Competition and facilitation between two herbivores on a temperate salt marsh

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Introduction

The topic 'herbivory' is not limited to modifications of the vegetation by animals, but also include complex interactions between plants and animals. Certain adaptations of plant species can for example prevent mostly negative changes to their tissue by grazing herbivores. The interactions between wild herbivores and vegetation and the interaction between different herbivores is a very complex but interesting matter. Herbivores modify their grazing strategy to match structure and composition of the vegetation, while the vegetation adapts its reaction to the grazing regime of herbivores. Herbivores influence the plant structure in two ways; they alter the vegetation physically by grazing and trampling, and they influence the plant phenology through consumption and thereby modify the chemical compositions of plant tissues (Coppock *et al.* 1983a,b). The chemical composition of the plant tissues does not only have a negative effect on the grazing of herbivores by producing feeding repellents, but also an effect of increased quality and thus a positive effect on grazing pressure. When vegetation is kept short by herbivory, total biomass decreases, but the quality of the forage increases, as the percentage of nitrogen (and thus, quality) is higher in newly produced leaf tips (Crawley, 1997). Another effect of intensive grazing is that the vegetation density increases as well (McNaughton, 1984). These so called grazing lawns are seen as an important aspect in the facilitary interactions between different herbivores and within herbivore species. By maintaining these grazing lawns, herbivores can increase the quality of the forage directly and thus create and maintain a better food resource.

In terms of competition and facilitation between herbivores, overlap in habitat use, sharing of food plants and limitation of food supply are necessary conditions (De Boer & Prins 1990). Although composition and facilitation might be two opposite effects, they often occur together in a relation between two herbivore species (Van der Wal *et. al.*, 1998). The interactions between resident herbivores and migrating herbivores are promising studies concerning competition and facilitation. In a relatively short period of the year, many interactions are feasible that are not present during the remainder of the year. Several studies have concentrated on the situation on the African savannahs with large migratory ungulate grazers (Maddock 1979; Jarman & Sinclair 1979; Prins & Olff 1999), where it is found that grazing of certain herbivore species is beneficial for other grazers. In this study we concentrated on another ecosystem, a temperate salt marsh on one of the islands of the Dutch Wadden Sea, Schiermonnikoog. Here the resident herbivores are brown hares, *Lepus europaeus*, and during spring the marsh is also intensively grazed by Palearctic geese migrating to their Arctic breeding sites. The geese compete for quality forage very intensively in a short period whereas the hares forage all year round. The two main goose species are barnacle geese, *Branta leucopsis*, and brent geese, *Branta bernicla bernicla*, which stay in large numbers on the salt marsh of Schiermonnikoog during early spring. These staging geese are selective grazers looking for high quality forage to fatten up for the migration and breeding. Because they are so selective, the geese are very sensitive to alterations of the vegetation by other herbivores (Stahl *et. al.*, 2001). Recent studies have tried to unravel the interactions between brown hares and geese and found both competitve and facilitary components. There is a competition for the same food resource, mainly *Festuca rubra* and *Juncus gerardi* in the same habitat (Van der Wal *et. al.*, 1998), but also a long-term indirect facilitation by hares for brent geese through selective removal of woody plant species which keeps the canopy low (Van der Wal *et al.* 2000). Drent & Van der Wal (1999) showed that hares facilitate goose grazing by retarding growth of woody plant species like *Atriplex portucaloides*. By removal of this plant material the area remains attractive for the geese as they avoid sites with a higher canopy and they do not eat woody plant species (Van der Wal *et. al.*, 2000). Another study showed that barnacle geese in early spring enhance the quality of the *Festuca* meadows on the salt marsh for the brent geese by maintaining grazing lawns (Stahl *et. al.*, 2001).

In this study we want to investigate the interactions between brown hares and barnacle geese in early spring. Early in the season, this relationship has not been studied yet and is interesting in comparison to the interactions between hares and brent geese later in the season. We assume that the facilitary effect of hare winter grazing also applies to the barnacle geese, so we focus on the direct interactions. It is known that hares avoid sites that are heavily grazed by geese (Van der Wal *et. al.*, 1998). Both herbivores graze on the salt marsh while the vegetation regrows in early spring and there has been no pre-grazing by other large herbivores. Thus interactions might differ from the already studied relationship between hares and brent geese. In our experimental set-up we offer different pre-grazed treatments to the wild herbivores by excluding either barnacle geese or brown hares or both using different types of exclosures. With these different pre-grazing regimes we create differences in the vegetation and offer the herbivores a choice in vegetation structures that have been grazed in different ways. After opening the exclosures to allow all herbivores access, we can study the reaction of wild herbivores grazing on the plots by measuring grazing pressure and several vegetation parameters. From these observations, we draw conclusions about facilitation and competition. We expect the same effects here as have been found for brent geese and hares later in spring, but possibly a little less obvious, as it is early in the season and the differences between vegetation parameters on the salt marsh are not as extreme yet.

Methods

Experiment I

The island of Schiermonnikoog was the location of the field experiments and this island is located in the eastern part of the Dutch Wadden Sea (53°30'N, 6°10'E). The salt marshes are situated at the eastern part of the island and the study area on the upper salt marsh was approximately 35 years of age (as described by Van der Wal et al. 1998). The experiments were performed during early spring 2002 and at the start of our experiment dead biomass and shoots of Festuca rubra and Juncus gerardi mainly dominated the vegetation. We concentrated on the *Festuca* meadows on the upper marsh, because *Festuca* accounts for 90% of the diet in staging barnacle geese (G. Van Dinteren, unpublished data) and for 51% of the estimated spring diet of brown hares (Van der Wal et al. 1998) during this period. The area we selected for our experiments is known as a site were brown hares are resident herbivores and both barnacle and brent geese are transient grazers. Barnacle geese exploit *Festuca* until their departure to the breeding grounds halfway during May.

At the end of February we built four types of exclosures (each 4 m x 4 m) in a blocked design, each having ten replicates, which we finished building on March 6. The four plots within one replicate were seperated by approximately three meters and the longest distance between two replicates was about 350 m. The full exclosure (type A) was built as a plot fenced by 50 cm high chicken wire to exclude the hares and two ropes were attached on top of the exclosure, making sure that no geese would land in the exclosure. The goose exclosure (type B) was constructed by four bamboo sticks connected by two ropes at different height (10 cm and 50 cm), allowing hares to graze the plot, but excluding geese by the attachment of two ropes on top of the exclosure. The hare exclosure (type C) had exactly the same construction as exclosure type A, because it is not possible to create an exclosure were only wild geese can graze. To simulate grazing by geese only we used two captive barnacle geese to graze these exclosures for 24 hours. This was done 18-24 days before we opened the exclosures. All droppings produced in these pregrazing rounds were collected, dried at 60 °C and weighed. The control exclosure (type D) was only marked by four sticks allowing both herbivores to graze these plots. All exclosures were removed on the 9th of April, four weeks after the set-up of the exclosures. Only the four sticks marking the corners of each plot remained in the exclosure and then the preference of the wild herbivores for the different pre-grazing treatments was measured.

The vegetation was measured three times; after building the exclosures (March 6 – March 8) to determine the composition at the beginning of the experiment; at the time of opening the exclosures (April 7- April 9) to monitor the effect of the treatments; and two weeks after the exclosures had been opened (April 23 – April 24) to monitor the effect of wild herbivore grazing. Biomass was measured by randomly taking three sods (10 cm x 10 cm) of each plot and all vegetation was cut off. Then the vegetation was sorted to seperate dead biomass from living biomass and the living biomass was sorted for different plant species. The sorted vegetation was then washed, dried at 60°C for at least 24 hours and weighed. In addition we also measured the leaf length of 25 randomly chosen living *Festuca* plants on each plot and we computed the total leaf length and the leaf length of the two youngest leaves as geese select the youngest leaves with a higher percentage of nitrogen. The first time we measured only ungrazed leaves to document the begin situation, the second time we measured both ungrazed leaves in the ungrazed treatments and grazed leaves for the grazed treatments to determine the effect of grazing. Higher vegetation is unattractive for geese to forage on and thus has an effect on grazing pressure and preference for foraging sites (Van der Wal et al. 1998).

This vegetation height was measured ten times for all the plots, by randomly dropping a styrofoam disk on the vegetation along a measuring stick. For all plots the average vegetation height was calculated from these ten measurements. A higher tiller density in theory correlates with a higher grazing pressure as plants invest in more tillers as they are grazed more intensively and therefore this might be a good parameter for our experiment (McNaughton, 1984). Tiller density was determined by averaging three counts of all living shoots in a square of 5 cm by 5 cm per plot. As a measure of forage quality we took samples of 1 gr *Festuca* leaf tips in five replicates, selecting only the part of the leaf geese would graze on. The total elemental nitrogen and carbon in this plant tissue (automated elemental analysis, Interscience EA 1110) was determined from samples taken at the time of opening the exclosures (April 9) and samples taken after the exclosures had been open for two weeks (April 23). To create a parameter that includes both biomass and quality of the forage we multiplied the *festuca* biomass of all plots with the percentage of nitrogen of the same plot to have a total grams of nitrogen for *Festuca* per sod (10 cm x 10 cm).

As an indicator of grazing pressure we took the number of droppings of both hares and geese on our plots. These droppings were counted on four occassions; after we built our exclosures to determine the homogeneity in grazing pressure of the area; before opening the exclosures to have an indication of pre-grazing pressure; one week after we opened the exclosures and two weeks after we opened the exclosures to determine the reaction of the wild herbivores on the pre-grazed treatments (see fig 1). To standardize the grazing pressure for both herbivores we computed an intake rate by multiplying the number of droppings by grams of intake per dropping per herbivore (1 hare dropping = 0.451 gram intake, 1 goose dropping = 1.299 gram intake) (see also Van der Wal et al. 1998). This intake is taken as a measure of numbers of herbivores on the plots within the counting interval, and is thus an indication of grazing pressure within that interval.

Experiment II

This experiment was set up to study the differences in digestibility between the treatments. The digestibility of the vegetation was computed after the treatments had developed for 52 days. To create also a digestibility value for the geese, we had captive geese graze the different treatments and studied whether there were differences in digestibility for both vegetation and droppings. This might also be an indication why herbivores chose for certain vegetation, as a good digestibility of the forage might be prefered.

For experiment II, treatments of the same type as earlier described were set up in an area with comparable vegetation. Each exclosure consisted of a block of seven replicates of 2 m x 4 m, totalling to a size of 14 m x 4 m for each treatment. The first block of replicates excluded all herbivores (full exclosure, A), the second allowed only hares (goose exclosure, B), the third only geese (hare exclosure / geese pregrazed, C) and the fourth was a control plot allowing all herbivores (control, D). The exclosures for this experiment were completely seperate from the ones used in experiment I.

The treatments A, B and D were set up and left to develop for 52 days until the grazing experiment. To simulate grazing by wild barnacle geese on the 'geese only' treatments, treatment C was pregrazed by captive barnacle geese 15 days after the set up of the exclosures. A moveable cage of 2 m x 4 m was put on each of the seven replicates and two captive barnacle geese grazed within the cage for 24 hours. The geese were supplied

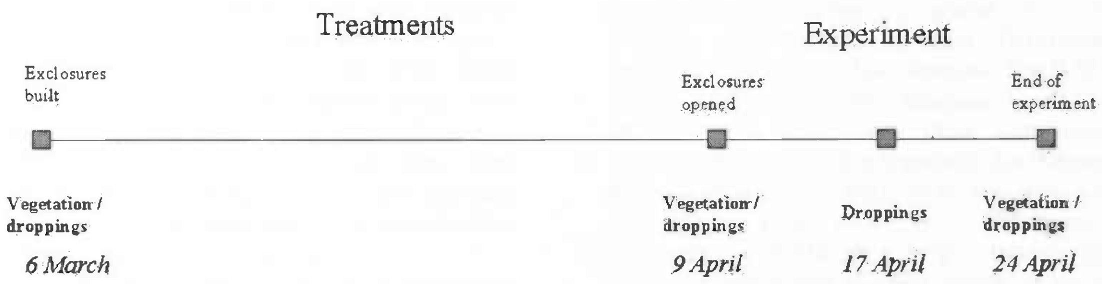

Figure 1 *: Time schedule of Experiment I*

with fresh water.

For the grazing experiment, four of the seven replicates were opened for two captive barnacle geese, the remaining three replicates were used for taking quality samples of the three most abundant plant species. Before the start of each grazing trial, two sods were taken in each replicate to determine biomass and composition of the vegetation. A cage (2 m x 4 m) was put on the replicate and the plot was cleaned of any remaining herbivore droppings. Two captive barnacle geese were then put in the cage and allowed to graze for 1.5 hours. After the first 1.5 hours all the droppings produced were collected and removed from the plot. As the geese were not kept from grazing overnight, these droppings might consist of material not taken from the current plot and could therefore not be used for the digestibility analysis. The geese were then allowed to graze for an additional 1.5 hours, after which all the droppings were counted and collected. Total grazing pressure for every 2 x 4 m plot was thus 3 hours with 2 geese. Every day two pairs of geese were grazing on two replicates of different treatments.

Quality samples of the three most abundant plant species, *Juncus gerardi*, *Plantago maritima*, and *Festuca rubra*, were taken of the three non-grazed replicates. This was done in the same way as for the herbivore exclosures of experiment I, but the amount taken here was 4 gr. Due to the relatively low overall *Festuca* cover, only one sample of this species was taken for every treatment. These samples were later analysed in the lab for ADF (Acid-Detergent Fiber) content to get a measure for quality of the forage in terms of fibre content. The method follows Van Soest & Wine (1967). Each sample was weighed and pulverised in a high-speed mixer. ADF solution consists of 20.0 gr of Cetyl-trimetyl-ammonium-bromide in 0.5M H_2SO_4 sulpheric acid. Of this solution 100 ml was added to each sample which is boiled at 60 °C and then filtered through a glass fiber filter. The residue was washed to neutral pH, and dried at 105 °C for 24 hours. The residue was then weighed and taken as the ADF content for this sample.

The droppings collected after three hours of grazing by the captive geese were dried in an oven at 60 °C for at least 24 hours, total weight was recorded, and were then grinded. The resulting powder was analysed for ADF content in the same way described for the vegetation samples above.

No data on the actual diet of the captive geese was collected, so it was not possible to determine a seperate digestibility for each of the three sampled plant species. Instead an average of ADF content was calculated per treatment, resulting in one ADF value per species for each treatment. From these values the % of ADF in all the living biomass was calculated. Then an average digestibility of the forage was calculated per treatment using the following formula :

Digestibility(%) =
[(ADF faeces – ADF vegetation)
/ ADF faeces] * 100%

Statistical tests

For all the statistical testing we used an Univariate Analysis of Variance, occasionally supplemented by a seperate linear regression, to correct for the effect of the blocked design. All the tests were done with the statistical package SPSS 10.0. We chose a stepwise exclusion of non-significant factors, resulting in a One-way ANOVA when treatment and replicate were excluded and in a Linear regression when a covariate was included. In the tests for experiment I, the random factor 'replicate' was always removed with the factor 'treatment' when the latter did not have any significant effect. This was done to prevent any possible 'masking' effects by the factor replicate.

Results

Experiment I

Is the area homogenous?

In experiment I we offered wild herbivores four different treatments of pre-grazing by creating different exclosures. First of all we had to test whether the study area we selected showed no differences in vegetation structure and herbivore grazing pressure. Any difference in biomass would create differences in attractivity for the wild herbivores and thus a biased preference. The measurements of biomass just after we built the treatments showed that the area was homogenous in terms of grams of living biomass and *Festuca* biomass (Univariate Analysis of Variance, live biomass: $F = 0.321$, $df = 3$, $p = 0.810$; *Festuca* biomass: $F = 0.188$, $df = 3$, $p = 0.903$) but there were some differences between the replicates for *Festuca* biomass (Univariate Analysis of Variance, live biomass: $F = 1.767$, $df = 9$, $p = 0.122$; *Festuca* biomass: $F = 2.314$, $df = 9$, $p = 0.044$). The total leaf length and the leaf length of leaves 1+2 were not significantly different between the treatments (Univariate Analysis of Variance, total leaf: $F = 0.702$, $df = 3$, $p =$

0.562; leaf 1+2: F = 0.478, df = 3, p = 0.701) or between the replicates (Univariate Analysis of Variance, total leaf: F = 2.039, df = 9, p = 0.091; leaf 1+2: F = 2.296, df = 9, p = 0.061). Also tiller density and vegetation height were homogenous between the treatments (Univariate Analysis of Variance, tiller density: F = 0.802, df = 3, p = 0.504; vegetation height: F = 2.267, df = 3, p = 0.103), but there was a significant difference for vegetation height between the replicates (Univariate Analysis of Variance, tiller density: F = 1.386, df = 9, p = 0.243; vegetation height: F = 5.979, df = 9, p = 0.000). See fig. 2.

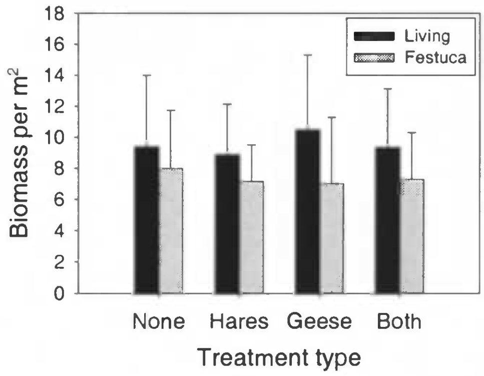

***Figure 2** : Average living and* Festuca *biomass in grams per m^2 per treatment type before the start of the experiment. Error bars represent standard deviations. N = 10.*

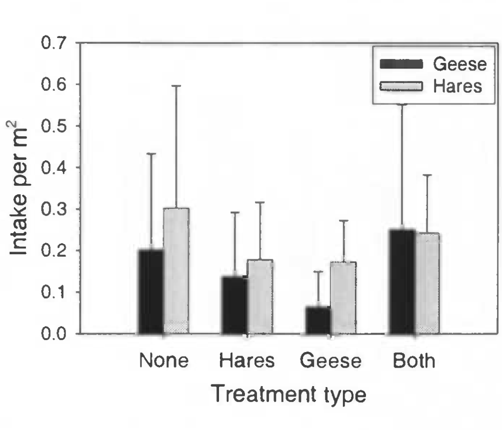

***Figure 3** : Average intake in grams per m^2 per treatment type for both geese and hares before the start of the experiment. Intake was calculated from dropping counts by multiplying with grams of intake per dropping. Error bars represent standard deviations. N = 10.*

The study area had to be homogenous in account to the grazing pressure for both geese and hares. Both intake of geese and intake of hares showed no differences between the treatments (Univariate Analysis of Variance, goose intake: F = 1.462, df = 3, p = 0.247; hare intake: F = 1.407, df = 3, p = 0.262) and replicates (Univariate Analysis of Variance, goose intake: F = 0.868, df = 9, p = 0.564; hare intake: F = 2.112, df = 9, p = 0.064). See fig. 3.

Did the treatments create differences?

The second time the vegetation had been measured was just before the exclosures were opened. These measurements should give an indication whether the treatments did exclude the herbivores on specific plots and if the different pre-grazing schemes created differences in the vegetation parameters. This would allow the herbivores to chose between the different treatments. The grazing pressure is affected by the exclosures. Both for geese as for hare intake a difference between the treatments is achieved (Univariate Analysis of Variance, goose intake: F = 32.184, df = 3, p = 0.000; hare intake: F = 23.228, df = 3, p = <0.0001) and there are no differences between the replicates (Univariate Analysis of Variance, goose intake: F = 2.048, df = 9, p = 0.071; hare intake: F = 0.861, df = 9, p = 0.570). See fig. 4.

The living biomass now did show differences between the treatments, although the *Festuca* biomass showed no difference before opening the exclosures (Univariate Analysis of Variance, live biomass: F = 4.655, df = 3, p = 0.010; *Festuca*: F = 2.010, df = 3, p = 0.136), while for the replicates both biomass measurements showed significant differences (Univariate Analysis of Variance, live biomass: F = 2.573, df = 9, p = 0.028; *Festuca*: F = 3.047, df = 9, p = 0.012). See fig. 5. The full exclosure had almost twice the living biomass of the hare exclosure, while the goose exclosure and the control plot differed not in living biomass (Tukey's test). The Festuca biomass showed the same trend as it is the main part of the total living biomass, although not significant. The total leaf length and the length of leaves 1 and 2 were also not homogenously distributed over the different treatments (Univariate Analysis of Variance, total leaf: F = 56.043, df = 3, p = 0.000; leaf 1+2; F = 32.291, df = 3, p = 0.000) and the replicates (Univariate Analysis of Variance, total leaf: F = 2.990, df = 9, p = 0.013; leaf 1+2; F = 3.662, df = 9, p = 0.004). The leaf length was the longest in the ungrazed treatments and shortest in the hare grazed treatments, see fig. 6. Both tiller density and vegetation height did not differ significantly between the treatments (Univariate Analysis of Variance, tiller density: $F = 0.729$, $df = 3$, $p = 0.543$; vegetation height: $F = 1.549$, $df = 3$, $p = 0.225$), but did differ between the replicates (Univariate Analysis of Variance, tiller density: $F = 3.383$, $df = 9$, $p = 0.007$; vegetation height: $F = 3.443$, $df = 9$, $p = 0.006$). The percentage of nitrogen, the quality of the forage, also differed significant between the treatments and replicates (Univariate Analysis of Variance, % N treatments: $F = 5.720$, $df = 3$, $p = 0.011$; % N replicates: $F = 14.417$, $df = 9$, $p = 0.000$). The geese grazed plots showed the highest percentage of nitrogen, while the ungrazed plots have the lowest percentage of nitrogen in the festuca leaf tips. See fig. 7. There was no significant difference between the plots in the parameter that combines biomass and quality between the treatments (Univariate Analysis of Variance, biomass x %N: $F = 0.797$, $df = 3$, $p = 0.519$) or between the replicates (Univariate Analysis of Variance, biomass x %N: $F = 2.709$, $df = 9$, $p = 0.081$).

There was a strongly negative correlation between the total living biomass and quality of the forage, as for festuca

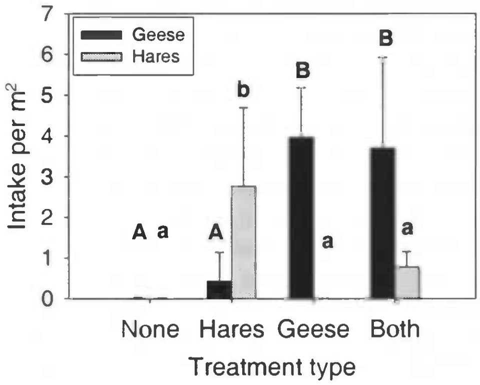

***Figure 4** : Average intake in grams per m² per treatment type for both geese and hares before before opening the exclosures. Intake was calculated from dropping counts by multiplying with grams of intake per dropping. Error bars represent standard deviations, letters are subgroups defined by a Tukey post-hoc test. N = 10.*

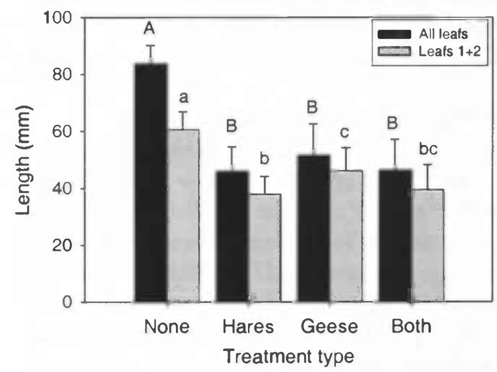

***Figure 6** : Average length of all leafs measured and two youngest leafs only before opening the exclosures, measured per* Festuca *tiller. Error bars represent standard deviations, letters are subgroups defined by a Tukey post-hoc test. N = 10.*

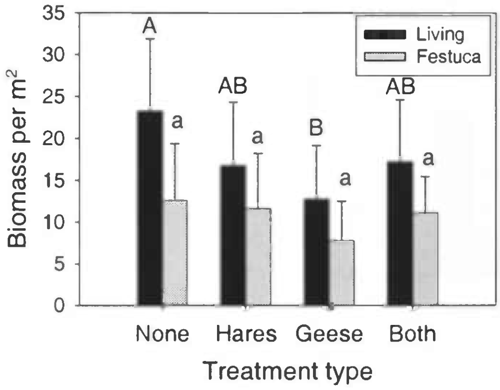

***Figure 5** : Average living and* Festuca *biomass in grams per m² per treatment before opening the exclosures. Error bars represent standard deviations, letters are the subgroups defined by a Tukey post-hoc test. N =10.*

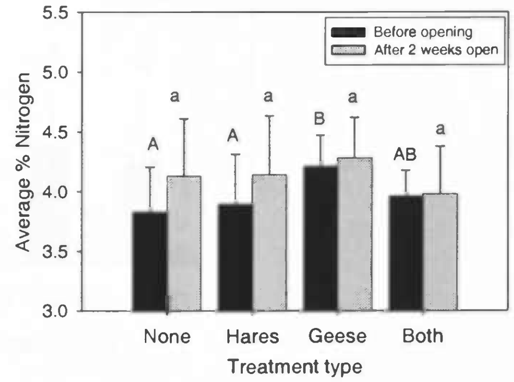

***Figure 7** : Average Nitrogen content in percentages per treatment, before opening the exclosures and after the exclosures had been open for two weeks. N content was determined from 1g samples of* Festuca *leaf tips, in half of the replicates. Error bars represent standard deviations, letters are subgroups defined by a Tukey post-hoc test. N = 5.*

biomass and quality of the forage (Bivariate correlation, live biomass x %N: Pearson = 0.614, p = 0.004; *Festuca* x %N: Pearson = 0.708, p = 0.005). The quality of the forage was highest on the plots with the lowest biomass for both total and Festuca biomass.

Reaction of wild herbivores on treatments

The next step in the experiment was to investigate whether the wild herbivores showed any preference for the different pre-grazed treatments. To test this, we plotted intake of the wild herbivores in the first week after opening the exclosures against the vegetation parameters we measured before opening. Only the vegetation parameters that showed significant differences between the treatments were suitable for testing the herbivore reaction on these treatments: biomass, leaf length and percentage of nitrogen. We separated the intake in three variables; goose intake, hare intake and total intake. The intake of the geese did not differ for the four treatments but the intake of the hares and the total intake did differ significantly between the treatments (Univariate Analysis of Variance, Goose intake: F = 2.545, df = 3, p = 0.077; hare intake: F = 9.889, df = 3, p = <0.001; total intake: F = 5.818, df = 3, p = 0.004). The intake for both herbivores was highest at the ungrazed plots and lowest for the control plots, pre-grazed by both hares and geese. The hare grazed and the goose grazed treatments were comparable considering the grazing pressure in the first week after opening the exclosures. There were also significant differences between the replicates (Univariate Analysis of Variance, goose intake: F = 6.894, df = 9, p = 0.000; hare intake: F = 3.523, df = 9, p = 0.006; total intake: F = 5.694, df 3, p = 0.000).

These intakes were tested against the vegetation parameters. The intake of the geese increased with increasing grams of living biomass on the plots (Linear regression, goose intake: $F_{1,39}$ = 15.721, p = <0.001) while the intake of hares did not show a significant effect (Univariate Analysis of Variance, hare intake: $F_{1,1}$ = 1.590, p = 0.219). The total intake of both herbivores did not depend on the total living biomass on the plots (Univariate Analysis of Variance, total intake: $F_{1,1}$ = 1.559, p = 0.223).

Goose intake increased significantly with increasing *Festuca* biomass (Linear regression, r^2 = 0.255, df = 1, F = 12.983, p = 0.001, b = 0.1955, see fig. 11) as did total intake (Univariate Analysis of Variance, $F_{1,1}$ = 4.370, p = 0.047). There was no significant effect on hare intake though (Univariate Analysis of Variance, $F_{1,1}$ = 0.431, p = 0.517). Similarily, hare intake increased significantly with increasing *Juncus* biomass (Univariate Analysis of Variance, $F_{1,1}$ = 6.708, p = 0.016), but *Juncus* biomass had no significant effect on either goose intake (Linear regression, r^2 = 0.055, df = 1, F = 2.190, p = 0.147) or total intake (Univariate Analysis of Variance, $F_{1,1}$ =

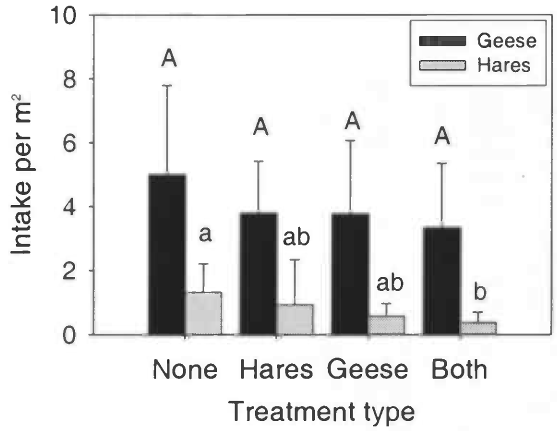

***Figure 8** : Average intake in grams per m² per treatment for both geese and hares, after the exclosures had been open for a week. Intake was calculated from dropping counts by multiplying with grams of intake per dropping. Error bars represent standard deviations, letters are subgroups defined by a Tukey post-hoc test. N = 10.*

0.005, p = 0.947).

The total leaf length had no significant effect on goose intake (Univariate ANOVA, $F_{1,1}$ = 0.327, p = 0.572), but both hare intake and total intake increased significantly with increasing total leaf length (Linear regression, hare intake : r^2 = 0.225, df = 1, F = 10.753, p = 0.002, total intake : r^2 = 0.171, df = 1, F = 7.650, p = 0.009). When looking only at the youngest two leafs, goose, hare and total intake all increased with increasing leaf length (Linear regression, goose intake : r^2 = 0.099, df = 1, F = 4.156, p = 0.048, hare intake : r^2 = 0.133, df = 1, F = 5.661, p = 0.023, total intake : r^2 = 0.150, df = 1, F = 6.535, p = 0.015).

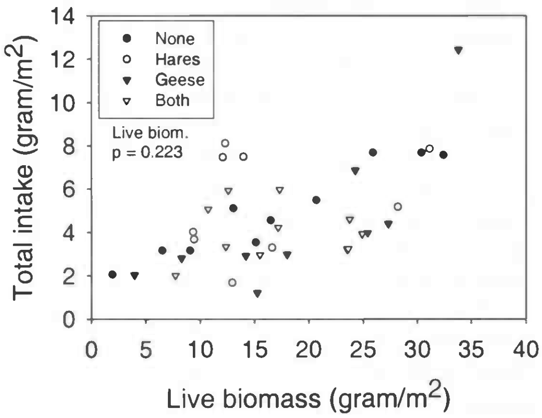

Figure 9 : Total intake in grams per m^2 after the exclosures had been open for a week plotted against total living biomass in grams per m^2 before the exclosures were opened. N = 39.

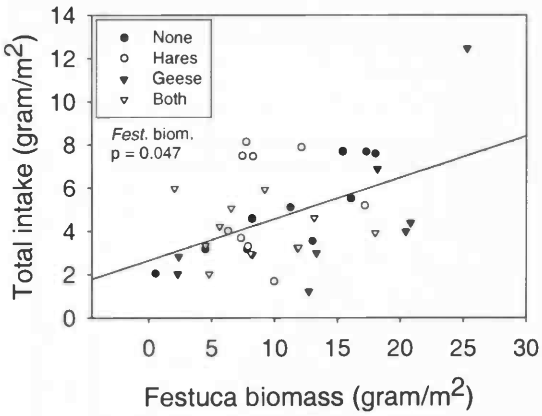

Figure 10 : Total intake in grams per m^2 after the exclosures had been open for a week plotted against total Festuca *biomass in grams per m^2 before the exclosures were opened. The line is a linear regression on the total data (all treatments pooled). N = 39.*

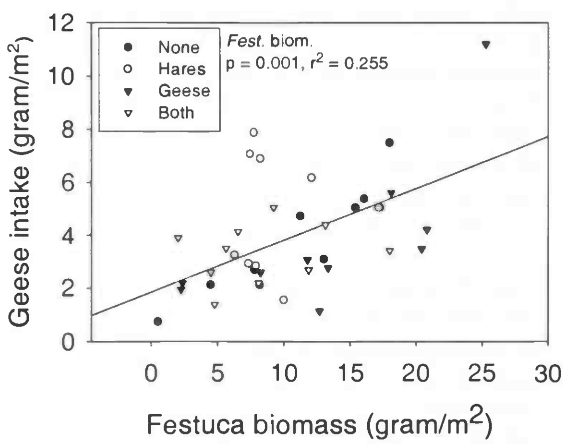

Figure 11 : Intake of geese in grams per m^2 after the exclosures had been open for a week plotted against total Festuca biomass in grams per m^2 before the exclosures were opened. The line is a linear regression on the total data (all treatments pooled). N = 40.

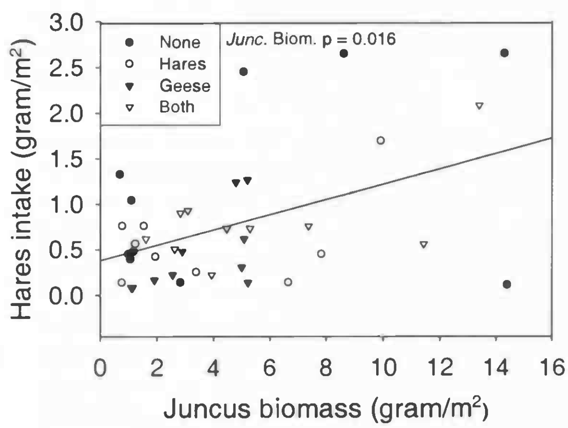

Figure 12 : Intake of hares in grams per m^2 after the exclosures had been open for a week plotted against total Juncus *biomass in grams per m^2 before the exclosures were opened. The line is linear regression on the total data (all treatments pooled). N = 39.*

The quality of the forage did not increase or decrease goose intake (Linear Regression, r^2 = 0.027, F = 0.504, df = 1, p = 0.487), or hares and total intake (Univariate ANOVA, hare intake: $F_{1,1}$ = 0.230, p = 0.640; total intake: $F_{1,1}$ = 0.003, p = 0.958) and the parameter that combined biomass and quality of the forage also showed no significant effect on the herbivore intakes (Univariate ANOVA, goose intake: $F_{1,1}$ = 3.543, p = 0.087; hare intake: $F_{1,1}$ = 0.214, p = 0.653; total intake: $F_{1,1}$ = , 1.619, p = 0.232).

On competition and facilitation

To investigate the possible facilitative and/or competitive interactions between the herbivores in the study area, the grazing pressure of each of the herbivore species one week after opening the exclosures was related to the grazing pressure exerted on the exclosures by the pregrazing. As such, the reaction of each of the species individually to the treatments and to each other could be measured in terms of grazing pressure.

In fig. 13, goose grazing pressure after the exclosures had been open for one week was plotted against the total grazing pressure during the pregrazing period. All the treatment types are represented in this plot. After the treatments were open for a week, there was no significant difference in goose grazing pressure between the treatments when tested in a Univariate ANOVA ($F_{1,3}$ = 2.545, p = 0.077). There was no significant linear relationship between goose intake one week after opening the exclosures and total intake during pregrazing (Linear regression, r^2 = 0.000, df = 1, F = 0.001, p = 0.973) when taking all the treatments together. The same was done for hare intake one week after opening the exclosures in fig. 14. There was a significant difference in hare grazing pressure between the treatments (Univariate Analysis of Variance, $F_{1,3}$ = 9.889, p = <0.001), and hare intake decreased significantly with increasing total intake during pregrazing (Linear regression, r^2 = 0.295, df = 1, F = 15.454, p = <0.001, b = -0.150).

To further investigate the preference of individual herbivore species, the analyses were repeated, plotting the grazing pressure of both herbivores (in terms of intake) against total intake during pregrazing for plots only pregrazed by hares (B) and geese (C). In fig. 15 goose intake on treatment types B and C is plotted against the pregrazing pressure in these plots. There was no significant effect of treatment (Univariate Analysis of Variance, $F_{1,1}$ = 0.051, p = 0.828). There was no relationship between goose intake and total pregrazing intake for plots B or plots C (Linear Regressions, B : r^2 = 0.200, df = 1, F = 1.750, p = 0.227, b = 0.467 and C : r^2 = 0.098, df = 1, F = 0.873, p = 0.377, b = 0.594). Looking at hare intake on treatments B and C, there was no significant effect of treatment (Univariate Analysis of Variance, $F_{1,1}$ = 0.225, p = 0.650). There was also no dependency of hare grazing pressure and pregrazing pressure for any of these treatments (Linear Regressions, B : r^2 = 0.363, df = 1, F = 3.996, p = 0.086, b = -$9.08*10^{-2}$ and C : r^2 = <0.001, df = 1, F = <0.001, p = 0.996, b = -$5.93*10^{-4}$). See fig. 16. The actual interaction at the same moment in time between the two herbivores was also investigated by plotting the hare

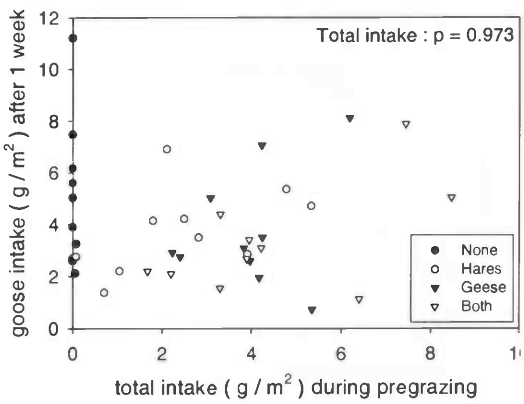

***Figure 13** : Average goose intake in grams per m^2 after the exclosures had been open for a week plotted against total intake in grams per m^2 before opening the exclosures. N = 40.*

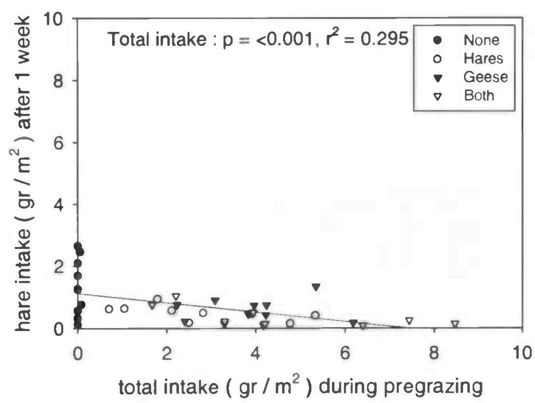

***Figure 14** : Average hare intake in grams per m^2 after the exclosures had been open for a week plotted against total intake in grams per m^2 before opening the exclosures. The line is a linear regression fit on the total data set (all treatments pooled).N = 39.*

grazing pressure against the goose grazing pressure one week after opening the exclosures

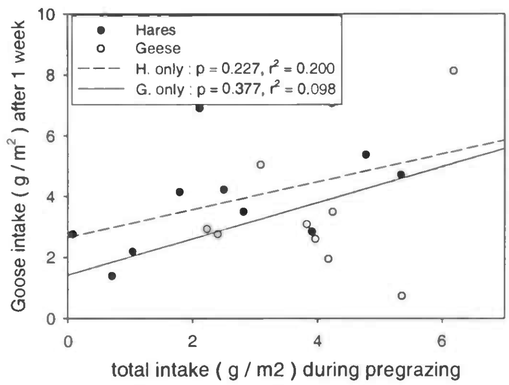

***Figure 15** : Goose intake in grams per m² after the exclosures had been open for a week plotted against total intake in grams per m² before opening the exclosures, for treatment 'Hares' (N = 9) and 'Geese' (N = 10) only. The dashed line is a linear regression on treatment 'Hares', the solid line a linear regression on treatment 'Geese'.*

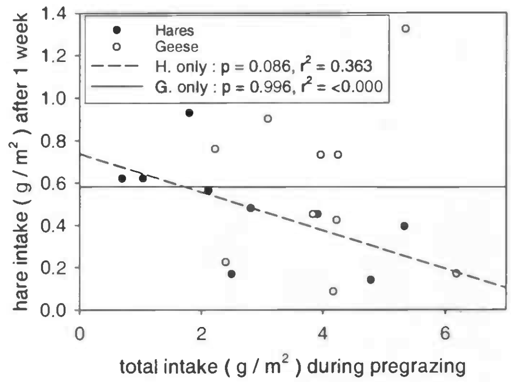

***Figure 16** : Hare intake in grams per m² after the exclosures had been open for a week plotted against total intake in grams per m² before opening the exclosures, for treatment 'Hares' (N = 9) and 'Geese' (N = 10) only. The dashed line is a linear regression on treatment 'Hares', the solid line a linear regression on treatment 'Geese'.*

in fig. 17. While both treatment and replicate had a significant effect on hare intake, it did not affect goose intake (Univariate Analysis of Variance; treatment : $F_{1, 3} = 7.081$, $p = 0.001$, replicate : $F_{1, 9} = 3.202$, $p = 0.010$; intake geese: $F_{1, 1} = 0.025$, $p = 0.875$). The same test was also done for goose intake versus hare intake. Without taking non-significant factors treatment and replicate into account, hare intake still did not significantly influence goose intake (Linear Regression, $r^2 = 0.001$, df = 1, F = 0.023, p = 0.880). Excluding some of the plots from the analysis (like the completely ungrazed and/or fully grazed plots) did not yield any significant effect of intake of either of the herbivores on the other.

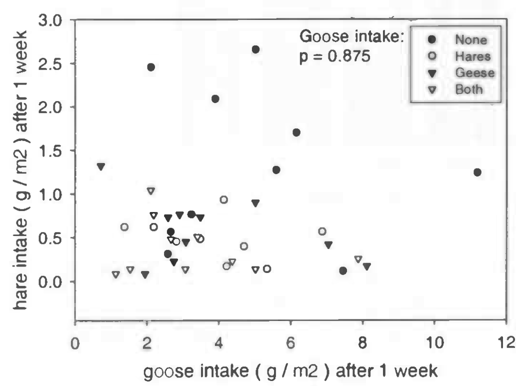

***Figure 17** : Intake of hares plotted against intake of geese in grams per m² one week after opening the exclosures. N = 39.*

Experiment II

Biomass analysis

Fig. 18 shows the availability of forage at the start of the grazing trials. Biomass of the three most abundant species were compared between the four treatments. *Juncus* was by far the most abundant species in all the four treatments, followed by *Festuca rubra* which was present in much more modest amounts. *Plantago maritima* was present in each treatment, but not very abundant. Additionally, some very small amounts of *Agrostis stolonifera* were found in some plots.

Living biomass differed significantly between treatments (Univariate Analysis of Variance, living biomass : $F_{1,3} = 6.822$, $p = 0.011$) but not between replicates ($F_{1,9} = 1.041$, $p = 0.420$). Tukey defines two subgroups, while the total living biomass was highest for the ungrazed and goose grazed plots. Dead biomass also differed significantly between treatments (Univariate Analysis of Variance, dead biomass : $F_{1,3} = 11.839$, $p = 0.002$) and not between replicates ($F_{1,9} = 0.389$, $p = 0.764$). For *Plantago* and *Festuca* there were no significant differences between either treatments (Univariate Analysis of Variance *Plant.* : $F_{1,3} = 1.492$, $p = 0.282$, *Fest.* : $F_{1,3} = 2.271$, $p = 0.149$) or replicates (*Plant.* : $F_{1,9} = 0.229$, $p = 0.874$, *Fest.* : $F_{1,9} = 0.765$, $p = 0.542$). *Juncus* however did show significant differences between treatments (Univariate Analysis of Variance, $F_{1,3} = 13.328$, $p = 0.001$) but not between replicates ($F_{1,9} = 1.000$, $p = 0.436$). The *Juncus* biomass shows the same trend as the total living biomass, with the ungrazed and goose only grazed treatments having the highest biomass. As *Juncus* determines the largest part of the total biomass, it therefore strongly influences the trend.

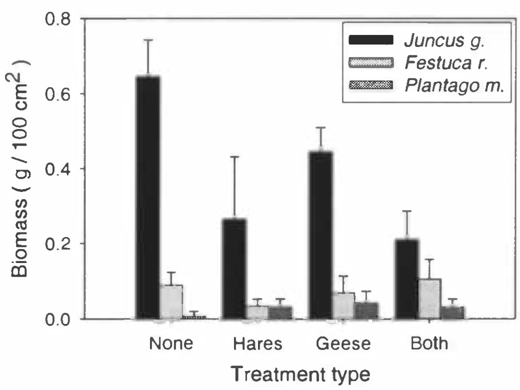

***Figure 18 :** Avergage biomass in grams per 100 cm^2 for three species per treatment type in experiment II. Error bars represent standard deviations, letters are subgroups defined by a Tukey post-hoc test. N = 4.*

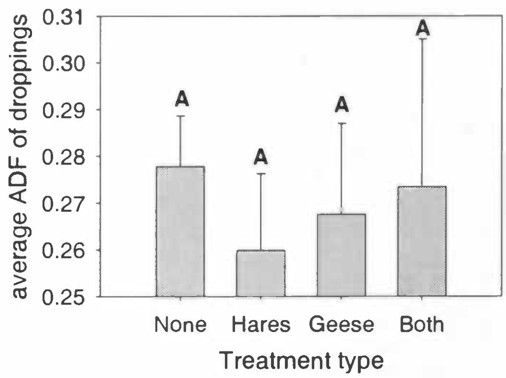

***Figure 19 :** Average ADF content of droppings of captive geese collected on each treatment in experiment II. Error bars represent standard deviations. None+Geese: N = 4, Hares+Both: N = 3.*

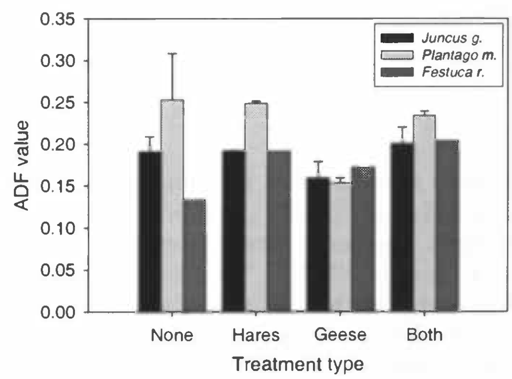

***Figure 20 :** Average ADF content of three plant species per treatment in experiment II. Per treatment: Juncus N = 3, Plantago N = 3, Festuca N = 1. Error bars represent standard deviations*

Digestibility analysis

ADF values of both vegetation and droppings were compared between treatments. No significant differences were found between the treatments or replicates for ADF values of the collected droppings (Univariate ANOVA, replica : $F_{1,3} = 2.209$, $p = 0.609$, treatment : $F_{1,2} = 0.528$, $p = 0.609$, see fig. 19). When looking at ADF *Plantago* and *Juncus*, there is an effect of treatment and species, *Plantago* has a significantly different ADF content compared to *Juncus* (Univariate ANOVA, replica : $F_{1,2} = 0.246$, $p = 0.785$, treatment : $F_{1,3} = 5.961$, $p = 0.006$, species (only *Juncus* and *Plantago*) : $F_{1,1} = 11.097$, $p = 0.004$). There was no effect

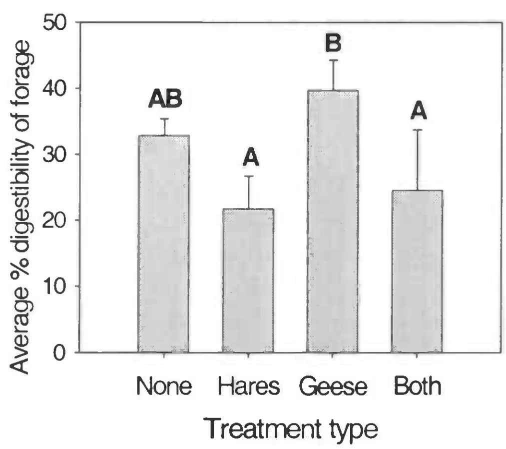

Figure 21 : Average digestibility of forage in percentages per treatment in experiment II. Digestibility was calculated from averaged ADF content of the three plant species and averaged ADF content of the collected droppings. Error bars represent standard deviations, letters are subgroups defined by a Tukey post-hoc test. N = 3.

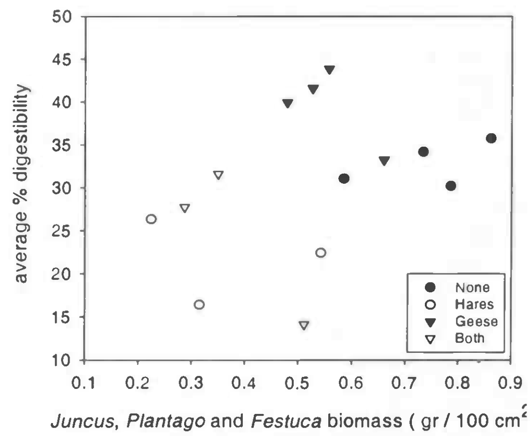

***Figure 22** : Average digestibility of available forage in percentages plotted against biomass of this forage in grams per 100 cm^2 in experiment II*

of replicates, though, see fig. 20. *Festuca* ADF values were not tested as N = 1 for each treatment for this species. In fig. 21 it is shown that average digestibility of the entire forage is higher in the fully grazed and the goose only grazed plots then in the other plots. (Univariate ANOVA, replicates : $F_{1,3} = 0.753$, $p = 0.555$, treatments : $F_{1,2} = 11.984$, $p = 0.004$).

An attempt was made to relate average digestibility to biomass. In fig. 22 the average digestibility is plotted against the total biomass of the three plant species. Taking treatment into account as a factor, average digestibility does not significantly increase or decrease with the biomass of *Juncus*, *Plantago* and *Festuca* taken together (Univariate Analysis of Variance : $r^2 = 0.829$, $F_{1,1} = 1.301$, $p = 0.284$).

Dropping weights and correlations

Total weight of all the droppings produced during the 3 hour grazing trial were taken as an indication for the grazing intensity of the captive geese on each treatment. There were no significant differences between replicates or treatments for droppings weights (Univariate ANOVA, replica : $F_{1,3} = 1.828$, $p = 0.230$, treatment : $F_{1,2} = 1.307$, $p = 0.345$). See fig. 23.

Grazing intensity (that is, total weight of all droppings) does not increase or decrease significantly with total living biomass (Linear regression : $r^2 = 0.061$, df = 1, $F = 0.780$, $p = 0.395$), nor with *Juncus, Plantago, Festuca* (Linear regression : $r^2 = 0.054$, df = 1, $F = 0.685$, $p = 0.424$, see fig. 24) or total dead biomass (Linear regression : $r^2 = 0.065$, df = 1, $F = 0.840$, $p = 0.377$). In the same way, average dropping weight was plotted against average digestibility in fig. 25. There turned out to be no significant relationship between average digestibility of the forage and grazing intensity (Linear regression : $r^2 = <0.001$, df = 1, $F = 0.001$, $p = 0.970$) and there also was no dependency of dropping weight on average ADF value of the forage (Linear regression : $r^2 = 0.007$, df = 1, $F = 0.091$, $p = 0.769$).

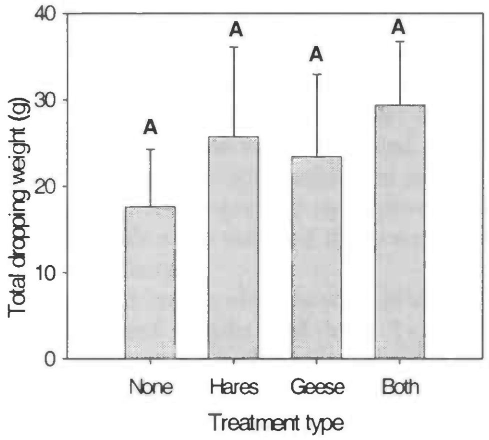

Figure 23 : Total weight of all the droppings collected on each treatment in experiment II. Error bars represent standard deviations. None+Geese: N = 4, Hares+Both: N = 3.

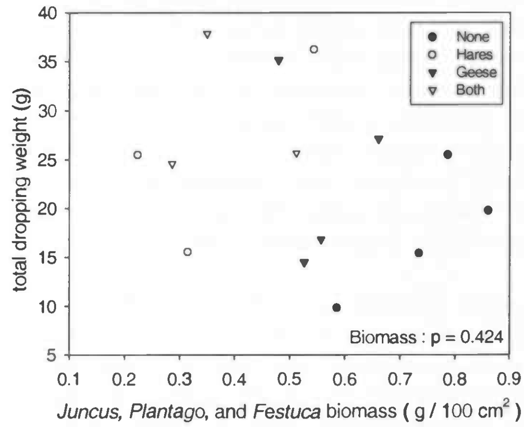

Figure 24 : Total weight of all the droppings collected on each treatment plotted against total forage biomass in grams per 100 cm^2 in experiment II.

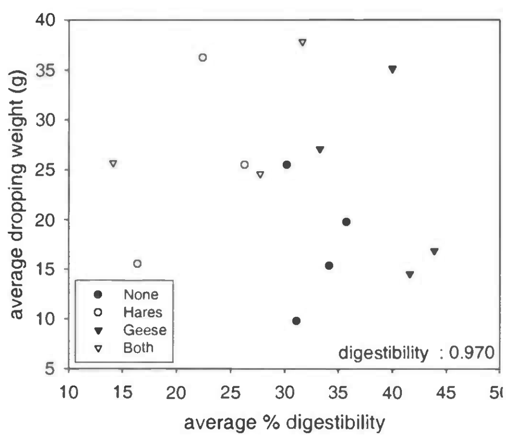

Figure 25 : Average dropping weight in grams plotted against average digestibility in percentages, per treatment in experiment II.

Discussion

Experiment I

Is the area homogenous?

When the experiment was set up, there were no differences in vegetation parameters like living biomass, festuca biomass, tiller height and vegetation height between the treatments. There were significant differences for some of these factors between individual replicates, but this can be explained by the fact that the replicates themselves were scattered throughout the experimental area, as the largest distance between them was approximately 350 m. There were also no significant differences in grazing pressure between the treatments when the experiment was set up, neither for geese nor for hares. However, it is evident that the total grazing pressure of geese was much lower than the total grazing pressure of the hares. Later in the season the number of foraging geese in the area increased and the total grazing pressure of geese started to top that of the hares.

The absence of any differences between the treatments leads to the conclusion that the experimental area was homogenous both in terms of vegetation as well as in distribution of grazing pressure of the herbivores, and that any change after the application of the treatments in either of these parameters is not due to initial differences within the area.

Did the treatments create differences?

Four weeks after the setup of the four different grazing regimes, the exclosures were removed to allow access to all herbivores, and all the vegetation parameters and dropping numbers were measured again. Additionally, quality samples of the leaf tips were taken. Both total living biomass and *Festuca* biomass were the highest in the completely ungrazed plots (A). The plots pregrazed by captive geese showed the lowest values, for both living biomass as well as for *Festuca*. These effects were only significant for living biomass, however. The fact that not the fully grazed plots, but the artificially pregrazed plots showed the lowest biomass, could be an indication that the pregrazing was too intensive and not comparable to wild goose grazing. But, even though the biomass in the pregrazed plots seemed to be unnaturally low compared to the other plots, no significant differences were found between intake of geese on the pregrazed plots C and the fully grazed plots D (that were grazed by wild herbivores only). In this respect, our pregrazing by captive geese was well within the range of the normal wild herbivore grazing.

Leaf length also showed differences: both total leaf lengths and leafs 1+2 were significantly longer in the ungrazed plot when compared to the fully grazed plot. Differences between the partially grazed plots and the fully grazed plot (B,C and D) were less apparent. According to previous research, differences between treatments for tiller densities could be expected, but none were found. There seems to be no response of density to differences in grazing regime. This is probably due to the short time period of our measurements, as other studies (McNaughton, 1984) did show a response of tiller densities over the course of several seasons of grazing. There were also no differences between treatments in vegetation height, so these parameters were not expected to influence herbivore choice. Quality measured as the % of nitrogen content of the leaf tips did however differ significantly between the treatments, the plots grazed by geese only being qualitatively better than the other treatments. Concerning intake, obvious differences were found: no (or negligable) intake for the exclosed herbivore species.

From this, the conclusion can be drawn that the treatments did have the desired effect, both in terms of development of the vegetation and the exclusion of grazing by specific herbivores. Thus difference in forage availability and quality was created for the herbivores to select on after removing the exclosures.

Reaction of wild herbivores on treatments

The measurements taken after the exclosures had been open for a week, lead to the conclusion that hares prefer completely ungrazed vegetation. The numbers of hare droppings on the ungrazed plots were significantly higher than the numbers on the fully grazed plots. The same pattern also applied to goose grazing : geese seem to prefer ungrazed plots, but this trend was not significant. Differences between the partially grazed plots (B and C) for both geese and hares were less apparent.

From the preference of the herbivores for specific treatments, it can be concluded that geese select for higher biomass. From correlations made between intake and biomass it is evident that goose intake increases with increasing living biomass. Hare intake did not increase with living biomass, while it did increase with increasing *Juncus* biomass. As *Juncus* formed only a small fraction of the entire living biomass, and assuming hares graze selectively on this plant, it can still be concluded that hares prefer higher biomass as well.

While no effects of total leaf length, quality of the forage or a combination parameter of quality and biomass could be found on intake, there still is a strongly negative effect of total living biomass on quality of the vegetation. So by selecting for a higher biomass, the herbivores inevitably take the vegetation of a relatively lower quality. This could be explained by the fact that this early in the season the actual differences in vegetation quality are not that pronounced yet, and that it still pays off to select for higher quantities instead of quality as there is not much forage available to begin with.

On competition and facilitation

Possible facilitative and/or competitive interactions between geese and hares were investigated by correlating grazing pressure in terms of intake of each of these herbivores in the first week after opening the exclosures with total pregrazing pressure. In other words, how does increasing pregrazing pressure (from both geese and hares) influence the grazing pressure of either one of the herbivores?

Geese did not show any significant reaction to increasing pregrazing pressure, while the intake of hares decreased as total pregrazing pressure increased. It can be concluded that hares avoid plots that have been more intensively grazed, and prefer less grazed vegetation. This is in line with the earlier conlcusion that hares (as well as geese) prefer higher biomass, as less grazed vegetation would logically have higher quantities of vegetation left. When looking only at the plots selectively pregrazed by one of the herbivores (B and C), there is an increasing trend visible in the goose intake with increasing pregrazing : geese seem to prefer plots that were more intensively pregrazed. However, this relationship was not significant for either of these plots. There was no reaction of the hares to increasing pregrazing pressure for these selectively pregrazed plots.

By relating intake of one of the herbivore species to the other one week after opening the exclosures, direct effects of the grazers on each other could be investigated. There were treatment effects, but no significant effects of intake of either of the herbivores on the other was found, which would lead to the conclusion that there was no direct interference between the herbivores one week after opening the exclosures.

The best evidence for some kind of facilitative interaction comes from the results of the dropping counts after four weeks of treatment (see fig. 4). When the two treatments then accesible to hares (one exclusively and the other also grazed by geese) are compared, a significantly higher number of hares visited the plots exclusively grazed by other hares. They avoided the geese also grazing plots D. This is also in line with work earlier done on hares and brent geese later in the season.

Experiment II

As it is impossible to get an estimate of digestibility in an experiment with wild herbivores like experiment I, we set up a second experiment. The aim was to collect data on digestibility of the forage within similar exclosures and treatments as in experiment I for captive geese, and later use these data with the results of the wild herbivore experiment to draw conclusions on digestibility there.

There were some differences in living biomass (treatment A having a slightly higher amount of living biomass) and dead biomass between the treatments, but for *Festuca* and *Plantago* specifically, there were no differences. There was significantly more *Juncus* present in treatments A and C, but as this is not normally considered to be an important food source for barnacle geese, this is not of any great importance.

The average digestibility for geese of the plots pregrazed by captive geese was significantly higher than the other plots. Although not measured, it was assumed that biomass is also much lower in these plots after the pregrazing, which would be in line with the fact that lower (or younger) vegetation is considered to be qualitatively better. For this experiment, dropping weights from each plot were taken as an indication of grazing intensity on that plot. Although grazing pressure was more or less standarised by having a fixed number of geese on a plot for three hours each time, the geese were expected to feed differently on each treatment as the properties of the vegetation are assumed to be different (in the same way as in experiment I).

As the forage on the treatment pregrazed by geese only was of the best quality in terms of digestibility for the geese, one might expect the plots with a better digestibility also to be grazed more intensively. This was not the case, however, as there was no significant dependency of average digestibility on grazing intensity. Neither did living biomass significantly influence grazing intensity.

Summary and general discussion

The aim of this study was the exploration of the facilatative and/or competitive interactions between barnalce geese and brown hares in a salt marh ecosystem in early spring. We tried to find evidence for food competition and facilitation and tried to seperate these effects by exposing wild herbivores to different pregrazing regimes.

The results of our study indicate that both geese and hares seem to prefer a higher biomass of the vegetation opposed to a higher quality. As both herbivores show a higher preference for the totally ungrazed plots, one could conclude that these herbivores select on quantity of the forage. This might be an indication for competition between hares and geese, although we cannot define stronger conclusions on competition or facilitation as we did not find any differences in preference for both hares and geese for the goose grazed or hare grazed plots. In earlier studies, Brent geese have been shown to specifically select the higher quality forage in terms of digestibility and N content, while hares prefer areas of higher biomass. However, while our treatments did create differences in quality of vegetation, especially for the plots pregrazed exclusively by geese, the geese did not show any preference for those plots in experiment I. As earlier suggested, the expected differences in vegetation structure, quality and digestibility for the geese this early in the season, are very small. The vegetation is developping, so the overall quality is approximately at the same, relatively high, level. As the vegetation just starts its growth, the differences in vegetation height are also not a selective factor. It is known that tiller density increases with intensive grazing, but this is a proces that takes several years, which is past the duration of this experiment. As there were no differences created in vegetation height and tiller density, we could not study the effect of these vegetation properties. Another interaction we could find, was the effect of hares avoiding sites that have been (pre) grazed by geese. This was already known and is a competitive element in the relationship of these two herbivores.

To get an indication of the effect of pregrazing on the digestibility of the forage we set up experiment II. We did create differences in digestibility, where the plots exclusively pregrazed by geese, show a higher digestibility. In experiment II, the captive geese did not graze the plots with a higher digestibility more intensively. When we try to link both experiments, we might thus conclude that geese do not select for vegetation with a higher digestibility, here being the goose grazed plots.

There were some drawbacks in linking these two experiments. The first objection would be that comparing captive goose grazing with wild goose grazing is not reliable. We acknowledge this problem, but it is also the only way to obtain an approximation of the digestibility of wild herbivores grazing in open exclosures. Here we assume the digestibility measures found for wild geese and captive geese on similar vegetation are reasonably comparable. Another problem was that the vegetation structure in the area of experiment II was rather different from the structure at the site of experiment I. The exclosures for experiment II were dominated by *Juncus*, while *Festuca* was much more dominant in the experiment I exclosures. But since geese are expected to be selective in their diet, the actual intake will possibly not differ much from that of the wild herbivores in experiment I. The third problem was that due to high water on the study area we were not able to collect all the data we wanted to collect, so part of the experimental data was not complete. In the end, the comparison and linking done between the two experiments ended up to be rather limited.

So the interactions between the three herbivores on the salt marsh of Schiermonnikoog are now more unwravelled. The brown hares facilitate for the geese by removing woody plant species and keep the vegetation low for the geese in the winter. In early spring, both geese and hares seem to prefer sites with a higher biomass as there are no clear differences in forage quality or digestibility this early in the season. Hares do seem to avoid sites that are heavily grazed by barnacle geese, so this indicates a competitive interaction between hares and geese. By grazing the salt marsh intensively, the barnacle geese increase the quality and the digestibility of the forage for the brent geese, which arrive later in the season and thus have a facilitative importance for the brent geese. By producing these so called grazing lawns, the barnacle geese enhance the quality of the food resource necessary for the migration and breeding season.

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