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**Manuscript**

# Response of Nitrogen Fixation and Biomass Productivity on Long-term Grazing and Fertilization by Barnacle Geese (*Branta leucopsis*) in High Arctic Tundra Vegetation

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## Abstract

The effect of grazing and fertilization by barnacle geese (*Branta leucopsis*) on cyanobacterial nitrogen fixation and plant biomass productivity in a high arctic habitat was studied in a long-term experiment. In an area with high natural grazing pressure moss-dominated vegetation was exclosed from geese grazing over a period of six growing seasons and annually manipulated by the following treatments: (i) clipping of the vegetation, (ii) addition of goose droppings, (iii) a combination of (i) and (ii), and (iv) exclosing without additional treatment. In order to compare the treated vegetation with naturally grazed vegetation, samples from the nearby surrounding of the exclosures were included as an additional treatment in the analyses. Plant biomass and cyanobacterial nitrogen fixation activity of the vegetation were measured, and the community structure of moss-associated cyanobacteria was analyzed. In general, when droppings were added to the vegetation, plant biomass production was increased while nitrogen fixation activity decreased. In respect to the biomass this may be explained by an enhanced primary production caused by a higher availability of nutrients, while nitrogen compounds released from the droppings inhibit the nitrogen fixation. Furthermore, the clipping treatment caused an increase both in plant biomass and in nitrogen fixation activity and can, in case of the biomass production, be explained by an overcompensation effect that is known and previously described for grazed plants. In case of nitrogen fixation the removal of biomass reduced the net nitrogen content of the soil, which in turn has a stimulating effect on nitrogen fixation. Although the grazing by geese outside the exclosure was more intensive ~~as~~ than the clipping, it caused only a slight increase in nitrogen fixation. This may be explained by the inhibitory effect of nitrogen compounds both from droppings originating from the grazing geese and the trampling effect of the geese increasing mineralization of plant litter. Biomass production in this treatment was partly reduced, i.e. the biomass of mosses was unaffected while the grass biomass dropped to zero, and is explained by the geese's high preference for grass plants as forage. No treatment effect on the cyanobacterial community could be detected. In conclusion, grazing and fertilization by geese have a significant effects on plant biomass production and nitrogen fixation activity without significantly altering the cyanobacterial community structure. Whether these effects are positive or negative depends on the process affected and on the intensity of the grazing and fertilization. To predict the total impact of geese grazing and fertilization in terrestrial arctic habitats all factors has to be considered.

## Introduction

There are three separated populations of barnacle geese (*Branta leucopsis*) in the world: a russian, a greenlandic, and the so-called 'Svalbard population' that has its summer grounds on the islands of the Svalbard archipelago, while they use an area at the border between England and Scotland for wintering. Leaving this area in mid-April the geese arrive in Svalbard in early May where they use the short arctic summer for reproduction and moulting before leaving again southwards in mid-September. The current population size is about 23,000 birds which is a quadruplication during the last three decades (Loonen et al., 1998; Tombre et al., 1998). This increase is thought to be related to changes in land use and wildlife management, i.e. hunting regulation and establishment of bird reservations both on the wintering grounds, along the migration route and in the breeding area (Ebbinge, 1985; Madsen, 1987; Ebbinge, 1991). Since herbivores in general strongly influence the composition and dynamics of plant communities (e.g. van de Koppel et al., 1997; Jefferies, 1999; Olff et al., 1999) such a severe increase in numbers of a herbivorous bird may be expected to lead to dramatic changes in the vegetation (Kotanen and Jefferies, 1997). In extreme cases intense grazing by geese is able to even completely destroy vulnerable vegetation in the Arctic (Kerbes et al., 1990; Kotanen and Jefferies, 1997). However, depending on the intensity and on the parts eaten by the geese, grazing can have either a positive or a negative influence on plant biomass production (Cargill and Jefferies, 1984; Jefferies, 1988; Kerbes et al., 1990). Intense grazing of above-ground and below-ground vegetation leads to reduced plant production and degradation of the vegetation cover, particulary in ecosystems like the High Arctic, where there is less time for recuperation from grazing due to the shortness of the growing season. Furthermore, nitrogen may be removed from the ecosystem when incorporated into the bodies of the geese that return to their winter grounds. Cargill and Jefferies (Cargill and Jefferies, 1984) estimated the maximum amount of nitrogen that is removed in that way by lesser snow geese to 2.2 g $m^{-2}$ $y^{1}$. Other effects that can be ascribed to grazing by geese and fertilization through goose feces may be a decline in soil temperature meditaed by a decrease in the thickness of the vegetation layer (van Der Wal et al., 2001), an alteration of the flora of marine and freshwater habitats nearby the grazing grounds (Rowcliffe et al., 2001; Kotanen, 2002), and even a change in forage supply for reindeers (Van der Wal and Loonen, 1998).

However, several studies have shown that moderate grazing of

above-ground vegetation may have positive effects on plant production and soil nutrient cycling (Cargill and Jefferies, 1984; Hik and Jefferies, 1990). These positive effects can be ascribed to a numbers of abiotic and biotic factors (Bazely and Jefferies, 1985; Hik and Jefferies, 1990). Primary production in terrestrial ecosystems, in general, are subject to several constraints in which availability of nitrogen often plays a key role (Vitousek et al., 1989). In terrestrial arctic habitats nitrogen often is the limiting factor for primary production (Nadelhoffer et al., 1992). Obviously, the addition of nitrogen in form of feces and urine increases the amount of nitrogen available in soils. However, the availability of nitrogen for plants in soil also strongly depends on the rates of net nitrogen mineralization. This process, in turn, is affected by soil conditions and the rates in which plant litter becomes decomposed by soil microorganisms. Zacheis et al. (2002) and Olofsson and Oksanen (2002) showed that not only the addition of feces and urine results in increased availability of nitrogen, but also that trampling may accelerate decomposition by fragmenting the dead plant material and increase the rates of net nitrogen mineralization by incorporation of the litter into the soil. Another source of nitrogen in these habitats are nitrogen-fixing cyanobacteria, which in case of tundra vegetation occur epiphytically on moss leaves (reviewed in Solheim and Zielke, 2002), while they commonly can be found in free-living form as pioneer colonizers on bare soils and in salt marshes (Bazely and Jefferies, 1989). In areas with low precipitation, and consequently low rates of dry and wet deposition of nitrogen, cyanobacterial nitrogen fixation is considered to be the main source of nitrogen (Alexander et al., 1978; Chapin et al., 1991; Lennihan et al., 1994; Solheim et al., 1996). Previous studies have shown that abiotic factors may have severe effects on the nitrogen fixation activity in terrestrial arctic ecosystems (Lennihan et al., 1994; Liengen, 1999; Zielke et al., 2002). However, while enhanced temperatures and increased soil water content have a stimulating effect on cyanobacterial nitrogen fixation activity (Zielke et al., 2002), it is repressed by available nitrogen, or even totally inhibited like in soils beneath bird cliffs where the soil nitrogen content is extremely high (Solheim et al., 1996).

With goose grazing plant biomass is removed, but goose droppings are added to the vegetation. These components affect nutrient cycling in different ways. The objective of this study was to determine the effects of removal of biomass and fertilization through goose droppings on the nitrogen fixation rates in vulnerable high arctic vegetation. Furthermore, we investigated how the different treatments affect the above-ground plant biomass production of grass and moss vegetation. In order to achieve that, five exclosures protecting vegetation against herbivory by geese were set up in an aerea that is exposed to heavy grazing by barnacle geese during summer. The exclosures recieved their treatments for grazing and fertilization experiments for four growing seasons before nitrogen fixation and plant biomass production were analyzed.

## Materials and Methods

*STUDY SITES AND EXPERIMENTAL SET-UP*

The experimental sites were located around the pond Solvannet in the vicinity of the research station Ny-Ålesund (5 m alt.) in northwestern Spitsbergen (78° 55´N, 11° 56´E), Svalbard, Norway. This location has a mean annual temperature of –6,3°C and an annual precipitation of 385 mm, which falls mostly outside the growing season (Norwegian Meteorological Institute, http://www.dnmi.no). In 1998 on 12 July five exclosures were erected in dry (Site 1), moist (Site 2 and 3) and wet vegetation (site 4 and 5), all dominated by mosses. The exclosures were built of wire gauze (145 cm × 145 cm × 50 cm) and prevented geese from grazing inside. Each exclosure were subdivided into four treatment plots separated from eachother and from the wire gauze by clearance zones of 15 cm. Five treatments were used in the experiment: simulated grazing (G), adding of goose droppings (D), a combination of simulated grazing and adding of droppings (GD), and exclosing without additional treatment (E). An area within 1 m distance from the exclosures with vegetation characterized by natural grazing (N) and sparse cover of goose droppings was also included as a sample site. The experiment was setup as a replicated block design with five replicates and five treatments with each block (including the unmanupulated treatment N outside the exclosure). All plots within a block were selected on similarity in vegetation composition. There was no selection for similarity between blocks and the blocks were at least 5 m apart from each other. To simulate grazing by geese in the exclosures, grass and dicotyls were clipped 5 mm above ground using sissors. In the treatments D and DG, 25 fresh droppings from adult geese, corresponding ca. 1.9 g of N $m^{-2}$ (Van der Wal and Loonen, 1998), were evenly distributed on the vegetation. Before adding new droppings the previous year's droppings were removed. The treatments were performed within a tree-days period around mid-July of the years 1998 to July 2002, i.e. in the period when also natural grazing takes place.

*NITROGEN FIXATION ACTIVITY*

On 19 August 2002 at all sites five samples per treatment were randomly collected with a cork borer (∅ 12 mm) and stored in glass vials at ambient temperature for about 6 h before they were assayed for nitrogen fixation activity using the acetylene reduction assay (Stewart et al., 1967). The upper 2 cm of the sample, containg the green and yellow parts of the moss plants, were placed in 12-ml glass vials and moistenized with 3 ml of tap water. The samples were pre-incubated in open vials in natural daylight at room temperature for at least 12 hours before excess of water was decanted and the vials sealed with a rubber septum. After withdrawing 1 ml of air, the same volume of acetylene was injected through the rubber septum giving a 10% acetylene (v/v) atmosphere. The samples were incubated in natural daylight at room temperature for 120 minutes before 1 ml of the head space was analysed for ethylene on a gas gas chromatograph as described previously (Zielke et al., 2002). In control experiments no ethylene production could be measured when samples were incubated in an atmosphere without acetylene.

*BIOMASS PRODUCTION*

The collection of samples for determination of the biomass production of grass and mosses was conducted on 05.08.1998 and 08.08.2002. The samples were taken randomly from each plot by cutting out turf pieces with a size of 5 × 5 cm. Within 12 h, all vegetation above the layer of dead moss or soillayer was clipped from the turfs and separated in three functional groups: moiss, grass and dicots. Grass biomass was separated in live and dead biomass. The plant material was stored in paper bags and dried in an oven at 60°C for 48 h and weighted to the nearest 0.001 g.

*ANALYSIS OF CYANOBACTERIAL COMMUNITY STRUCTURE BY T-RFLP*

In order to analyze the cyanobacterial community structure of the vegetation from all treatment plots, a 20 × 20 cm sample of the vegetation including the upper soil layer was collected using a knif.

After collection, these samples were stored in zip-lock bags at ambient temperatures for about 6 h before they became frozen and kept at -20°C until analyzed. From each sample five subsamples of about 2 g were randomly taken and analyzed following the protocols for DNA-extraction, prediction of TRFs from 16S rDNA sequences, PCR amplification of 16S rDNA, restriction digest and analysis of TRFs, data processing, and multivariate analysis as described in Zielke et al. (2003a), but only the TRF profiles obtained by the restriction enzyme *Eco*R I were used for the data processing and multivariate analysis.

*STATISTICS AND MULTIVARIATE ANALYSIS*

We used a factorial ANOVA (STATISTICA for Windows, version 6, StatSoft, Inc., 1998, Tulsa, OK, USA) to examine the effects of different treatments and experimental sites on the nitrogen fixation activity. To analyze and compare the community structures of the vegetation after different treatments multivariate analysis and analysis of similarities (ANOSIM) (Clarke, 1999) were used as described previously (Zielke et al., 2003a).

## Results

*NITROGEN FIXATION*

Nitrogen fixation activity showed a clear response to all treatments (Fig. 1) with a significant differences between treatments (Tab. 1). Treatment D resulted in the lowest nitrogen fixation activity, followed by DC, G, E, and N. The results from a Tukey's posthoc-test revealed that all treatment pairs were significant different ($P < 0.01$). Nitrogen fixation activity was also affected by the sites (Tab. 1 and Tab. 2). However, no significant interaction between site and treatment effects could be found (Tab. 1).

*TABLE 1*

*Results from factorial ANOVA (P = 0.05) using treatments and sites as factors, and ethylene production as depending variable.*

| Factor | DF | *F*-value | *P*-value |
|---|---|---|---|
| Treatment | 4 | 283,13 | > 0.001 |
| Site | 4 | 10,48 | > 0.001 |
| Treatment × site | 16 | 0,87 | 0.607 |

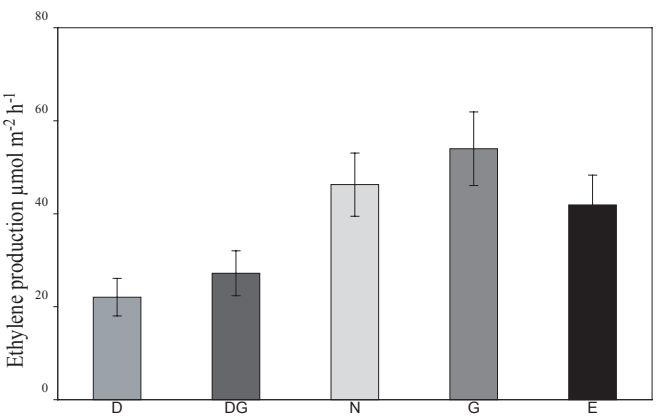


*FIGURE 1: Treatment response of ethylene production. Values are means (n = 25) ± SD.*

*TABLE 2*

*Results from Tukey's posthoc-test for significant differences between sites, using ethylene production as depending variable. Astrixes indicate significant (P < 0.05) differences between site.*

| Site | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| 2 | 0.229 | | | |
| 3 | 0.001* | 0.309 | | |
| 4 | < 0.001* | 0.015* | 0.712 | |
| 5 | < 0.001* | 0.013* | 0.686 | 0.999 |

*TABLE 3*

*Number of replicate samples (out of 25) in which of a certain TRF could be detected.*

| | bp | D | GD | N | E | G |
|---|---|---|---|---|---|---|
| CYA 792r | 54 | 16 | 18 | 16 | 20 | 18 |
| | 55 | 14 | 14 | 15 | 17 | 17 |
| | 58 | 20 | 23 | 21 | 24 | 25 |
| | 59 | 19 | 23 | 21 | 24 | 24 |
| | 61 | 16 | 15 | 14 | 16 | 12 |
| | 64 | 7 | 2 | 1 | 0 | 1 |
| | 68 | 1 | 2 | 10 | 6 | 1 |
| | 70 | 6 | 12 | 8 | 17 | 12 |
| | 74 | 13 | 20 | 16 | 23 | 18 |
| | 80 | 2 | 2 | 6 | 4 | 3 |
| | 90 | 1 | 0 | 3 | 1 | 1 |
| | 94 | 19 | 23 | 20 | 24 | 25 |
| | 95 | 19 | 23 | 19 | 24 | 25 |
| | 98 | 20 | 23 | 21 | 24 | 25 |
| | 110 | 0 | 6 | 0 | 4 | 4 |
| | 254 | 12 | 16 | 16 | 19 | 15 |
| | 255 | 3 | 4 | 4 | 10 | 8 |
| | 350 | 11 | 16 | 9 | 14 | 9 |
| | 351 | 7 | 12 | 9 | 10 | 4 |
| | 353 | 18 | 23 | 21 | 23 | 23 |
| | 354 | 19 | 20 | 19 | 21 | 22 |
| CYA 432f | 51 | 8 | 4 | 2 | 2 | 4 |
| | 54 | 8 | 5 | 4 | 5 | 7 |
| | 56 | 1 | 3 | 2 | 6 | 6 |
| | 57 | 14 | 11 | 13 | 8 | 11 |
| | 58 | 19 | 23 | 19 | 24 | 23 |
| | 59 | 18 | 21 | 20 | 19 | 24 |
| | 62 | 20 | 23 | 21 | 24 | 25 |
| | 68 | 13 | 9 | 5 | 9 | 3 |
| | 70 | 5 | 10 | 14 | 14 | 15 |
| | 75 | 3 | 9 | 9 | 8 | 9 |
| | 80 | 4 | 6 | 6 | 5 | 3 |
| | 82 | 11 | 18 | 13 | 20 | 16 |
| | 86 | 6 | 10 | 11 | 16 | 13 |
| | 90 | 2 | 3 | 6 | 9 | 8 |
| | 95 | 8 | 9 | 9 | 9 | 6 |
| | 99 | 17 | 23 | 19 | 24 | 24 |
| | 100 | 16 | 20 | 20 | 23 | 22 |
| | 105 | 1 | 0 | 2 | 6 | 4 |
| | 111 | 0 | 7 | 0 | 6 | 3 |
| | 126 | 18 | 19 | 20 | 24 | 24 |
| | 136 | 2 | 4 | 7 | 10 | 8 |
| | 139 | 12 | 13 | 19 | 21 | 23 |
| | 166 | 10 | 13 | 8 | 12 | 1 |
| | 168 | 12 | 20 | 17 | 21 | 17 |
| | 177 | 16 | 17 | 20 | 24 | 22 |
| | 252 | 19 | 23 | 21 | 24 | 24 |
| | 254 | 17 | 19 | 17 | 17 | 16 |
| | 255 | 16 | 21 | 20 | 22 | 20 |
| | 272 | 2 | 2 | 0 | 1 | 0 |
| | 352 | 8 | 6 | 7 | 8 | 6 |
| | 354 | 18 | 19 | 18 | 23 | 23 |

*CYANOBACTERIAL COMMUNITY STRUCTURE*

The results from our analysis of cyanobacterial community structures in moss-dominated vegetation revealed a high diversity of epiphytic cyanobacteria. Table 3 shows the pattern of distribution

of the TRFs from restriction digests of PCR-products of both primers. In total 21 and 31 different TRFs could be obtained using *Eco*R I digest products of CYA 792r-amplicons and CYA 432f-amplicons, respectively. The majority of the TRFs, i.e. 90% of the ones obtained from CYA 432f-amplicons and 86% of the ones obtained from CYA 792r-amplicons, were present in samples from all treatments. On the other hand no TRFs appeared to be treatment specific, i.e. were found solely in samples of one type of treatment. An ANOSIM showed significant differences between the TRF profiles ($P < 0.001$), but also relative high variances within treatments (groups) compared to inter-group variances ($R = 0.055$).

*BIOMASS PRODUCTION*

While the moss biomass outside the exclosure (N) did not significantly alter, the moss biomass for the four other treatments responded with a clear increase (Fig. 2). The increase was highest for the treatments with added droppings, i.e. D and DG, namely about 230 and 160%, respectively. The biomass of the moss vegetation with treatment E and G inceased both with about 77%.

In case of the grass biomass for treatments D, DG, and G resulted in an 150, 50, and 100% increase of biomass, respectively (Fig. 3), while the biomass of grass in treatment E only increased by 10%.However, the biomass of the grass vegetation outside the exclosures (N) dropped to zero, that means no grass plants could be found any longer in 2002.

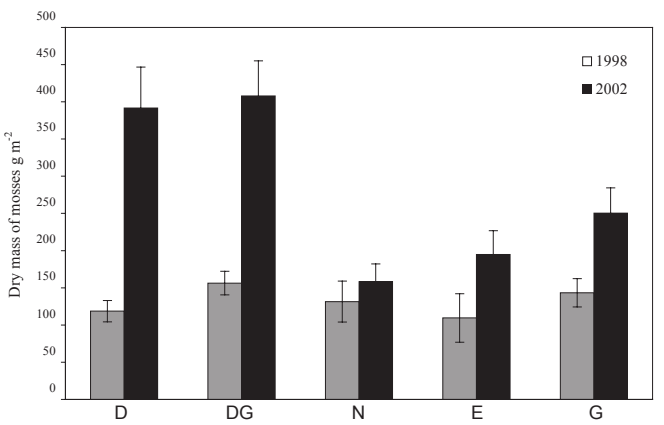


*FIGURE 2: Biomass of moss in response to four years of experimental treatment. Values are means (n = 5) ± SEM.*

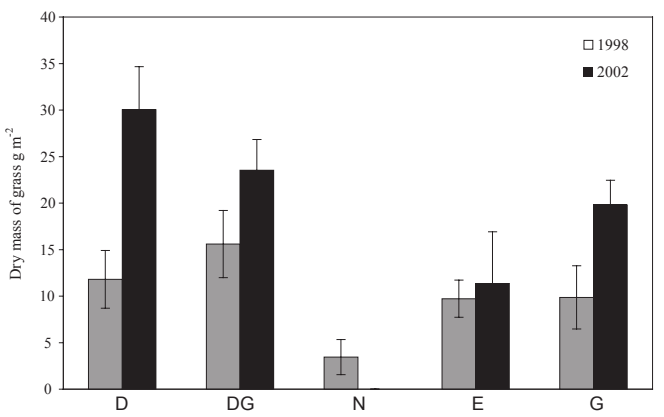


*FIGURE 3: Biomass of grass in response to four years of experimental treatment. Values are means (n = 5) ± SEM.*

## Discussion

*NITROGEN FIXATION*

The results from the ANOVA (Tab. 1) show that cyanobacterial nitrogen fixation activity became significantly affected by the treatments. Although the sites had an effect on the rates of nitrogen fixation (Tab. 1) there are no significant treatment×site interactions, i.e. the effects of the sites are the same for all treatments. However, the differences between the sites (Tab. 2) may be explained by the corresponding differences in their water status.

Treatment E of our experimental setup has to be regarded as the pristine state of the vegetation and nitrogen fixation activity. The activity clearly declines when high amounts of nitrogen in form of goose droppings (D and DG) is added to the soil/vegetation. This is consistent with findings of other studies where nitrogen fixation activity of cyanobacteria was reduced due to enhanced levels of organic or inorganic nitrogen compounds (reviewed in Flores and Herrero, 1994; Solheim et al., 1996) which mediate an inhibition of heterocyst differentiation (Wolk et al., 1994) and *nif* gene expression (Meeks et al., 1983) when assimilated by cyanobacteria. The opposite effect is found in treatment G where the removal of nitrogen from the system had a stimulating effect on the nitrogen fixation activity. The simulated grazing caused less dead plant material that otherwise had been decomposed and released as nitrogen compounds. This positive effect may also explain the higher nitrogen fixation rates in treatment DG *vs*. D. The nitrogen fixation rates of samples taken outside the exclosures (N) are lower than in treatment G even if the natural grazing by geese is more intensive than achieved by clipping. This may be explained by the fact that the net nitrogen removal is lower in N than in G due to an increased nitrogen availability caused by (i) addition of nitrogen by goose feces, and (ii) by enhanced litter incorporation into soil, which in turn results in higher rates of decomposition and mineralization of the dead plant material (Zacheis et al., 2002).

*CYANOBACTERIAL COMMUNITY STRUCTURE*

In a previous studies Zielke et al. (2003a; 2003b) used the same molecular approach to characterize cyanobacterial communities in moss-dominated arctic vegetation. Using the same combination of primer and restriction enzyme as in the present study, they found 31 and 37 different operational taxonomic units (OTU). This is in the same range as our findings and suggests that the species richness of cyanobacteria is not affected by vegetation removal and/or goose dropping addition. Thus, changes in the rates of nitrogen fixation in the vegetation layer is not caused by a shift in the composition of the cyanobacterial communities to more non- or less nitrogen-fixing species, but by a down-regulating of the nitrogen fixation process of the cyanobacteria - either on a physiological or a genetic level (Meeks et al., 1983; Wolk et al., 1994). This becomes confirmed by an ANOSIM. Although the low *P*-value of the ANOSIM suggests significant treatment-specific differences between the cyanobacterial community structures, the very low *R*-value reveals that these differences may be caused by higher within-group variances compared to the inter-group variances. However, due to the high number of replicates and taxa (TRFs) even very small differences in the profiles become identified by the ANOSIM (Clarke, 1999) and may account for significant inter-group differences.

*BIOMASS PRODUCTION*

The high input of nitrogen, phosphorus and other nutrients (for details see (Van der Wal and Loonen, 1998)) through added goose droppings in treatment D and DG clearly resulted in an increased

above-ground biomass of grass plants and mosses (Fig. 2 and 3). This increase is obviously caused by improved primary production due to a higher availability of otherwise strongly limited nutrients. However, the increase in moss biomass for the two treatments was about 100% higher than corresponding values for grass. This can be explained by the ability of mosses to acquire effectively nutrients through their entire surface because they lack a cutile (Brown and Bates, 1990), which allows the mosses to take up soluble nutrients before they reach the grass roots in the lower parts of the vegetation layer. Furthermore, in treatment E, which involved only prevention of grazing, the moss plants responded with a 77% increase of the biomass, while the grass biomass was elevated by 10%. This dissimilarity may have its reason in the fact that the majority of the mosses habor epiphytic cyanobacteria that additionally 'provide' their hosts with fixed nitrogen. This also shows that even under harsh environmental arctic conditions the vegetation can slightly increase its biomass as long as it is not disturbed. Nevertheless, the results from treatment G reveal that under moderate removal of biomass, as occured by the simulated grazing, the vegetation is even able to increase the plant biomass production. However, since in this experiment no nutrients were added, the enhanced primary production has to go to the expense of limited available soil nutrients, and thus finally may not be sustainable. There was also an obvious difference between the biomass production of mosses and grass at sites with natural grazing (N). Due to the geese's preference for grass as forage plants the grazing pressure for mosses was not so high as for grass. The high number of geese during the study period led to a severe grazing pressure in the experimental area, and consequently to a state without any grass shoots, while the moss vegetation could cope with that and kept its biomass on a pre-study level.

In arctic areas grazing by geese and their input of nutrients by feces have significant effects on the the terrestrial primary production, including plant biomass production and nitrogen fixation. The effects may be sometimes in oposite directions, that means stimulating or inhibitory depending on the intensity of the affecting factor and the process affected. Nitrogen fixation, a key process in the ecosystem, is stimulated by grazing, while it is reduced by the nitrogen compounds stored in goose droppings, which in turn are an important contributor of nutrients for plants. This shows that there exists a fragile balance between these processes and ecological functions. In addition, several other factors, such as climate change, have to be included to get a better understanding of this vulnerable ecosystem.

## Acknowledgements

The authors thanks Kings Bay AS, Nork Polar Institutt and Ocean Wide Expeditions for logistic support. Kings Bay AS and Ny-Ålesund Science Managers Committee (NySMAC) for permission to build the exclosures. Julia Stahl and Peter Tolsma for help setting up the experiment. The work was partly supported by grants for M.Z. from the Roald Amundsen Centre for Arctic Research and the Norwegian Committee on Polar Research.

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