

Compensatory growth of *Festuca rubra* after grazing: can migratory herbivores increase their own harvest during staging?

A. J. VAN DER GRAAF,*† J. STAHL*‡ and J. P. BAKKER§

*Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, PO Box 14, 9750 AA Haren, the Netherlands, ‡Landscape Ecology Group, University of Oldenburg, 26111 Oldenburg, Germany, and §Community and Conservation Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands

Summary

1. The grazing optimization hypothesis predicts 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 the grazing intensity of *Festuca rubra* swards through trials with captive geese in early spring. Levels on experimental grazing matched levels of natural grazing pressure. The growth response of individually marked tillers was measured over 6 weeks.
3. Above-ground biomass production of individual tillers was not different among different grazing intensities. Lost biomass in grazed tillers was compensated by a lower rate of senescence.
4. Grazing affected sward characteristics significantly: 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 compared with ungrazed swards at levels of natural spring grazing.
6. This experiment demonstrates an increase in the carrying capacity of the staging site for migratory geese through grazing. When comparing the experiment with grazing levels of wild Barnacle Geese, it is clear that current goose densities maximize potential harvest.

Key-words: Barnacle Goose, carrying capacity, forage quality, grazing optimization hypothesis, herbivory

Functional Ecology (2005) **19**, 961–969
doi: 10.1111/j.1365-2435.2005.01056.x

Introduction

In the 1970s Dyer (1975) and McNaughton (1979) postulated the grazing optimization hypothesis, which describes the reaction of plants to increasing herbivory. The hypothesis 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 have demonstrated a positive response of plant tissue production on grazing (Cargill & Jefferies 1984b; Frank & McNaughton 1993), but evidence is limited to certain ecosystems, and remains controversial (Belsky 1986; Belsky *et al.*

1993). Responses of various plant traits, such as total production, final biomass, root biomass and relative growth rate, differ among species (Ferraro & Oosterheld 2002). In general, relative growth rate has been shown to increase under defoliation.

It is important to note that facilitation of grazing is not caused solely by increased tissue production and biomass (grazing optimization). Further reactions of vegetation to grazing comprise increased nutrient concentration, denser sward, and decreased cover of standing dead material. Sites that are repeatedly grazed by herbivores, often referred to as grazing lawns (McNaughton 1984; Drent & Van der Wal 1999), are characterized by these traits.

McNaughton (1979) developed the theoretical framework of grazing optimization in view of the large-scale

movements of herbivores in the Serengeti (such as Wildebeest, *Connochaetes taurinus*). In ecosystems visited periodically by many migratory herbivores, grazing facilitation can be of great importance. Here, plant regrowth might counteract forage depletion, thereby allowing repeated foraging 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 3000 Barnacle Geese and 1500 Brent Geese forage on the salt marsh during March–May (Bos & Stahl 2003). During these months, both goose species accumulate body reserves before their migration to the Arctic (Prop & 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 & Spaans 1995). It has been suggested that Brent Geese, *Branta bernicla bernicla*, adopt a cyclic grazing pattern through which they optimize their protein intake (Ydenberg & Prins 1981; Drent & 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 the literature. We present an experimental field test to interpret the consequences of successive waves of grazing on biomass production at a major staging site of arctic geese. We tested the predictions of the grazing optimization 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 *F. rubra* was followed for 6 weeks. Our aim was to explore the scope for grazing optimization 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. At these salt-marsh sites about 2500 Barnacle Geese were present during the experiments (goose count March/April 2002, unpublished data). At the same time, about 1000 Brent Geese (unpublished data) along with 350 Brown Hares (D.P.J. Kuijper, personal communication) used the 1350-

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, Van de Koppel & Sagel 1998) in the *Festuca* community, where the vegetation mainly consists of Red Fescue (*F. 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, ≈20% of the total area. *Festuca* forms ≈90% of the diet of Barnacle Geese (Van Dinteren 1988) and ≈50% of the diet of Brent Geese (Van der Wal *et al.* 2000). The diet of resident Brown Hares, *Lepus europaeus*, contains ≈70% *Festuca* in early spring (Van der Wal, Van de Koppel & Sagel 1998).

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 in the same places. Grazing intensity was calculated by multiplying these field measures of dropping density with field observations on dropping intervals of Barnacle Geese. Prop & Vulink (1992) recorded dropping intervals of 4.4 min for Barnacle Geese foraging on *Festuca* at this site in spring. The cumulative grazing intensity of wild Barnacle Geese amounted to 13.9 ± 1.5 min m⁻² (mean ± SE, *N* = 30) for 2 weeks in mid-March.

In 2002, five replicate sites were selected and matched for homogeneity of the *Festuca* sward. Sites were ≈100 m apart from each other. At each site, an area of 2 × 12 m was fenced with chicken wire to exclude grazing by wild geese and hares. Other herbivores are virtually absent from these marshes. Fences were erected in mid-March 2002 before the 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 m² to each treatment. Five treatments characterized by different grazing intensities were created through controlled grazing with two captive Barnacle Geese for a fixed period. This experimental design was adopted from a study by Hik & Jefferies (1990), who studied growth stimulation through grazing in a subarctic 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 2-week period in mid-March 1998. The timing of these measurements corresponds with the period between erection of the enclosures and experimental grazing in our experiments.

On the day before 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 the 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 having to be caught, and stress was reduced to a minimum. The grazing took place on five consecutive days (25–29 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 2 weeks before the experiment.

MEASUREMENTS ON *F. 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 sward with a high proportion of litter, instead we adopted a detailed approach that 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 three square frames of 5.5 × 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 *F. rubra* were marked individually in each plot. In each of two sections of 10 × 25 cm, 10 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 dead parts. Following the first marking, tillers were measured six times with intervals of 1 week.

We started out with 20 marked tillers in each replicate of the treatments. Mortality accounted for ≈5% of the loss of 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 tiller loss of 16%, and did not differ between treatments (univariate ANOVA, $F_{4,20} = 0.449$, $P = 0.772$).

Therefore sample sizes decreased to ≈15 tillers per plot at the end of the season. To avoid pseudo-replication, measurements of 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 *F. rubra* was collected to establish a conversion between leaf length and leaf biomass. On each occasion about 100 leaves were measured, dried and weighed (in total ≈2.5 m). Average dry weight of *Festuca* leaves was 0.034 mg mm⁻¹ (±0.0007).

Additionally, samples of green leaf tips for chemical analysis were collected 2, 4 and 6 weeks after grazing. Samples were oven-dried at 60 °C for at least 48 h and ground in a Idar-Oberstein planetary micro-mill (Pulverisette 7, Fritsch GmbH, Germany), at a rotational speed of 750 rpm, for 3 × 3 min. Ground samples were analysed for total nitrogen and carbon content 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 (Bakker & Loonen 1998): increment in standing crop; above-ground biomass production, including both increment in standing crop and senescence; and number of leaf births and deaths. Increment in standing crop is a frequently used measure (McNaughton 1979; Hik & Jefferies 1990; Frank & McNaughton 1993); however, Bakker & Loonen (1998) suggested above-ground biomass production 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 *F. rubra* (0.034 mg mm⁻¹) to convert the measure of leaf length into yield to grazers as g DW m⁻². Nitrogen yield (g N m⁻²) was calculated by multiplying yield to grazers with the N concentration (g N g⁻¹ DW) of leaves of the different treatments.

Finally, the carrying capacity of the area (262 ha of mid-marsh dominated by *F. 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, Deerenberg & Owen 1991). From these data, total biomass removal by the geese was calculated over 8 weeks, a period corresponding to the interval between 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. As we were interested in the yield to grazers after specific periods, subsequently the tests were performed separately for every measurement date. For all tests a randomized block design was used, with treatment as fixed factor and replicate as random factor, with an additional Tukey *post hoc* test for differences between treatments. All analyses were performed using SPSS for Windows, version 12.0.1.

Results

GROWTH AFTER GRAZING

Average live biomass per tiller was reduced after the experimental grazing bouts by ≈ 13 mm in all grazed treatments. A repeated-measures ANOVA showed significant differences between treatments for both live above-ground biomass (Fig. 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 treatments; for live above-ground 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. When analysed per measuring date, above-ground biomass of the ungrazed treatment exceeded that of all grazed treatments during the first 3 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, $F_{4,16} = 2.533$, NS; $F_{4,16} = 2.780$, NS for weeks 5 and 6, respectively,

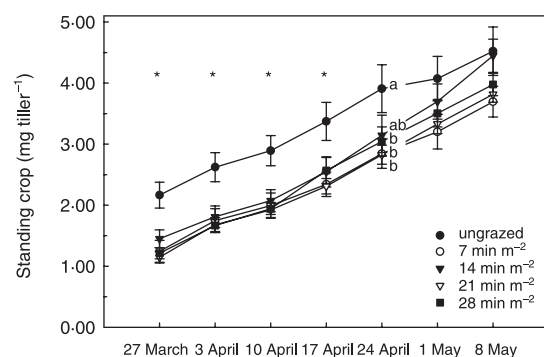


Fig. 1. Seasonal change in standing crop for different grazing intensities. Values represent means \pm SE ($n = 5$). Asterisks denote significant differences ($P < 0.05$) between ungrazed and all grazed treatments. Different letters denote significant differences between treatments ($P < 0.05$).

replicate, $F_{4,16} = 4.716$, $P = 0.010$ and $F_{4,16} = 2.860$, NS). This suggests a greater increase in live biomass (increment in standing crop) in the grazed treatments. We found a significant effect of grazing treatment on increment in standing crop in week 6 after grazing (treatment, $F_{4,16} = 3.029$, $P = 0.049$; replicate, $F_{4,16} = 0.827$, NS; Fig. 2a), caused by the difference between the ungrazed treatment and that receiving 14-min grazing (*post hoc* Tukey).

Tiller senescence differed significantly between treatments. In the ungrazed treatment more biomass died than in each of the grazed treatments (treatment, $F_{4,16} = 7.224$, $P = 0.002$; replicate, $F_{4,16} = 7.557$, $P = 0.001$; Fig. 2b). When combining the measures of increment of standing crop and tiller senescence with the parameter of total above-ground biomass production, we found no effect of treatment ($F_{4,16} = 0.871$, $P = 0.503$; Fig. 2c) or replicate ($F_{4,16} = 2.230$, NS). This suggests that the growth of tillers in all treatments was equal, but more material 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 compared with the 14- and 21-min grazing treatments (live biomass 70 vs 79 and 77%; treatment, $F_{4,16} = 4.905$, $P = 0.009$; replicate, $F_{4,16} = 0.760$, NS; Fig. 3a).

INCREASED TILLERING AFTER GRAZING

At the beginning of the experiment, tiller density was 2574 ± 303 tillers m^{-2} , and the number of leaves per tiller was equal for all treatments (treatment, $F_{4,16} = 0.690$, NS; 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 clear that grazing at an intermediate intensity increased the number of axillary shoots (Fig. 3b; treatment, $F_{4,16} = 3.493$, $P = 0.031$; replicate, $F_{4,16} = 1.276$, NS). The number of leaves of the main shoot (treatment, $F_{4,16} = 0.842$, NS; replicate, $F_{4,16} = 5.104$, $P = 0.008$), and the number of leaves per axillary shoot, did not differ significantly between treatments (treatment, $F_{4,13} = 0.274$, NS; replicate, $F_{4,13} = 1.719$, NS).

INCREASED QUALITY AFTER GRAZING

For N concentration, taken as a measure of forage quality, we found a significant difference between treatments (repeated-measures 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 the N concentration of leaf material in the ungrazed treatment was significantly lower than in the 21- 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

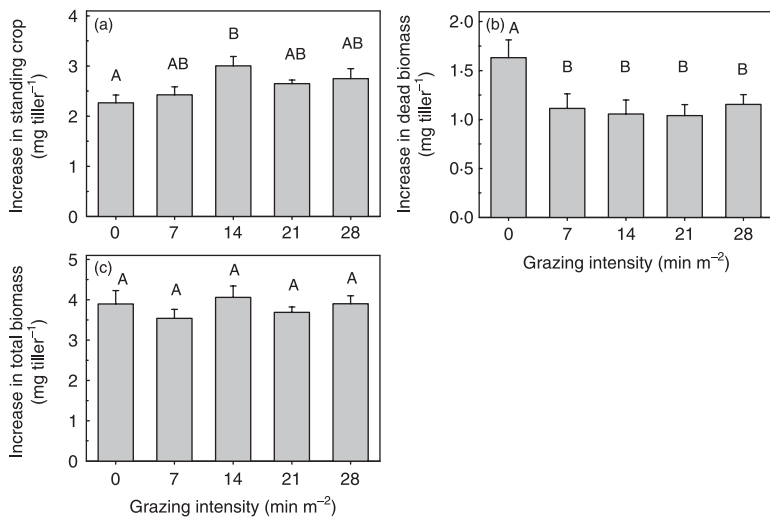


Fig. 2. Increment of standing crop (a), increase in dead biomass (b) and total biomass production (c) over 6 weeks, given as mean + SE ($n = 5$) for different treatments. Different letters denote significant differences, $P < 0.05$.

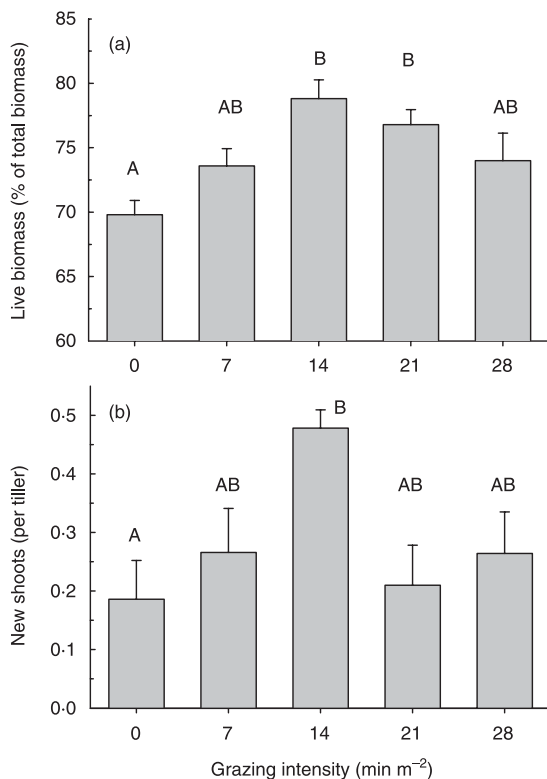


Fig. 3. Effects of grazing intensity on sward characteristics: (a) percentage of live biomass in the vegetation; (b) number of new shoots per tiller 6 weeks after experimental grazing treatment. Bars represent overall mean + SE ($n = 5$).

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 N content was similar (treatment, $F_{4,16} = 1.180$, NS; replicate, $F_{4,16} = 0.275$, NS).

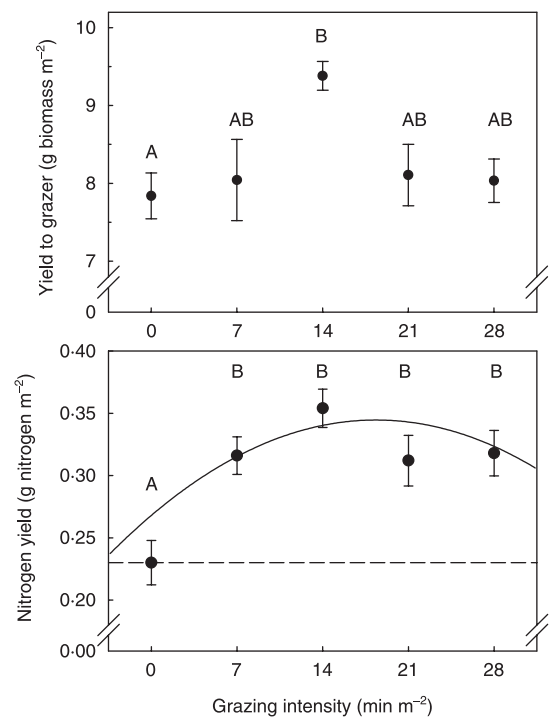


Fig. 4. (a) Yield to grazers and (b) nitrogen yield 6 weeks after experimental grazing for all grazing intensities (mean \pm SE). Different letters in (a) denote significant differences between treatments ($P < 0.05$). The curve in (b) shows the quadratic regression: $y = 0.2373 + 0.0123x - 0.0003x^2$ ($F_{2,22} = 10.5031$, $P = 0.0006$, $R^2 = 0.488$); dashed reference line gives potential harvest for ungrazed swards.

YIELD TO GRAZERS

Figure 4(a) shows that yield to grazers increased by $\approx 20\%$ in the intermediate, 14-min grazing treatment (treatment, $F_{4,16} = 3.420$, $P = 0.033$; replicate, $F_{4,16} = 1.518$, NS). Also in the intermediate 14-min grazing treatment we found an increase of $\approx 40\%$ in N yield, and an increase of $\approx 25\%$ in all other grazed treatments, compared with the ungrazed treatment (treatment, $F_{4,16} = 5.936$, $P = 0.004$; replicate, $F_{4,16} = 0.568$, NS; Fig. 4b). Subsequently, carrying capacity also showed an optimum at the 14-min grazing treatment (Fig. 5).

Discussion

We can distinguish four ways in which herbivores might positively alter the availability and quality of plant resources through grazing: (1) maintenance of phenologically young plant stages leading to a high nutrient concentration in leaf material; (2) stimulation of growth leading to increased biomass; (3) 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 in senescing tissue. The second point has received most attention, and the controversy regarding the mechanism has produced evidence both for it (Ydenberg & Prins 1981; Hik & Jefferies 1990; Pandey & Singh 1992; Frank &

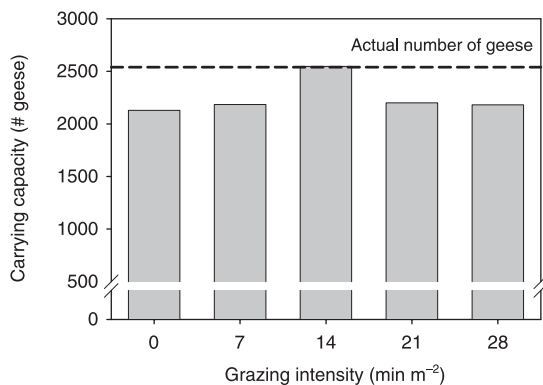


Fig. 5. Estimate of carrying capacity in response to grazing intensity and average number of geese observed in the area (dashed line).

McNaughton 1993; Nolet 2004), and against it (Belsky 1986; Zellmer *et al.* 1993; Beaulieu, Gauthier & Rochefort 1996). An increase in the nutrient concentration in previously grazed tissue is a well reported effect of grazing in many different ecosystems (Ydenberg & Prins 1981; Gauthier *et al.* 1995; Ruess *et al.* 1997; Fox *et al.* 1998; Green & Detling 2000; but see also Piedboeuf & Gauthier 1999; Leriche *et al.* 2003). Alterations in shoot density or live/dead ratios are often reported as side-effects in grazing studies (Coughenour 1991; Van de Koppel *et al.* 1996; Loonen & Solheim 1998; Zacheis, Hupp & Ruess 2001), but usually do not receive much attention.

In our study, grazing did not increase biomass production, yet we found effects on sward characteristics such as tiller density (increase in tillering, Fig. 3b) and vegetation composition (increased percentage of live biomass, Fig. 3a). When considering the increment of standing crop alone, we found evidence for overcompensation in grazed plants (Fig. 2a). However, when correcting for senescence of leaf tissue through the measure of above-ground biomass production, the difference between grazing treatments disappeared (Fig. 2c). At the end of the experiment, the biomass in the grazed treatments had recovered to that of the ungrazed treatment (Fig. 1). Therefore we conclude that *F. rubra* compensated, but did not overcompensate, for biomass lost through grazing. We stress the importance of incorporating leaf senescence in all measurements, and of avoiding measuring only the increment in standing crop. Single measurements of increment in standing crop overestimate plant production, increasing the risk of drawing erroneous conclusions about overcompensation under grazing. Bakker & Loonen (1998) stressed this point, and depict studies in which 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 (Fig. 1a) and increase in new shoots (Fig. 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 *F. rubra* in our study, we argue that goose grazing increased harvestable biomass and N. We have shown that yield to grazers was increased by $\approx 20\%$ in the intermediate, 14-min grazing treatment (Fig. 4a). Because of their limited digestive volume, geese and other small herbivores are restricted to high-quality diets (Demment & Van Soest 1985). Therefore we used N yield, the amount of nitrogen per m², as a measure of forage quality (Fig. 4b). In line with the grazing optimization hypothesis of McNaughton (1979), we fitted a quadratic curve to our data (Fig. 4b); the curve shows an optimum of N 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 2000–02, unpublished data) matches the maximum carrying capacity as calculated from our experiment (Fig. 5).

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 N concentration of grazed tissue as well as increased growth rates and increased tiller densities (Ruess, McNaughton & Coughenour 1983; Cargill & Jefferies 1984b; Ruess *et al.* 1997; Frank, Kuns & Guido 2002; but see also Zacheis, Hupp & Ruess 2002). It is assumed that nutrient limitation of the vegetation, and the ability of plants to profit directly from the released nutrients, are important prerequisites for enhanced growth of plants following grazing (Yamauchi & Yamamura 2004). Hik & Jefferies (1990) tested the predictions of the grazing optimization hypothesis in a subarctic ecosystem characterized 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 & Jefferies (1990) demonstrated that goose grazing enhanced productivity of these species. However, the increase of above-ground production of grazed swards of *P. phryganodes* depended entirely on the input of goose faeces (Hik & Jefferies 1990). As the subarctic marsh at that site is primarily N-limited (Cargill & Jefferies 1984a), the increase in biomass production in grazed swards was explained by an acceleration of the N 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 N and phosphorus had no effects on the biomass of *F. rubra* (Kiehl, Esselink & Bakker 1997; Van Wijnen & Bakker 1999). Additionally, Van Wijnen, Van der Wal & Bakker (1999) demonstrated that the total N input from droppings on a temperate salt marsh is negligible when compared with the inorganic N released by mineralization. We therefore argue that fertilization by droppings is an unlikely cause of increased tillering of grazed plants at our temperate salt-marsh site.

The second mechanism, a reduction of shading through removal of other, taller species (McNaughton 1979) through a reduction in standing dead biomass (Frank & McNaughton 1993) or a reduction in self-shading (Wegener & Odasz 1997; Nolet 2004), has received less attention. McNaughton (1976) first reported the higher productivity of vegetation on grazed sites compared with 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 neighbouring plant species' intolerance of grazing and trampling.

In the case of *F. rubra* nutrient stores are maintained mainly below-ground, which reduces N loss through above-ground grazing (Berendse, Elberse & Geerts 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 & Krahlulec 1992). If *Festuca* reacts to improved light conditions with increased tillering after grazing, this may explain the increased sward density found in our grazing experiment. Further experimental field studies are needed on the mechanism behind plant responses to grazing in non-nutrient-limited systems.

Conclusions

Although the mechanism is not yet completely understood, 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 & Spaans 1995). We conclude that the geese optimize grazing of the area, thereby ensuring a maximum carrying capacity. This is an interesting finding, in contrast to that of McNaughton (1979) who showed that natural grazing intensities of wildebeest in his savanna study system are higher than optimal. Two studies that experimentally manipulated grazing frequency in disparate ecosystems (a mixed-grass prairie in the USA grazed mainly by Bison, *Bison bison*, Green & Detling 2000; and hayfields in Iceland grazed by Greenland White-fronted Geese, *Anser albifrons flavirostris*, Fox *et al.* 1998) found comparable results: an increase in N yield at grazing frequencies that corresponded to natural levels. Other experimental field tests generally did not apply multiple levels of grazing intensity (e.g. Frank & 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 & Jefferies 1990). For our study, we suggest that the observed optimal level of grazing intensity results from a decline in foraging intake of the geese at non-optimal grazing intensities. At low grazing intensities the vegetation will eventually become too tall for the geese and intake rate will decline (Van der Wal *et al.* 1998); at high grazing intensities the 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, Van de Koppel & Weissing (2004).

Acknowledgements

Many people were very supportive with the logistics in the field and care of the captive geese: we especially thank J. Minderman, R. Mullers and K. Soepboer. Vereniging Natuurmonumenten kindly allowed us to conduct the project within the borders of the National Park Schiermonnikoog. We thank M. Wandago, B. Venema and N. Eck for handling of the nitrogen samples and for assistance in the laboratory, and R. Jefferies, R. Drent and two anonymous referees for critical discussions and valuable advice on earlier drafts. Dick Visser skilfully prepared the figures. The project was supported financially by the Deutsche Forschungsgemeinschaft in a grant to J.S. and the University of Groningen.

References

- Bakker, C. & Loonen, M.J.J.E. (1998) The influence of goose grazing on the growth of *Poa arctica*: overestimation of overcompensation. *Oikos* **82**, 459–466.

- Beaulieu, J., Gauthier, G. & Rochefort, L. (1996) The growth response of graminoid plants to goose grazing in a High Arctic environment. *Journal of Ecology* **84**, 905–914.
- Belsky, A.J. (1986) Does herbivory benefit plants? A review of the evidence. *American Naturalist* **127**, 870–892.
- Belsky, A.J., Carson, W.P., Jensen, C.L. & Fox, G.A. (1993) Overcompensation by plants: herbivore optimization or red herring? *Evolutionary Ecology* **7**, 109–121.
- Berendse, F., Elberse, W.T. & Geerts, M.H.M.E. (1992) Competition and nitrogen loss from plants in grassland ecosystems. *Ecology* **73**, 46–53.
- Black, J.M., Deerenberg, C. & Owen, M. (1991) Foraging behaviour and site selection of barnacle geese *Branta leucopsis* in a traditional and newly colonised spring staging habitat. *Ardea* **79**, 349–358.
- Bos, D. & Stahl, J. (2003) Creating new foraging opportunities for Dark-bellied Brent *Branta bernicla* and Barnacle Geese *Branta leucopsis* in spring – insights from a large-scale experiment. *Ardea* **91**, 153–166.
- Bos, D., Van de Koppel, J. & Weissing, F.J. (2004) Dark-bellied Brent Geese aggregate to cope with increased levels of primary production. *Oikos* **107**, 485–496.
- Cargill, S.M. & Jefferies, R.L. (1984a) The effects of grazing by lesser snow geese on the vegetation of a sub-arctic salt marsh. *Journal of Applied Ecology* **21**, 669–686.
- Cargill, S.M. & Jefferies, R.L. (1984b) Nutrient limitation of primary production in a sub-arctic salt marsh. *Journal of Applied Ecology* **21**, 657–668.
- Coughenour, M.B. (1991) Biomass and nitrogen responses to grazing of upland steppe on Yellowstone's northern winter range. *Journal of Applied Ecology* **28**, 71–82.
- De Jong, D.J., Dijkema, K.S., Bossinade, J.H. & Janssen, J.A.M. (1998) *Salt 97 – Classificatieprogramma voor kweldervegetaties*. Rijkswaterstaat and IBN-DLO, Middelburg, the Netherlands.
- Demment, M.W. & Van Soest, P.J. (1985) A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *American Naturalist* **125**, 641–672.
- Drent, R.H. & Van der Wal, R. (1999) Cyclic grazing in vertebrates and the manipulation of the food resource. *Herbivores: Between Plants and Predators* (eds H. Olff, V.K. Brown & R.H. Drent), pp. 271–299. Blackwell Science, Oxford.
- Dyer, M.I. (1975) The effects of red-winged blackbirds (*Agelaius phoeniceus*) on biomass production of corn grains (*Zea mays* L.). *Journal of Applied Ecology* **12**, 719–726.
- Ebbinge, B.S. & Spaans, B. (1995) The importance of body reserves accumulated in spring staging areas in the temperate zone for breeding in Dark-bellied Brent geese *Branta b. bernicla* in the high Arctic. *Journal of Avian Biology* **26**, 105–113.
- Ferraro, D.O. & Oesterheld, M. (2002) Effects of defoliation on grass growth. A quantitative review. *Oikos* **98**, 125–133.
- Fox, A.D., Kristiansen, J.N., Stroud, D.A. & Boyd, H. (1998) The effects of simulated spring goose grazing on the growth rate and protein content of *Phleum pratense* leaves. *Oecologia* **116**, 154–159.
- Frank, D.A. & McNaughton, S.J. (1993) Evidence for the promotion of aboveground grassland production by native large herbivores in Yellowstone National Park. *Oecologia* **96**, 157–161.
- Frank, D.A., Kuns, M.M. & Guido, D.R. (2002) Consumer control of grassland plant production. *Ecology* **83**, 602–606.
- Gauthier, G., Hughes, R.J., Reed, A., Beaulieu, J. & Rochefort, L. (1995) Effect of grazing by greater snow geese on the production of graminoids at an arctic site (Bylot Island, NWT, Canada). *Journal of Ecology* **83**, 653–664.
- Green, R.A. & Detling, J.K. (2000) Defoliation-induced enhancement of total aboveground nitrogen yield of grasses. *Oikos* **91**, 280–284.
- Hik, D.S. & Jefferies, R.L. (1990) Increases in the net above-ground primary production of a salt-marsh forage grass – a test of the predictions of the herbivore-optimization model. *Journal of Ecology* **78**, 180–195.
- Kers, A.S., Van den Burg, S.R., Schoen, L., Bos, D. & Bakker, J.P. (1998) *Vegetatiekartering Oost-Schiermonnikoog*. Laboratory of Plant Ecology, University of Groningen, Groningen, the Netherlands.
- Kiehl, K., Esselink, P. & Bakker, J.P. (1997) Nutrient limitation and plant species composition in temperate salt marshes. *Oecologia* **111**, 325–330.
- Leriche, A., Le-Roux, X., Desnoyers, F., Benest, D., Simioni, G. & Abbadie, L. (2003) Grass response to clipping in an African savanna: testing the grazing optimization hypothesis. *Ecological Applications* **13**, 1346–1354.
- Loonen, M.J.J.E. & Solheim, B. (1998) Does arctic vegetation change when grazed by barnacle geese? A pilot study. *Norsk Polarinstitutt Skrifter* **200**, 99–103.
- McNaughton, S.J. (1976) Serengeti migratory wildebeest: facilitation of energy flow by grazing. *Science* **191**, 92–94.
- McNaughton, S.J. (1979) Grazing as an optimization process: grass–ungulate relationships in the Serengeti. *American Naturalist* **113**, 691–703.
- McNaughton, S.J. (1984) Grazing lawns: animals in herds, plant form and coevolution. *American Naturalist* **124**, 863–886.
- Nolet, B.A. (2004) Overcompensation and grazing optimisation in a swan–pondweed system? *Freshwater Biology* **49**, 1391–1399.
- Olf, H., De Leeuw, J., Bakker, J.P., Platerink, R.J., Van Wijnen, H.J. & De Munck, W. (1997) Vegetation succession and herbivory in a salt marsh: changes induced by sea level rise and silt deposition along an elevational gradient. *Journal of Ecology* **85**, 799–814.
- Pandey, C.B. & Singh, J.S. (1992) Rainfall and grazing effects on net primary productivity in a tropical savanna, India. *Ecology* **73**, 2007–2021.
- Piedboeuf, N. & Gauthier, G. (1999) Nutritive quality of forage plants for greater snow goose goslings: when is it advantageous to feed on grazed plants? *Canadian Journal of Zoology* **77**, 1908–1918.
- Prop, J. & Deerenberg, C. (1991) Spring staging in Brent Geese *Branta bernicla*: feeding constraints and the impact of diet on the accumulation of body reserves. *Oecologia* **87**, 19–28.
- Prop, J. & Vulink, T. (1992) Digestion by barnacle geese in the annual cycle: the interplay between retention time and food quality. *Functional Ecology* **6**, 180–189.
- Prop, J., Black, J.M., Shimmings, P. & Owen, M. (1998) The spring range of barnacle geese *Branta leucopsis* in relation to changes in land management and climate. *Biological Conservation* **86**, 339–346.
- Ruess, R.W., McNaughton, S.J. & Coughenour, M.B. (1983) The effects of clipping, nitrogen source and nitrogen concentration on the growth responses and nitrogen uptake of an East African sedge. *Oecologia* **59**, 253–261.
- Ruess, R.W., Uliassi, D.D., Mulder, C.P.H. & Person, B.T. (1997) Growth responses of *Carex ramenskii* to defoliation, salinity, and nitrogen availability: implications for geese–ecosystem dynamics in western Alaska. *Ecoscience* **4**, 170–178.
- Skalova, H. & Krahulc, F. (1992) The response of three *Festuca rubra* clones to changes in light quality and plant density. *Functional Ecology* **6**, 282–290.
- Van de Koppel, J., Huisman, J., Van der Wal, R. & Olff, H. (1996) Patterns of herbivory along a productivity gradient: an empirical and theoretical investigation. *Ecology* **77**, 736–745.
- Van der Wal, R., Van de Koppel, J. & Sagel, M. (1998) On the relation between herbivore foraging efficiency and plant standing crop: an experiment with barnacle geese. *Oikos* **82**, 123–130.

- Van der Wal, R., Van Lieshout, S.M.J., Bos, D. & Drent, R.H. (2000) Are spring staging Brent geese evicted by vegetation succession? *Ecography* **23**, 60–69.
- Van Dinteren, G. (1988) De benutting van de Oosterkwelder-vegetatie op Schiermonnikoog door de brandgans (*Branta leucopsis*). MSc Thesis, University of Groningen, Groningen, the Netherlands.
- Van Wijnen, H.J. & Bakker, J.P. (1999) Nitrogen and phosphorus limitation in a coastal barrier salt marsh: the implications for vegetation succession. *Journal of Ecology* **87**, 265–272.
- Van Wijnen, H.J., Van der Wal, R. & Bakker, J.P. (1999) The impact of herbivores on nitrogen mineralization rate: consequences for salt-marsh succession. *Oecologia* **118**, 225–231.
- Wegener, C. & Odasz, A.M. (1997) Effects of laboratory simulated grazing on biomass of the perennial Arctic grass *Dupontia fisheri* from Svalbard: evidence of overcompensation. *Oikos* **79**, 496–502.
- Yamauchi, A. & Yamamura, N. (2004) Herbivory promotes plant production and reproduction in nutrient-poor conditions: effects of plant adaptive phenology. *American Naturalist* **163**, 138–153.
- Ydenberg, R.C. & Prins, H.H.T. (1981) Spring grazing and the manipulation of food quality by barnacle geese. *Journal of Applied Ecology* **18**, 443–453.
- Zacheis, A.B., Hupp, J.W. & Ruess, R.W. (2001) Effects of migratory geese on plant communities of Alaskan salt marsh. *Journal of Ecology* **89**, 57–71.
- Zacheis, A.B., Hupp, J.W. & Ruess, R.W. (2002) Response of a subarctic salt marsh plant community to foraging by captive lesser snow geese. *Ecoscience* **9**, 320–331.
- Zellmer, I.D., Clauss, M.J., Hik, D.S. & Jefferies, R.L. (1993) Growth responses of arctic graminoids following grazing by captive lesser snow geese. *Oecologia* **93**, 487–492.

Received 14 February 2005; revised 30 May 2005 accepted 20 June 2005