

Figure 5.5: Vegetation heights in centimetres for the different treatments in Session I and Session II. Significant differences (P<0.05) using the Tukey's multiple comparisons test are indicated with different letters; * and ** indicate significant effects (P<0.05 and P<0.01 resp.) and n.s. stands for non-significant effects using ANOVA. C: Control; F: Fertilisation; M: Mowing; F+M: Fertilisation + Mowing.

The main species found on the site of the experiment were *Festuca rubra*, *Juncus gerardii* and *Agrostis stolonifera*. The coverage of these species and *Elymus athericus* on the different experimental plots is presented in Figure 5.6. Species composition was not different between the treatments in either Session I or Session II.
In Session I, the vegetation was generally composed of 35-45% *Festuca rubra*, 25-35% *Agrostis stolonifera* and 15-25% *Juncus gerardii* while in Session II, these three species were generally more equally distributed, within the range of 15-35%.

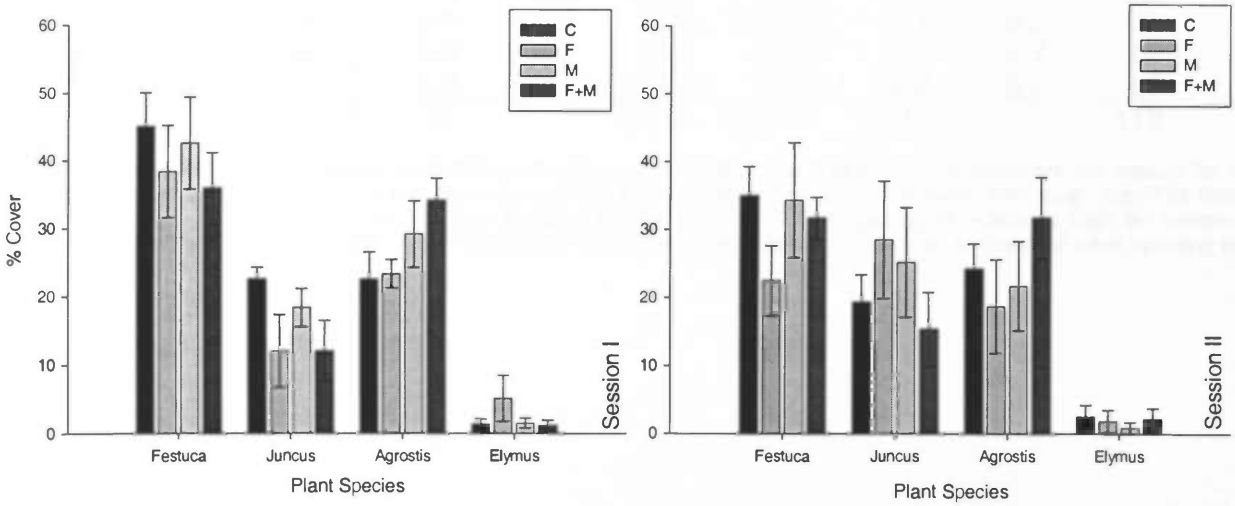

Figure 5.6: Percentage cover of *Festuca rubra*, *Juncus gerardii*, *Agrostis stolonifera* and *Elymus athericus* for the different treatments of Session I and Session II. C: Control; F: Fertilisation; M: Mowing; F+M: Fertilisation + Mowing.

Hare grazing intensity expressed as the amount of collected hare droppings found on the experimental sites is shown in Table 5.1. The numbers of counted hare droppings found on the experimental plots show considerable temporal fluctuations which makes it rather complicated to find any trend in hare feeding preference. The droppings found as soon as possible after opening of the experiment could be argued to be the most relevant. The first day with a high grazing pressure is therefore selected for analysis. This shows the initial preference, as afterwards, the plots are not in their original state anymore and it is expected that differences will diminish as the experiment progresses.

For Session I, this means that the count performed only 21 days after opening the exclosure is the most relevant when a total of 154 hare droppings were found in contrary to the 'counting days' before, when only 11 and 18 hare droppings were found during the first and second week respectively. However using a univariate analysis of variance on the accumulative total after 21 days, no significant treatment effects were found for fertilisation or mowing, i.e. no significant preference by the grazing hares (ANOVA fertilisation: df=1, F=1.828, P=0.191 mowing: df=1, F=0.001 P=0.973, fertilisation * mowing: df=1, F=0.179, P=0.677).

Regarding Session II, which opened later in the season, the first day of high grazing pressure was apparent after 13 days when a total of 496 hare faeces were found. Although there appears to be a clear trend with higher number in the fertilised and the fertilised + mown treatments, the huge standard errors caused by the unequal distribution of hare faeces within the experimental plots of similar treatments undermines this trend. A univariate analysis of variance on the accumulative counts after 13 days supports this observation. Again no significant feeding preference by hares could be demonstrated experimentally (ANOVA fertilisation: df=1, F=0.912, P=0.351 mowing: df=1, F=0.054 P=0.819, fertilisation * mowing: df=1, F=3.358, P=0.082). For more detailed information on statistics, see Appendix 10.2.

Session I (29/5/2002)

Date 2002	6/6		13/6		19/6		26/6	
Total days	8		15		21		28	
	mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.
Control	0.2	0.2	0.2	0.2	5.5	1.8	10.5	4.2
Fertilised	0.3	0.4	0.8	0.7	7.5	2.0	5.5	1.3
Mown	0.0	0.0	1.7	0.8	10.8	4.9	5.2	1.5
Fertilised + Mown	1.3	1.2	0.3	0.2	1.8	1.4	11.0	2.3
Total	11		18		154		193	

Session II (4/7/2002)

Date 2002	11/7		17/7		24/7		1/8	
Total days	7		13		20		28	
	mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.
Control	0.3	0.2	16.3	9.7	3.3	1.7	0.2	0.2
Fertilised	0.0	0.0	25.8	16.0	0.2	0.2	9.7	4.2
Mown	0.2	0.2	12.0	4.1	1.2	0.7	4.7	1.5
Fertilised + Mown	1.2	0.7	28.5	6.8	1.0	0.3	4.2	2.4
Total	10		496		34		112	

Table 5.1: Hare dropping counts for the different treatments of Session I and Session II. Shown are the means for each treatment, the standard errors (s.e.) and the total amount of hare droppings found on each "counting" day. The data on the grey background is the most relevant data because (1) the yield of hare droppings is relatively high (in contrary to totals < 20 for example) for a possible significant result and (2) data were obtained as soon as possible after opening of the experiment.

5.3 Long term (multiple years) effects: Cattle-exclosures and hare grazing

5.3.1 The D-exclosure: Cattle grazing excluded for 4 year

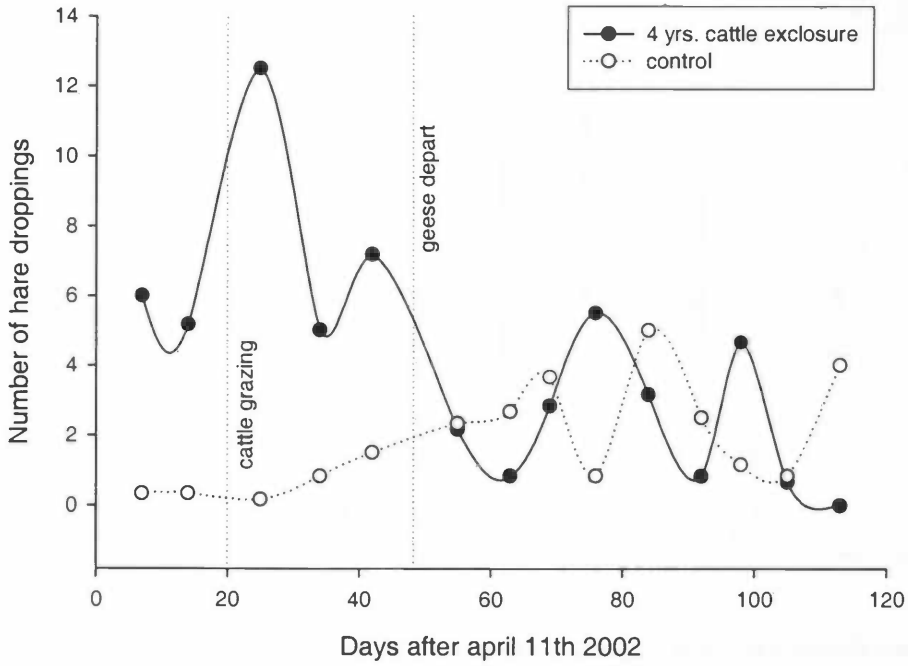

Figure 5.7: Number of hare droppings found inside (black circles) and outside (open circles) the area exclosed for 4 years for the period April 18 and August 1, 2002.

Figure 5.7 shows the results of hare dropping counts inside and outside the 4 years-old exclosure. Until about the end of May (day 50), hares tended to be grazing mostly inside the exclosure. After this day the grazing intensity inside and outside the exclosure seemed to fluctuate around an equilibrium.

In contrary to the results from the experimentally clipped plots, grazing had no effect on the quality of *Festuca rubra*. The nitrogen content of *Festuca rubra* inside and outside the exclosure did not differ (Figure 5.8.A; df=10, F=5.605, P=0.826). The biomass and the height of the vegetation measured over a period of 2 months during spring 2002 both inside and outside the exclosure increased although this increase was significantly different between the grazed and the ungrazed areas (Figure 5.8.B and C; Biomass 22/5: df=10, F=0.041, P=0.001; 24/6: df=10, F=0.268, P=0.169; 24/7: df=10, F=4.132, P=0.036; Vegetation Heights 22/5: df=10, F=0.000, P=0.000; 24/6: df=10, F=7.890, P=0.000; 24/7: df=10, F=9.484, P=0.000). There was a considerable and significant increase in vegetation biomass due to 4 years of excluding cattle grazing.

Figure 5.9 shows the distribution of different plant species inside and outside the 4 year-old exclosure. *Limonium vulgare*, *Juncus gerardii* and *Puccinellia maritima* were the most common species on the grazed areas. *Artemisia maritima* and *Agrostis stolonifera* dominated the cattle-exclosure. *Festuca rubra* was present in practically equal amounts both inside and outside the exclosure.

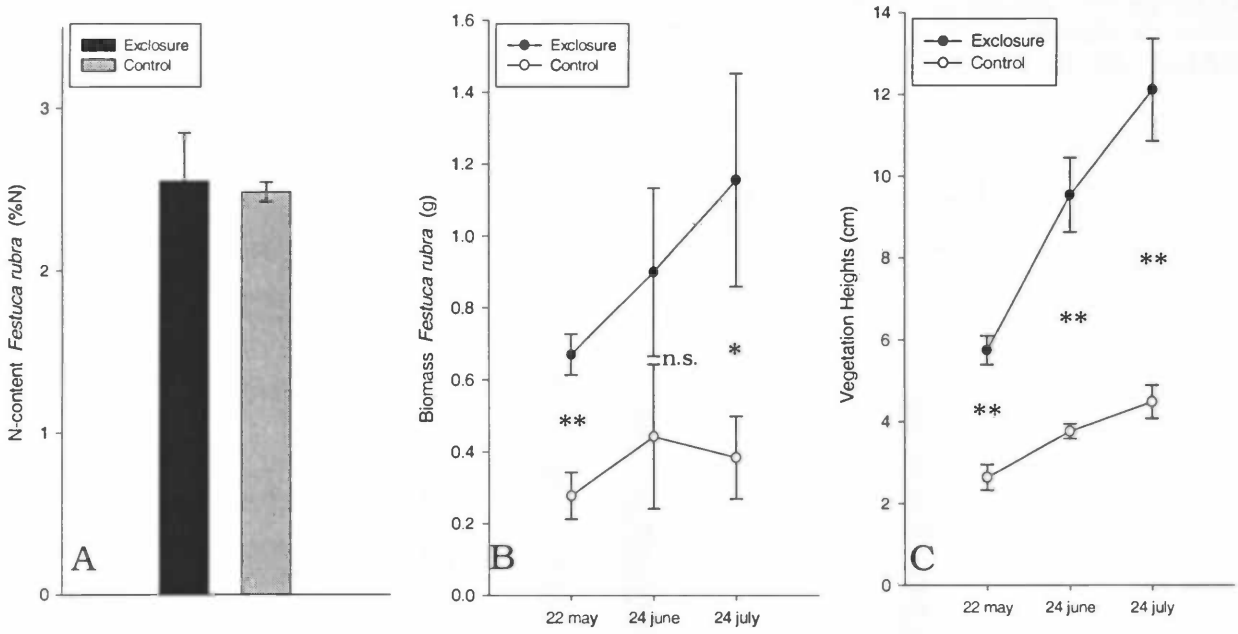

Figure 5.8: A. Quality of *Festuca rubra*, expressed as the percentage nitrogen, inside and outside the 4 year-old exclosure; B. Biomass of *Festuca rubra* in grams inside and outside the 4 year-old exclosure for 3 sampling times in the spring of 2002; C. Height of the vegetation inside and outside the 4 year-old exclosure for 3 sampling times in the spring of 2002. * and ** indicate significant differences (P<0.05 and P<0.01 resp.) and n.s. stands for non-significant effects using independent samples T-test.

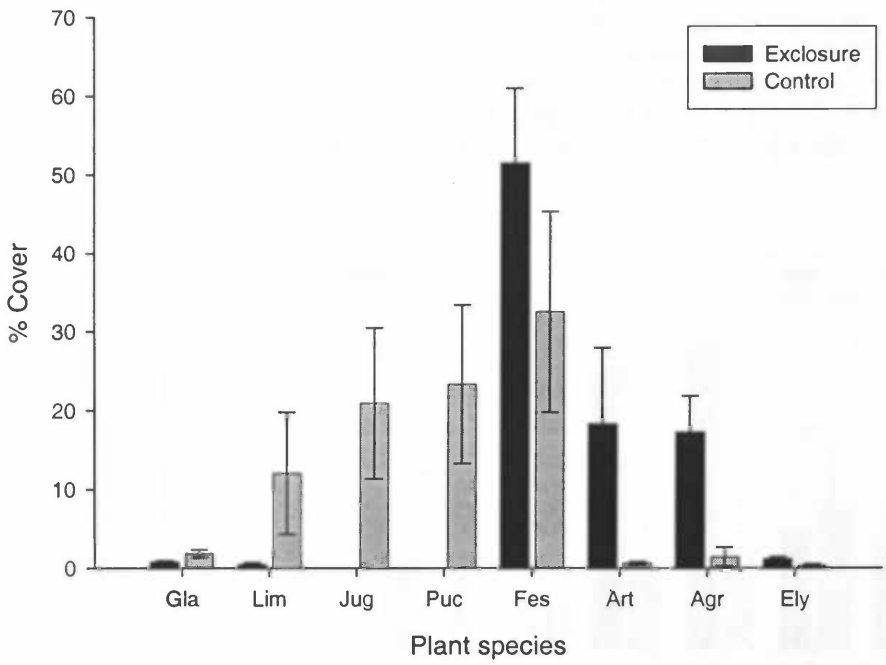

Figure 5.9: Percentage cover of different plant species inside and outside the 4 year-old exclosure. Gla: *Glaux maritima*; Lim: *Limonium vulgare*; Jug: *Juncus gerardii*; Puc: *Puccinellia maritima*; Fes: *Festuca rubra*; Art: *Artemisia maritima*; Agr: *Agrostis stolonifera*; Ely: *Elymus athericus*

5.3.2 The old exclosures: Cattle-grazing excluded for 30 years

Figure 5.10 shows the results of the hare dropping counts inside and outside the exclosures. Hare dropping density was found to be significantly higher outside all exclosures compared to inside, with the exception of exclosure III. In exclosure III, hare dropping density was significantly higher inside the exclosure than outside (I: df=10, F=161.893, P=0.37; II: df=10, F=145.960, P=0.030; III: df=10, F=4.363, P=0.21; IV: df=10, F=15.077, P=0.008; V: df=10, F=13.999, P=0.018).

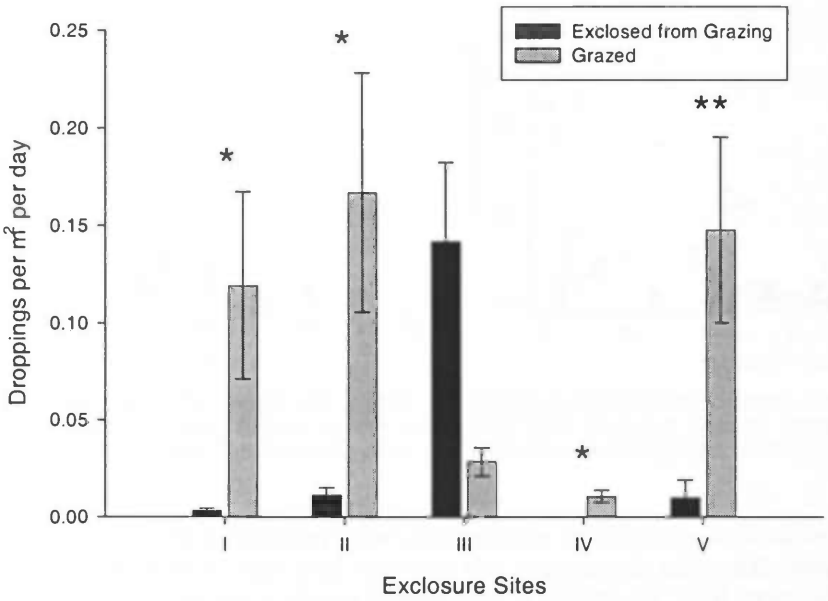

Figure 5.10: Hare dropping density inside and outside the areas (I-V) which have been exclosed from cattle grazing for 30 years. * and ** indicate significant differences (P<0.05 and P<0.01 resp.) using independent samples T-test.

Figure 5.11.A shows the presence of *Festuca rubra* inside and outside the exclosures. The *Festuca rubra* cover of exclosure number I is equal inside and outside the exclosure (3% on average). Exclosure number II has a 30% cover of *Festuca rubra* on average, compared to 10% on average outside. Exclosure number III has a more than 50% on average inside and 25% outside. In both exclosure number IV and V the *Festuca rubra* cover is around 20% on average outside the exclosures while inside there is no *Festuca rubra*. (Figure 5.11.A; I: df=10, F=0.017, P=0.903; II: df=10, F=0.785, P=0.118; III: df=10, F=0.291, P=0.125, IV: df=10, F=43.821, P=0.010; V: df=10, F=22.631 P=0.023).

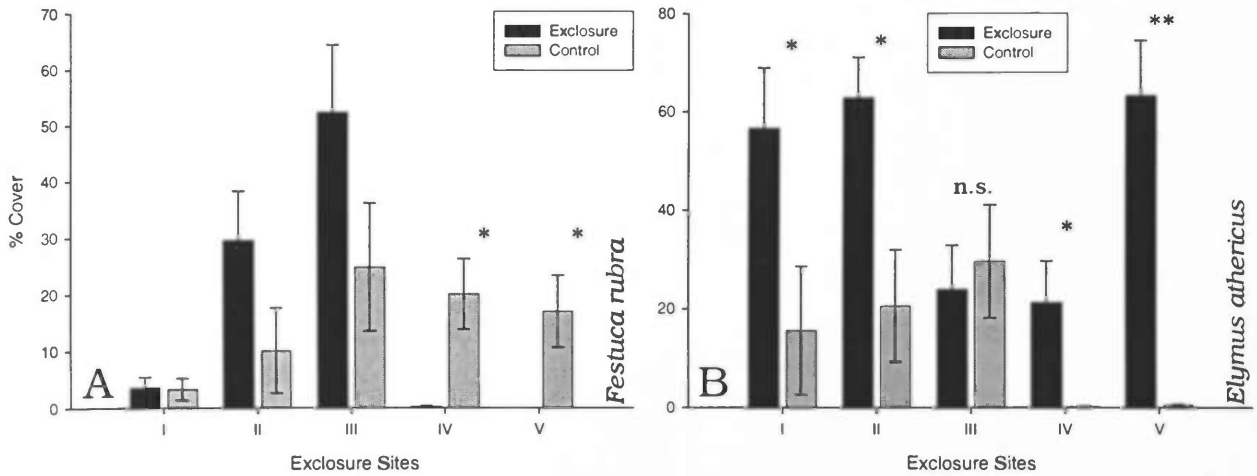

Figure 5.11: Percentage cover of *Festuca rubra* (A) and *Elymus athericus* (B) inside and outside the areas (I-V) which have been exclosed from cattle grazing for 30 years. * and ** indicate significant differences (P<0.05 and P<0.01 resp.) and n.s. stands for non-significant effects using independent samples T-test.

In all the exclosures, the relative abundance of *Elymus athericus* is significantly higher compared to outside the exclosures, with the exception of exclosure III where there is no difference. (Figure 5.11.B; I: df=10, F=0.081, P=0.45; II: df=10, F=1.945, P=0.013; III: df=10, F=1.331, P=0.708; IV: df=10, F=29.386, P=0.031; V: df=10, F=18.375, P=0.000).

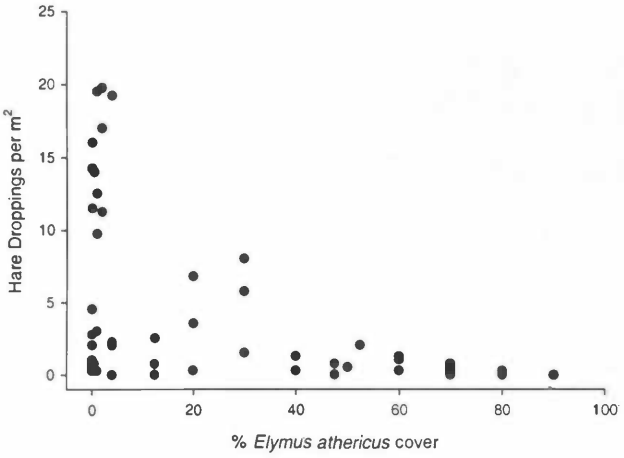

Figure 5.12: Relation between the percentage cover of *Elymus athericus* and hare dropping density inside and outside the areas which have been exclosed for 30 years.

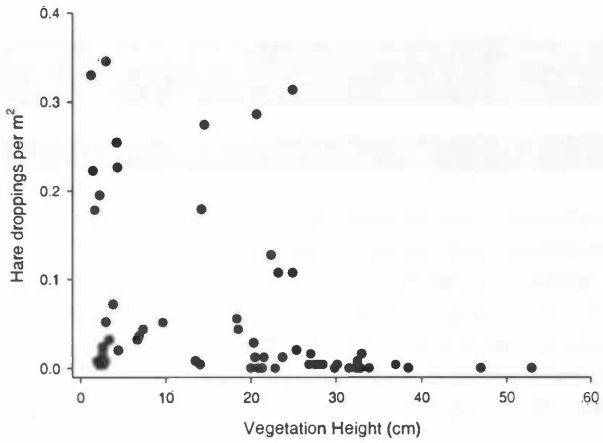

Figure 5.13: Relation between the height of the vegetation and hare dropping density inside and outside the areas that have been exclosed for 30 years.

Figure 5.12 shows the relation between the abundance of *Elymus athericus* and hare dropping density for all the plots both inside and outside the long-term exclosed areas. The plots with a cover of *Elymus athericus* less than about 30% show a relatively high grazing intensity by hares. The highest are found on areas lacking *Elymus athericus*. Similarly, the sites which show lowest hare grazing intensities have the highest *Elymus athericus* cover.

To a lesser extent, a similar relation could be found between the vegetation height and hare grazing intensity. Lowest numbers of hare droppings were found at plots with a vegetation higher than 25 centimeter (Figure 5.13).

6. Discussion

6.1 Selective Grazing Behaviour

As a confirmation of earlier studies (van der Wal 1999), *Festuca rubra* appeared to be the forage species which was mostly found in the diet of the hares in spring. Hares actively select for *Festuca rubra* in both grazed and ungrazed sites and avoid species like *Elymus athericus* and *Juncus gerardi*.

6.2 Short-term (seasonal) effects by cattle grazing: Hare feeding preference for quality or biomass

6.2.1 Early in the season (Session I)

Both mowing and fertilisation enhanced the quality of *Festuca rubra*, supporting the hypothesis that cattle grazing can effect the quality of the plant species in the short term. No significant effects on the biomass of *Festuca rubra* were found among the different treatments, while in contrast, there were significant effects on the total biomass of the standing vegetation. This suggests that the biomass of *Festuca rubra* did not seem to be altered by fertilisation or mowing, in contrary to the total vegetation biomass. However, fertilisation and mowing had no effect on the plant species composition. *Festuca rubra* was the main species to be found on all different plots, followed by *Juncus gerardi* and *Agrostis stolonifera*.
In summary, there was a significant effect of the treatments on quality of *Festuca rubra* but not on biomass. This means that hypotheses that hares would show preference or avoidance of manipulations of the biomass of *Festuca rubra* can not be tested as the biomass manipulations were not effective enough. No significant difference in hare grazing densities among the different treatments could be found, which means that the hares had no clear preference or avoidance of manipulations in quality. There might be a possibility that the differences among the treatments decreased in course of the experiment, but it seems unlikely to happen so quickly.

6.2.2 Later in the season (Session II)

As for Session I, both mowing and fertilisation significantly enhanced the quality of *Festuca rubra* in Session II. Mowing reduced the standing biomass of *Festuca rubra*, as well as the total biomass. Although fertilisation had no significant effect on the biomass of *Festuca rubra*, there was a big increase in the biomass of the total vegetation. Compared to the values of Session I, the biomass is much higher in Session II. This data was taken later in the season, when growth of the vegetation had progressed further. Again, the trends in biomass values mirror the trends in the height values of the vegetation. Mowing reduced the vegetation height and fertilisation on the unmown plot enhanced vegetation growth.
However, fertilisation and mowing again had no effect on the plant species composition. *Festuca rubra* together with *Juncus gerardi* and *Agrostis stolonifera* were the main species to be found on all plots.
At time of opening, the experimental plots exhibited clear differences in both quality and biomass of *Festuca rubra* at the moment of opening in contrast to Session I, though no differences in plant species composition.
However, no significant difference in hare grazing densities among the different treatments could be found, which means that the hares showed no clear preference or avoidance of manipulations in quality and biomass.
Again there might be a possibility that the differences among the treatments decreased in course of the experiment, but it seems unlikely to happen in such a short period.

An explanation for the low values of hare droppings at the beginning of both experiments might be that hares had to become accustomed to the 'new' situation of the experiment in the field. However, once they finally entered the area, their grazing intensity was very high, compared to the rest of the grazed salt marsh. The grazing intensities were 0.267 and 0.861 hare droppings per m^2 per day for Session I and Session II respectively, in contrary to the average grazing intensity of the grazed salt marsh for the period of half May until the end of July, which was only 0.0944 hare droppings per m^2 per day. Though it is no clear experimental evidence for this thesis, it is a strong indication that the experiment had an attractive effect on the hares of the salt marsh.

6.3 Long term (multiple years) effects: Cattle-exclosures and hare grazing

6.3.1 The D-exclosure: Cattle grazing excluded for 4 year

Hare dropping counts performed inside and outside the exclosure show a moderate change in grazing intensity on the grazed and ungrazed areas. There seems to be a clear preference for grazing inside the exclosure before the end of May while after this date, grazing inside and outside appears to be equal. Competition with Brent Geese (*Branta bernicla bernicla*), which depart around May, for the same foodplant (van der Wal, 1998) might be the cause. This is supported by the lower biomass of *Festuca rubra* and the decreased height of the vegetation at the end of May outside the exclosure (Figure 5.8.B and 5.8.C 22 May) These particular differences maintained by cattle-grazing does not effect hare grazing, as a confirmation of the short-term experiment.

Nevertheless, an effect of 4 years of cattle-grazing exclusion on the vegetation could be observed. Species found inside the exclosure represent comparably later successional stages than the species found outside the exclosure, which suggests successional retarding by cattle-grazing. Personal observations in the field confirm this idea, namely that inside the exclosure, as opposed to outside the exclosure, a fair amount of large *Elymus athericus* patches were observed. *Elymus athericus* is known to be the latest successional species on a salt marsh, which becomes dominant by outcompeting all the other plant species. Apparently the permanent plots used in this project were placed in such a way that they were not representative of the vegetation within the exclosures and missed the large *Elymus athericus* patches.
However, despite the change in vegetation within the exclosure, *Festuca rubra* is still abundant and grazing pressure by hares is equal inside and outside the exclosure.

6.3.2 The old exclosures: Cattle-grazing excluded for 30 years

With respect to the old exclosures, hares appear to avoid areas which have been excluded from grazing for 30 years, except one exclosed area (exclosure number III) which shows the reverse situation. These exclosures are characterised by old successional stages (van Wijnen, 1999).
Festuca rubra has been found to be the main food plant that hares consume (van der Wal, 1998) and actively select for (section 6.1) This might be an explanation for the observed hare grazing results. Inside exclosure number III, with a *Festuca rubra* abundance of more than 50% on average, a relatively high hare grazing density is found. However exclosure number II, with a *Festuca rubra* cover of 30% on average, showed a relatively low hare grazing density. A high hare grazing density is found on the area around exclosure number I, which has a low *Festuca rubra* cover (<5% on average). In summary, no clear relation could be found between *Festuca rubra* cover and hare grazing density.

Elymus athericus has been shown to be a strong light-competitor, which at old successional stages outcompetes shorter plant species (Olff *et al.* 1997), including *Festuca rubra*, and thus has the potential to effect the availability of *Festuca rubra*. The abundance of *Elymus athericus*, is significantly higher inside the exclosures, except for exclosure number III, which has an equal abundance inside and outside.
There is a relation between the percentage cover of *Elymus athericus* in the vegetation and hare dropping density. It shows that few hare droppings are found on areas with higher covers than 30% of *Elymus athericus* and the highest densities of counted hare droppings are found on areas where *Elymus athericus* is absent (Figure 5.12).
The low cover of *Elymus athericus* (and the high cover of *Festuca rubra*) inside exclosure number III can probably be explained by ant activity (personal observation). The high cover of *Elymus athericus* cover on the grazed areas surrounding exclosure number III (and exclosure number I and II), can be explained by the presence of *Juncus maritimus* patches, which are avoided by cow grazing and can be considered to be 'natural cattle-exclosures'.
The low cover of *Elymus athericus* inside exclosure number IV can be explained by the large abundance of the annual, *Atriplex prostrata*, which might be dispersed during storm surges (personal observation).

This hypothesis of the effect of structural plants is supported by experiments performed by Kuijper (2000), where hare grazing intensity was measured at sites in a *Festuca rubra* vegetation type with different densities of plastic plants, which mimicked *Elymus athericus* plants. Hare grazing intensities decreased at sites with higher concentrations of the imitation plants (Figure 3.5).

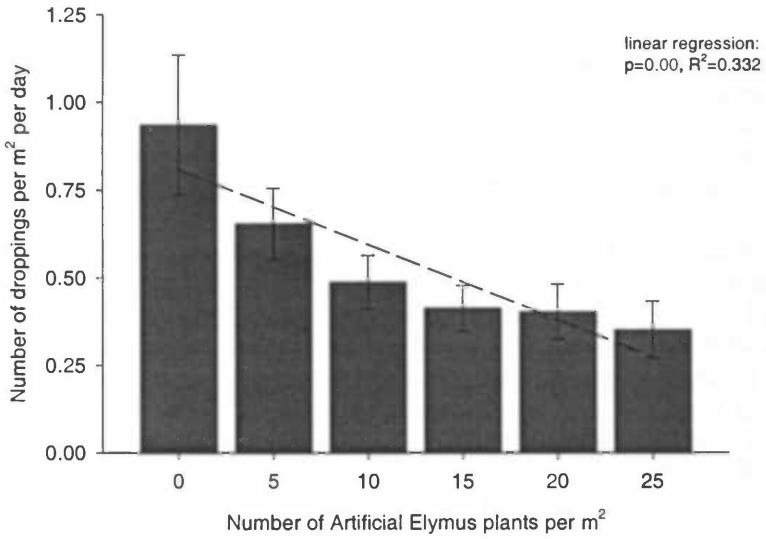

Figure 3.5: Relation between hare grazing intensity and the density of artificial plants, which mimic *Elymus athericus* plants, on the eastern part of Schiermonnikoog (unpublished results D. Kuijper)

7. Conclusions

On the salt marsh of the island of Schiermonnikoog, hares tend to actively select for *Festuca rubra*; 50 to 60 percent of their diet consists of this monocotyledonons plant.

Neither quality nor biomass manipulations of *Festuca rubra* caused the hares to show significant preference, not in the early growing season, neither later in the season.

Exclusion from cattle grazing for 4 years increased standing biomass, increased the height of the vegetation and had an effect on the composition of the vegetation. Later successional species were more abundant in the ungrazed area, which indicated that cattle grazing retards vegetation succession. Furthermore *Festuca rubra* was equally abundant inside and outside the exclosure. Hares did not show a clear preference for the grazed or the ungrazed areas.

Areas which have been excluded from cattle grazing for 30 years, characterised by old successional stages (van Wijnen, 1999), experienced very little to no hare grazing. The abundance of *Elymus athericus* appeared to be the most important factor, which deters hares. Extremely low hare grazing intensity was found in vegetation made up with more than 30% of *Elymus athericus* coverage and the highest dropping densities were found on sites with lacking *Elymus athericus*. The distribution and abundance of *Festuca rubra* cannot explain the hare grazing density results. Therefore it seems that the hypothesis concerning the indirect facilitative effect of cattle grazing on hare grazing, is not applicable. This suggests the need for alternate explanations about effects of structural plants, such as *Elymus athericus*, on hare grazing density.

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10. Appendices

10.1 Appendix 1: Identification Key of Plant Fragments in Hare Faeces

Resource: van Lieshout (1995)

1. * Huidmondjes 2
   * Geen Huidmondjes 19
2. * Huidmondjes zijn Haltervormig 3
   * Huidmondjes zijn Boontjes 8
3. * Celstructuur rechthoekig, vaak geribbelde cellen 4
   * Celstructuur opgeblazen, cellen glad 7
4. * Tussencellen Vierkant = *Puccinellia maritima* (OZ)
   Verdere kenmerken: randcellen bol, dakpansgewijs gerangschikt. Huidmondjes geconcentreerd per rij van cellen. Haltervormige huidmondjes (zonder ellips?) NB. Tussencellen hoeven niet vierkant te zijn, maar er zijn altijd vierkante aanwezig.
   * Tussencellen Nooit Vierkant 5
5. * Huidmondjes in rijen, ononderbroken door cellen. Ellips om haltertjes = *Elymus athericus* (OZ)
   * Niet in ononderbroken lijnen 6
6. * Onderscheid bedenken tussen *Spartina* en de bovenkant van *Elymus athericus*. *Elymus athericus* heeft dakpancellen als *Festuca rubra*, maar dan spits.
7. * Tussencellen aanwezig, haren uit tussencellen. Huidmondjes lang en smal = *Festuca rubra* (BZ)
   * Tussencellen niet aanwezig, geen haren maar wel korte stekels (?), huidmondjes verspreid = *Puccinellia maritima* (BZ)
   * Huidmondjes haltervormig en Ribbels in nerf = *Agrostis stolonifera*
8. * Dubbele Boontjes 9
   * Geen dubbele Boontjes 10
9. * Regelmatig, huidmondjes in rijen, gescheiden door rijen met lange smalle cellen. Cellen tussen huidmondjes zijn vierkant. Boontjes zijn soms bruin gekleurd. Evenwijdige nerven overeenkomstig met rijen smalle cellen = *Triglochin maritima*
   * Minder regelmatig, geen duidelijke indeling in rijen, cellen tussen de huidmondjes niet duidelijk vierkantig = *Armeria maritima*
10. * Huidmondjes op scheiding van twee cellen. Lijken in een grote cel te liggen omdat de scheiding van de twee cellen moeilijk zichtbaar is = *Plantago maritima*
    * Huidmondjes Niet op scheiding van twee cellen 11
    Steeltjes aanwezig of cellen op steeltjes (*Atriplex* + *Glaux*) 10B
    10 B: * Steeltjes, verder kunnen cellen gegolfd zijn, dikkere celwanden = *Glaux maritima*
    * Steeltjes of met een cel erop, verder cellen hoekig. Geen dikke celwanden onregelmatige structuur = *Atriplex portulacoides*
11. * Celwanden geribbeld als grassen, maar alleen aan de rand smalle rechthoekige cellen soort van dubbele boontjes = *Juncus gerardi*
    * Niet 12
12. * Cellen gegolfd 13
    * Cellen hoekig, tot afgerond 15
13. * Cellen licht gegolfd = *Artemisia maritima*
    * Cellen sterk gegolfd 14
14. * Huidmondjes groot en dik en in ander vlak i.t.t. *Spergularia maritima*. Cellen met dikke dubbele celwanden. Steeltjes! = *Glaux maritima*
    * Huidmondjes klein, cellen op rijen (?) Ook steeltjes (?) = *Spergularia maritima*
15. * Cellen rond huidmondjes kleiner. Rommelige structuur, cellen variabel, cellen geconcentreerd rond huidmondjes = *Limonium vulgare*
    * Niet 16
16. * Huidmondjes een beetje kleiner dan de omliggende cellen = *Aster tripolium*. Huidmondjes enigzins bovenop? Bijna bolrond, veel huidmondjes
    * Huidmondjes duidelijk een stuk kleiner dan de omliggende cellen 17
17. * Cellen op steeltjes = *Atriplex portulacoides*
    * Niet 18
18. * Huidmondjes onregelmatig van grootte. Veel huidmondjes, langwerpige boontjes ingeklemd. Grote hoekige cellen = *Sueda maritima*

* Huidmondjes regelmatig van grootte, cellen minder hoekig, veel huidmondjes = *Salicornia europaea*

19. * Celstructuur lange rechthoekige cellen, geribbeld, met smalle korte tussencellen = *Festuca rubra* (OZ)
    * Niet 20
20. * Weefsel bestaand uit heel veel kleine celletjes = *Enteremorpha*
    * Niet? Tja, dan houdt het op!

BZ/OZ = Bovenzijde/ Onderzijde

10.2 Appendix 2: Hare Preference Experiment Statistics

Session I
TREATMENT

Descriptives

	TREATMEN			Statistic	Std. Error
DROPPING	1.00	Mean		7.6250	1.66029
		95% Confidence Interval for Mean	Lower Bound	4.1904	
			Upper Bound	11.0596	
		5% Trimmed Mean		6.6667	
		Median		6.0000	
		Variance		66.158	
		Std. Deviation		8.13373	
		Minimum		.00	
		Maximum		34.00	
		Range		34.00	
		Interquartile Range		8.7500	
		Skewness		1.903	.472
		Kurtosis		4.283	.918

Tests of Normality

		Kolmogorov-Smirnov[a]			Shapiro-Wilk		
	TREATMEN	Statistic	df	Sig.	Statistic	df	Sig.
DROPPING	1.00	.190	24	.025	.805	24	.000

a. Lilliefors Significance Correction

Univariate Analysis of Variance

Tests of Between-Subjects Effects

Dependent Variable: DROPPING

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	1171.500[a]	3	390.500	.669	.581
Intercept	10668.167	1	10668.167	18.283	.000
FERTIL	1066.667	1	1066.667	1.828	.191
MOWING	.667	1	.667	.001	.973
FERTIL * MOWING	104.167	1	104.167	.179	.677
Error	11670.333	20	583.517		
Total	23510.000	24			
Corrected Total	12841.833	23			

a. R Squared = .091 (Adjusted R Squared = -.045)

Session II
TREATMENT

Descriptives

	TREATMEN			Statistic	Std. Error
DROPPING	1.00	Mean		21.0833	4.82330
		95% Confidence Interval for Mean	Lower Bound	11.1056	
			Upper Bound	31.0611	
		5% Trimmed Mean		18.3519	
		Median		14.0000	
		Variance		558.341	
		Std. Deviation		23.62923	
		Minimum		.00	
		Maximum		98.00	
		Range		98.00	
		Interquartile Range		25.7500	
		Skewness		1.809	.472
		Kurtosis		3.724	.918

Tests of Normality

		Kolmogorov-Smirnov[a]			Shapiro-Wilk		
	TREATMEN	Statistic	df	Sig.	Statistic	df	Sig.
DROPPING	1.00	.186	24	.031	.800	24	.000

a. Lilliefors Significance Correction

Univariate Analysis of Variance

Tests of Between-Subjects Effects

Dependent Variable: DROPPING

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	270.458[a]	3	90.153	1.441	.261
Intercept	1395.375	1	1395.375	22.305	.000
FERTIL	57.042	1	57.042	.912	.351
MOWING	3.375	1	3.375	.054	.819
FERTIL * MOWING	210.042	1	210.042	3.358	.082
Error	1251.167	20	62.558		
Total	2917.000	24			
Corrected Total	1521.625	23			

a. R Squared = .178 (Adjusted R Squared = .054)