Geese on a green wave
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Compensatory growth of *Festuca rubra* after grazing – Can migratory herbivores increase their own harvest during staging?

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**Summary**

1. The grazing optimisation hypothesis predicts an increased production and quality of plants grazed at intermediate grazing pressures. Following this hypothesis, herbivores will be able to increase their own harvest by repeated grazing. We tested the predictions of this hypothesis for Barnacle Geese, *Branta leucopsis*.

2. We manipulated grazing intensity of *Festuca rubra* swards through trials with captive geese in early spring. Levels of experimental grazing matched levels of natural grazing pressure. Growth response of individually marked tillers was measured over six weeks.

3. Aboveground biomass production of individual tillers was not different among different grazing intensities. Lost biomass in grazed tillers was compensated by a lower senescence.

4. Grazing significantly affected sward characteristics; the proportion of dead biomass in the vegetation was reduced and production of additional axillary tillers increased.

5. When extrapolating the experimental findings to foraging opportunities for staging geese, we calculate an increase in potential harvest for grazed as compared to ungrazed swards at levels of natural spring grazing.

6. The experiment demonstrates an increase in carrying capacity of the staging site for migratory geese through grazing. When comparing the experiment with grazing levels of wild Barnacle Geese, it is obvious that current goose densities maximise potential harvest.
Introduction

In the 1970s, Dyer (1975) and McNaughton (1979) postulated the grazing optimisation hypothesis (GOH). This hypothesis describes the reaction of plants to increasing herbivory. It predicts that grazing at intermediate intensities stimulates plant production and enhances the net primary production of grazed plants above that of ungrazed plants. Several studies demonstrated a positive response of plant tissue production on grazing (Cargill and Jefferies 1984b; Frank and McNaughton 1993), but evidence is limited to certain ecosystems and remains controversial (Belsky 1986; Belsky et al. 1993). Responses of various plant traits like total production, final biomass, root biomass and relative growth rate differ among species (Ferraro and Oesterheld 2002). In general, relative growth rate increased under defoliation. It is important to note that grazing facilitation is not caused solely by increased tissue production and biomass (i.e. grazing optimisation). Further reactions of vegetation to grazing comprise an increased nutrient concentration, denser sward and decreased cover of standing dead material. Sites which are repeatedly grazed by herbivores, often referred to as grazing lawns (McNaughton 1984; Drent and Van der Wal 1999), are characterised by these traits.

McNaughton (1979) developed the theoretical framework of grazing optimisation in view of the large-scale movements of herbivores in the Serengeti (e.g. wildebeest, Connochaetes taurinus). In ecosystems periodically visited by many migratory herbivores, grazing facilitation can be of great importance. Here, plant regrowth might counteract forage depletion and thereby allowing repeated usage of forage by passing herbivores within one season. In the Northern Hemisphere, avian herbivores (mainly geese and swans) commute between tundra sites in the High Arctic and coastal sites in the temperate zone. At different staging sites, forage plants repeatedly experience short periods of heavy grazing, mostly during the start of the growing season when different waves of migratory birds pass through.

At the Dutch island of Schiermonnikoog, about 3,000 Barnacle Geese and 1,500 Brent Geese forage on the salt marsh during the months of March, April and May (Bos and Stahl 2003). During these months, both goose species accumulate body reserves prior to their migration to the Arctic (e.g. Prop and Deerenberg 1991). The salt-marsh grass Festuca rubra is an important component of the diet of both species. For long-distance migrating geese, consequences of foraging performance at a staging site are far-reaching: improved foraging opportunities during spring translate into improved body condition and subsequently into successful reproduction at the Arctic breeding grounds (Ebbinge and Spaans 1995). It was suggested earlier that Brent Geese, Branta bernicla bernicla, adopt a cyclic grazing pattern by which they optimise their protein intake (Ydenberg and Prins 1981; Drent and Van der Wal 1999). We argue that the potential importance of grazing facilitation of large numbers of avian herbivores concentrating at coastal sites during short periods of spring migration has been largely ignored in literature.
Compensatory growth of Festuca rubra after grazing

We present here an experimental field test to interpret the consequences of successive waves of grazing on biomass production at a major staging site of Arctic geese. In a field experiment, we tested the predictions of the grazing optimisation hypothesis on a temperate salt marsh in North-Western Europe. Using captive geese, different grazing schemes were applied to the grass sward and the growth response of individual tillers of Festuca rubra was followed for six weeks. Our aim was to explore the scope for grazing optimisation on a temperate salt marsh that is a key site for staging migratory geese and to examine consequences for the carrying capacity of these sites.

Methods

Study area

Our study area was located at the eastern salt marsh of the island of Schiermonnikoog in the Dutch Wadden Sea (53°30’N, 6°10’E) which is an area unaffected by livestock grazing throughout the year (Box 1). At these salt-marsh sites, about 2,500 Barnacle Geese were present during the experiments (pers. obs. – goose count March/April 2002). At the same time, about a 1000 Brent Geese (pers. obs.) along with 350 brown hares (D.P.J. Kuijper, pers. comm.) used the 1,350 ha study area on the salt marsh. With regard to the grazing of small herbivores, our study area is one of the most intensively used salt-marsh areas on the island in spring (Van de Koppel et al. 1996). We conducted the grazing experiment on the high salt marsh (for description see Olff et al. 1997; Van der Wal et al. 1998b) in the Festuca community, where the vegetation mainly consists of Red Fescue, Festuca rubra, combined with the Salt-marsh Rush, Juncus gerardi, and sparsely distributed rosettes of Sea Plantain, Plantago maritima. On our study site (1350 ha), the Festuca community (De Jong et al. 1998; Kers et al. 1998) covers 262 ha, which amounts to about 20% of the total area. Festuca forms about 90% of the diet of Barnacle Geese (Van Dinteren 1988) and about 50% of the diet of Brent Geese (Van der Wal et al. 2000a). The diet of resident Brown Hares, Lepus europaeus, contains about 70% Festuca in early spring (Van der Wal et al. 1998b).

Grazing treatments

In 1998, fresh droppings were counted weekly on 30 plots of 4 m² marked by a PVC tube, to allow for repeated counts on the same places. Grazing intensity was calculated by multiplying these field measures of dropping densities with field observations on dropping intervals of Barnacle Geese. Prop and Vulink (1992) recorded dropping intervals of 4.4 min for Barnacle Geese foraging on Festuca at this site in spring. Cumulative grazing intensity of wild Barnacle Geese amounted to 13.9 ± 1.5 min m⁻² (mean ± SE, N=30) for two weeks in mid March.
In 2002, five replicate sites were selected and matched for homogeneity of the *Festuca* sward. Sites were about 100 m apart from each other. At each site, an area of 2 by 12 m was fenced with chicken wire in order to exclude grazing by wild geese and hares. Other herbivores are virtually absent on these marshes. Fences were erected in mid-March 2002 prior to arrival of wild geese on the salt marsh and were maintained throughout the measuring period. Within these fences, we randomly appointed one plot of 4 m\(^2\) to each treatment. Five treatments characterised by different grazing intensities were created through controlled grazing with two captive Barnacle Geese for a fixed time period. This experimental design was adopted from a study by Hik and Jefferyes (1990), studying growth stimulation through grazing in a sub-Arctic salt marsh.

For the experimental grazing with captive geese, five different treatments were created: 0, 7, 14, 21 or 28 min grazing m\(^{-2}\). The grazing intensity recorded for wild geese at that site (14 min m\(^{-2}\)) was represented within the range of experimentally chosen grazing bouts. Natural grazing pressure on *Festuca* swards is based on measurements at the same site during a two-week period in mid March 1998. The timing of these measurements corresponds with the time period between erection of the exclosures and experimental grazing in our experiments.

On the day prior to experimental grazing, a holding pen was erected surrounding the treatments. During the night preceding the experiment, two geese stayed on a depleted plot adjacent to the trial plots to increase feeding susceptibility of the geese. In the morning of the grazing trials the geese were allowed to enter the first plot. Grazing time of both geese was recorded to the nearest second and trials stopped when the amount of grazing time specified for a treatment was reached cumulatively by both geese. Then the geese had to graze an adjacent plot until plots of all treatments had received grazing. By arranging plots in a line, the geese could be driven to the next plot without catching, and stress was reduced to a minimum. The grazing took place on five consecutive days (25-29 of March 2002) for the five replicates. Experimental grazing with captive geese was conducted under licence of the ethical committee for use of experimental animals of the University of Groningen (DEC RuG, licence number 2734). The Barnacle Geese were born in captivity and kept on a grass diet for more than two weeks prior to the experiment.
Measurements on Festuca rubra

The biomass response of the *Festuca* sward to the different treatments is a crucial parameter in our analyses. As destructive biomass sampling is connected with rather large measuring errors in this type of short grass swards with high proportions of litter, we instead adopted a detailed approach which combines measurements of tiller densities, leaf length and length-to-biomass calibrations to a fine-tuned measure of biomass. Directly after experimental grazing tiller density was counted within 3 square frames of 5.5 x 5.5 cm in every replicate of the treatments. All 15 counts were grouped per replicate and the average tiller density at the start of the experiment was calculated from the averages of the five replicates.

At the same time, 20 tillers of *Festuca rubra* were marked individually in each plot. In each of two sections of 10 cm x 25 cm, ten tillers were selected close to the centre of each plot to prevent edge effects. For the grazed treatments we selected tillers of which at least one leaf had been grazed, for the 'no grazing' treatment we selected ungrazed tillers. The leaves of every tiller were measured to the nearest millimetre and marked with Indian ink for subsequent identification in the following week. With this method, we were able to follow individual leaves from their emergence until their death. For all leaves, we measured the length of the living and the dead parts. Following the first marking, tillers were measured six times with intervals of one week.

We started out with 20 marked tillers in each replicate of the treatments. Mortality accounted for approximately 5% of the loss in tillers and was not significantly different between treatments (Univariate ANOVA $F_{4,20} = 0.229$, $P =0.919$). Reasons other than mortality accounted for a loss in tillers of 16% and did not differ between treatments (Univariate ANOVA $F_{4,20} = 0.449$, $P =0.772$). Therefore, sample sizes decreased to about 15 tillers per plot at the end of the season. To avoid pseudo-replication measurements of the individual tillers were averaged per replicate per treatment. Only tillers that were still present at the last measurement were taken into account. On three occasions covering the whole period of the experiment leaf material of *Festuca rubra* was collected in order to establish a conversion between leaf length and leaf biomass. On each occasion, about 100 leaves were measured, dried and weighed (in total about 2.5 m). Average dry-weight of *Festuca* leaves was 0.034 mg mm$^{-1}$ (± 0.0007).

Additionally samples of green leaftips for chemical analysis were collected two, four and six weeks after grazing. Samples were oven-dried at 60°C for at least 48 hours and ground in a planetary micro mill (Pulverisette 7, Fritsch GmbH, Idar-Oberstein Germany), on a rotational speed of 750 rpm, for 3 x 3 minutes. Ground samples were analysed for total nitrogen and carbon contents using an automated CNHS-analyser (automated element analysis, Interscience EA 1110, New York, USA).
Calculations and Statistics

Tiller growth was calculated in the following ways (see Bakker and Loonen 1998): Increment in standing crop (ISC); aboveground biomass production (ABP) including both ISC and senescence; and number of leaf births and deaths. Increment in standing crop is a frequently used measure (e.g. McNaughton 1979; Hik and Jefferies 1990; Frank and McNaughton 1993), however Bakker and Loonen (1998) suggested ABP as a more specific measure of plant response.

Yield to grazers was calculated as the harvestable biomass at the end of the experiment (6 weeks after experimental grazing) plus the harvest during experimental grazing. Harvestable biomass at the end of the experiment was calculated per tiller, assuming a maximum bite size of 3 cm per leaf. This means that for every leaf on a tiller the harvestable biomass was set at either 3 cm or the entire length of the leaf if the leaf was shorter than 3 cm. The harvestable biomass of all leaves on a tiller was summed to calculate the harvestable biomass per tiller. This was multiplied by the tiller density at the start of the experiment (2574 m⁻²) and the dry-weight of Festuca rubra (0.034 mg mm⁻¹) to convert the measure of leaf length into yield to grazers as g dwt m⁻². Nitrogen yield (g N m⁻²) was calculated by multiplying yield to grazers with the nitrogen concentration (g N g⁻¹ dwt) of leaves of the different treatments.

Finally, carrying capacity of the area (262 ha of mid-marsh dominated by Festuca rubra) was calculated, using published data on intake rate and feeding time. For Barnacle Geese feeding on Festuca in spring, intake rate was measured as 0.19 g min⁻¹ (Prop et al. 1998) and feeding time as 907 min day⁻¹ (Black et al. 1991). From these data total biomass removal by the geese during 8 weeks was calculated, a period corresponding with the interval between the establishment of the exclosures and the last measurement.

To test for trends over time, a repeated measures ANOVA was used with week as the repeated factor, treatment as the fixed factor and replicate as the random factor; a post-hoc Tukey test was used to test for differences between treatments. Since we were interested in the yield to grazers after specific periods, the tests were subsequently performed separately for every measurement date. For all tests a Randomised block design was used with treatment as fixed factor, and replicate as random factor with additional Tukey post-hoc test to test for differences between treatments. All analyses were performed using the SPSS for Windows, version 12.0.1.
Results

Growth after grazing

Average live biomass per tiller was reduced after the experimental grazing bouts by approximately 13 mm in all grazed treatments. A repeated measurement ANOVA showed significant differences between the treatments for both live aboveground biomass (Figure 7.1; Treatment: $F_{4,16}=6.153, P=0.002$; Replicate: $F_{4,16}=6.659, P=0.001$) and dead biomass (Treatment: $F_{4,16}=4.782, P=0.010$; Replicate: $F_{4,16}=17.322, P<0.001$). For dead biomass the ungrazed treatment was higher than all grazed treatment for live aboveground biomass the 14-min grazing treatment did not differ significantly from either the other grazed or the ungrazed treatments, while the ungrazed treatment differed significantly from the grazed treatments.

Figure 7.1: Seasonal change in standing crop for the different grazing intensities. Values represent means with SE (n=5). Asterisks denote significant differences (P<0.05) between the ungrazed and all grazed treatments. Different letters denote significant differences between treatments (P<0.05).
When analysed per measuring date, aboveground biomass of the ungrazed treatment exceeded that of all grazed treatments during the first three weeks after experimental grazing (Treatment $P<0.005$; Replicate $P<0.005$). In the fourth week, the 14 min-grazing treatment was not significantly different from the ungrazed (Treatment: $F_{4,16}=4.635$, $P=0.011$; Replicate: $F_{4,16}=5.613$, $P=0.005$) and in the fifth and sixth weeks, there were no differences between any of the grazed treatments and the ungrazed treatment (Treatment: $F_{4,16}=2.533$ n.s. and $F_{4,16}=2.780$ n.s. for week 5 and 6 respectively and Replicate: $F_{4,16}=4.716$, $P=0.010$ and $F_{4,16}=2.860$ n.s.). This implies a greater increase in live biomass (increment in standing crop – ISC) in the grazed treatments. We found a significant effect of grazing treatment on ISC in week six after grazing (Treatment: $F_{4,16}=3.029$, $P=0.049$; Replicate: $F_{4,16}=0.827$ n.s.; Figure 7.2A), caused by the difference between the ungrazed and the treatment receiving 14-min grazing (post hoc Tukey).

**Figure 7.2:** Increment of standing crop (A), increase in dead biomass (B) and total biomass production (C) over six weeks, given as mean + SE ($N=5$) for the different treatments. Different letters denote significant differences with $P<0.05$. 
Tiller senescence differed significantly between treatments: In the ungrazed treatment more material died than in each of the grazed treatments (Treatment: $F_{4,16}=7.224, P=0.002$; Replicate: $F_{4,16}=7.557, P=0.001$; Figure 7.2B). When combining the measures of increment of standing crop and tiller senescence to the parameter of total aboveground biomass production (ABP), we found no effect of treatment ($F_{4,16}=0.871, P=0.503$; Figure 7.2C) or replicate ($F_{4,16}=2.230$ n.s.). This implies that the growth of tillers in all treatments was equal, but more biomass died in the ungrazed treatment. Interestingly, the amount of biomass that died in the ungrazed treatment equals the amount of biomass that was eaten in the grazed treatments. At the end of the experiment this resulted in a significantly lower percentage of live biomass in the ungrazed treatment as compared to the 14 and 21 min-grazing treatments (live biomass 70% versus 79 and 77%; Treatment $F_{4,16}=4.905, P=0.009$; Replicate $F_{4,16}=0.760$, n.s., Figure 7.3A).

**Increased tillering after grazing**

At the beginning of the experiment tiller density was 2574 ± 303 tillers m$^{-2}$. At the beginning of the experiment the number of leaves per tiller was equal for all treatments (Treatment $F_{4,16}=0.690$, n.s.; Replicate $F_{4,16}=21.526$, $P<0.001$). When comparing the number of new axillary shoots between different treatments at the end of the measuring period (first week of May) it is obvious that grazing at an intermediate intensity increased the number of axillary shoots (Figure 7.3B Treatment $F_{4,16}=3.493$ $P=0.031$; Replicate $F_{4,16}=1.276$, n.s.). The number of leaves of the main shoot (Treatment $F_{4,16}=0.842$, n.s.; Replicate $F_{4,16}=5.104$, $P=0.008$) and the number of leaves per axillary shoot did not differ significantly between treatments (Treatment $F_{4,13}=0.274$, n.s.; Replicate $F_{4,13}=1.719$, n.s.).

![Figure 7.3](image1.png)

**Figure 7.3:** The effects of grazing intensity on sward characteristics: (A) The percentage of live biomass in the vegetation. (B) The number of new shoots per tiller six weeks after experimental-grazing treatment. Bars represent overall mean + SE ($N=5$).
**Increased quality after grazing**

For nitrogen concentration, taken as a measure of forage quality, we found a significant difference between treatments (Repeated measurements ANOVA, Treatment $F_{4,16}=4.316$, $P=0.015$; Replicate $F_{4,16}=12.852$, $P<0.001$). A post-hoc Tukey test revealed that nitrogen concentration of leaf material in the ungrazed treatment was significantly lower than in the 21 min- and 28 min- grazed treatments. Quality in all treatments decreased throughout the measuring period, but the decline in the ungrazed treatment was distinctly stronger than in the grazed treatments. Five weeks after grazing the 28 min-grazing treatment was significantly different from the ungrazed treatments (Treatment $F_{4,16}=3.266$, $P=0.039$; Replicate $F_{4,16}=4.115$, $P=0.018$). Twelve weeks after grazing all differences between treatments had disappeared and nitrogen contents were similar (Treatment $F_{4,16}=1.180$, n.s.; Replicate $F_{4,16}=0.275$, n.s.).

**Yield to grazers**

Figure 7.4A shows that yield to grazers increased by approximately 20% in the intermediate, 14-min grazing treatment (Treatment $F_{4,16}=3.420$, $P=0.033$; Replicate $F_{4,16}=1.518$, n.s.). Also in the intermediate, 14-min grazing treatment we found an increase of about 40% in nitrogen yield, and of about 25% in all other grazed treatments as compared to the ungrazed treatment (Treatment $F_{4,16}=5.936$, $P=0.004$; Replicate $F_{4,16}=0.568$, n.s; Figure 7.4B). Subsequently, carrying capacity also showed an optimum at the 14-min grazing treatment (Figure 7.5).

![Figure 7.4: (A) Yield to grazers and (B) Nitrogen yield 6 weeks after experimental grazing for all grazing intensities (mean + SE). Different letters in (A) denote significant differences between treatments ($P<0.05$). The curve in (B) shows the quadratic regression: $y=0.2373+0.0123x-0.0003x^2$ ($F_{2,22}=10.5031$, $P=0.0006$, $R^2=0.488$), the dashed reference line gives the potential harvest for ungrazed swards.](image_url)
Compensatory growth of Festuca rubra after grazing

Discussion

We can distinguish four ways in which herbivores might positively alter availability and quality of plant resources through grazing: (1) the maintenance of phenologically young stages of plants leading to a high nutrient concentration in leaf material; (2) the stimulation of growth leading to increased biomass; (3) the stimulation of tillering which increases shoot density; and (4) a shift in vegetation composition which can increase plant cover and reduce that of standing dead biomass, through selective foraging and a reduction of senescing tissue. The second point has received most attention and the controversy about the mechanism has produced evidence for (Ydenberg and Prins 1981; Hik and Jefferies 1990; Pandey and Singh 1992; Frank and McNaughton 1993; Nolet 2004) and against it (Belsky 1986; Zellmer et al. 1993; Beaulieu et al. 1996). An increase of the nutrient concentration in previously grazed tissue is a well-reported effect of grazing in many different ecosystems (Ydenberg and Prins 1981; Gauthier et al. 1995; Ruess et al. 1997; Fox et al. 1998; Green and Detling 2000; but see also Piedboeuf and Gauthier 1999; Leriche et al. 2003). Alterations in shoot densities or live/dead ratios are often reported as side-effects in grazing studies (Coughenour 1991; Van de Koppel et al. 1996; Loonen and Solheim 1998; Zacheis et al. 2001), but usually do not receive much attention.

In our study, grazing did not increase biomass production, yet we found effects on sward characteristics like tiller density (increase in tillering, Figure 7.3B) and composition of the vegetation (increased percentage of live biomass, Figure 7.3A). When considering the increment of standing crop alone, we found evidence of overcompensation in grazed plants (Figure 7.2A). However, when correcting for senescence of leaf tissue through the measure of aboveground biomass production, the difference between grazing treatments disappeared (Figure 7.2C). At the end of the experiment, the biomass in the grazed treatments had recovered to that of the ungrazed treatment (Figure 7.1). Therefore, we conclude that Festuca rubra did compensate, but not overcompensate, for biomass lost through grazing. We stress the importance of incorporating leaf senescence in all measurements and to avoid measuring increment in standing crop alone. Single measurements of increment in standing crop overestimate plant production, increasing the risk of making erroneous conclusions about overcompensation under grazing. Bakker and Loonen (1998) already stressed this point and depict studies where proof of overcompensation disappeared when senescence was incorporated in the calculations.

We acknowledge that in all grazing treatments the individual tillers that we measured were grazed to the same extent. However, the sward received different grazing intensities and our results show that this has effects on the growth response of the individual tiller. Different treatment responses concerning the increase in standing crop (Figure 7.1A) and increase in new shoots (Figure 7.3B) suggest that these growth differences have repercussions for the total yield to grazers.
Grazing facilitation through increased (nitrogen) yield

Although experimental grazing did not increase biomass production of Festuca rubra in our study, we argue that goose grazing increased harvestable biomass and nitrogen. We have shown that yield to grazers was increased by approximately 20% in the intermediate, 14-min grazing treatment (Figure 7.4A). Because of their limited digestive volume, geese and other small herbivores are restricted to high quality diets (Demment and Van Soest 1985). Therefore we used nitrogen yield, the amount of nitrogen per square meter, as a measure of forage quality (Figure 7.4B). In line with the grazing optimisation hypothesis by McNaughton (1979) we fitted a quadratic curve to our data (Figure 7.4B); the curve shows an optimum of nitrogen yield at an intermediate grazing pressure (14-min m\(^{-2}\)). It is important to note that this intermediate grazing pressure corresponds with the natural grazing pressure of wild Barnacle Geese at this site.

The carrying capacity of this salt-marsh area is increased by grazing, with an optimum at the natural grazing intensity. Interestingly, the current number of wild Barnacle Geese that rely on Festuca swards as spring forage (on average 2540 Barnacle Geese, annual counts for the period 2000-2002, own observations) matches the maximum carrying capacity as calculated from our experiment (Figure 7.5).

![Figure 7.5: Estimate of the carrying capacity in response to grazing intensities and average number of geese observed in the area (dashed line).](image)

Figure 7.5: Estimate of the carrying capacity in response to grazing intensities and average number of geese observed in the area (dashed line).
Compensatory growth of Festuca rubra after grazing

**Mechanisms for (over)compensatory growth**

In the literature, two mechanisms of how plants can profit from grazing are generally discussed. The first, and most studied focuses on the interaction of grazing and an increased nutrient availability through nutrient input by faeces or urine. The second mechanism relates to the effects of shading by taller neighbouring species, by standing dead biomass or by the plant itself (self-shading) and the removal of competition for light through grazing.

Combined effects of grazing and nutrient input through droppings on the growth of forage plants have been found in many studies in various ecosystems. These studies often report increased nitrogen concentration of grazed tissue as well as increased growth rates and increased tiller densities (Ruess *et al.* 1983; Cargill and Jefferies 1984b; Ruess *et al.* 1997; Frank *et al.* 2002; but also see Zacheis *et al.* 2002). It is assumed that nutrient limitation of the vegetation and the ability of the plants to profit directly from the released nutrients are important prerequisites for the occurrence of enhanced growth of plants following grazing (Yamauchi and Yamamura 2004). Hik and Jefferies (1990) tested the predictions of the grazing optimisation hypothesis in a sub-Arctic ecosystem characterised by extensive but periodic grazing by large numbers of breeding Lesser Snow Geese, *Chen caerulescens caerulescens*, during summer. At their study site, the salt marsh of La Pérouse Bay, Canada, the vegetation is dominated by the graminoids *Puccinellia phryganodes* and *Carex subspathacea*. Hik and Jefferies demonstrated that goose grazing enhanced productivity of these species. However, the increase of aboveground production of grazed swards of *P. phryganodes* depended entirely upon the input of goose faeces (Hik and Jefferies 1990).

As the sub-Arctic marsh at that site is primarily nitrogen-limited (Cargill and Jefferies 1984a), the increase in biomass production in grazed swards was explained by an acceleration of the nitrogen cycle caused by a combination of grazing and subsequent deposition of droppings. In several studies on temperate salt marshes in the Wadden Sea, addition of nitrogen and phosphorus had no effects on the biomass of *F. rubra* (Kiehl *et al.* 1997; Van Wijnen and Bakker 1999). Additionally, Van Wijnen *et al.* (1999) demonstrated that the total nitrogen input from droppings on a temperate salt marsh is negligible when compared to the inorganic nitrogen released by mineralisation. We therefore argue that fertilisation by droppings is an unlikely cause of increased tillering of grazed plants at our temperate site.
The second mechanism, a reduction of shading through removal of other taller species (McNaughton 1979), through reduction in standing dead biomass (Frank and McNaughton 1993) or through reduction of self-shading (Wegener and Odasz 1997; Nolet 2004) has received less attention. McNaughton (1976) first reported the higher productivity of vegetation on grazed sites compared to non-grazed sites in the Serengeti short-plains. These grasslands were dominated by the grass *Andropogon greenwayi*, which disappeared when a site remained ungrazed (McNaughton 1979). Belsky (1986) demonstrated that *A. greenwayi* profits from grazing which opens up the dense canopy, and facilitates the production of new tillers. The grass takes advantage of the intolerance of neighbouring plant species to grazing and trampling.

In the case of *Festuca rubra*, nutrient stores are maintained mainly below-ground, which reduces nitrogen-loss to aboveground grazing (Berendse *et al.* 1992). This can be interpreted as an adaptation to grazing. Kiehl *et al.* (1997) suggested that self-shading may decrease tillering in *Festuca* swards. In an experimental set-up non-shaded *Festuca* clones produced significantly more tillers than artificially shaded clones, resulting in a denser sward of the non-shaded clones (Skalova and Krahlulec 1992). If *Festuca* reacts with increased tillering to improved light-conditions after grazing, this can explain the increased sward density found in our grazing experiment. We call for further experimental field studies on the mechanism behind plant responses to grazing in non-nutrient limited systems.
Conclusions

Although the mechanism is not entirely understood yet, our data demonstrate that geese can increase their harvest and the quality of their forage through grazing. This can have far-reaching consequences for their survival and breeding performance, as improved foraging opportunities during spring translate into improved body condition and subsequently into successful reproduction at the Arctic breeding grounds (Ebbinge and Spaans 1995). We conclude that the geese optimise grazing of the area, thereby ensuring a maximum carrying capacity. This is an interesting finding contrasting that of McNaughton (1979) who showed that natural grazing intensities of wildebeest in his savannah study system are higher than optimal. Two studies that experimentally manipulated grazing frequency in disparate ecosystems such as a mixed-grass prairie in the USA grazed mainly by bison, *Bison bison*, (Green and Detling 2000) and hayfields on Iceland grazed by Greenland White-fronted Geese, *Anser albi*frons *flavirostris* (Fox *et al.* 1998) found comparable results; an increase in nitrogen yield at grazing frequencies that corresponded to natural levels. Other experimental field tests did generally not apply multiple levels of grazing intensity (for example: Frank and McNaughton 1993; Gauthier *et al.* 1995; Ruess *et al.* 1997; Fox *et al.* 1998) or do not provide the natural level of grazing intensity (Hik and Jefferyes 1990). For our study, we suppose that the observed optimal level of grazing intensity results from a decline of foraging intake of the geese at non-optimal grazing intensities; at low grazing intensity the vegetation will eventually become too tall for the geese and intake rate will decline (Van der Wal *et al.* 1998b); at high grazing intensities intake rate will also decline because of lower food availability and higher levels of interference competition. This so-called dome-shaped functional response was recently described for Dark-bellied Brent Geese (*Branta bernicla bernicla*) by Bos *et al.* (2004).

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Holding pen on the salt marsh of Schiermonnikoog with two captive Barnacle Geese in the night pen (top) and grazing on one of the plots (bottom).