Hare diet selection and feeding patch choice in relation to their food quality and availability in a salt marsh habitat

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1. Introduction

Herbivores make complex foraging decisions concerning the diet they select and where they choose to feed. Their foraging behaviour will be influenced by their own nutritional requirements and by the quality, availability and distribution of the food where they live, in addition to other necessities such as predator avoidance. The following study investigates the diet selection and feeding site choice of the Brown Hare (*Lepus europaeus*) within the salt marsh of the island of Schiermonnikoog (Netherlands).

Diet selection

Selection has been defined as an animal's preference modified by the possibilities the environment offers in selecting (e.g. Hodgson 1979). A selected diet can be seen as the combined result of food preference and food availability in the area in which the herbivore lives (Norbury & Sanson 1992). A herbivore's perception of food availability may be influenced by the abundance, distribution and accessibility of the food source (Crawley 1983).

There is no general agreement on which plant characteristics best explain herbivore food preference. Parameters used to describe food quality for herbivores are digestible energy, nutrient content (e.g. nitrogen), the proportion of digestibility reducing substances such as fibre content, lignins and tannins and the presence or absence of toxins (e.g. cyanogenic glycosides). The nutritional quality a food source has for a herbivore will depend on both the chemical components of the plant and on the nutritional requirements of the animal and the digestive system it is equipped with (Iason & van Wieren 1999).

Where herbivores choose to graze

Foraging efficiency is considered an important determinant of feeding patch choice by herbivores (Langvatn & Hanley 1993). Feeding patch quality for a herbivore is then sensibly looked at in terms of attainable energy or nutrient intake rate. Parameters affecting this intake can be summarized as the herbage quality and availability (Ungar & Noy-Meir 1988). The herbage quality in terms of nutritional quality of the different food plants can influence intake rate due to the selective feeding of the herbivore itself (Parker *et al* 1996) and due to the rate of food processing by the digestive system (Iason & van Wieren 1999). Food availability within a feeding patch is the vertical and horizontal distribution of herbage mass. Studies have demonstrated the relationship between herbage intake rate and different sward characteristics such as biomass, sward height and bulk density. Accordingly, these are the main parameters used to describe availability of food within a patch (Arnold 1987; Illius *et al* 1992; Parsons *et al* 1994).

Species composition of a feeding site can be expected to influence herbivore feeding patch choice in several ways. A high abundance of good quality food plants can be assumed to have a positive effect as it may enable a higher nutrient intake rate. The occurrence of less palatable plants among food plants can lower the encounter rate of the herbivore with it's food. These not eaten food plants can chemically mask the occurrence food species via toxins or odours or interfere with the abilities to find and feed on the food plants via large size or structures such as spines (Atsatt & Dowde 1976; Hay 1986).

The hares

Due to their small body size hares have a high metabolic rate that leads to high energy requirements. Small herbivores consume more food per unit body mass than larger herbivores. They are expected to require more high quality food than larger bodied grazers (Kleiber 1961). Hares are known to perform caecotrophy, which enables a more efficient digestion of the food. Brown Hares appear to perform caecotrophy less frequently than rabbits (van Laar 1995). A comparison between the diet of Brown Hares and that of their lagomorph relatives the Wild Rabbit (*Oryctolagus cuniculus*) showed that the latter was a more generalist feeder whereas hares were more selective for higher quality food (Chapius 1990). This difference was related to the different feeding ranges of the two species. While rabbit feeding is constrained to the close vicinity of their burrows, hares forage over larger areas with a wider range of food sources.

Brown Hares had fixed home ranges in the salt marsh. By radio-tracking hares all year round Kunst & Baarspul (1997) determined a home range size of 34 ha in my study site. The radio-tracked hares showed a large overlap in their home ranges (Kunst & Baarspul 1997). The same study also discovered that the hares spent a lot of time during the day in the dunes. Van der Wal *et al* (1998b) showed for spring that the hares mainly grazed on the salt marsh from evening to the early morning hours. Predators present that are known to attack adult hares are feral cats and two species of birds of prey, the Marsh Harrier (*Circus aeruginosus*) and Hen Harrier (*Circus cyaneus*) (pers. observation R. Drent).

Study objective

The hares on the saltmarsh of Schiermonnikoog with it's comparably low number of plant species and species compositions offer a good opportunity for investigating their diet selection and factors influencing where they choose to feed. My study lies within the context of ongoing research in the Schiermonnikoog salt marsh where the effect of different herbivores on plant competition is being studied. Previous studies on the interaction between hares and the island salt marsh vegetation showed that their winter feeding habits had a large impact on the system by retarding succession and thereby facilitating goose grazing (van der Wal *et al.* 1998d). Little is known on how the hares utilize the saltmarsh over the summer and what influences their distribution.

This study aims at investigating both hare diet selection and feeding patch choice in relation to seasonal food quality and availability in the salt marsh.

The research questions and hypotheses are the following:

1) I hypothesized that hares would selectively graze on high quality food due to higher nutrient per body mass requirements.

research questions:

2) How is hare choice of a feeding site affected by food availability and nutritional quality?

3) Do structure plants influence hare patch choice?

The thesis is divided into 3 parts consistent with the hypothesis and questions raised above:

The first section deals with the hare diet composition in relation to food plant availability and nutritional quality.

The second part concentrates on hare grazing preference for three vegetation types with high abundances *of Festuca rubra* in relation to the sward characteristics species composition, *F. rubra* biomass, *F. rubra* nutritional quality and cover of structure plants. *F. rubra* is expected to be the most important food plant over the summer (van der Wal *et al* 1998d).

Thirdly, an experiment was set up to test the effect of structure plants on hare feeding patch choice.

2. Materials and methods

The field season for the following study took place from 23 July to 15 December 1999. Many of the below described measurements were taken at three different times during this period. The timing of these measurements coincided with three periods distinguished within the field season as presented in table 1.

2.1. Study area

This study took place in the salt marsh of the Dutch Wadden Sea island Schiermonnikoog (fig.1). The marsh is situated on the eastern section of the island bordered in the North by dunes, which separate it from the North Sea. My study site lies within the ungrazed marsh around the 8th gully. This area was discovered to have the highest hare densities within the island salt marsh (Drost 2000).

The salt marsh vegetation begins at the edge of the mud flats with the Salicornia zone. Further inland follows the Limonium vegetation type and an area with the so-called "island vegetation" consisting of a mosaic of lower situated gullies with Puccinellia vegetation and slightly elevated "islands" with Artemisia vegetation. Along the lower edge of the 8th gully we find the Atriplex/Limonium zone. The middle marsh consists of *Festuca rubra* dominated vegetation, which can be sub-divided into the Festuca/Artemisia, Festuca and the Festuca/Elymus types, listed in order of increasing elevation height. Higher on the salt marsh lays the Elymus athericus zone followed by dune vegetation with high covers of *Ammophila arenaria* and *Elymus farctus.*

Table 1: Field season divided into three periods. Timing of the different measurements taken in the field.

Period:	1 23-Jul – 18-Aug	2 18-Aug – 20-Oct	3 20-Oct – 30-Nov
Number of dropping counts	4	4	3
Sampling of droppings for faecalanalyses	7.7 21.7 4.8	10.9 26.9 13.10	11.11 20.11 29.11
Biomass samples	20-Jul	4-Sept	6-Dec
Plant quality samples	9-Jul – 14-Jul	6-Sept – 11-Sept	31-Oct – 3-Nov
Grazing intensity veg. type level: - 8 veg. types		7-Oct - 10-Oct	
- Festuca, Artemisia, Festuca/Artemisia veg.	2-Aug – 17-Aug	7-Oct – 10-Oct	14-Dec – 15-Dec
Grazing intensity within Artemisia & Festuca/Artemisia veg.			28-Oct 29-Oct
Vegetation relevees	point quadrat: 26-Jun – 17-Jul	LONDO: 15-Oct – 18-Oct	

The main study area within which all measurements took place is situated on the low to middle marsh vegetation (fig.1, site B). A further section of the salt marsh mentioned in this thesis is an area selected on the basis of the hare home range size, referred to as site A (fig.1).

In spring during the main bird breeding season entrance to the salt marsh in strictly limited. From summer to winter all visitors have free access to the marsh. The *Puccinellia maritima* and *Festuca rubra* sites within the study area are frequented by Barnacle and Brent geese in spring, which leave for their breeding grounds around mid April and end of May, respectively. In autumn some geese return to the island, but are mainly in the polder area. Hares and rabbits are the only herbivores resident all year round. Rabbits are mainly found on the higher marsh and in the dunes, where they have their burrows. This leaves only the hares that utilize the middle to lower salt marsh vegetation during the summer and autumn months when my field work took place.

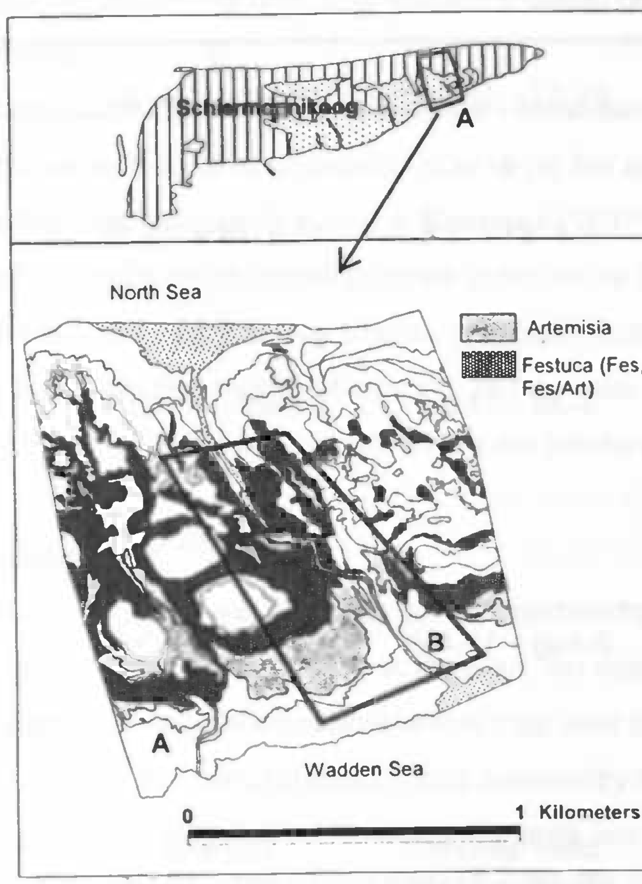


Figure 1: Study site on the island of Sciermonnikoog. Site A presents the area for which hare food availability was estimated. Site B is the main study area in which all measurements were taken.

2.2. Hare diet

Hare diet composition was determined by microscopial faecal analysis based on surface area of epidermal fragments (Steward 1967). The fragments were identified according to characteristics of the epidermal cells such as cell size, shape and hairs. Both half-digested epidermis fragments and the indigestible cuticule, which shows an imprint of the epidermal cells, are present in the faeces and enable this procedure. I did not correct for differences in leaf area verses biomass or for differential digestibility of different species.

Droppings for the faecal analyses were collected during dropping counts. A mixed sample consisting of about 40 droppings was collected from plots spread over the whole study site. The samples were frozen for later analyses. Hare diet composition was determined for three periods to take into account seasonal changes (tab.1). Three mixed samples collected during three successive dropping counts were analysed per period.

The faecal analyses were performed as described by De Jong (1997). For the analyses the de-frozen pellets of each sample were rubbed between fingers until they crumbled into a mass of plant fragments. A few grams fresh weight of the fragment mixture of each sample was blended with a mixer and washed over a bacterial sieve in order to free the cuticular epidermal structure from other cell material and wash away the smaller unidentifiable fragments. Per sample I estimated the area of 100 identified epidermal fragments using an ocular micrometer. A magnification of 80x was used. Epidermal fragments smaller than 4 micrometer grid squares were ignored. Those fragments not identifiable to species level were classed as monocotyledon, dicotyledon or unknown.

Percentages of the diet results were arcsine transformed for statistical analyses (Zar 1996).

2.3. Diet selection

I looked at diet selection by comparing food availability in the area with percentage in the diet. It was assumed that neutral feeding takes place when the proportion of a species in the area equals the proportion in the diet. A preference for a species being shown when the percentage in the diet is higher than the proportional availability and a non-preference when *vice versa* is the case (Crawley 1983).

A frequently used method of looking at diet selection is to calculate a selectivity index using the ratio between percentage in the diet and availability

(Norbury & Sanson 1992). However, due to the rough estimation of availability used in this study and generally due to difficulties in estimating food availability (Crawley 1983; Norbury & Sanson 1992) the following method as also used by van der Wal *et al* (1998c) was chosen. Hare plant species selection was looked at by plotting percentage in the diet on the y-axis against availability on the x-axis. A line was drawn at x=y to divide between preferred and non-preferred. A species was named preferred if it lay above the line and twice the standard deviation did not overlap the line. The same went for non-preferred species below the line. The rest were called neutral species (van der Wal *et al* 1998c).

In order to compare the diet results with food availability, home range size of the hares was used to decide on how large the area should be in which food availability was estimated. Kunst & Baarspul (1997) determined a home range size of 34 ha by radio-tracking hares in my study area. I selected a section of the island in such a way that an area with a radius of at least 660m (represents two times the radius of a round 34 ha home range size) surrounding each dropping plot lay within the set borders (fig.1, site A)

2.3.1. food availability

Proportional cover was used as an estimation of availability of potential food plants for hares occurring in the study area. An existing vegetation map of the island and the vegetation releveés this map was based on (Kers *et al* 1996) were used for the calculations of food availability described below. The eastern section of the island in which my study area lies was mapped in 1996 by the vegetation dynamics course of the University of Groningen. During the course borders of the different vegetation types were first drawn using an infra-red image of Schiermonnikoog taken in 1992. These borders were then checked in the field and changed when necessary. Classification of the different vegetation types was based on vegetation releveés made over the whole eastern part of the island.

The abundance of each potential food species was calculated as follows: the average percentage cover of each food species within a vegetation type was multiplied by the area this vegetation type covered within the selected area. For each species these multiplications for all vegetation types they occurred in where summed up. The sum per species was divided by the total area covered by all food species and multiplied by 100. In this way percentage cover of each food species within the area was estimated as a proportion of the total cover of all potential food species.

2.3.2. seasonal changes in food availability

The above described calculation of food availability does not account for seasonal changes and thereby remains a rough estimate. In order to receive a measure of change in hare food supply that took place during the field season vegetation releveés of eight main salt marsh vegetation types were made twice during the season (tab.1). These communities listed from high to low salt marsh are: Festuca/Elymus, Juncus, Festuca, Festuca/Artemisia, Artemisia, Limonium, Atriplex/Limonium and Puccinellia. I made the first releveés using the point-quadrat method (Grant 1981) end June - mid July (tab.1). For time reasons the second releveés end of October (tab.1) were made using an estimation of cover according to Londo-scale (Londo 1976). As these second releveés were done at a time when several species were dying or dead, in addition to percentage cover of each species, I also recorded whether dead or alive. The vegetation releveés made in the Festuca, Festuca/Artemisia and Artemisia communities were additionally important for the more detailed investigations of hare grazing preference of these types in relation to different sward characteristics (section 2.6.).

In order to compare the two methods two point quadrat releveés were additionally made in 5 vegetation types (Juncus, Festuca, Festuca/Artemisia, Artemisia and Limonium) during the same period in which the vegetation relevees were made according to Londo-scale.

2.4. Plant nutritional quality

The following chemical characteristics were chosen as quality parameters of potential hare food plants: digestibility, fibre content (Neutral Detergent Fibre) and nitrogen content. Neutral detergent fibre (NDF) represents the cellulose and hemicellulose of the cell wall including lignin and condensed tannins. These plant components are difficult to digest to indigestible substances. Less fibre content means a higher proportion of easily digestible cell contents and *vice versa*. NDF together with digestibility of the food plant give an indication of how much of the forage is actually available to the herbivore. Nitrogen content is used as a rough measure for the proportion of protein within organic substances. Proteins characteristically have 16 % nitrogen and represent a major component of the animal body and have numerous important functions (Robbins 1993). A sufficient supply of proteins is crucial in the life of an animal (Robbins 1993).

Chemical analyses were performed by Tjakkie van der Laan at the University of Wageningen. Potential digestibility was measured with the *in vitro* digestibility method as described by Tilly & Terry (1963). The procedure consists of leaving the plant material in the rumen fluid of a cow for 48 hrs and determining how much was digested. This can be considered a relative measure of digestibility in order to compare different species. For the automated determination of nitrogen in the plant material, organic matter was oxidized and digested using hydrogen peroxide and sulphuric acid (Novozamsky *et al* 1983). For more detailed description of the methods of analyses see appendix.

The following species were sampled: *Festuca rubra, Puccinellia maritima, Elymus athericus, Elymus farctus, Agrostis stolonifera, Juncus gerardii, Artemisia maritima, Atriplex portulacoides*. The decision which plant parts should be sampled was based on information from former studies on hares on Schiermonnikoog (van der Wal *et al* 1998b,d; Bestman & Keizer 1997). Plant parts sampled also coincided with grazing marks observed during the field season. Leaves were collected for all species. For the monocotyledons, samples consisted of leaf tips and for the dicotyledons whole leaves were taken. Additionally, stems of *A. maritima* and *A. portulacoides* were analysed. Plant samples were collected three times during the field season in order to account for seasonal changes in quality. The sampling dates coincided with the different periods as indicated in table 1. For all species except *Festuca rubra* (section 2.6.1.) one sample was collected in each period.

2.5. Relationship between number of hare droppings and grazing pressure

In this study number of hare droppings was used as a measure of hare grazing pressure. The relationship between hare grazing and droppings was tested by comparing the results of dropping counts with a measure of grazing intensity. This was done on two scales relevant for this study: on the vegetation type level over eight vegetation types and on a smaller scale of $4m^2$ plots within two vegetation types.

The vegetation types listed according to decreasing height above sea level were: Festuca/Elymus, Juncus, Festuca, Festuca/Artemisia, Artemisia, Limonium, Atriplex/Limonium and Puccinellia. Relationship between number of droppings and grazing pressure on the smaller scale was tested within the Festuca/Artemisia and the Artemisia vegetation types.

The vegetation types Festuca, Festuca/Artemisia and Artemisia were investigated in more detail concerning hare grazing preference in relation to different vegetation parameters (section 2.6.). Dropping counts in these vegetation types were performed on a one to two weekly basis throughout the field season (tab.1) and grazing intensity measurements were conducted three times representing the three periods shown in table 1. For the purpose of testing for a correlation between number of droppings and grazing intensity on the vegetation type level dropping counts over all eight vegetation types were performed from 7 July to 18 August and the grazing intensity measurement took place in August after the last dropping count (tab.1). Within the vegetation types Festuca/Artemisia and Artemisia grazing intensity on the $4m^2$ plot level was measured end of October (tab.1). This measurement was related to the dropping counts that until then had taken place throughout the field season in these two communities.

2.5.1. dropping counts

For counting droppings ten $4m^2$ dropping plots were set out per vegetation type within site B (tab.1). The center of each plot was marked with a plastic pipe. Counting was done by checking the ground around the pipes using a rope with a length of 1,33 m (radius of a $4m^2$ circle) to mark the $4m^2$ area. All plots were cleared of droppings during each count.

Droppings found were divided into three categories: hare, unknown and rabbit. Hare and rabbit droppings were differentiated according to size and form based on measurements and observations made before the field season. Hare droppings were defined as being longer than 12,5 mm. Rabbit droppings were identified as those smaller than 12,5 mm and totally round in shape. The rest was classified unknown.

In order to insure that number of droppings counted was not influenced by flooding two test plots, each filled with 20 droppings, were set out for each of the four lower salt marsh vegetation types (Atriplex/limonium, Limonium, Puccinellia/Suaeda & Artemisia). The number of droppings re-found in these 30x30 cm^2 plots was noted for each dropping count date. In each case the plots were cleared and filled with 20 fresh droppings from the area. Dropping count results per vegetation type were expressed as average dropping densities (no. droppings / $4m^2$) per day to account for the differing time lengths between count dates. For further analyses results were log-transformed to approach statistical assumptions (Zar 1996). Differences in dropping densities between the Festuca, Festuca/Artemisia and the Artemisia vegetation types were tested using a general linear model with repeated samples.

2.5.2. grazing intensity

The performed grazing intensity measurements had two aims: to test the relationship between number of droppings and frequency of grazed shoots and in order to collect data on the plant species eaten and how frequently each species was grazed within the three vegetation types Festuca, Festuca/Artemisia and Artemisia., which were investigated in more detail (section 2.6.).

Frequency of grazed shoots was measured using a grid with 20 5x5 cm^2 squares. Each square was checked for grazed shoots and recorded as grazed or not grazed. Number of grazed shoots per 5x5 cm^2 was not counted. Only green shoots were taken into account. Grazed shoots were assumed to be mainly caused by hares as they were the main herbivores grazing on the salt marsh at the time. Rabbits are only expected to graze the salt marsh close to dune areas. At least six weeks lay between the measurements of frequency of grazed shoots for the Festuca, Festuca/Artemisia and Artemisia communities. The turn-over rate of most leaves is expected to be fast enough so that green grazed shoots present at each measuring date represented hare grazing pressure that mainly took place after the last measurement.

For data on grazing intensity of the different species eaten within the Festuca, Festuca/Artemisia and Artemisia vegetation type, each 5x5 cm^2 square was also checked for occurrence/absence of each of the potential food plants. Both occurrence and whether they were grazed/not grazed was recorded. Potential food plants were those known to be eaten by hares according to previous faecal analyses performed with hare droppings from Schiermonnikoog (Bestman & Keizer 1997; van der Wal *et al* 1998b,d). On the vegetation type level the grid was thrown haphazardly onto each vegetation type 12 times. Within the two vegetation types the grid was laid down systematically eight times within each of the ten $4m^2$ plots in order to avoid repeated measurements of the same spot.

2.5.3. procedure of looking for a correlation between number droppings and frequency of grazed shoots

Since the frequency of green grazed shoots found in the vegetation represented hare grazing over an unknown period of time, it was important to compare the measured grazing intensity with number of droppings accumulated over different time spans. Starting with the last dropping count that took place before the grazing intensity measurement, previous counts were added up step-wise resulting in a row of numbers of droppings for each plot that represented an accumulation over different lengths of time. Bivariate two-tailed Pearson correlations were performed to test the relationship between grazing intensity and all values of dropping numbers calculated in the above way.

2.6. Sward characteristics of the Festuca, Festuca/Artemisia and Artemisia vegetation types

Factors determining hare grazing preference for the vegetation types Festuca, Festuca/Artemisia and Artemisia were studied in more detail. These vegetation types occur at different elevations of the salt marsh, Festuca situated on the higher middle marsh followed by Festuca/Artemisia and then the Artemisia community lower in the marsh. They were chosen due to their high percentage cover of *Festuca rubra*, which was expected to be the most important food plant over the summer (van der Wal *et al* 1998d). I expected differences in where hares chose to graze on this food plant based on the species it occurs together with, the available biomass and the nutritional quality of the leaves. A comparison between hare grazing preference for the three communities and the sward characteristics was undertaken for the three successional time periods indicated in table 1. Hare grazing preference was based on the dropping counts (section 2.5.1.) and the grazing intensity measurements (section 2.5.2.). Vegetation relevees of the three vegetation types were performed as described in section 2.3.2..

2.6.1. Festuca rubra leaf nutritional quality

Leaf samples for the Festuca and Festuca/Artemisia vegetation types were collected for all three periods (tab.1). In both types four samples were collected in both July and October/November and a single sample in the middle period in September. *Festuca rubra* leaves from the Artemisia vegetation type were only sampled in September and October/November, but then in the same way as described above.

2.6.2. biomass samples

Biomass samples were taken in the Festuca, Festuca/Artemisia and Artemisia at three different times during the field season (tab.1) in order to take into account seasonal changes in food availability and differences between the different types. Six biomass samples were taken per type from 20x20 cm^2 plots spread haphazardly within the area where droppings were counted (tab.1, site B). Vegetation was clipped at ground level. The green plant material in each sample was sorted into species. Standing dead was lumped. The sorted samples were dried at 75°C for 48 hrs and weighed.

Differences in *Festuca rubra* leaf nutritional quality, Festuca rubra biomass and in grazing intensity from the different sites were tested with a oneway ANOVA including post hoc tests. Percentages were arcsine transformed (Zar 1996).

2.7. The effect of structure plants on hare feeding patch choice

An experiment was conducted in order to test for the effect of "structure" plants standing among a food plant species on feeding patch choice by hares. Structure plants were defined as not eaten species that stand above a layer of eaten species.It was hypothesized that structure plants hamper hare grazing making the covered food plants less attractive.

The two vegetation types Festuca/Artemisia and Puccinellia where selected for the experiment, *Festuca rubra* and *Puccinellia maritima* being the food plants under investigation. *Artemisia maritima* in the Festuca/Artemisia community and *Salicornia spec.* and *Suaeda maritima* in the Puccinellia type were the structure plants. In each vegetation type five random 1 m^2 experimental plots with a same-sized neighbouring control were selected. The structure species *A. maritima* and *Suaeda maritima* and *Salicornia spec.* were removed by hand from the experimental plots. Droppings were counted on all plots on a one to two weekly basis for six weeks. It was assumed that within this relatively short period changes in the abiotic conditions due to removal of the structure plants would not yet lead to changes in the remaining vegetation that would interfere with the objective of the experiment.

Counted droppings were accumulated per plot and log transformed (Zar 1996) for further analyses. A paired samples T-Test was used to test for differences between control and experimental plot within each vegetation type.

3. Results

3.1. Hare diet selection

3.1.1. Hare diet

Epidermal fragments of 12 different plant species were found in the analysed hare dropping samples. The proportion of unknown fragments ranged between 2 and 5 %. The percentage of unknown dicotyledons and monocotyledons were 1-3 % and 3-10 %, respectively.

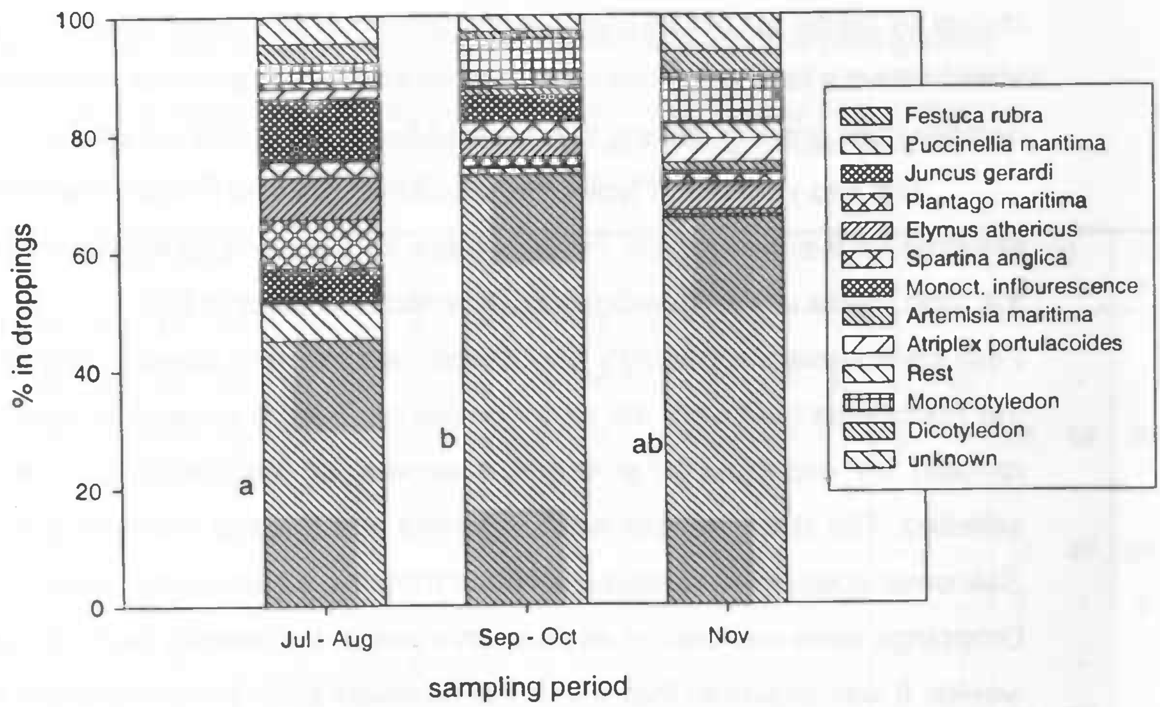


Figure 2: Hare diet based on faecal analyses for three different periods of the year. Species never reaching more than 1 % in the droppings are included in Rest. Different letters indicate significant differences in percentage *Festuca rubra* between periods for arcsine transformed percentages (oneway ANOVA, Tukey posthoc; $p < 0.05$; $n = 3$). Rest = *Limonium vulgare, Spergularia spec., Ammophila arenaria* and *Elymus farctus.*

Festuca rubra was the most important food plant for hares throughout the summer and early autumn. The proportion of *F. rubra* in the diet was lowest in July at 45% and showed a significant increase later in the season to 75 % in September. The slight decrease down to an average of 65% in November was not significantly lower than September values nor significantly higher than in July. Other important hare food plants in July were *Plantago maritima, Juncus gerardii, Elymus athericus* and *Puccinellia maritima*, each making up between 5 and 10 % of the diet. Epidermal fragments identified as being part of monoctyledon inflourescences took up 12% of the hare diet in July. These fragments indicate the importance of monocotyledon seeds as a hare food source within this period. In September and November no single species apart from *F. rubra* made up more than 5 % of the diet. Fragments showing a marked decrease in average proportion of the diet from July to November were *Plantago maritima*, *Juncus gerardii*, *Puccinellia maritima* and monocotyledon Hüllspelzen.

3.1.2. Food species availability

The calculated proportion cover of the potential food plants in the area are listed in table 2. *Festuca rubra* clearly represents the most available food plant with a proportional cover among potential food plants in the area of 28 %. The next most abundant species is *Elymus athericus* taking up a proportion of 12 %.

Table 2: Percentage cover of the different potential hare food plant species calculated as a proportion of total cover of these species in the hare home range area.

	Proportional cover
Festuca rubra	30.3
Elymus athericus	12.6
Juncus gerardi	10.0
Agrostis stolonifera	9.5
Artemisa maritima	8.9
Limonium vulgare	7.5
Ammophila arenaria	5.4
Pucinellia maritima	4.9
Plantago maritima	3.6
Elymus farctus	3.2
Atriplex portulacoides	2.3
Triglochin maritimum	1.3
Spartina anglica	0.4

3.1. Comparison between the point quadrat and Londo method (tab.3)

The comparison between the two methods used for the vegetation releveés undertaken in October showed partly large differences between the results of the different methods on the same site. For example, in *Festuca rubra* and in *Limonium vulgare* cover in the different vegetation types. These differences can mainly be put down to the estimation of cover (Londo) taking

Table 3: Comparison between vegetation relevees made with the point quadrat method and estimating cover according to Londo-scale. Relevees are not complete, only selection of species are presented here. Londo-scale values are transformed into percentages. Jun = Juncus, Fes = Festuca, F/A = Festuca/Artemisia, Art = Artemisia, Lim = Limonium, P = point quadrat, L = Londo.

Vegetation type:	Jun 1		Jun 2		Fes 1		Fes 2		F/A 1		F/A 2		Art 1		Art 2		Lim1		Lim 2	
Method:	P	L	P	L	P	L	P	L	P	L	P	L	P	L	P	L	P	L	P	L
J. gerardi (dead)	50	40	61	60	3	1	4	1	3	0	0	0	-	-	-	-	-	-	-	-
F. rubra	29	30	21	20	63	90	54	90	48	60	55	85	54	80	45	70	-	-	-	-
Lim. vulgare	5	20	3	13	0	1	1	2	0	0	0	0	0	1	0	1	33	58	30	60
Plant. maritima	1	2	1	4	2	4	2	4	0	1	0	0	-	-	-	-	-	-	-	-
Puc. maritima	0	0	1	1	-	-	-	-	-	-	-	-	-	-	-	-	11	20	31	30
A. portulacoides	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	1	2	1
A. stolonifera	9	8	4	4	2	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-
S.maritima & Salicornia spec.	0	0	6	1	-	-	-	-	-	-	-	-	0	1	0	1	38	20	28	20

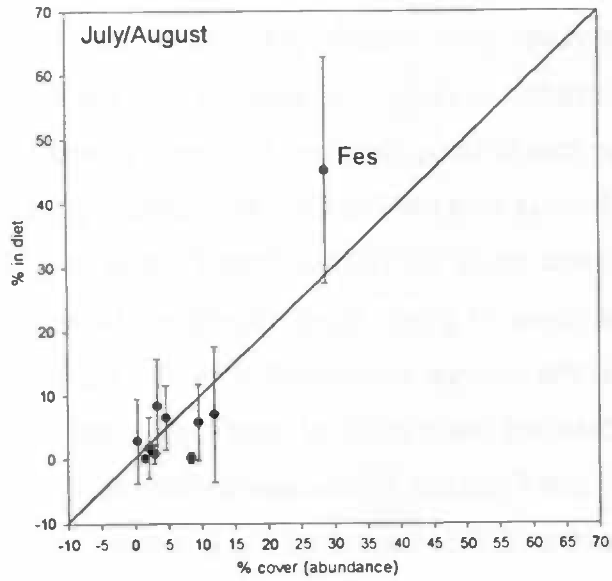
into account the double cover of the different vegetation strata, e.g. the layer dominated by *F. rubra* and the higher *L. vulgare* towering above this layer. This can result in overall covers of over 100%. In contrast, the results per releveé of the point quadrat method as performed here always added up to 100%. However, both methods are measuring relative cover of different species within a site. The overall picture of the plant composition stays the same. For example, cover of *Artemisia maritima* on the releveé sites within the Festuca/Artemisia and the Artemisia community showed a similar trend according to the two methods. Festuca/Artemisia had a lower *A. maritima* cover than the Artemisia vegetation. Percentage *Festuca rubra* cover for the different sites showed a similar ranking order for releveés made with the two methods. The highest *F. rubra* cover being found in the Festuca and the Festuca/Artemisia vegetation relevees, followed by the Artemisia relevees and then the Juncus relevees with lowest *F. rubra* cover.

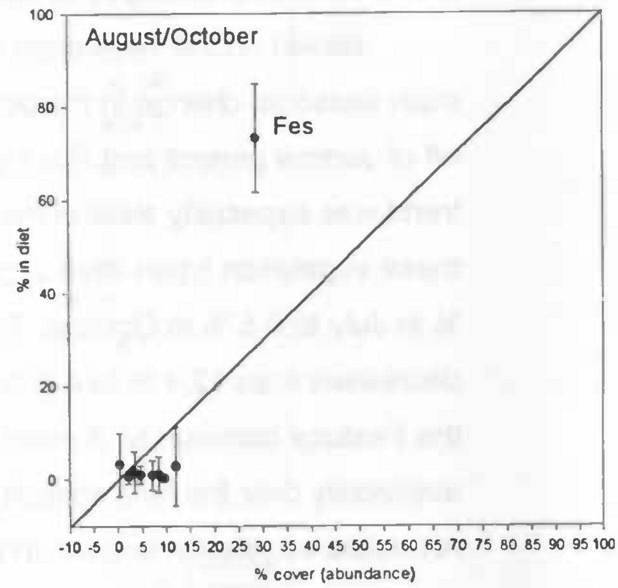
3.1.4. Seasonal changes in food availability *(tab.4)*

Based on the vegetation relevees performed in July and October the main seasonal change in the occurrence of hare food species was the dying off of *Juncus gerardi* and *Plantago maritima* by October. For both species this trend was especially clear in the Juncus and the Festuca vegetation types. In these vegetation types alive *J. gerardi* cover decreases from 72.4 % and 23.5 % in July to 0.5 % in October. The cover of green *Plant. maritima* shoots decreases from 12.4 % to 4.6 % in the Juncus and from 9.5 % to 2.95 % in the Festuca community. A more detailed description of hare food plant availability over the field season in the Festuca, Festuca/Artemisia and Artemisia vegetation is given in section 3.3.5. based on the biomass samples.

Table 4: A selection of species from vegetation releveés made in eight salt marsh vegetation types in July and October. Different methods were used for the different periods: July – point quadrat (PQ) and October – Londo-scale (LO). Londo-scale results were transformed into percentages.

	Festuca Elymus		Juncus		Festuca		Festuca / Artemisia		Artemisia		Limonium		Atriplex / Limonium		Puccinellia	
	Jul PQ	Oct LO	Jul PQ	Oct LO	Jul PQ	Oct LO	Jul PQ	Oct LO	Jul PQ	Oct LO	Jul PQ	Oct LO	Jul PQ	Oct LO	Jul PQ	Oct LO
E.athericus	32	29	0	0.2	0.1	0.1	-	-	-	-	0.1	0	-	-	-	-
Juncus gerardi	-	-	72	0.5	24	0.5	9	0	0.6	0	-	-	-	-	0.4	0
Festuca rubra	26	17	3	20	57	73	59	71	47	63	0.1	0.1	-	-	0	0.2
Lim. vulgare	-	-	5	10	3	3	4	3	4	6	49	48	20	20	10	8
Plant. maritima	0.3	0.2	12	5	10	3	0.8	0	-	-	0	0.1	-	-	0.2	0.3
Art.maritima	-	-	0	0.2	0.2	0	25	11	44	35	0	0	3	0	-	-
Puc. maritima	-	-	-	-	-	-	0.1	0	0.5	0	9	8	3	3	22	18
A.portulacoides	-	-	-	-	-	-	-	-	0	0.1	3	3	47	58	6	4
Sua. maritima	-	-	0.1	0.4	-	-	-	-	0.4	0.4	7	3	9	3	18	19
Salicornia spec.	-	-	0	0.1	-	-	-	-	-	-	11	6	5	4	22	16
Standing dead	15	32	0.4	63	1	40	0.9	36	1	13	2	53	1	14	4	23





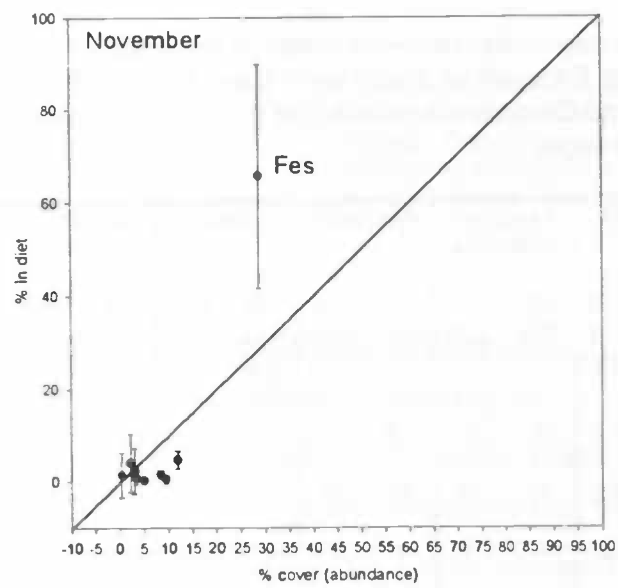


Figure 3: Hare diet in relation to plant species abundance in July/August (A), August/October (B) and November (C). Mean values are given for proportion in the diet with 2x the standard deviation as error bars. The line x = y is used as an indication of preference or non-preference. Fes = *Festuca rubra*.

3.1.5. Food plant species selection (fig.3,A-C)

Festuca rubra is the only clearly preferred food plant in all three periods when comparing percentage in the diet with estimated availability in the selected area based on hare home range size (tab.1, site A). All other potential food plant species occurred in both low percentages in the diet and with low percentage cover in the area making statements on preference or not problematic. Small differences in the calculated percentage cover compared with actual availability and in the results of the faecal analyses compared with the actual diet could easily lead to different conclusions.

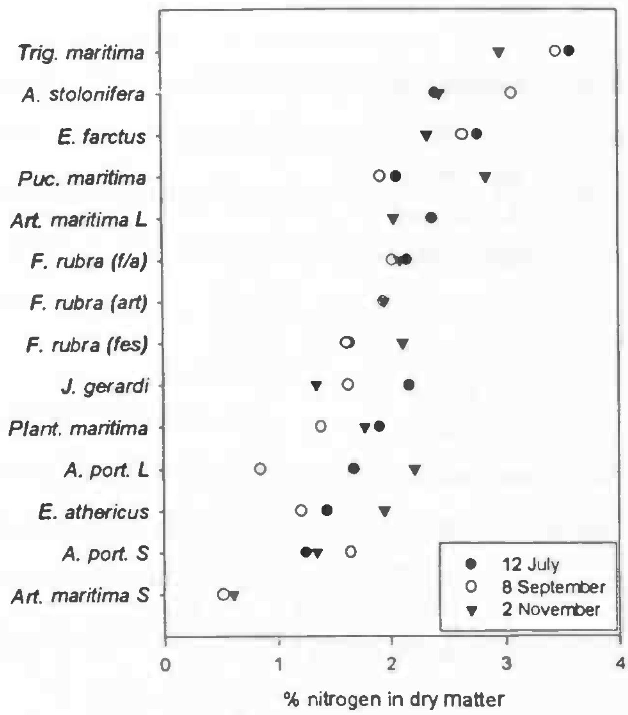


Figure 4: Percentage nitrogen in dry matter of hare food species ranked according to decreasing nitrogen content. Different times of the year are indicated with different symbols. S = stem, L = leaf, fes = Festuca veg., f/a = Festuca/Artemisia veg., art = Artemisia veg., A. port. = *A. portulacoides*.

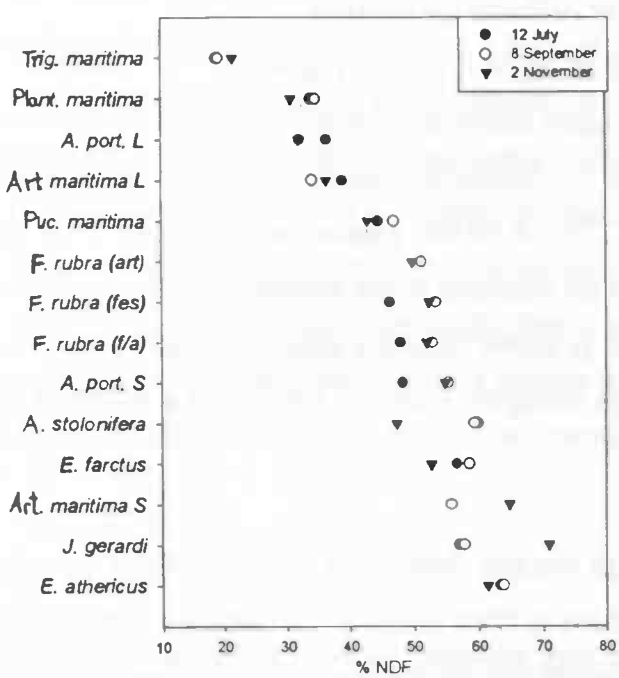


Figure 5: Percentage neutral detergent fibre in dry matter of potential hare food plant species ranked according to increasing average. Different times of the year are indicated by different symbols. S = stem,L = leaf, A. port. = *Atriplex portulacoides*.

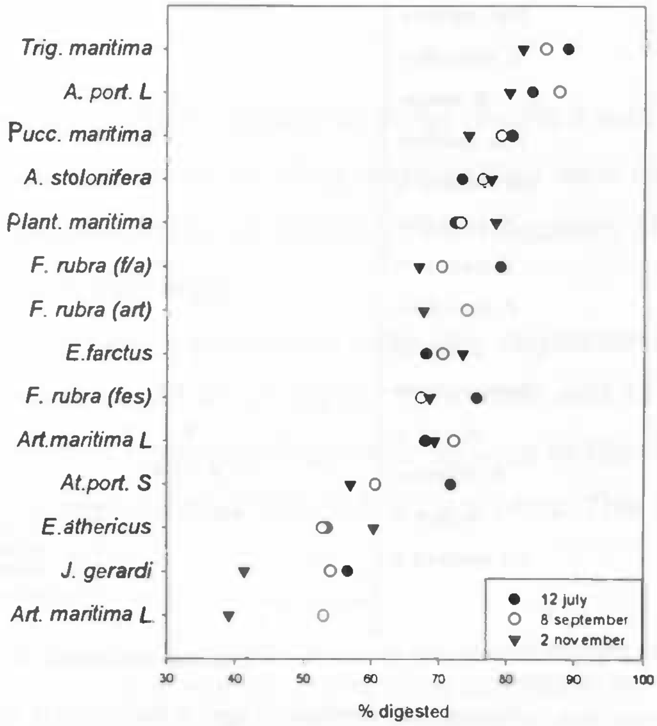


Figure 6: Dry matter digestibility of potential hare food species ranked according to decreasing average. Different times of the year indicated by different symbols. S = stem, L = leaf, A. port. = *Atriplex portulacoides*.

3.1.6. Plant nutritional quality

% nitrogen in organic matter (fig.4)

Nitrogen content in organic matter of the sampled species ranged from 0.5 to 3.58 %. *Triglochin maritima* had the highest average percentage nitrogen (2.97 - 3.58 %). Lower values (0.5-1.6 %) were found for the dicot stems and for *Festuca rubra* leaves from the Festuca/Elymus vegetation. Among the grasses *Agrostis stolonifera* and *Elymus farctus* had a higher percentage nitrogen. *Festuca rubra* had a nitrogen content of around 1.6 to 2.3 %.

Percentage Neutral Detergent Fibre (NDF) in dry matter (fig.5)

Values of fibre content for sampled species ranged between 19 and 72 %. Dicotyledon leaves always contained less percentage NDF than the grass species. *Triglochin maritima* had the lowest percentage NDF within each sampling period with values around 19 to 21.5 %, followed by *Plantago maritima*, *Atriplex portulacoides* and *Artemisia maritima* leaves with values between 30 and 40 %. Fibre content of the dicotyledon stems was comparable to values of most grasses. *Elymus athericus* samples had the highest percentage NDF among the grasses (61.5 - 63.9 %). *Puccinellia maritima* samples always had lowest fibre content among the grasses within each period (43 - 47 %).

in vitro dry matter digestibility (fig.6)

Highest dry matter digestibility was found for *Triglochin maritima* (82.3 – 89 %) and *Atriplex portulacoides* (80.4 – 87,7 %) leaves within all sampling periods. Samples with a lower digestibility throughout the season came from the dicotyledons stems and the monocotyledons *Juncus gerardi* and *Elymus athericus*.

combined quality parametres

In summary *Triglochin maritima* is the best quality food plant according to the performed analyses. *Festuca rubra* leaves always lay in the upper middle section of the nutritional quality ranking. Further species often amongst the qualitatively higher ranked species are *Puccinellia maritima*, *Atriplex portulacoides* leaves, *Agrostis stolonifera* and *Elymus farctus*. *Puc. maritima* had a high nitrogen content, high digestibility and relatively low fibre content. *A. portulacoides* leaves had a low fibre content, relatively high digestibility, but a lower percentage nitrogen. *Plant. maritima* samples showed low fibre content and ranked around the median in nitrogen content and in digestibility. Leaves of the other species sampled and the sampled stems were found at the lower end of the ranking. Only *Artemisia maritima* leaves had a relatively high nitrogen content, but showed low quality in all other measured parameters.

3.2. Relationship between number of hare droppings and grazing intensity

No extreme floodings took place from July to September before the grazing intensity measurement over all eight vegetation types was made. Test plot results show that droppings re-found were never below 50% and mostly above 75% per count date (tab.5). Based on these results it was decided that the dropping counts performed within these communities were usable to test for a relationship between number of droppings and frequency of grazed shoots on the vegetation type level.

The two dropping counts performed within the vegetation types Festuca, Festuca/Artemisia and Artemisia on 13 October and 11 November were excluded from further analyses because droppings re-found in the Artemisia vegetation were less than 75% in both test plots. This is of importance for section 3.3..

Table 5: Results of the dropping test plots set up in lower salt marsh vegetation types to test for the effect of flooding on number of droppings counted in the salt marsh. Numbers represent re-found droppings out of 20. Dropping counts excluded from further analyses are in bold italics. Art = Artemisia, Lim = Limonium, Puc = Puccinellia, Atr = Atriplex portulacoides.

date	art 1	art2	lim 1	lim 2	lim 3	puc 1	puc 2	atr 1	atr 2
21-Jul	20	19	17	18	14	19	13	14	12
4-Aug	19	17	19	15	12	18	14	12	13
18-Aug	15	20	18	11	18	21	17	13	19
1-Sep	19	21	16	14	10	18	14	19	16
10-Sep	20	25	12	14	17	21	14	15	11
26-Sep	18	20	16	16	15	19	19	17	19
13-Oct	***1***	***12***	***5***	***2***	***3***	***5***	***20***	***3***	***8***
20-Oct	17	19	17	13	16	16	11	16	12
27-Oct	17	15	14	15	15	20	21	17	14
11-Nov	***0***	***8***	***16***	***17***	***11***	***11***	***15***	***14***	***22***
20-Nov	20	20	15	12	16	20	18	18	16
30-Nov	19	18	13	12	18	16	14	17	17

There was a good correlation between number of droppings and grazing intensity on both the vegetation type level and on the smaller $4m^2$ plot scale within the Artemisia and Festuca/Artemisia vegetation types.

On the vegetation type level the correlation was significant for all dropping numbers representing the different time spans (tab.6). Within the Artemisia vegetation, correlations are significant at the 0.05 level for droppings accumulated over 10 and 27 days (tab.7). For numbers of droppings accumulated over 43 days and longer, correlations with the measured grazing intensity were highly significant. Correlations found between dropping numbers and grazing intensity within the Festuca/Artemisia vegetation were significant at the 0.05 level (tab.7). No significant correlation was found between number of droppings accumulated over the shorter periods of three and ten days within the Festuca/Artemisia and over three days within the Artemisia vegetation. This is not unusual as the grazed shoots found in the vegetation probably originate from hare grazing over a longer period than ten days.

Table 6: Results of bivariate correlations between number of droppings and frequency of grazed shoots measured in 8 different vegetation types.

Length of period (in days)	r	p≤
17	0.948	0.000
33	0.874	0.005
42	0.892	0.003
55	0.895	0.003
65	0.901	0.002
75	0.916	0.001
82	0.927	0.001

Table 7: Results of bivariate correlations between numbers of droppings and frequency of grazed shoots measured within the Festuca/Artemisia and the Artemisia vegetation types.

Length of period	Festuca/Artemisia		Artemisia	
(in days)	r	p ≤	r	p ≤
3	0.317	0.373	0.552	0.098
10	0.302	0.397	0.632	0.050
27	0.805	0.005	0.638	0.047
43	0.828	0.003	0.865	0.001
52	0.822	0.004	0.900	0.000
74	0.826	0.003	0.898	0.000
88	0.804	0.005	0.929	0.000
102	0.791	0.006	0.951	0.000
116	0.766	0.010	0.935	0.000

3.3. Hare grazing in the Festuca, Festuca/Artemisia and Artemisia communities

3.3.1. Vegetation descriptions and structure plants

All three communities had a high average *Festuca rubra* cover (tab.4). The Festuca and Festuca/Artemisia vegetation types with 56.7% / 73% and 58.6% / 70.5% respectively. The Artemisia vegetation showed slightly lower values of 46.5% and 63%. In the Festuca vegetation type there was a higher cover of the hare food plants *Juncus gerardi* and *Plantago maritima* than in the other two.

The following species were defined as structure plants within the Festuca, Festuca/Artemisia and the Artemisia vegetation: Artemisia maritima and Limonium vulgare. Both the point quadrat releveés in July and the releveés according to Londo-scale in October showed significant differences in percentage cover of structure plants between the three communities (fig.7). The highest percentage cover being found in the Artemisia, followed by the Festuca/Artemisia and then the Festuca community.

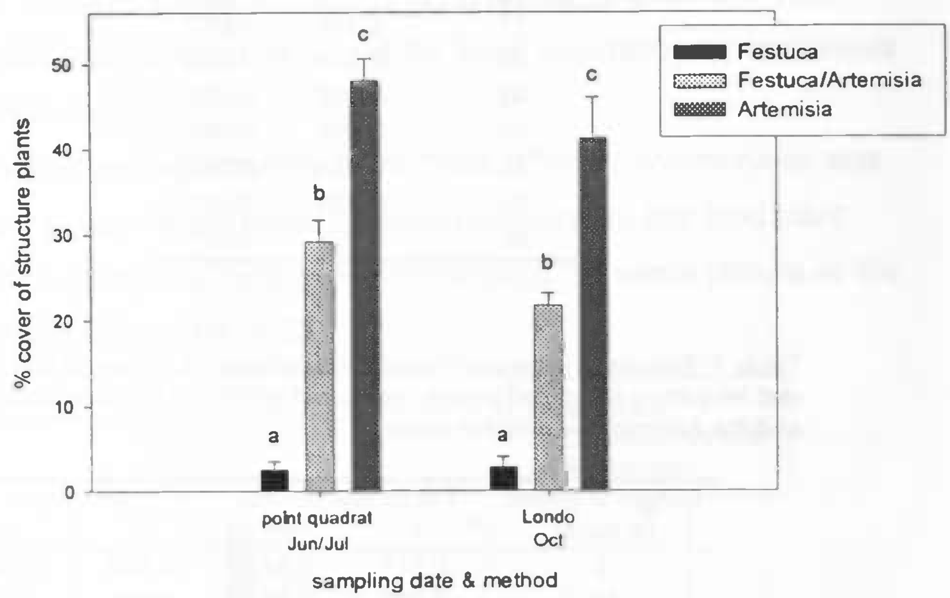


Figure 7: Percentage cover of structure plants in the Festuca, Festuca/Artemsia and Artemisia vegetation types in June/July based on relevees using the point quadrat method and in October using an estimation of cover according to Londo-scale. Different letters indicate significant differences within a sampling period for arcsine transformed percentages (oneway ANOVA, Tukey post hoc; $p < 0.001$; $n = 10$).

3.3.2. Grazing preference based on dropping counts

Dropping numbers on the vegetation types Festuca, Festuca/Artemisia and Artemisia were looked at in more detail in order to relate them with results from the biomass samples and *Festuca rubra* leaf nutritional quality taken in these sites. In order to relate different biomass parametres with the hares preference for vegetation type, count dates were divided into periods which are indicated by the dotted lines (fig.8).

There was never a significant difference between dropping densities in the Festuca and Festuca/Artemisia vegetation. In the first two periods dropping densities on the Artemisia vegetation were significantly lower than on the Festuca and Festuca/Artemisia. In the last period there were no significant differences in dropping densities between the three i.e. in the end of November until end of October hares did not show a preference for one of the three vegetation types.

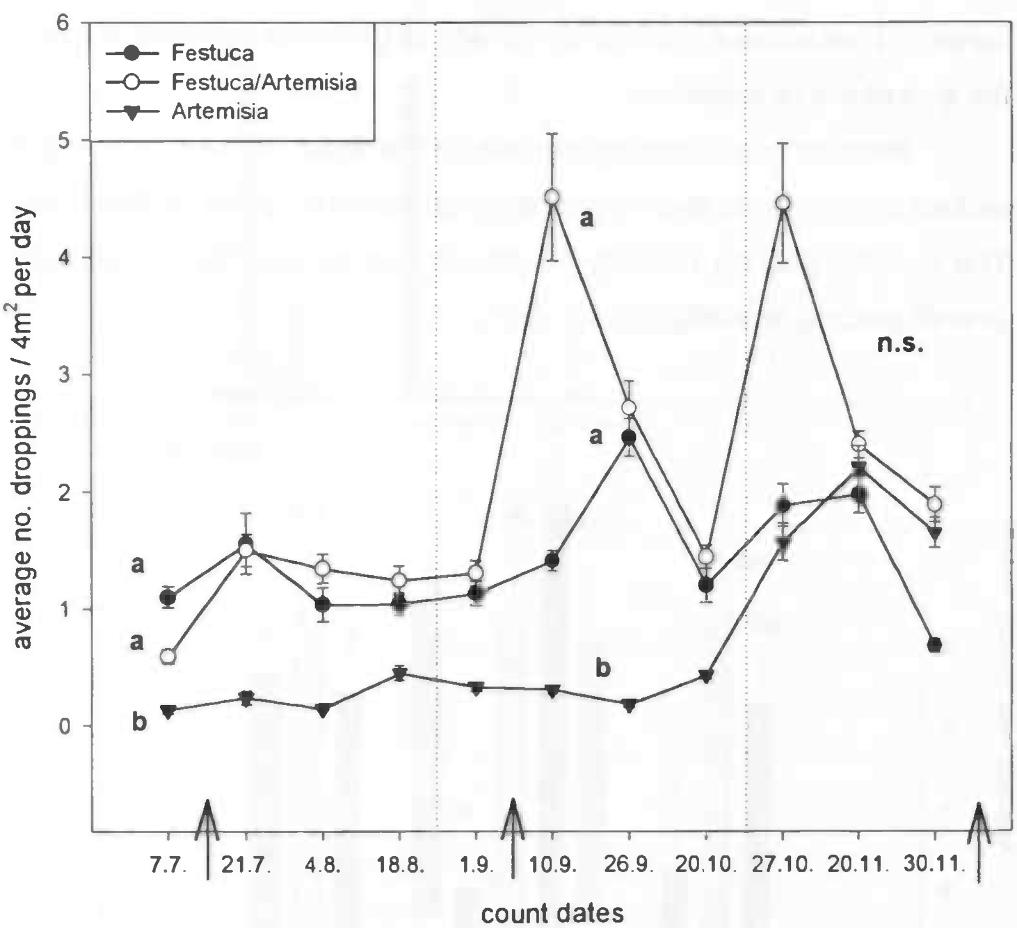


Figure 8: Average number of droppings / $4m^2$ per day for each count date in the vegetation types Festuca, Festuca/Artemisia and Artemisia vegetation types. Average dropping densities per count date expressed as average dropping densities per day in order to account for different time lengths between count dates. Dotted lines indicate division in 3 periods. Arrows indicate biomass sampling dates. Different letters indicate significant differences within periods (GLM repeated measures; $p < 0.05$; $n = 10$).

3.3.3. Grazing preference based on grazing intensity

In the first period, i.e. the results from August, no significant difference was found in frequency of grazed shoots between the Festuca and the Artemisia vegetation types (fig.9). This differs from the results of dropping densities described above. The grazing intensity of the Festuca/Artemisia vegetation was significantly higher than the grazing on the Artemisia type. Measurements of grazing intensity in October and December, representing periods 2 and 3, showed the same pattern as the dropping counts. Festuca and Festuca/Artemisia did not differ in frequency of grazed shoots in period 2, whereas grazing intensity in the Artemisia vegetation was significantly lower than in the other two types. Also according to frequency of grazed shoots hares did not show a preference for any of the three vegetation types towards the end of the field season.

Festuca rubra grazing intensity in the three different communities was looked at in order to see where hares preferred to graze on this food plant. The *F. rubra* grazing intensity measurements showed the same picture as the overall grazing intensity (fig.10, A-C).

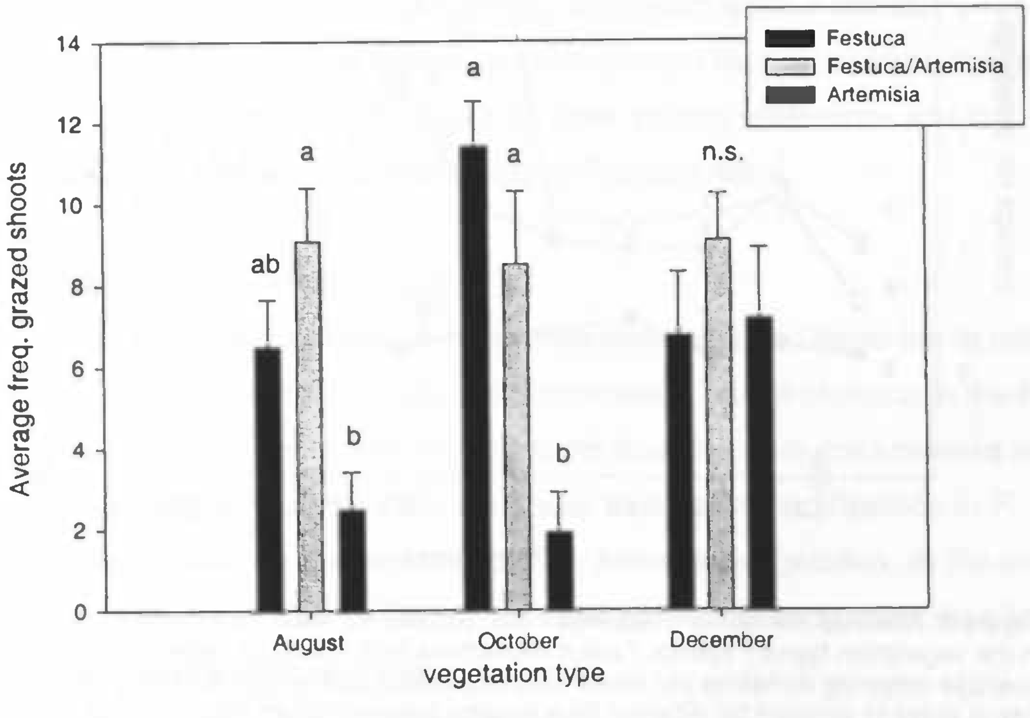


Figure 9: Frequency of grazed shoots as a measure of hare grazing pressure in the Festuca, Festuca/Artemisia and Artemisia vegetation types at three times of the year. Different letters indicate significant differences within periods (oneway ANOVA, Tukey post hoc; $p < 0.05$; $n = 12$).

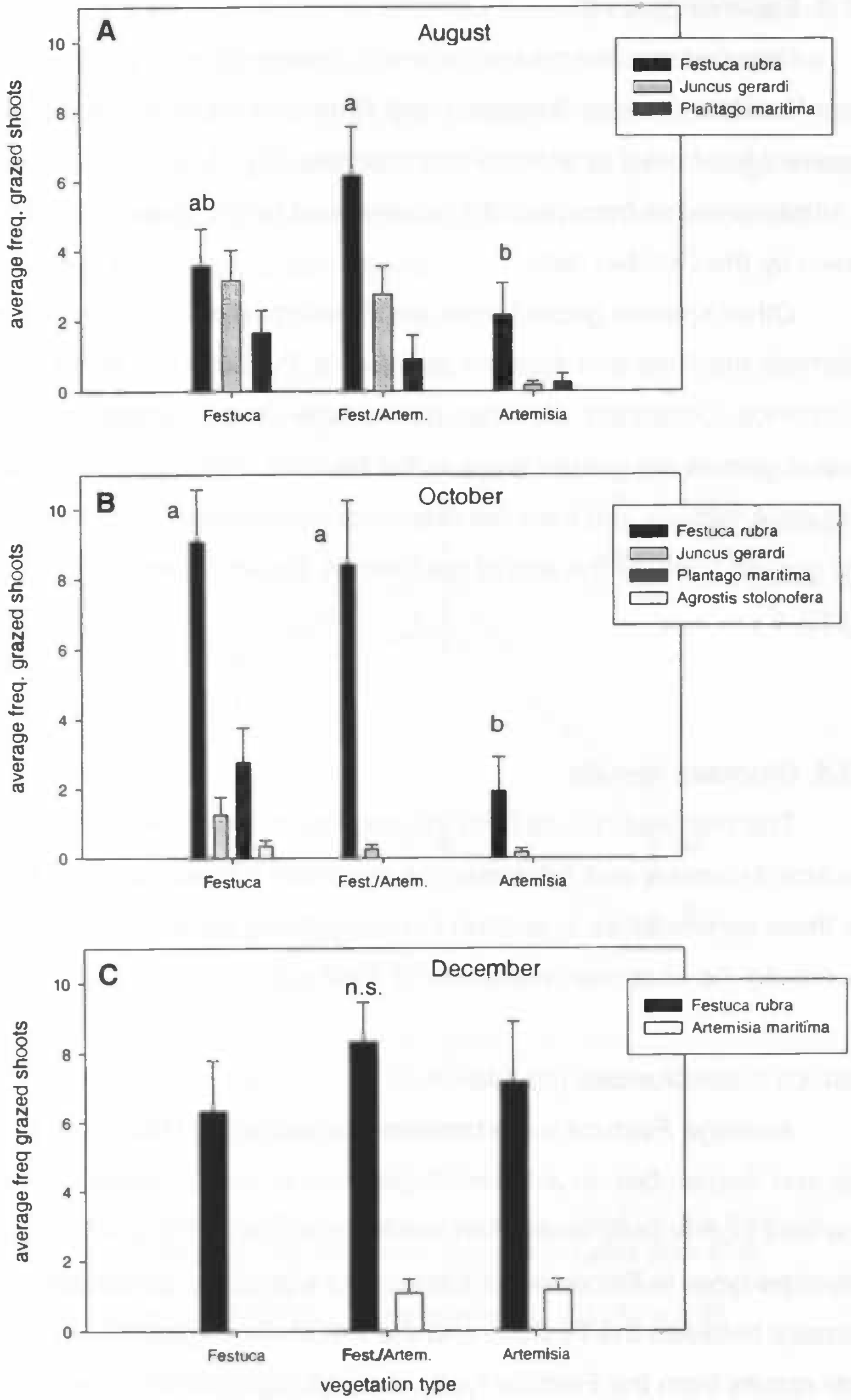


Figure 10: Average frequency grazed shoots of different species in the Festuca, Festuca/Artemisia and Artemisia vegetation types in 3 different periods. Different letters indicate significant differences between Festuca rubra grazing intensity in different vegetation types (oneway ANOVA, Tukey post hoc; $p < 0.05$; $n = 12$).

3.3.4. Species grazed

Results from the grazing intensity measurements within the vegetation types Festuca, Festuca/Artemisia and Artemisia show that *Festuca rubra* is an important food plant in all three communities (fig.10, A-C). The importance of *F. rubra* increases from period 1 represented by the August results to period 2 shown by the October data.

Other species grazed upon are *Plantago maritima*, *Juncus gerardi*, *Artemisia maritima* and *Agrostis stolonifera*, the latter not being of much importance. Consistent with their percentage cover *Plantago maritima* and *Juncus gerardi* are grazed more in the Festuca vegetation, followed by the Festuca/Artemisia and then the Artemisia community. *Artemisia maritima* was only grazed towards the end of the year as shown by results from December (fig.10, C).

3.3.5. Biomass results

The biomass results from the vegetation types Festuca, Festuca/Artemisia and Artemisia are important for two reasons: for comparing the three communities in relation to hare grazing preference and for describing the seasonal availability of *Festuca rubra*.

Festuca rubra biomass (fig.11)

Average *Festuca rubra* biomass decreased in December in relation to July and September. In July and September *F. rubra* biomass in the Festuca type was significantly lower than results from the Festuca/Artemisia and Artemisia type. In December there was no significant difference in *F. rubra* biomass between the Festuca and the Artemisia vegetation. At the end of the year results from the Festuca type were still significantly lower than for the Festuca/Artemisia vegetation.

percentage standing dead biomass (fig.12)

There was a strong increase in percentage standing dead in the three vegetation types throughout the field season, with an especially strong increase from around 15-30 % in September to between 60 and 80 % in December. Percentage standing dead biomass between the Festuca and the Artemisia vegetation was significantly different for all periods. In July the Artemisia vegetation had significantly higher values compared with the Festuca vegetation values. In September and December percentage standing dead in the Festuca vegetation was significantly higher than in both the Artemisia and the Festuca/Artemisia types.

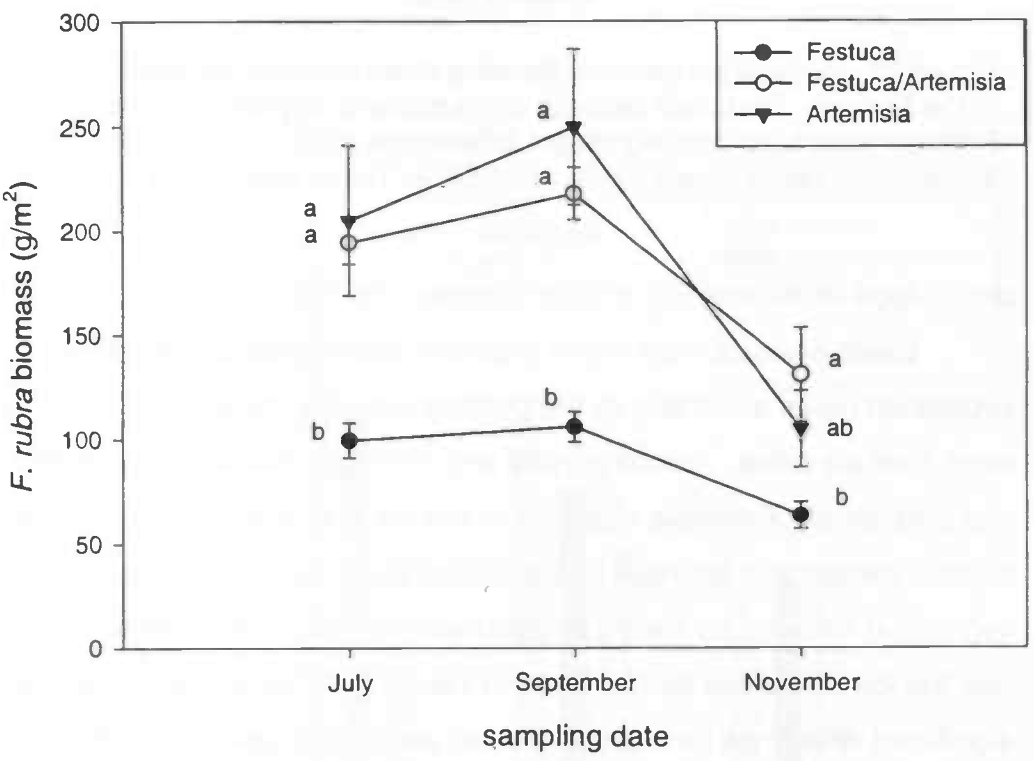


Figure 11: Average *Festuca rubra* biomass (g/m^2) in the Festuca, Festuca/Artemisia and Artemisia vegetation types over time. Different letters indicate significant differences within sampling dates (one-way ANOVA, Tukey post hoc;$p < 0.05$; $n = 6$).

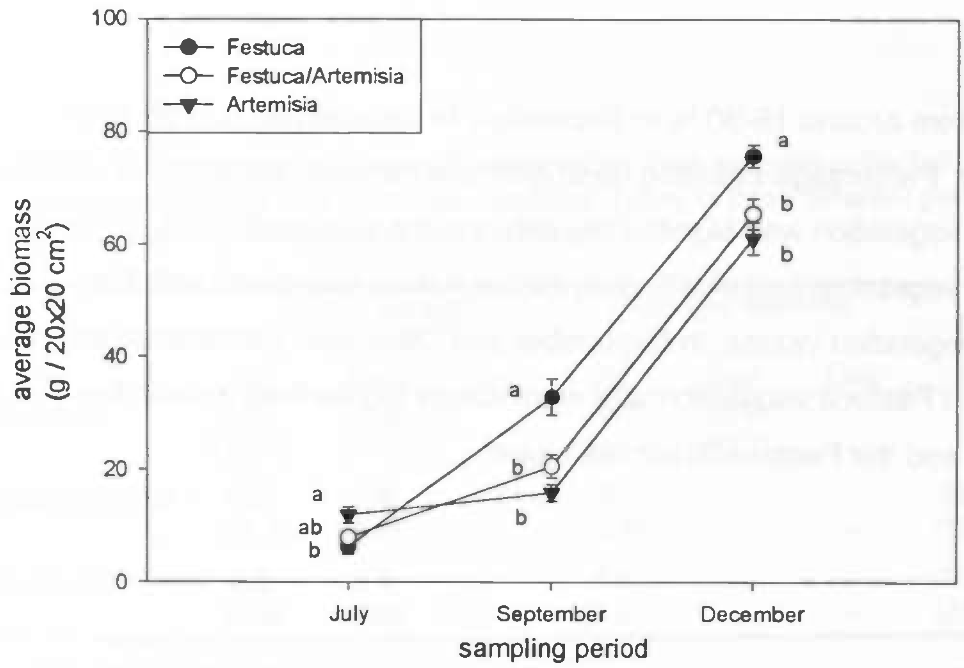


Figure 12: Average percentage standing dead biomass (of total biomass) in the Festuca, Festuca/Artemisia and Artemisia vegetation types in 3 periods. Different letters indicate significant differences within periods for arcsine transformed percentages (oneway ANOVA, Tukey post hoc; $p < 0.05$; $n = 6$).

percentage eaten species of total biomass (fig. 13)

Eaten species were those regularly found grazed in the three vegetation types according to the grazing intensity measurements. These were *Festuca rubra*, *Juncus gerardi* and *Plantago maritima* in period 1 and 2 and additionally *Artemisia maritima* in period 3. In July and September the highest percentage biomass of eaten species was found in the Festuca vegetation followed by the Festuca/Artemisia type. The Artemisia community had the lowest values for the first two periods. In December there was no significant difference between the three vegetation types. This change between September and December results is to a large extent due to *Artemisia maritima* being included to the eaten species.

Juncus gerardi, Plantago maritima and Artemisia maritima biomass (tab.8)

Overall *Juncus gerardi* biomass shows a strong decrease from July over September to December in all three vegetation types. This is due to senescence. In in December no green J. gerardi shoots were found. *Artemisia maritima* biomass in the Festuca and Festuca/Artemisia vegetation shows a strong decrease from September to December where occure in the Festuca/Artemisia and Artemisia communities. In July *Plantago maritima* was found in biomass samples within all three plant communities. In September this species was only found in the biomass samples from the Festuca site where this species occurred more frequently (tab.4). This could be explained by the patchy occurrence of this species together with it's low cover in the Festuca/Artemisia and Artemisia vegetation types (tab.4).

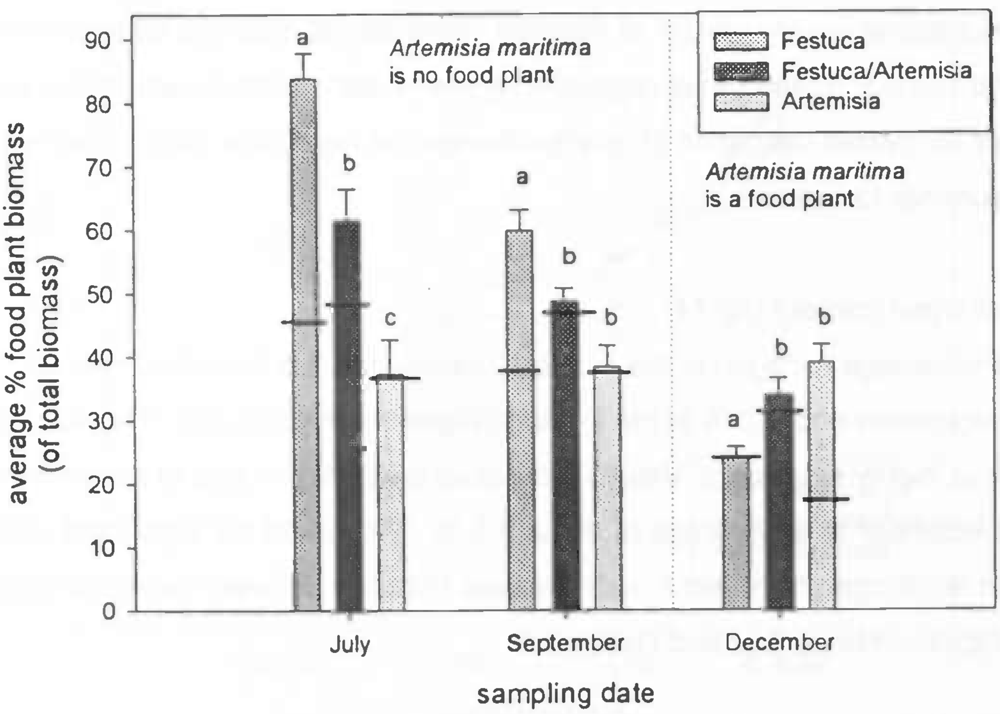


Figure 13: Average percentage biomass of hare food plants of total biomass in the vegetation types Festuca, Festuca/Artemisia and Artemisia for three different periods. Food plants are *Festuca rubra*, *Juncus gerardi* and *Plantago maritima*, in December additionally *Artemisia maritima*. Different letters indicate significant differences within periods for arcsine transformed percentages (oneway ANOVA, Tukey posthoc; $p < 0.05$; $n = 6$). Horizontal lines through the bars indicate average percentage *Festuca rubra*.

Table 8: Biomass in g/m2 for different species from samples collected in the Festuca, Festuca/Artemisia and Artemisia vegetation types in three different periods over the field season. Standard errors are in brackets, n = 6.

	Juncus gerardi			*Plantago maritima*			*Artemisia maritima*		
	Jul	Sep	Dec	Jul	Sep	Dec	Jul	Sep	Dec
Festuca	64.5 (14.9)	23.8 (6.8)	-	26.8 (11.4)	33.6 (10.2)	-	-	-	-
Festuca/Artemisia	33.4 (13.1)	7.6 (2.4)	-	19.3 (12.9)	-	-	69.5 (15.3)	120.3 (19.0)	30 (8.6)
Artemisia	8.6 (6.9)	8.8 (8.8)	-	4.9 (4.9)	-	-	254.1 (25.1)	272.7 (13.3)	81.9 (11.2)

3.3.6. Nutritional quality of Festuca rubra leaves

Nutritional quality results of *Festuca rubra* leaves over the season is important for comparing the three vegetation types under closer investigation, but also as an overall indication of quality change the hares are confronted with from summer to autumn.

nitrogen content (fig.14)

Percentage nitrogen in the *F. rubra* leaves was 1,6 % in the Festuca vegetation and 2,2 % in the Festuca/Artemisia type in July. This difference was highly significant. Values increased towards the end of the year in December to an average of about 2,5 %. There was no significant difference in % nitrogen between *F. rubra* leaves from the different vegetation types in October/November and December.

dry matter digestibility (fig.15)

Dry matter digestibility of *Festuca rubra* leaves decreased throughout the season from 75 to 78 % in July to about 67 % in November. In July *F. rubra* was significantly more digestible lower on the salt marsh in the Festuca/Artemisia vegetation (75 %) than in the Festuca vegetation (78 %).

fibre content (fig.16)

Percentage Neutral Detergent Fibre (dry matter) in the leaves showed a decrease in quality from summer to autumn. In July values were around 46 and 48 % increasing to 52 % in November for the Festuca and Festuca/Artemisia types. Samples from the second period indicate that this increase could have already taken place in September. In November fibre content of *F. rubra* in the Artemisia vegetation (50 %) was significantly lower than in the other two vegetation types higher on the saltmarsh.

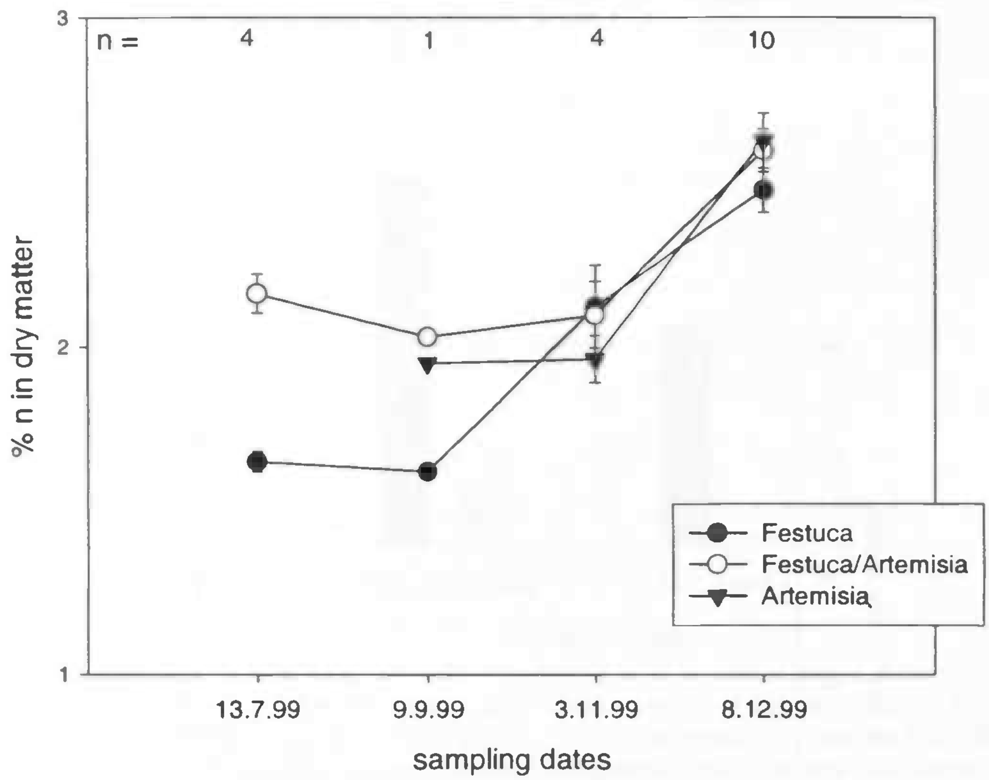


Figure 14: Nitrogen content in dry matter of Festuca rubra leaves in the Festuca,Festuca/Artemisia and Artemisia vegetation types over time. Different letters indicate significant differences within sampling dates (one-way ANOVA,Tukey post hoc; $p < 0.05$).

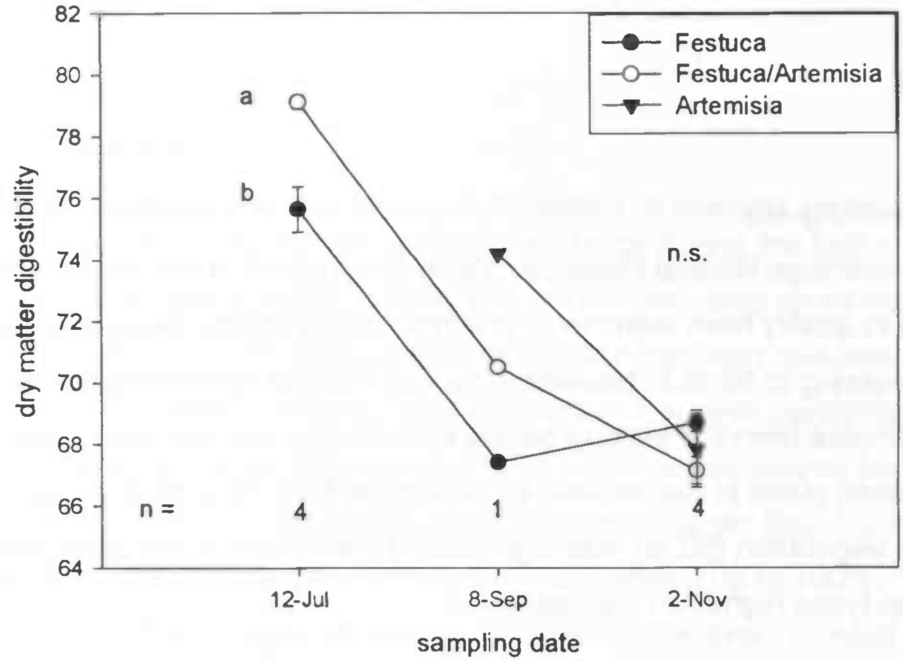


Figure 15: Dry matter digestibility of *Festuca rubra* leaves in the Festuca, Festuca/Artemisia and Artemisia vegetation types at different times of the year. Different letters indicate significant differences within sampling periods (oneway ANOVA, Tukey post hoc test; $p < 0.05$).

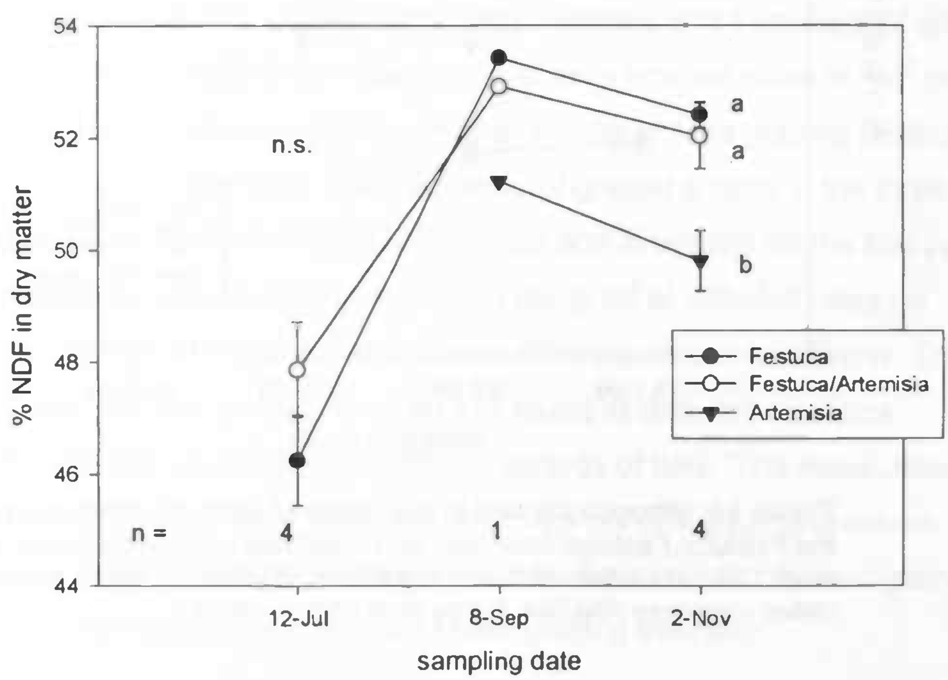


Figure 16: Percentage Neutral Detergent Fibre in dry matter in *Festuca rubra* leaves in the Festuca, Festuca/Artemisia and Artemisia vegetation types at different times of the year. Different letters indicate significant differences within periods (oneway ANOVA, Tukey post hoc; $p < 0.05$).

3.4. Effect of structure plants on hare feeding patch choice

For the Puccinellia vegetation type removal of *Suaeda* and *Salicornia spec.* had a significantly positive effect on patch choice by hares (p< 0,05) (fig.17). Removing *Artemisia maritima* within the Festuca/Artemisia vegetation did not have a significant effect on hare patch choice. There was, however, a clear trend that hares preferred the experimental patches where structure plants had been removed.

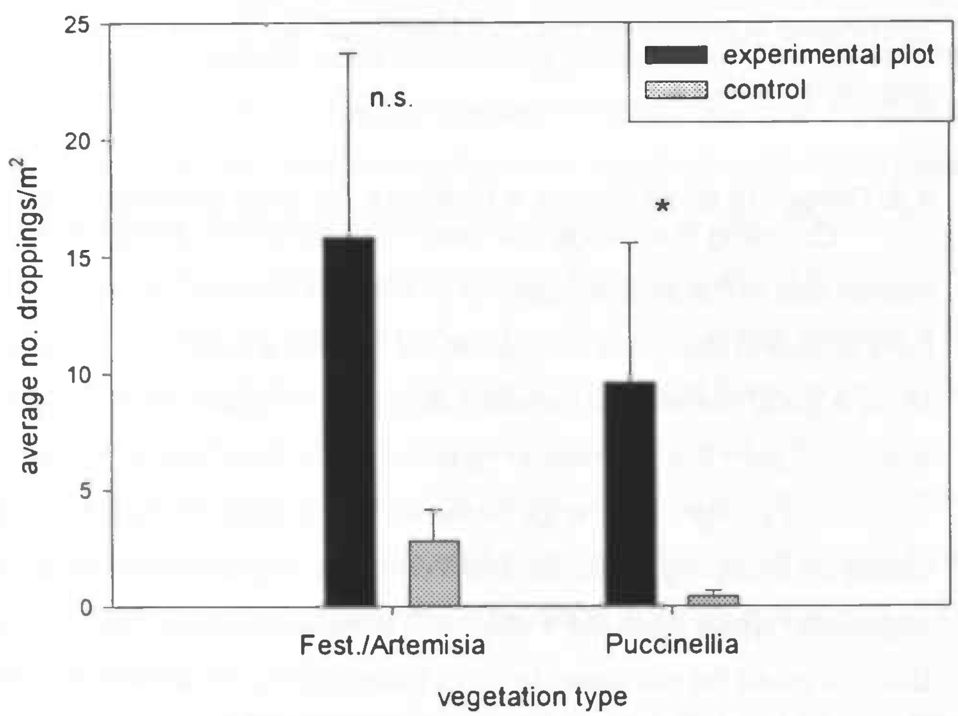


Figure 17: The effect of experimental removal of structure plants in two vegetation types on hare patch choice. Removal of Artemisia from the Festuca/Artemisia veg., removal of *Suaeda maritima* and *Salicornia* spec. from the Puccinellia veg. (paired t-test, n = 5; Festuca/Artemisia : n.s.; Puccinellia: t = 3.064, p < 0.05)

4. Discussion

4.1. Point quadrat method verses estimation of cover (Londo-scale)

Vegetation relevees were performed twice during the field season. In July using the point quadrat method and in October using an estimation of cover (Londo-scale). Results on the comparison between relevees made with both methods partially showed large differences between percentages cover of some species. Large differences can be explained by overall percentages of the Londo-relevees often reaching values much larger than 100%, whereas values from the point quadrat relevees always added up to 100%. The relative cover of the different species among each other, however, showed a similar pattern in both methods. Both methods represent a description of species composition within a site. The similarities between the two methods is considered sufficient for the conclusions drawn in this study based on the vegetation releveés.

4.2. Dropping densities as a measure for hare grazing pressure

Counting droppings has been considered an adequate measure for habitat use in hares (Langbein *et al* 1999). However, no study directly related hare dropping densities to intensity of grazed shoots. In this study I could show a good correlation between dropping densities and frequency of grazed shoots on both the vegetation type level and on a smaller scale of $4m^2$ plots. There was a slight difference between the ranking of hare grazing preference based on dropping densities and frequency of grazed shoots in the three vegetation types Festuca, Festuca/Artemisia and Artemisia for the first period. But this could be put down to plant leaves dying off at different rates on different locations of the salt marsh due to differing abiotic conditions. This would mean that the green grazed shoots found at different locations represent grazing pressure over differing periods of time. The measurement of grazing intensity used here is a rough estimate of hare grazing pressure. However, it is considered accurate enough for the purpose of investigating whether dropping densities represent hare grazing intensity.

4.3. Effect of structure plants on hare patch choice

It was experimentally shown that structure plants can have an effect on hare patch choice. A significant effect was, however, only found in the Puccinellia vegetation where the structure species *Salicornia spec.* and *Suaeda maritima* were removed from patches of *Puc. maritima*. It appears likely that structure plants lower hare foraging efficiency of *Puc. maritima* by getting in the way while foraging. However, the exact mechanism how these species deter hare grazing was not investigated in this study.

4.4. Hare diet composition

4.4.1. Hare diet in relation to food plant quality and availability

This study showed that the diet of the Brown hare in the salt marsh was dominated by grasses throughout the field season from July to November. The grass species *Festuca rubra* clearly took up the largest proportion among all other food species. A comparison between the availability of *F. rubra* and the proportion in the hare diet showed that this was a preferred food plant. This species had a medium to high quality according to the measured parameters nitrogen content, digestibility and fibre content (NDF).

Further studies on the diet of hares in grassland areas showed a similar dominance of grasses throughout the year in the diet of these animals (Brüll 1976; Wolfe *et al* 1996). Brüll's (1976) results also showed that *Festuca rubra* took up a large proportion of the diet of hares occurring in the mainland salt marshes and in agricultural grasslands further inland in Schleswig-Holstein. However, in this study no comparison was made with the availability of this species in the area.

The hares were found to have a more diverse diet in July than later in the year. Monocotyledon seeds were an important food item for hares at this time of the year. Seeds have a high energy content (Robbins 1993) and can thus be considered a good food source. Further species taking up between five and ten percent of the diet were the monocotyledons *Juncus gerardi*, *Puccinellia maritima* and *Elymus athericus* and the dicotyledon *Plantago maritima*.

Considering their low abundances within the home range area (tab.1, site A), the relatively high percentage of *Puc. maritima* and *Plant. maritima* in the July diet is consistent with the better nutritional quality of these species.

The sampled *J. gerardi* leaves had a similar nitrogen content to *F. rubra*, *Plant. maritima* and *Puc. maritima*, but had a low digestibility and a high fibre content. As already mentioned, *J. gerardi* leaves sampled mostly had brown tips. Younger shoots can be expected to have a better quality. Only few totally green shoots could be found during my field season. It can not be stated whether hares also fed on the dying *J. gerardi* shoots.

E. athericus which was found in the hare diet throughout the year in percentages of 3 to 5% has a poor quality according to the measured parametres. However, it is the second most abundant food species in the area. Considering the similar percentages of the species *Puc. maritima*, *Plant. maritima* and *E. athericus* in the diet in July and much higher availability of *E. athericus* it can be assumed that the hares preferred *Puc. maritima* and *Plant. maritima* over latter.

Triglochin maritima, the best quality food plant according to the performed analyses, was not found in the hare diet. Grazed shoots were found, but seldom. This species is quite rare in the area and is additionally known to contain cyanogenic glycosides (Beath, Draize & Eppson 1933). Both can play a role in explaining it's absence in the hare diet.

4.4.2. Seasonal changes in diet composition

The main seasonal change in the hare diet composition over the field season took place between July/August and September/October. There was a decrease in proportion of seeds and the species *Juncus gerardi*, *Plantago maritima* and *Puccinellia maritima* and a consequent increase in percentage *Festuca rubra*.

The decreasing importance of *Juncus gerardi* can be related to decreasing availability due to senescence as shown by the biomass results and the vegetation relevees. Also the decrease in proportion of seeds in the hare diet can be explained by lack of these plant parts later in the year. Biomass results did not show a clear decrease in Plant. maritima biomass by September, but this species had died off to a large extent by the time the vegetation relevees were taken in October. October represents the end of the second period (tab. 1). The decline in proportion of *Plant. maritima* in the second period is therefore likely to be due to dying off of this plant species. This is not the case for *Puccinellia maritima*.

Puc. maritima shows no clear decrease in percentage cover later in the year (tab. 4). The observation that *Puc. maritima* was increasingly overgrown by *Salicornia spec.* and *Sua. maritima* offers an explanation. *Puc. maritima* always occurred among high densities of *Salicornia spec.* and *Sua. maritima* within the study area. The latter two had their main growth period later in the summer when they grew tall above the *Puc. maritima* layer. The performed experiment showed that removal of *Salicornia spec.* and *Sua. maritima* had a positive effect on feeding patch choice by the hares showing that these structure species make *Puc. maritima* less attractive for the hares.

4.4.3. Comparing the summer to autumn diet with the winter and spring diet based on previous studies

By comparing my results on the diet of Brown hares over the summer and autumn months with results of previous studies on their winter and spring diet in the salt marsh a more complete picture arises on choices these animals make concerning their food plants.

Bestman & Keizer (1997) performed faecal analyses for the period February to May based on hare droppings found in salt marsh areas to the east and to the west of my study area and from the dunes bordering my study site. The larger size of their sampling area doesn't enable an exact comparison with my results. However, for a general picture the overall availability of plant species is similar enough between the two areas.

Their results show that also the winter and spring diet of the hares was dominated by monocotyledon species. Important monocotyledons in the winter were *Festuca rubra*, *Agrostis stolonifera* and *Elymus farctus*. The percentage of *F. rubra* increased from 20 to 50 % from February to May, reaching a similar value I measured in July. *Juncus gerardi* covered 10 to 15 % of the diet during May, again similar to my results in July. The increase in *F. rubra* and *J. gerardi* is consistent with the beginning of the growing season in spring.

Bestman & Keizer (1997) furthermore showed that the dicotyledon *Atriplex portulacoides* took up 20 % of the hare diet in February, decreasing down to very low values in May. Also van der Wal *et al* (1998d) found that the proportion of this species increased in the hare diet in the Schiermonnikoog saltmarsh over the winter.

Based on my study both dicotyledons *Artemisia maritima* and *Atriplex portulacoides* played a minor role in the hare summer diet. Leaves of both species had a lower fibre content than the grasses. This is consistent with other studies that have shown lower fibre contents in dicotyledons when compared with monocotyledons (Iason & van Wieren 1999). *A. portulacoides* also had a relatively high digestibility. However, dicotyledons are generally known to contain more secondary compounds than monocots. Bryant & Kuropat's (1980) study on winter diet selection in snowshoe and mountain hares (*Lepus americanus* and *L. timidus*) showed that these animals preferred feeding on plant species and plant parts with less secondary plant metabolites. For example, monoterpenoid substances in *Artemisia* are assumed to deter herbivores from grazing on this *genus* (Narjisse *et al* 1997). Secondary plant compounds these species contain could make them unattractive for the hares as long as enough alternative food sources are available.

Consistent with the results of Bestman & Keizer (1997) and van der Wal *et al* (1998a) the faecal analyses I performed showed that *A. portulacoides* tended to be eaten more often in November than over the summer months. This species is one of the few salt marsh plants that stays green over the winter. The results of my study also show that *Artemisia maritima* stems were clearly grazed more often in autumn than during the summer. Grazed off *A. maritima* stems, which are left laying on the ground, have often been observed in both autumn and early spring (van der Wal *et al* 1998d). Hares have also been observed to chew on the lower end of the bitten off stem (D. Bos pers. comment). It is assumed that they feed on the sweeter lower part of the stem where the plant stores it's sugars over the winter as the leaves die off (R. van der Wal pers. comment).

That hares more frequent graze *A. maritima* and the trend in eating more *A. portulacoides* during this study can be related to the strong decrease in *Festuca rubra* availability towards the end of the year as shown by the biomass samples. Both total *F. rubra* biomass decreased and ratio of standing dead to alive *F. rubra* increased. A similar switch from more grasses in the summer to more woody plants in the winter when grasses are less available is also known for the mountain hare, *Lepus timidus* (Iason & Waterman 1988).

4.5. What influences where hares choose to feed on Festuca rubra?

The results on hare grazing preference for the three vegetation types Festuca, Festuca/Artemisia and Artemisia showed that hares clearly preferred grazing in the Festuca and the Festuca/Artemisia vegetation than in then Artemisia vegetation in July to October. Hares did not show a preference between the Festuca and the Festuca/Artemisia vegetation as a food site. In November the hare grazing pattern changed. Hares did not show any preference between the three feeding sites anymore. The following questions concerning these results will be discussed below:

1) Why didn't hares graze more in the Festuca/Artemisia vegetation compared with the Festuca type over the summer considering the biomass and the quality of the preferred food plant *Festuca rubra* in the first was higher?
2) How can the very low hare grazing pressure in the Artemisia vegetation type be explained?
3) What caused the change in hare grazing pattern towards the end of the year in November when no preference was shown anymore between the three vegetation types?

4.5.1. No difference in hare grazing preference between the Festuca and the Festuca/Artemisia communities in July to October

Although *Festuca rubra* nutritional quality in July was worse and the biomass lower in the Festuca vegetation (lower nitrogen content and digestibility) than in the Festuca/Artemisia type no significant difference in hare overall grazing intensity nor in *F. rubra* grazing intensity was found between the two types.

In both July and September *Juncus gerardi* and *Plantago maritima* were frequently grazed, especially in the Festuca vegetation where these two species had a higher biomass than in the other two types. The total percentage biomass of eaten species being significantly higher in the Festuca than in the Festuca/Artemisia community combined with the better quality *F. rubra* in the latter could explain why hares did not show a grazing preference for one of the two.

This does not, however, necessarily explain why hares did not show differences in *F. rubra* grazing intensity between the two vegetation types in July and September. Considering *F. rubra* leaves in the Festuca vegetation are still of relatively good quality it may not pay to select for only *P. maritima* and *J. gerardi* amongst the more abundant *F. rubra*. Arnold (1987) showed that sheep were less selective when quality differences between species were smaller. A similar case may be found here. Grazing all three species may enable an overall higher nutrient and/or energy intake rate than being more selective.

4.5.2. Low hare grazing pressure in the Artemisia vegetation type in relation to the Festuca and Festuca/Artemisia communities in July to October

Little can be said on *Festuca rubra* nutritional quality in the Artemisia vegetation due to the missing samples in July. However, the samples analysed for the three vegetation types in September do not indicate that *F. rubra* in the Artemisia area had a lower nutritional quality than in the other two communities. Olff *et al* (1997) showed for spring that the nitrogen content in *F. rubra* leaves even increased from high to low salt marsh. This is consistent with the higher nitrogen content found in *F. rubra* leaves from the Festuca/Artemisia vegetation than in the Festuca community, which lies higher on the salt marsh. It is possible that *F. rubra* in the Artemisia area has a higher percentage nitrogen than in the other two communities. Nutritional quality of *F. rubra* is not likely to be the reason why hares chose to graze there so seldom.

The lower *Festuca rubra* cover in the Artemisia than in the Festuca and Festuca/Artemisia vegetation types as shown by the vegetation relevees in

July and October may indicate a lower availability of this species from a hare perspective. Hares mainly grazed on the upper part of the leaves i.e. that biomass may not be a good indication for food availability. The similar *F. rubra* biomass in the Festuca/Artemisia and Artemisia vegetation, although *F. rubra* cover was clearly lower in the Artemisia type, can be explained by the longer leaves in the latter community. Van der Wal *et al* (1998a) showed for geese that short-term food intake was strongly related to percentage cover of the their food plant *F. rubra*. In contrast, geese showed lowest intake rates on high biomass patches (van der Wal *et al* 1998a). Measuring intake rates for hares would be a difficult procedure. Assuming foraging efficiency is an important parameter when it comes to their choice of a feeding site, hares may find the long leafy swards of the Artemisia vegetation unattractive for grazing due to a lower intake rate.

In a similar line of argumentation, the high cover of *Artemisia maritima* in the Artemisia community when compared with the Festuca and Festuca/Artemisia vegetation types may hinder hare foraging efficiency. The conducted experiment in this study showed that structure plants can have an effect on feeding patch choice by hares, although the removal of *A. maritima* showed no significance. Nevertheless, results showed a clear tendency. The experiment was performed on patches with lower *A. maritima* cover than found in most areas of the Artemisia vegetation. The effect of *A. maritima* on hare feeding patch choice may become stronger the higher the percentage cover of this species. This would be an interesting question for future research.

A further factor possibly playing a role in where hares choose to feed is predation risk. Hares may feel hindered in their ability to detect approaching predators when feeding in high vegetation. On the other hand high vegetation can also offer protection from predators.

Based on this study three factors are named that may explain why hares fed so rarely in the Artemisia vegetation over the summer months: predation risk and the two parameters long leafy swards and structure plants that may lower accessibility of the food plant *F. rubra*.

4.5.3. No grazing preference between the Festuca, Festuca/Artemisia and Artemisia communities in November

The changing hare grazing pattern towards the end of the year could be due to a decrease in the magnitude of differences between the different feeding sites from a hare's point of view, but also to the overall seasonal change in food availability. As WallisDe Vries & Daleboudt (1994) pointed out, selectivity between feeding sites could be more rewarding if the differences between food patches are larger. It has also been shown that as food gets scarce herbivores can be less selective in the foods they eat (Sinclair 1975). This could also go for choices they make concerning where they graze. In this case, due to decreasing *F. rubra* availability hares may choose to feed on this species in areas they found unattractive in times when this food source was abundant. Murton *et al* (1966) showed a similar phenomenon with Wood pigeons. When the overall clover availability decreased they started feeding in areas with lower clover cover which they had avoided when clover was abundant.

Biomass results give few indications for a decreasing difference between the three vegetation types, which could explain the increasing grazing preference for the Artemisia vegetation. The December samples show a strong decrease in *Artemisia maritima* biomass. However, the vegetation relevees made in October still showed similar percentage cover of structure plants within the three types. The Artemisia vegetation still had the highest percentage cover of structure plants, followed by Festuca/Artemisia and then Festuca. This vegetation description took place about 12 days before higher dropping densities were found in the Artemisia area making it unlikely large changes took place before the turning point in hare grazing preference took place.

The decreasing *A. maritima* biomass in December is likely to be caused by a combination of hare grazing and senescence. By including *A. maritima* to the eaten species in December the percentage biomass of eaten species becomes significantly higher in the Festuca/Artemisia and Artemisia vegetation than in the Festuca type. It must be kept in mind, however, that *F. rubra* can still be expected to be preferred over *A. maritima* i.e. a higher percentage biomass of eaten species can not in itself be interpreted as a measure for a better feeding site. The herbivore's differing preference for different plant species must be taken into account.

Nutritional quality analyses of *F. rubra* leaves do show less differences between the three vegetation types in October/November than in July. Both nitrogen content and digestibility no longer differ between the different sites. However, as stated in section 4.5.2. it is unlikely that *F. rubra* leaf quality was worse in the Artemisia vegetation when compared with the other two vegetation types. Decreasing differences in nutritional quality does not offer an explanation why hares showed no preference between the three vegetation types.

Concluding it can be stated that the changes in hare grazing pattern in November is probably mainly due to the strong decline in *F. rubra* availability towards the end of the vegetation growing season. As this important food became scarce hares started to feed on it in areas they found unattractive while food was abundant.

4.6. General conclusion

The hare diet composition consisted mainly of medium to high quality food plants. This result is consistent with the expected high nutritional requirements of these animals. However, food nutritional quality alone could not explain the hare diet composition over the summer to autumn. Availability of the food species appeared to play an important role. Selecting to feed on high amounts of a very high quality food plant, which is barely present means longer searching times and herewith probably overall lower nutrient or energy intake rates. Under the aspect of foraging efficiency *Festuca rubra* with it's high abundance and relatively good nutritional quality represents the best combination of quality and availability in the study area over the summer. This can explain the large proportion of this species in the hare diet during this period. *A. portulacoides* and *Artemisia maritima* become a more important food source for the hares when the major summer food source *F. rubra* declines in availability in autumn and over the winter. Secondary plant compounds may affect hare food choices when it comes to these species.

Neither biomass nor nutritional quality of *F. rubra* leaves alone could explain where hares chose to feed. According to these two parameters, the

Festuca/Artemisia and the Artemisia vegetation type offered the best feeding sites. Biomass was higher in the Festuca/Artemisia and Artemisia vegetation types when compared with the Festuca type. In July nutritional quality of *F. rubra* was clearly better in the Festuca/Artemisia vegetation than in the Festuca type. Based on the study by Olff *et al* (1997) it could even be expected that *F. rubra* quality was the best in the Artemisia vegetation earlier in the year. Hares, however, rarely grazed in the Artemisia and grazed frequently in the Festuca and the Festuca/Artemisia communities.

The sward structure in terms of long leaves and presence of structure plants may have a negative influence on where hares choose to graze by lowering their foraging efficiency. The occurrence of other good quality food plants appeared to have a positive effect on hare feeding site choice in the Festuca vegetation, which again could be interpreted in terms of an overall higher nutrient and/or energy intake rate.

Based on the results of this study both hare diet selection and where these small herbivores chose to feed did not depend on food nutritional quality alone. These two aspects of hare foraging behaviour in the salt marsh were closely related to the availability of the food. On a larger scale *Festuca rubra* clearly represented the most available food plant for hares over the summer. On a smaller scale within the three plant communities investigated in more detail here, a defintion of *F. rubra* availability from the perspective of a hare is more difficult. Biomass appeared not to be a good measure.

Hare feeding site choice was shown to not only depend on the food availability in the sites themselves, but on the overall food availability within their home range at the time of the year.

5. Summary

Diet selection and factors influencing feeding patch choice of the Brown Hare (*Lepus europaeus*) were studied in relation to their food quality and availability in a salt marsh habitat. The study took place from July to December on the Wadden Sea island Schiermonnikoog (Netherlands). Hare diet composition and plant nutritional quality in terms of nitrogen content, fibre content (NDF) and *in vitro* digestibility were determined for three different periods within the field season. Diet selection was looked at by comparing proportion of species in the diet with an estimation of food species availability within an area based on hare home range size. Hare grazing preference for three vegetation types with high abundance of the important food plant *Festuca rubra* was investigated. These plant communities differed in species composition, *F. rubra* biomass and quality. Additionally, an experiment was set up to test for the effect of less palatable structure plants on feeding patch choice by hares.

F. rubra was the main hare food plant over the season. When compared with it's availability this species was also a preferred food source. Hare diet selection could be explained by a combination of food quality and availability following the principals of foraging efficiency. In July the hare diet was more diverse than later in the year. The seasonal decline in proportion of *Plantago maritima*, *Juncus gerardi* and monocotyledon inflourescences could be related to a decline in their availability. Hares started to graze more frequently on the less preferred species *Artemisia maritima* and *Atriplex portulacoides* in November/December when their major food plant *F. rubra* became less available due to scenescence and a high proportion of standing dead.

Hare grazing preferences over the three vegetation types with a high cover of *Festuca rubra* showed that neither biomass nor nutritional quality alone could explain hare feeding site choice. The presence of further good quality food plants among the stands of *F. rubra* appeared to have a positive effect on their choice of where to feed. Long leafy swards and the occurrence of structure plants could have had a negative effect on where the hares chose to feed. The experiment showed that structure plants can have an effect on

hare feeding patch choice. Towards the end of the year when overall F. rubra was less available the hares changed their grazing preferences. Hares became less selective of their feeding sites towards the end of the year when *F. rubra* became less available. They started grazing on *F. rubra* in sites they avoided while this food source more available.

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Appendix I: Abbreviations

A. portulacoides	*Atriplex portulacoides*
A. prostrata	*Atriplex prostrata*
A. stolonifera	*Agrostis stolonifera*
A. tripolium	*Aster tripolium*
Arm. maritima	*Armeria maritima*
Art. maritima	*Artemisia maritima*
E.athericus	*Elymus athericus*
F. rubra	*Festuca rubra*
G. maritima	*Glaux maritima*
J. gerardi	*Juncus gerardi*
L. vulgare	*Limonium vulgare*
Pla. maritima	*Plantago maritima*
Puc. maritima	*Puccinellia maritima*
Spa. anglica	*Spartina anglica*
Sua maritima	*Suaeda maritima*
Tri. maritimum	*Triglochin maritimum*
Tri. repens	*Trifolium repens*
st. dead	standing dead

Appendix II: Vegetation relevees performed in June/July with the point quadrat method

Artemisia 19-28.7.99

plot no.	*F. rubra*	*J. gerardi*	*L. vulgare*	*Art. maritima*	*Puc. maritima*	*A. prostrata*	*Tri. maritimum*	*A. tripolium*	*Sua. maritima*	litter	st. dead	soil
1	40	0	1	48	2	1	0	0	1	5	2	0
2	57	0	6	32	0	0	1	0	0	1	2	1
3	44	0	8	45	0	0	0	0	0	1	1	1
4	44	0	3	48	0	0	0	0	0	0	1	4
5	38	2	3	47	2	2	1	0	0	0	2	3
6	55	0	2	36	0	0	0	0	3	1	2	1
7	53	4	10	32	0	0	0	0	0	1	1	0
8	38	0	10	52	0	0	0	0	0	0	0	0
9	56	0	1	40	0	0	0	1	0	0	0	2
10	40	0	0	56	1	1	0	0	0	0	2	0

Festuca 26.6.-10.7.99

plot no.	*F. rubra*	*J. gerardi*	*Pla. maritima*	*A. stolonifera*	*E. athericus*	*L. vulgare*	*Odontites spec.*	*G. maritima*	*Centaurium spec.*	*Tri. repens*	*Art. maritima*	*Arm. maritima*	litter	st. dead	soil
1	44	35	13	0	0	1	3	0	1	0	0	0	1	0	0
2	61	21	10	2	0	0	6	0	0	1	0	0	0	3	0
3	46	25	1	2	0	0	16	0	1	8	0	0	1	0	0
4	62	23	4	1	0	2	1	1	0	1	0	0	0	1	0
5	51	17	25	0	1	0	2	0	0	0	0	0	1	4	0
6	63	10	14	0	0	7	0	1	0	0	1	0	4	0	0
7	42	34	14	0	0	8	0	0	0	0	0	0	1	0	1
8	61	31	5	1	0	0	1	0	0	0	0	0	0	1	0
9	79	12	3	1	0	2	0	0	0	0	1	1	0	0	1
10	58	27	6	0	0	5	0	0	0	0	0	1	1	2	0

Juncus 26.6.-8.7.99

plot no.	*J. gerardi*	*F. rubra*	*Pla. maritima*	*A. stolonifera*	*L. vulgare*	*G. maritima*	*Art. maritima*	*Puc. maritima*	*A. prostrata*	*Tri. maritimum*	*A. tripolium*	*Sua. maritima*	litter	st. dead	soil
1	80	6	1	7	4	0	0	0	0	0	0	0	0	2	0
2	70	1	7	12	7	0	1	0	0	0	0	0	0	2	0
3	67	9	12	5	4	0	0	0	1	2	0	0	0	0	0
4	68	1	14	5	7	0	0	0	1	0	3	0	0	0	1
5	82	1	6	0	2	0	0	0	0	8	0	1	0	0	0
6	73	1	21	0	1	0	0	0	0	1	0	0	0	0	3
7	64	1	19	0	12	1	0	2	0	0	0	0	0	0	1
8	75	3	6	3	9	0	0	0	3	0	0	0	0	0	1
9	86	2	0	0	6	0	0	0	1	5	0	0	0	0	0
10	59	1	38	0	2	0	0	0	0	0	0	0	0	0	0

Festuca/Artemisia 28.6.-15.7.99

plot no.	*F. rubra*	*J. gerardi*	*Pla. maritima*	*L. vulgare*	*Art. maritima*	*Puc. maritima*	litter	st. dead	soil
1	49	27	0	0	22	0	2	0	0
2	59	7	0	0	33	0	0	1	0
3	50	18	3	0	27	0	0	2	0
4	45	8	0	1	41	0	2	3	0
5	67	12	2	0	17	0	0	1	0
6	69	0	1	11	17	0	1	1	0
7	53	15	1	20	8	1	0	1	1
8	72	0	1	10	17	0	0	0	0
9	54	3	0	0	41	0	2	0	0
10	68	3	0	2	25	0	2	0	0

Festuca/Elymus 15-20.7.99

plot no.	*F. rubra*	*Pla. maritima*	*A. stolonifera*	*E. athericus*	*Tri. repens*	*Arm. maritima*	*litter*	*st dead*	*bare*
1	24	0	12	35	0	0	16	11	2
2	33	0	7	31	0	0	10	18	1
3	21	0	12	31	1	0	20	11	3
4	20	0	13	32	3	0	13	16	3
5	25	3	3	29	0	1	14	22	3
6	25	0	7	37	0	0	20	11	0
7	25	0	5	37	0	0	14	19	0
8	30	0	17	23	0	0	16	14	0
9	25	0	9	37	0	0	16	13	0
10	27	0	1	28	0	0	25	19	0

Puccinellia 16.7.99

plot no.	*Puc. maritima*	*J. gerardi*	*Pla. maritima*	*Spa. anglica*	*L. vulgare*	*Tri. maritimum*	*A. tripolium*	*Sua. maritima*	*Salicornia spec.*	*A. portulacoides*	*Spe. maritima*	*litter*	*st dead*	*soil*
1	25	0	2	5	22	3	2	23	14	1	0	0	2	1
2	9	0	0	1	0	1	0	24	44	2	0	0	8	11
3	10	0	0	2	17	20	0	11	21	19	0	0	0	0
4	14	0	0	0	22	17	0	16	23	6	0	0	0	2
5	36	0	0	1	32	4	2	12	6	0	0	0	1	6
6	25	4	0	6	2	0	0	24	27	2	0	0	4	6
7	29	0	0	23	0	0	0	23	7	0	0	3	11	4
8	20	0	0	1	3	3	0	16	41	0	1	0	5	10
9	20	0	0	10	3	13	8	14	14	10	1	0	4	3
10	35	0	0	2	0	0	0	16	20	23	0	0	2	2

Limonium 27.6.-5.7.99

plot no.	*Puc. maritima*	*Tri. maritima*	*L. vulgare*	*Art. maritima*	*A. tripolium*	*Sua. maritima*	*Salicornia spec.*	*A. portulacoides*	*Spe. maritima*	*G. maritima*	*F. rubra*	*E. athericus*	*litter*	*st dead*	*soil*
1	13	2	36	0	0	1	21	0	1	0	0	0	0	0	16
2	15	14	27	0	0	2	11	0	2	0	0	0	0	1	28
3	10	1	40	0	0	1	15	0	0	0	0	0	0	7	26
4	0	0	50	0	0	7	6	12	4	0	0	0	0	1	20
5	1	0	60	0	0	1	2	5	8	0	0	0	0	3	20
6	8	1	56	0	0	17	4	2	2	6	1	0	0	0	2
7	5	0	44	0	0	10	23	7	1	0	0	1	1	1	7
8	17	0	60	0	3	6	8	3	0	0	0	0	0	0	3
9	12	1	54	1	5	10	9	0	0	2	0	0	0	1	4
10	4	3	62	0	0	12	12	1	1	0	0	0	0	1	4

Atriplex/Limonium 27.-28.6.99

plot no.	*Puc. maritima*	*Tri. maritimum*	*L. vulgare*	*Art. maritima*	*Sua. maritima*	*Salicornia spec.*	*A. portulacoides*	*Spe. maritima*	*litter*	*st. dead*	*soil*
1	2	0	33	0	8	8	40	1	0	0	8
2	0	0	0	0	13	7	71	0	0	2	7
3	0	0	11	0	11	8	61	0	0	1	8
4	0	0	33	1	4	4	49	2	0	1	6
5	0	0	38	0	7	3	43	1	0	3	5
6	2	0	26	0	10	10	30	1	2	2	17
7	2	0	23	0	4	1	53	1	0	0	16
8	1	5	36	6	5	0	36	1	0	0	10
9	5	1	0	20	10	4	45	0	0	2	13
10	19	6	2	0	21	2	43	0	0	2	5

Appendix III: Vegetation relevees performed in October using an estimation of cover according to Londo-scale

Atriplex/Limonium 18.10.99

plot no.	*Puc. maritima*	*Tri. maritimum*	*A. tripolium*	*Spa. anglica*	*Spe. maritima*	*Salicornia spec.*	*Sua. maritima*	*A. portulacoides*	*L. vulgare*	st. dead	bare
1	3	0.5	0.5	0	0.5	7.5	3	47.5	30	10	30
2	1.5	0.5	0	0	0.5	3	1.5	60	30	10	20
3	1.5	0	0	0	0.5	1.5	1.5	60	30	10	10
4	1.5	0.5	0	0	0	0.5	0.5	80	20	5	20
5	20	0	0.5	0	0	3	3	70	0.5	5	10
6	0.5	0	0	0	0	3	3	47.5	40	20	20
7	0.5	0.5	0	0	0	3	3	47.5	20	20	20
8	0.5	0	0.5	0	0.5	7.5	7.5	40	30	20	20
9	0.5	0	0	0.5	0	3	3	47.5	1.5	30	30
10	0.5	0	0	0.5	0	3	3	80	0.5	5	10

Festuca 16.10.99

plot no.	*F. rubra*	*J. gerardi*	*PLa. maritima*	*A. stolonifera*	*E. athericus*	*Arm. maritima*	*L. vulgare*	*Tri. repens*	*Odontites spec.*	*G. maritima*	st. dead	bare
1	80	0.5	3	0.5	0.5	0	0.5	0.5	0.5	0.5	30	2
2	70	0.5	3	1.5	0	0.5	1.5	3	0.5	0.5	20	2
3	70	0.5	0.5	1.5	0	0.5	0	7.5	3	0	40	1
4	80	0.5	3	0.5	0	0.5	0	7.5	0.5	0	30	1
5	80	0.5	12.5	0.5	0	0	1.5	0.5	0.5	0.5	20	3
6	80	0.5	3	0.5	0	0.5	7.5	0.5	0	0.5	30	2
7	40	0.5	0.5	3	0.5	0.5	12.5	0	0	0.5	50	3
8	70	0.5	3	1.5	0	0.5	0.5	0.5	0.5	0	60	5
9	80	0.5	0.5	0.5	0	0.5	1.5	0.5	0	0	60	5
10	80	0.5	0.5	0.5	0	0.5	1.5	0.5	0	0	60	5

Festuca/Artemisia 15.10.99

plot no.	*F. rubra*	*Art. maritima*	*L. vulgare*	st. dead	bare
1	60	12.5	1.5	40	2
2	85	20	1.5	20	3
3	60	7.5	0.5	40	2
4	60	12.5	1.5	35	3
5	60	12.5	1.5	30	2
6	90	12.5	7.5	35	2
7	80	1.5	7.5	35	1
8	80	7.5	3	45	2
9	70	20	1.5	35	4
10	60	7.5	0.5	45	2

Artemisia 18.10.99

plot no.	*F. rubra*	*Art. maritima*	*Sua. maritima*	*A. prostrata*	*L. vulgare*	*G. maritima*	*A. portulacioides*	st. dead	bare
1	70	47.5	0.5	0.5	0.5	0	0	10	1
2	70	40	0.5	0.5	0.5	0	0	15	1
3	60	40	0.5	0	3	0	0	10	1
4	80	30	0	0	12.5	0	0	10	1
5	90	7.5	0	0	1.5	0.5	0	10	1
6	47.5	52.5	0.5	0.5	0.5	0	0.5	15	4
7	80	7.5	0	0	20	0	0	15	3
8	52.5	47.5	0.5	0	20	0	0	10	3
9	40	40	0.5	0.5	0.5	0	0	15	1
10	40	40	0.5	1.5	0.5	0	0	15	3

Limonium 18.10.99

plot no.	*Puc. maritima*	*Pla. maritima*	*F. rubra*	*Spa. anglica*	*A. portulacoides*	*A. tripolium*	*Tri. maritimum*	*L. vulgare*	*Sua. maritima*	*Salicornia spec.*	*Spe. maritima*	st. dead	bare
1	7.5	0	0	0	0.5	0.5	0.5	40	0.5	12.5	0.5	50	30
2	20	0.5	0	0	0	0.5	0.5	40	0.5	7.5	0.5	50	40
3	12.5	0	0	0.5	0.5	0	0.5	40	1.5	12.5	0.5	50	40
4	0.5	0	0	0	20	0	0	40	1.5	3	0.5	60	40
5	0.5	0	0	0	0.5	0	0	40	0.5	3	0.5	60	50
6	12.5	0	0.5	0.5	0.5	7.5	0	52.5	7.5	3	0.5	60	20
7	3	0	0	0	7.5	1.5	0.5	52.5	3	3	0.5	50	40
8	12.5	0	0.5	0.5	0.5	3	0.5	60	3	3	0.5	50	20
9	7.5	0.5	0	0	0.5	7.5	0.5	70	3	3	0.5	50	20
10	7.5	0	0	0	0.5	1.5	0.5	47.5	7.5	7.5	0.5	50	40

Puccinellia 18.10.99

plot no.	*Puc. maritima*	*Pla. maritima*	*Spa. anglica*	*F. rubra*	*A. portulacoides*	*A. tripolium*	*Tri. maritimum*	*L. vulgare*	*Salicornia spec.*	*Sua. maritima*	st. dead	bare
1	12.5	0.5	1.5	1.5	3	1.5	0.5	7.5	12.5	20	10	40
2	3	0	0.5	0	0.5	0.5	0.5	0.5	20	30	40	50
3	30	0	0.5	0	12.5	0.5	0.5	7.5	12.5	12.5	20	30
4	30	0	0.5	0	3	0	0.5	30	7.5	7.5	30	30
5	30	0.5	1.5	0	0.5	1.5	0.5	20	7.5	7.5	10	40
6	20	0	1.5	0	0.5	0.5	0.5	0.5	30	30	30	30
7	12.5	0	20	0	0.5	0.5	0.5	0	12.5	20	10	40
8	7.5	1.5	0.5	0	0	0.5	1.5	1.5	20	20	40	40
9	12.5	0.5	3	0	3	7.5	1.5	7.5	12.5	20	20	30
10	20	0	1.5	0	12.5	1.5	0.5	0.5	20	20	20	30

Juncus 16.10.99

plot no.	*F. rubra*	*J. gerardi*	*A. stolonifera*	*Pla. maritima*	*Puc. maritima*	*E.athericus*	*Tri. maritimum*	*Spe. maritima*	*A. portulacoides*	*Art. maritima*	*G. maritima*	*A. tripolium*	*L. vulgare*	st. dead	bare
1	70	0.5	3	0.5	0	0.5	0	0	0.5	0	0.5	0	3	40	2
2	30	0.5	7.5	1.5	0	0.5	0	0	0.5	0	0.5	0.5	20	40	10
3	40	0.5	1.5	1.5	0	0.5	0	0	0.5	0	0	0	1.5	40	4
4	12.5	0.5	3	7.5	0	0	0	0	0.5	0	0	1.5	12.5	60	10
5	0.5	0.5	0	7.5	0	0	0	0	0.5	0	0.5	1.5	3	90	15
6	12.5	0.5	0.5	20	0	0	0	0	0.5	0.5	0.5	0.5	0.5	70	10
7	3	0.5	3	1.5	0.5	0	0	0	0.5	0	0.5	0	30	70	15
8	20	0.5	3	3	0.5	0	0	0.5	3	0.5	0.5	0.5	12.5	60	5
9	3	0.5	3	1.5	0	0	0	0.5	3	0.5	0	0.5	12.5	90	4
10	12.5	0.5	1.5	1.5	0.5	0	0.5	0	3	0	0	0	3	70	5

Festuca/Elymus 15.11.99

plot no.	*F. rubra*	*A. stolonifera*	*E. athericus*	*Pla. maritima*	*Sedum acre*	*Sonchus*	*Pla. coronopus*	*Centaurium spec.*	*Arm. maritima*	*Tri. repens*	st. dead	bare	moss
1	20	12.5	20	0	0.5	0	0	0	0	0	40	10	10
2	30	12.5	20	0	0	0	0	0	0	0	40	5	0
3	20	20	20	0.5	0	0	0	0	0	0.5	30	10	10
4	20	12.5	30	0	0.5	0	0.5	0.5	0	0.5	30	10	20
5	20	12.5	30	0.5	3	0	0	0	0.5	0.5	30	5	10
6	12.5	7.5	40	0	1.5	0	0	0	0	0.5	30	10	3
7	7.5	30	20	0.5	3	0	0	0	0	0	25	15	10
8	7.5	12.5	40	0	0.5	0.5	0	0	0	0	30	15	3
9	12.5	7.5	40	0	0.5	0	0	0	0	0	30	10	1
10	20	7.5	30	0.5	0.5	0	0.5	0	0	0.5	30	10	5

Appendix IV: Method of chemical analysis used for determining nitrogen content of plant material

2.2 DIGESTION IN TUBES WITH H_2SO_4 - SALICYLIC ACID - H_2O_2 AND SELENIUM

2.2.1 Field of application

This digestion is in particular suited for routine work on large series of plant samples and automated determinations. It can be applied for the determination of Ca, K, Mg, Mn, N-total, Na, P, and Zn in plant material.

2.2.2 Principle

The larger part of organic matter is oxidized by hydrogen peroxide at relatively low temperature. After decomposition of the excess H_2O_2 and evaporation of water, the digestion is completed by concentrated sulphuric acid at elevated temperature under the influence of Se as a catalyst.

Remarks:

1. Salicylic acid is added to prevent loss of nitrate.
2. A precipitate of $CaSO_4$ may be formed when cooling after completing the digestion; it will dissolve in 18 — 20 hours after the addition of water. Therefore, Ca can be measured only after this period.

2.2.3 Apparatus

Aluminium heating block with holes for digestion tubes.
Metal weighing funnels with long spouts.(see Fig. 1)
Digestion tubes, 100 ml, with narrowed neck (see Fig. 2).

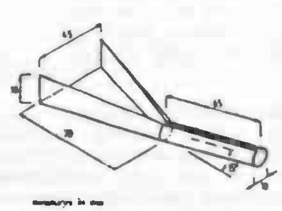

Fig. 1 Weighing funnel

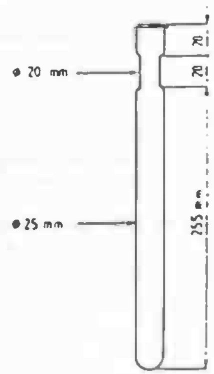

Fig. 2 Digestion tube

Remarks:

3. Dried plant material may easily stick to glass when the relative humidity of the air is low. These home-made weighing funnels (stainless steel or aluminium) do not show this effect.
4. These weighing funnels have been designed with an extra long spout, so that the plant material is released below the narrowed neck.
5. The dimensions of digestion tubes may be different from those indicated in Fig.2, as long as they fit exactly into the holes of the heating block used and have a length of at least 15 cm.
6. In the authors' laboratory, a series consists of 30 tubes: 24 samples, 2 blanks, 1 plant sample with known low concentration (in duplicate) and 1 with known high concentration (also in duplicate). These known samples serve as internal quality control.

2.2.4 Reagents

(1) Sulphuric acid, 96 % (w/w), $c(H_2SO_4)$ = 18 mol/l (d = 1.84 g/ml).
(2) Hydrogen peroxide 30 % (w/w).
(3) Selenium, powder.
(4) Salicylic acid, powder.
(5) Sulphuric acid - selenium mixture. Dissolve 3.5 g of selenium (3) in 1 litre of sulphuric acid (1) by heating to about 300 °C, while covering the beaker with a watch glass. The originally black colour of the suspension turns via green/blue into clear light-yellow. The entire process takes 3-4 hours.
(6) Digestion mixture. Dissolve 7.2 g of salicylic acid (4) in 100 ml of the sulphuric acid-selenium mixture (5). This digestion mixture should not be stored for more than 48 h.

Remarks:

7. In the authors' routine laboratory, where this digestion is applied every day, the plant material is dried again at 70 °C just before weighing; at that moment its moisture content is only 1 — 2 %, so that concentrated sulphuric acid may be used for the digestion. When the drying is not repeated, the plant sample may contain up to 10 % moisture. The use of concentrated sulphuric acid then causes a

Appendix V: Method of chemical analysis used for determining Neutral Detergent Fibre content

Measurement of N.D.F.

The sample is weighed and boiled in a tube with N.D.R. (Neutral Detergent Reagent) solution. The contents of the cell dissolves.
After filtration the cell wall fraction, N.D.F (neutral detergent Fibre) stays in the crucible. This fraction is rinsed, dried and weighted.

Equipment:
- 250 ml boiling tubes
- heating block
- glassfibre crucibles (D2 or P2) with outlets connected to an aspirator (2)
- stove and crucible tongs
- balance (4 decimals)
- tubes with ice (see sample)
- acetone
- oven (550 °C)
- exsiccator
- aspirator
- büchner funnel (3+4)

Chemicals:
- distilled water
- Titriplex III [Na_2EDTA]
- di-sodium tetraborate decahydrate [$NA_2B_4O_7.10H_2O$]
- di-sodium hydrogen phosphate dihydrate [$Na_2HPO_4.2H_2O$]
- dodecyl sulfate sodium salt [$C_{12}H_{25}NaO_4S$]
- ethylene glycol monethyl ether [$C_4H_{10}O_2$]

Method:
- Mix the sample (dried and passed through a 1mm sieve) and weigh 0.9 grams on a weight paper or open funnel with a long neck. Transfer the sample in a 250 ml boiling tube with the help of a brush.
- Add 100 ml N.D.R. solution to each tube. (measured from a 100 ml measuring cylinder). Shake the tubes.
- Switch on the heating block at 170 °C and put for example every 5 minutes a tube in the block. Hang a test tube with ice above the boiling tube to avoid evaporation.
- Record the time that it starts to boil for each tube.
- Replace the tube with ice after boiling for 30 minutes.
- After boiling for total 60 minutes the sample is filtered over a glassfibre crucible placed on a büchner funnel which is connected to an aspirator.
- Transfer the rest of the sample with hot distilled water into the crucible. Wash the crucible four times with hot distilled water.
- There after wash the sample twice with a little acetone. Fill the crucible half with acetone and keep it there for at least one minute.
- Dry the crucibles in a stove at 103 °C for eight hours.
- Weigh the crucibles one by one.
- Place the crucibles in an oven for 3 hours at 550 °C.
- If the samples have cooled down a bit, put them in order in the stove at 103 °C.
- After one hour the samples are cooled down enough to be weighed (ash weight).

Calculation:
% cell wall in the organic matter:

$$\% \, NDF = \frac{\text{dry weight(with crucible)} - \text{ash weight(with crusible)}}{\text{starting weight} * \frac{\% \, dm.}{100} * \frac{\% \, om.}{100}} * 100 \, \%$$

All weights are in grams.
Allowed differences between duple's:

amount	accuracy
<10%	0.2% abs.
10-20%	2% rel.
20-40%	0.4% abs.
>40%	1% rel.

Solutions:

NDR-solution with EDTA.
- Dissolve by heating 465,25 g. Na_2EDTA (titriplex III), distributed over 2 beakers (3 L.) with each two litre distilled water.
- Dissolve by heating 170,25 g. $Na_2B_4O_7.10H_2O$ in two litre distilled water.
- Dissolve by heating 114,00 g. $Na_2HPO_4.2H_2O$ in two litre distilled water.
- Dissolve by heating 750 g. $C_{12}H_{25}NaO_4S$ distributed over 3 beakers (4 L.) in hot distilled water.
- Transfer all solutions into a 25 L. barrel.
- Add 250 ml $C_4H_{10}O_2$ (ethylenglycol monoethylether) step by step to limit foam.
- Fill up to 24 L. with distilled water and cool down.
- Fill up till 25 L. and mix well.
- Measure pH, it has to be between 6.9 and 7.1.
- If necessary correct with 0.1 N H_2SO_4 or 0.1 N NaOH.

Appendix VI: Method of chemical analysis used for determining *in vitro* digestibility of plant material

ANALYSE VOORSCHRIFT

Bepaling : **Verteerbaarheid van de organische stof *in vitro* volgens Tilley en Terry.**

1. Onderwerp.

De bepaling van de verteringscoëfficiënt organische stof van plantaardige produkten met behulp van penssap afkomstig van schapen.

2. Toepassingsgebied.

Het voorschrift is van toepassing op vrijwel alle ruwvoeders en alle vochtrijke en droge krachtvoeders, hetzij enkelvoudig hetzij gemengd, behalve wanneer stoffen zijn toegevoegd die een remmende werking hebben op de pensflora.

3. Beginsel.

Het verteringsproces van de herkauwer wordt *in vitro* nagebootst door een incubatie met pensvloeistof, gevolgd door een incubatie met een pepsine/zoutzuur oplossing.
Door standaardmonsters met bekende *in vivo* waarden voor verteerbaarheid van de organische stof mee te analyseren, kan een regressielijn berekend worden die het verband aangeeft tussen de *in vitro* en *in vivo* verteerbaarheid. Met behulp van deze regressielijn wordt voor de analysemonsters de *in vivo* verteerbaarheid van de organische stof geschat.

4. Toestellen en hulpmiddelen.

4.1 Centrifugebuizen, inhoud ca. 100 ml. De buizen worden voorzien van een maatstreep bij 50 ml.
4.2 Rubber stoppen voorzien van een gas uitlaatventiel; zie figuur 1.
4.3 Automatische pipet en voorraadfles; zie figuur 2., of b.v. een instelbare slangenpomp.
4.4 Waterbad 39°C ± 1°C. Afmetingen afhankelijk van gebruikte voorraadfles.
4.5 CO_2-gas.
4.6 Droogstoof 103 °C ± 2°C .
4.7 Broedstoof 39°C ± 1°C.
4.8 Moffeloven 550°C ± 10°C.
4.9 Analytische balans, nauwkeurig tot op 0,1 mg
4.10 Glasfilterkroezen, porositeit P3, gevuld met 1,5 cm gewassen en uitgegloeid zilverzand.
4.11 Exsiccatoren met droogmiddel.
4.12 Centrifuge 1400 g.
4.13 Thermosflessen.
4.14 Plastic-buis van ca. 45 cm lengte, ϕ 3 cm. Deze buis is aan de onderzijde afgesloten door een rubber stop. De buiswand is geperforeerd.
4.15 Roermotor, voorzien van een roervin met grote schoepen zodat goed gemengd kan worden bij een laag toerental; dit om beschadiging van micro-organismen zoveel mogelijk te voorkomen.
4.16 Kaasdoek, borduurstramien 16 draden per cm (in beide richtingen).
4.17 Nylondoek (voeringstof).
4.18 Vacuum inrichting voor het afzuigen van filterkroezen en Büchner trechters.
4.19 Wisser, glasstaaf voorzien van een stukje rubberslang.

5. Reagentia.

Alle hoeveelheden zijn gebaseerd op een serie van 100 bepalingen.
Tenzij anders vermeld, bedraagt de uiterste houdbaarheid van de reagentia 1 jaar.

5.1 Water.

Indien niet anders aangegeven, wordt hier gedemineraliseerd water bedoeld met een geleidbaarheid niet groter dan 2 μS.

5.2 Geconcentreerde fosfaat-bicarbonaatbuffer.

46,5 g $Na_2HPO_4.12H_2O$; 49,0 g $NaHCO_3$; 2,35 g NaCL en 2,85 g KCL oplossen in een maatkolf van 1 l met water, aanvullen en mengen. (Steeds vers bereiden.)

5.3 $MgCl_2$ oplossing 0,63 mol/l.

Los 12,8 g $MgCl_2.6H_2O$ op in een maatkolf van 100 ml. Aanvullen en mengen.

5.4 $CaCl_2$ oplossing 0,36 mol/l.

Los 5,3 g $CaCl_2.2H_2O$ op in een maatkolf van 100 ml. Aanvullen en mengen.

5.5 Verdunde bufferoplossing.

Breng in de voorraadfles: 1000 ml oplossing (5.2), 10 ml van oplossing (5.3) en 10 ml van oplossing(5.4). Los 12,5 g caseïne (b.v. Sigma artikel c 626 enzymatisch hydrolysaat) op in ± 200 ml water, voeg dit ook toe en vul daarna aan tot 5000 ml met water. Sluit de voorraadfles af met de rubberstop, voorzien van 3 openingen (* zie figuur 2). Zet de roermotor in werking. Breng de vloeistof op een temperatuur van 38-39°C met behulp van het waterbad en leid gedurende minimaal een uur CO_2 door (1 à 2 l/minuut) zodat de pH 6,9 wordt.
Opmerking: -Deze bufferoplossing steeds vers bereiden, voor iedere charge.

5.6 Pensvloeistof

Tenminste van 2 hamels, welke voorzien zijn van een zogenaamde pensfistel, wordt voldoende pensvloeistof getapt in voorverwarmde thermosflessen (maximaal kan per keer 750 ml pensvloeistof per fistelschaap getapt worden). Vlak voor het tappen worden de flessen gevuld met CO_2 gas.
Het tappen gebeurt 2 uur na het voeren. De hamels worden ad libitum gevoerd met hooi van redelijke kwaliteit en krijgen ieder 100 g schapenbrok per dag. Het is niet wenselijk vaker dan 2 keer per week (met een minimale tussentijd van 48 uur) pensvloeistof af te tappen.

5.7 Pensvloeistof-buffer.

Filtreer de getapte pensvloeistof door dubbelgevouwen kaasdoek. Vang het filtraat op in een voorverwarmde fles gevuld met CO_2. Zorg er voor dat de temperatuur van de vloeistof niet noemenswaardig zakt door de gebruikte attributen van te voren in de broedstoof op te warmen. Voeg 1250 ml gefiltreerde pensvloeistof toe aan de warme verdunde buffer oplossing 5.5. Leid onder roeren nogmaals 15 minuten CO_2 door. Daarna is de pensvloeistof-buffer gereed voor gebruik.

5.8 Na_2CO_3 oplossing 0,95 mol/l.

Los in een maatkolf van 1000 ml 100 g $Na_2CO_3.0H_2O$ op in warm water. Koel af, vul aan en meng.

5.9 Zoutzuur-oplossing 1 mol/l.

Breng 83 ml zoutzuur 37 % in een maatkolf van 1000 ml, vul aan en meng.

5.10 Pepsine-zoutzuur oplossing.

Breng in de voorraadfles 5100 ml water. Voeg daaraan toe 580 ml van oplossing 5.9. Weeg 11,6 g pepsine {2000 FIP-U/g, 30000 E/g (NFx11=1:10000)} bijvoorbeeld Merck 7190 af en breng dit met behulp van 120 ml water over in de voorraadfles. Plaats de fles in het waterbad en laat de oplossing op temperatuur komen terwijl geroerd wordt.

5.11 Standaardreeks.

Er wordt een tiental standaardmonsters, vergelijkbaar met het te onderzoeken produkt, meebepaald. Van deze monsters is de verteerbaarheid *in vivo*, middels verteringsproeven met hamels op onderhoudsniveau gevoerd, vastgesteld.

Zorg ervoor dat verteringscoëfficiënten van de standaardmonsters die gebruikt worden, qua spreiding, in het zelfde gebied liggen als de te verwachten coëfficiënten van de te onderzoeken monsters.
Indien voor het te analyseren produkt niet genoeg standaardmonsters aanwezig zijn, dient men altijd middels een duplo-bepâling van één of meerdere standaardmonsters het aantal van minimaal 10 te handhaven. Een minimum van 6 verschillende standaardmonsters zal echter altijd aanwezig moeten zijn. Standaardmonsters waarvan de verteringscoëfficiënt ver buiten de totale groep van standaarden ligt en daardoor sterk de hellingshoek bepalen, worden bij voorkeur in duplo bepaald.

6. **Analysemonster.**

Bereid het analyse monster overeenkomstig de richtlijnen vermeld in NEN 3328. Droog niet boven de 70° C en maal met een kruisslagmolen door een zeef van 1 mm.

7. **Werkwijze.**

Er kunnen meerdere series, van dezelfde of andere produkten, tegelijkertijd in bewerking worden genomen.
Regel hierbij is dat per serie steeds één standaardreeks en drie blanco's worden mee bepaald. Zorg ervoor dat de in bewerking genomen monsters steeds in dezelfde volgorde in het tijdschema behandeld worden.

7.1 Inwegen.

Weeg van het te onderzoeken luchtdroge monster circa 0,50 g ±0,05 g tot op 0,1 mg nauwkeurig af en breng dit over in een centrifugebuis.

7.2 Incubatie met pensvloeistof-buffer.

7.2.1 Wanneer alle monsters zijn ingewogen, de rekken met monsters voorverwarmen in de broedstoof bij 38°C.

7.2.2 Spoel de automatische pipet voor met de warme pensvloeistof-buffer oplossing (5.7).

7.2.3 Haal een monsterrek uit de broedstoof en hou dit op temperatuur.

7.2.4 Breng met de automatische pipet (4.3) 50 ml warme pensvloeistof-buffer oplossing (5.7) in iedere buis en sluit terstond af met een ventielstop (4.2). Zorg er voor dat het monster eerst met een weinig vloeistof goed bevochtigd wordt voordat de 50 ml in totaal wordt toegevoegd. Bij het vullen van de buis met pensvloeistof-buffer wordt CO_2 in de buis geleid.

7.2.5 Wanneer een rek gevuld is, dit direct weer in de stoof plaatsen.

7.2.6 1 uur nadat de laatste buis van de charge gevuld is de buizen zwenken zó dat er zo weinig mogelijk materiaal aan de wand blijft kleven. **Zorg er voor dat bij het zwenken de vloeistof nooit de rubber stop raakt!**

7.2.7 Herhaal het zwenken ca. 6, 22 en 30 uur na het inzetten van de bepaling.

7.3 Beëindiging incubatie 7.2.

7.3.1 Verwijder na 46 uur de ventielstoppen; indien er zich onverhoopt toch deeltjes aan de stoppen bevinden, deze met een spuitfles met demiwater terug in de buis spoelen.
7.3.2 Beëindig de incubatie (7.2) door 5 ml Na_2CO_3 oplossing (5.8) aan de buizen toe te voegen en te mengen.
7.3.3 Centrifugeer de buizen gedurende 10 minuten bij 1400 G.

7.4 Incubatie met pepsine/zoutzuur oplossing.

7.4.1 Schenk de bovenstaande vloeistof af over het over een Büchner trechter gespannen nylondoek.
7.4.2 Spuit met de warme oplossing 5.10 de deeltjes die op het doek achterblijven terug in de buis via een kleine trechter.
7.4.3 Maak de deeltjes die aan de wand kleven los met de wisser en spoel ze naar beneden in de buis en roer de massa op.
7.4.4 Vul de buis met de oplossing 5.10 aan tot de maatstreep van 50 ml.
7.4.5 Plaats de ventielstoppen (4.2) terug op de buizen.
7.4.6 Zet elk gereed rek terug in de broedstoof.
7.4.7 Zwenk de inhoud van de buizen na 1 uur, vervolgens na 5, 21 en 29 uur.

7.5 Beëindiging incubatie 7.4.

7.5.1 Verwijder na 48 uur de ventielstoppen. Indien er zich onverhoopt toch deeltjes aan de stoppen bevinden, deze met een spuitfles met demiwater terug in de buis spoelen.
7.5.2 Centrifugeer de buizen 10 minuten bij 1400 G.
7.5.3 Schenk de bovenstaande vloeistof af over het nylondoekfilter.
7.5.4 Spoel met zo weinig mogelijk water de vaste deeltjes op het nylondoek terug in de buis via een trechter.
7.5.5 Spoel de trechter na met een weinig demiwater.
7.5.6 Werk deze procedure rek voor rek af.

7.6 Filtreren.

7.6.1 Plaats de filterkroezen op de vacuüminrichting.
7.6.2 Breng de inhoud van de buizen kwantitatief over in de filterkroezen.
7.6.3 Zuig de vloeistof door het kroesje en spoel na met demiwater. Was het residu nog eenmaal met demiwater.

7.7 Drogen, wegen en verassen.

7.7.1 Plaats de kroesjes minstens 6 uur in de droogstoof op 104° C (± 2° C).
7.7.2 Plaats maximaal 8 kroezen in een exsiccator en koel af gedurende 1 uur.
7.7.3 De kroezen uit één exsiccator worden steeds achter elkaar, op 0,1 mg nauwkeurig, gewogen.
7.7.4 Plaats de monsters in een moffeloven en veras gedurende minstens 2 uur op een temperatuur van 550° C.
7.7.5 Koel af tot 104° C in de droogstoof
7.7.6 Plaats de kroezen in een exsiccator en koel af.
7.7.7 Weeg de kroesjes op 0,1 mg nauwkeurig terug.

8. **Berekening.**

8.1 De Verterings**C**oëfficiënt van de **O**rganische **S**tof(VC_{os} *in-vitro*) in procenten wordt als volgt berekend:

$$VC_{os} \textit{ in vitro} = 100 * \left\{1 - \frac{(A-B-C) * 1000}{D*(E-F)}\right\}$$

Waarin :

VC_{os} = verteringscoëfficiënt van de organische stof
A = gewicht kroesje na drogen in g.
B = gewicht kroesje na verassen in g.
C = gemiddelde gloeiverlies blanco's in g.
D = Ingewogen in gewicht in g.
E = droge stof gehalte, g/kg van het luchtdroge materiaal.
F = as gehalte, g/kg in de luchtdroge stof.

8.2 Schatting VC_{os} *in vivo*.

Met behulp van de meegeanalyseerde reeks standaardmonsters wordt via lineaire regressie de relatie berekend tussen de VC_{os} *in vitro* en de VC_{os} *in vivo*.

Geschatte VC_{os} *in vivo* = a x VC_{os} *in vitro* + b.

Met behulp van deze regressie lijn wordt de VC_{os} *in vivo* van de analysemonsters geschat. De RSD van de regressielijn moet kleiner zijn dan 2,0 % eenheden. Indien dit niet het geval is, verwijder de uitbijters (maximaal 3). Analysemonsters, waarvan de verteringscoëfficient meer dan 5 % -eenheden onder of boven deze van de standaardreeks ligt, mogen niet gecorrigeerd worden en dienen opnieuw geanalyseerd te worden.

9. **Herhaalbaarheid.**
Het verschil tussen de uitkomsten van 2 analyses welke in verschillende series met verschillende partijen pensvloeistof zijn verkregen mag maximaal 2 % eenheden bedragen.

10. **Verslag.**

De uitslagen worden gerapporteerd tot op 0,1 % eenheid VC_{os}.

Appendix VII: Results of the biomass samples taken in Festuca, Festuca/Artemisia and Artemisia vegetation types at three different periods during the field season (in g/m^2).

Festuca/Artemisia 20/7/99

	F. rubra	*F. rubra-stems*	*A. maritima*	*J. gerardi*	*Pla. maritima*	*L. vulgare*	*E. athericus*	*Sua. maritima*	*Spe. maritima*	*Puc. maritima*	*A. tripolium*	st. dead	sum
1	196.25	15.5	82.5	82.25	17.5	0	0	0	0	0	0	24.25	418.25
2	207.75	4.75	74.25	22.5	82	0	0	0	0	0	0	40.25	431.5
3	177.25	4	46	16	3	112.25	0	0	3.75	3.75	1.75	41.75	409.5
4	161.25	0	113.5	4.75	13.5	0	22	0	0	0	0	35.25	350.25
5	234.25	8.5	7.75	65	0	71.25	0	0	0	0	0	14.25	401
6	189.75	21.75	93.25	10	0	41.25	0	0	0	0	0	31.25	387.25
average	194.42	9.08	69.54	33.42	19.33	37.46	3.67	0.00	0.63	0.63	0.29	31.17	399.63
ste	10.30	3.31	15.34	13.13	12.88	19.11	3.67	0.00	0.63	0.63	0.29	4.26	11.62

Festuca/Artemisia 3&4/9/99

	F. rubra	*F. rubra-stems*	*A. maritima*	*J. gerardi*	*Pla. maritima*	*L. vulgare*	*E. athericus*	*Sua. maritima*	*Spe. maritima*	*Puc. maritima*	*A. tripolium*	st. dead	sum
1	199.5	5.5	97.25	8.25	0	14.75	0	0	0	0	0	96.25	421.5
2	209.75	0	111.5	17.25	0	0	0	0	0	0	0	97.75	436.25
3	172.75	12.75	203.5	0.5	0	0	0	0.5	0	0	0	50.75	440.75
4	231.25	0	76.5	9.75	0	50.25	0	0	0	0	0	82.5	450.25
5	231	0	90.75	3	0	44.5	0	0	0	0	0	129.25	498.5
6	262.25	0	142	7	0	0	0	0	0	0	0	118.5	529.75
average	217.75	3.04	120.25	7.63	0.00	18.25	0.00	0.08	0.00	0.00	0.00	95.83	462.83
ste	12.60	2.14	18.97	2.38	0.00	9.53	0.00	0.08	0.00	0.00	0.00	11.32	17.14

Festuca/Artemisia 5&6/12/99

	F. rubra	*F. rubra-stems*	*A. maritima*	*J. gerardi*	*Pla. maritima*	*L. vulgare*	*E. athericus*	*Sua. maritima*	*Spe. maritima*	*Puc. maritima*	*A. tripolium*	st. dead	sum
1	46.25	0	19	0	0	0	0	0	0	0	0	225.25	290.5
2	107.75	0	27	0	0	20	0	0	0	0	0	274.5	429.25
3	113.5	0	15.25	0	0	0	0	0	0	0	0	274.75	403.5
4	134.25	0	46	0	0	0	0	0	0	0	0	297.5	477.75
5	189.75	0	8.5	0	0	0	0	0	0	0	0	307	505.25
6	192.5	0	64.25	0	0	0	0	0	0	0	0	382.25	639
average	130.67	0.00	30.00	0.00	0.00	3.33	0.00	0.00	0.00	0.00	0.00	293.54	457.54
ste	22.56	0.00	8.64	0.00	0.00	3.33	0.00	0.00	0.00	0.00	0.00	21.17	47.34

Artemisia 26/7/99

	F. rubra	*F. rubra-stems*	*A. maritima*	*J. gerardi*	*Pla. maritima*	*L. vulgare*	*Sua. maritima*	*Salicornia spec.*	*Puc.maritima*	*A.prostrata*	*A. stolonifera*	st.dead	sum
1	309.5	10.5	153.75	9.5	0	2	1.75	0	0	1	0	107.75	595.75
2	142.75	0	261	0	0	17.25	0	0	0	0	0	38.75	459.75
3	140.5	1.75	276.25	0	0	8.25	15.25	0	0	35.5	0	56.25	533.75
4	269.5	12.75	278.25	42	29.25	18.25	0	0	0	0	0	63.5	713.5
5	270	16.25	220.25	0	0	0	0	0	10.5	26.25	0	82	625.25
6	97.5	1.75	335.25	0	0	0	0.5	0	0	4	0	61.25	500.25
average	204.96	7.17	254.13	8.58	4.88	7.63	2.92	0.00	1.75	11.13	0.00	68.25	571.38
ste	36.01	2.80	25.11	6.86	4.88	3.43	2.48	0.00	1.75	6.39	0.00	9.72	37.70

Artemisia 4/9/99

	F. rubra	F. rubra-stems	A. maritima	J. gerardi	Pla. maritima	L. vulgare	Sua. maritima	Salicornia spec.	Puc.maritima	A.prostrata	A. stolonifera	st.dead	sum
1	231	9.5	313.25	0	0	0	0	0	0	0	0	86	639.75
2	237.5	0	315.25	52.75	0	4.25	2.5	0	0	0	0	112.25	724.5
3	175.25	0	254	0	0	83.5	0	0	0	0	0	145	657.75
4	315.25	5.5	254.5	0	0	17.5	1.5	0	0	0	0	96	690.25
5	392	0	257.75	0	0	12.25	0	0	0	0	0	141.5	803.5
6	146	0	241.5	0	0	0	3.5	5	0	0	3	56	455
average	249.50	2.50	272.71	8.79	0.00	19.58	1.25	0.83	0.00	0.00	0.50	106.13	661.79
ste	37.12	1.66	13.33	8.79	0.00	13.10	0.62	0.83	0.00	0.00	0.50	13.93	47.64

Artemisia 5&6/12/99

	F. rubra	F. rubra-stems	A. maritima	J. gerardi	Pla. maritima	L. vulgare	Sua. maritima	Salicornia spec.	Puc.maritima	A.prostrata	A. stolonifera	st.dead	sum
1	107	0	82.75	0	0	0	0	0	0	0	0	425.25	615
2	93.25	0	92	0	0	0	0	0	0	0	0	296.25	481.5
3	143	0	80.5	0	0	0	0	0	0	0	0	306.5	530
4	103.5	0	58.5	0	0	0	0	0	0	0	0	293.75	455.75
5	28	0	50.25	0	0	0	0	0	0	0	0	142.5	220.75
6	153.5	0	127.5	0	0	0	0	0	0	0	0	269	550
average	104.71	0.00	81.92	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	288.88	475.50
ste	18.14	0.00	11.16	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	36.88	55.77

Festuca 20/7/99

	F. rubra	F. rubra-stems	J. gerardi	Pla. maritima	A. stolonifera	G. maritima	Trig. maritimum	Centaurium spec.	Odontites spec.	Tri. repens	L.vulgare	A.tripolium	Arm. maritima	st.dead	sum
1	107.5	15.5	79.25	30	3.25	9.75	0.25	0.25	1	9.5	0	0	0	11.5	267.75
2	79.25	9	28.25	0	0	0	0	0	12.25	4.25	0	0	0	17.5	150.5
3	84.25	5.5	30	73.5	0	0	0	0	0	0	0	0	0	6.75	200
4	82	3.5	39.75	1	0	1	0	0	0	0	21.75	0	0	16.25	165.25
5	120.5	10	106.5	16	5.25	0	0	0	0	0	0	0	0	15	273.25
6	123.75	6.5	103.5	40	0	0	0	0	0	2.5	0	0	0	9.25	285.5
average	99.54	8.33	64.54	26.75	1.42	1.79	0.04	0.04	2.21	2.71	3.63	0.00	0.00	12.71	223.71
ste	8.25	1.73	14.85	11.35	0.93	1.60	0.04	0.04	2.01	1.53	3.63	0.00	0.00	1.73	24.19

Festuca 3/9/99

	F. rubra	F. rubra-stems	J. gerardi	Pla. maritima	A. stolonifera	G. maritima	Trig. maritimum	Centaurium spec.	Odontites spec.	Tri. repens	L.vulgare	A.tripolium	Arm. maritima	st.dead	sum
1	113.25	12.5	43.25	64.5	5.5	0	0	0	0	4.25	0	0	0	59.5	302.75
2	111.5	3.5	19.5	0	8	0	0	0	0	14.5	0	0	0	108.25	265.25
3	95.75	1.75	14.75	24.5	13.75	0	0	0	0	1.5	0	0	0	97.5	249.5
4	92.75	3	7	61.75	19.25	0	0	0	0	0	0	0	0	71.75	255.5
5	87.25	0	12.25	24.75	8.25	0	0	0	0	3	0	0	0	74.5	210
6	135	8	45.75	26	13	0	0	0	0	0	0	0	0	116	343.75
average	105.92	4.79	23.75	33.58	11.29	0.00	0.00	0.00	0.00	3.88	0.00	0.00	0.00	87.92	271.13
ste	7.20	1.89	6.77	10.16	2.05	0.00	0.00	0.00	0.00	2.23	0.00	0.00	0.00	9.21	18.94

Festuca 5&6/12/99

	F. rubra	F. rubra-stems	J. gerardi	Pla. maritima	A. stolonifera	G. maritima	Trig. maritimum	Centaurium spec.	Odontites spec.	Tri. repens	L.vulgare	A.tripolium	Arm. maritima	st.dead	sum
1	52	0	0	0	2	0	0	0	0	2.5	0	0	0	152.25	208.75
2	84.25	0	0	0	15	0	0	0	0	2.5	0	0	0	210	311.75
3	44	0	0	0	0	0	0	0	0	0.25	0	0	0	182	226.25
4	74.75	0	0	0	0	0	0	0	0	0	0	0	0	260.25	335
5	71.75	0	0	0	0	0	0	0	0	0	0	0	0	252	323.75
6	54.75	0	0	0	0	0	0	0	0	0	0	0	0	193.75	248.5
average	63.58	0.00	0.00	0.00	2.83	0.00	0.00	0.00	0.00	0.88	0.00	0.00	0.00	208.38	275.67
ste	6.36	0.00	0.00	0.00	2.46	0.00	0.00	0.00	0.00	0.52	0.00	0.00	0.00	16.99	22.21