Grazing by captive Barnacle geese affects graminoid growth and productivity on Svalbard

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Abstract: Migratory geese breed in Svalbard in summer and return to Western Europe for the winter, feeding on wetlands and agricultural fields. Recent changes in climate, land use and the implementation of protective measures dramatically improved the birds' ability to survive the winter, increasing population sizes and thus the potential grazing impact on Svalbard. This study measured live leaf length and aboveground productivity of *Alopecurus borealis* and *Dupontia fisheri*, widespread forage grasses on Svalbard, in order to make a quantitative assessment of the short term effects of different intensities of goose grazing. In addition we wanted to establish whether warming could enhance graminoid growth and regenerative capacity of grazed grasses. We carried out a factorial experiment of grazing (control, normal and high grazing pressure) using captive wild barnacle geese and temperature manipulation using open top chambers (OTCs) in a mesic and wet habitat in Adventdalen, Svalbard (78°N, 16°E), following the growth of individual tillers before grazing and up until 20 days after grazing. OTCs enhanced temperatures and growth rates for *Alopecurus* in the mesic habitat, but slightly decreased belowground temperatures and early season growth for *Dupontia* in the wet habitat. Grazing stimulated growth rates resulting in increased cumulative leaf length production. The strength of response was greater for *Alopecurus* than *Dupontia*. We suggest that nutrients released by goose faeces were taken up by *Alopecurus* thus enhancing their growth rates, but that the thick layer of mosses prevented the addition of faeces from benefitting *Dupontia* as much.

key words: goose herbivory, climatic warming, compensation, High Arctic, tundra grasses

1. Introduction

Herbivores can affect vegetation in profound ways through selective removal of biomass, grazing and trampling and nutrient enrichment (*e.g.* McNaughton, 1979; Cooper and Wookey, 2001) and thus change species composition, resource allocation and phenology and modify growth rates (Jefferies *et al.*, 1992). This can be especially important in fragile arctic environments where soils are thin, plants are small, vegetation cover may be patchy and slow to establish. Tundra vegetation is generally slow to recover from damage inflicted by grazing because of a low net primary production and a short growing season (Gauthier *et al.*, 1995; Bazely and Jefferies, 1997; AMAP, 1998).

Grazing impact on plant production depends on the part of the plant removed and the intensity and timing of grazing (Cargill and Jefferies, 1984b; Jefferies, 1988; Kerbes *et al*., 1990; Hik *et al*., 1991). Graminoids have earlier growth than herbs and shrubs and are nutrient rich and so are preferentially grazed by geese early in the season (Prop and Deerenberg, 1991; Gadallah and Jefferies, 1995). Geese are important grazers in arctic ecosystems, and moderate grazing can enhance primary production (Cargill and Jefferies, 1984b; Hik and Jefferies, 1990). However, decreases in plant production occur when the plants capacity to recover is exceeded (Gauthier *et al*., 1995). Rapid increases in lesser snow goose numbers in La Pérouse Bay in Low-Arctic Canada, largely due to human activities (Bazely and Jefferies, 1997), led to extremely high grazing pressures and a degradation of the vegetation (Jefferies, 1988; Jano *et al*., 1998). Grubbing, in which the belowground parts of the plant are removed by geese, as well as trampling destroys plant meristems (Iacobelli and Jefferies, 1991; Jefferies and Bryant, 1995), thus reducing the speed at which plants can respond (Zellmer *et al*., 1993). Furthermore, trampling reduces the thickness and thus the insulating effect of the moss layer, allowing soil to warm (Van der Wal *et al*., 2001; Van der Wal and Brooker, 2004), and also affects the competition for available nutrients between graminoids and mosses (Gauthier *et al*., 1995; Van der Wal and Brooker, 2004).

Since geese are migratory birds, breeding in the Arctic in summer and returning to temperate locations for the winter, their population size is not regulated as much by density dependence in the arctic areas as non-migratory herbivores (Drent and Mehlum, 1998; Aanes *et al*., 2000). Differing carrying capacities of overwintering (southern) areas and summer breeding grounds (arctic) have resulted in increased grazing pressure in several arctic areas (Reed, 1990; Drent and Mehlum, 1998; Jano *et al*., 1998). Changes in European land use policies and milder winters have led to increased food availability in overwintering areas in Europe (Prop and Black, 1998), and bird protection measures have reduced the numbers of geese hunted (Bø *et al*., 1998; Drent and Mehlum, 1998). As a result, populations of all three goose species breeding on Svalbard have increased dramatically in size (3, 3 and 30-fold, Pink-foot goose *Anser brachyrhynchus*, light bellied Brent goose *Branta bernicla hrota*, and Barnacle goose *Branta leucopsis*, respectively) in the last 50 years (Madsen *et al*., 1998). This has led to a concern regarding the vegetation on Svalbard and its interaction with increasing goose numbers. Even with less severe grazing pressure than experienced in Canada, impacts on individual plant production, community dynamics and vegetation structure are important for areas around lakes and tundras and associated wildlife (Loonen and Solheim, 1998). Future climate conditions in the Arctic are predicted to be warmer than today (Houghton *et al*., 2001; ACIA, 2004). Responses to warming treatments in mesic or wet habitats in various arctic areas generally show an enhanced growth of graminoids (Arft *et al*., 1999). It is therefore possible that changes in climatic conditions may interact with graminoid responses to grazing, and so should be taken into account when trying to predict the future impact of increasing geese populations on arctic tundra.

The objective of this study was to measure live leaf length and aboveground productivity of *Alopecurus borealis* and *Dupontia fisheri*, widespread forage grasses on Svalbard, and to make a quantitative assessment of the short term effects of different

intensities of goose grazing. In addition we wanted to find out whether warming could enhance graminoid growth and regenerative capacity of grazed grasses. Previous studies of goose grazing on the growth of arctic plants have either used captive goslings (*e.g.* Zellmer *et al.*, 1993) or comparisons of growth inside and outside of exclosures in areas of natural grazing by wild adult geese (Bazely and Jefferies, 1986; Gauthier *et al.*, 1995; Bakker and Loonen, 1998). Our experiment is the first to use wild adult geese in the field in the Arctic with controlled duration of access to plants on experimental plots. In addition we factorially combined grazing of different intensities with a temperature manipulation treatment.

2. Methods

2.1. Site description

The experiment was carried out in Adventdalen, 15 km east of Longyearbyen, Svalbard (78°N, 16°E) in two habitats representative of those used by geese in summer; a mesic tundra vegetation with dwarf shrubs, forbs and graminoids (dominant species, most abundant first, vascular plants then mosses: *Salix polaris*, *Bistorta vivipara*, *Alopecurus borealis*, *Dryas octopetala*, *Hylocomium splendens*, *Tomentypnum nitens* and *Sanionia uncinata*, live moss depth *c*. 10 mm) and a wet moss-dominated vegetation with horsetail and graminoids (*Equisetum arvense*, *Dupontia fisheri*, *Eriophorum scheuchzeri*, *Calamagrostis stricta*, *Carex subspathacea* and *Calliergon richardsonii*, live moss depth *c*. 75 mm). The wet habitat was at the side of a stream transporting meltwater away from a small glacier, Foxfønna, and as such, had a constant throughput of cold water. *Alopecurus* grew in the mesic habitat at an average shoot density of $609 \pm 44/m^2$ whereas *Dupontia* in the wet habitat had a density of $1452 \pm 161/m^2$. Geese graze in this area early in spring before moving on to their summer breeding grounds and also in autumn before their migration south. Reindeer are present in the area year-round, but were kept out of our experiments by fences.

2.2. Experimental design and measurements

Temperature manipulation (two levels) and grazing treatments (three levels) were applied to plots of 2×2 m in a factorial randomised block design, with five replicated blocks in each habitat. Plexiglass open top chambers (OTCs) were used as small greenhouses to passively increase the temperature of the air and ground. They were placed on the plots soon after snowmelt (17 June 2003) and left in place thereafter, only being removed for the application of the grazing treatments, (maximum of 12 hours in a 6 week period). OTCs increased July mean temperatures at the surface during the afternoons (Fig. 1a and 1b). They also raised the soil temperatures of the mesic site during the night but had a slight cooling effect belowground at the wet site. Temperature sums for 6–26 July 2003 (Table 1) were higher in the OTCs than the ambient plots at the surface for both sites and in the mesic site. At the wet site the belowground temperature sums were lower in the OTCs than in the ambient plots.

Wild adult Barnacle geese used for the grazing treatments were captured in Ny-Ålesund (Svalbard) in June and kept in cages of 2×2 m with access to natural vegetation in the field area during the experimental period and subsequently released.
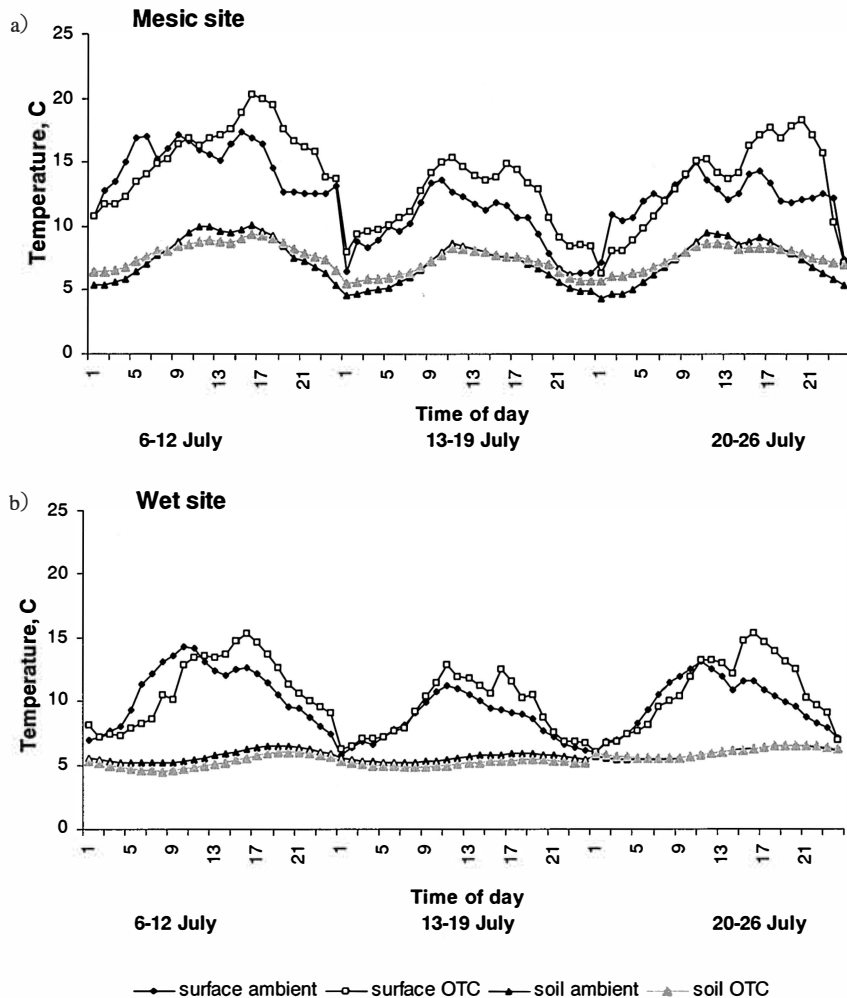
Fig. 1. *Diurnal surface and soil temperature for ambient and OTC plots for 6–26 July 2003, averaged for each of three weeks. Temperatures recorded hourly by 'Tinytag' loggers (8 in mesic site, 6 in wet site). Below ground measurements were taken at the moss-soil interface, approx 7 cm depth. a) mesic site, b) wet site. Calculated from raw data collected by S. Sjögersten.*

Before grazing the geese were starved for two hours. During a grazing treatment, two geese were put on the experimental plots for one or five hours, to simulate 'natural' and 'high' grazing pressure. The grazing pressure created with captive geese on experimental plots for one hour was similar to that observed in natural systems on Svalbard for both mesic and wet habitats, and the 5 hour treatment achieved a grazing pressure much higher than that observed experimentally in one hour or in natural systems on Svalbard (Cooper *et al*., 2004). The grazing treatments took place 2–18 July 2003.

Within each 2×2 m plot, five plants were randomly chosen and labelled with a 3 mm high plastic collar around the base. The live and dead length of all leaves of marked

Table 1. *Temperature sums (℃) for 6–26 July 2003. Temperatures recorded hourly by 'Tinytag' loggers (8 in mesic site, 6 in wet site). Below ground measurements were taken at the moss-soil interface, approx 7 cm depth. a) mesic site, b) wet site. Calculated from raw data collected by S. Sjögersten.*

	Ambient	OTC
Mesic site		
Surface	258	286
Below ground	151	157
Wet site		
Surface	202	216
Below ground	121	115

plants were measured immediately before and after the grazing treatments were applied and at 10 and 8–9 day intervals (*Alopecurus* and *Dupontia*, respectively) up to 20 and 17 days after grazing to determine grazing responses. To examine the effect of the length of time the geese had access to the plants on the length grazed and subsequent growth responses, a grazing gradient was established in each habitat with plots exposed to grazing for different lengths of time (0, 0.5, 2, 3, 5 and 7 hours in both sites, and additionally 4 hours in the wet site), with grazing carried out during 2–18 July 2003. In each of these plots, ten plants were marked and measured as in the factorial experiment. Cumulative leaf length production was calculated as the sum of the total length produced by all leaves at each time of measurement (including both green and senesced tissue produced) in addition to amount of material removed by grazing. Growth rate was calculated as the change in cumulative leaf production between the day after grazing and the last day of measurement over time.

2.3. Statistical analysis

Statistical analyses were carried out using the program 'R' (R Development Core Team, 2004). The mean values of 5 marked shoots per plot immediately before grazing and 17 and 20 days after grazing (*Dupontia* and *Alopecurus*, respectively) were used. Grazing (3 levels) and OTC (2 levels) were used as fixed factors and block as a random factor in a two way ANOVA with interactions. The response variables were total live leaf length per plant (before grazing, immediately after, and 20 days after grazing for *Alopecurus* (17 days after for *Dupontia*)—separate analysis was carried out for the 3 occasions), length grazed, growth rate over the experimental period following grazing and cumulative leaf length production during the whole measurement period. Post-hoc multiple comparisons were performed using Tukey's test to find significant differences between means with significance level set at $p < 0.05$. Responses to number of hours of grazing treatment and to length grazed were tested by regression analysis using data from individual plants in the grazing gradient (70 plants in the mesic site, 80 plants in the wet site). Regression analyses (growth rate and leaf production against grazed length) were also carried out on data from all grazed plants from ambient plots (85 *Alopecurus* and 66 *Dupontia*).

3. Results

Before grazing, *Alopecurus* plants growing inside the OTCs had longer total live leaf lengths than those in the ambient plots ($F_{1,20}=6.39$, $p=0.020$) (Fig. 2a), whereas for *Dupontia*, smaller plants were measured within the OTCs than in the ambient plots ($F_{1,20}=5.119$, $p=0.035$) (Fig. 2b).   The final live length of *Alopecurus* measured 20 days after grazing (Fig. 2a) showed significant effects due to OTC ($F_{1,20}=7.90$, $p=0.011$) and
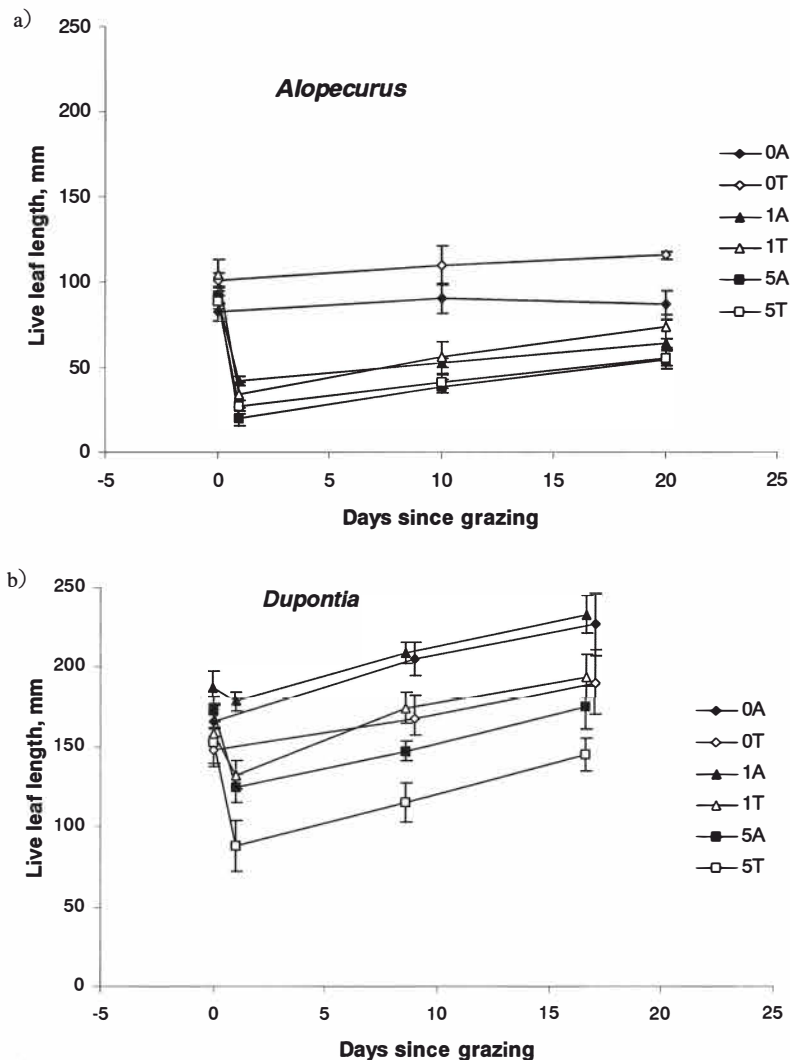

Fig. 2.   *Live leaf lengths of the grasses in response to the OTC treatment (A=ambient; T=OTC) and three intensities of grazing (0=no grazing; 1=one hour of grazing; 5=five hours of grazing) by Barnacle geese, Adventdalen, Svalbard, 2003.*
a) Alopecurus borealis, from the day before grazing until 20 days after grazing.
b) Dupontia fisheri, from the day before grazing until 17 days after grazing.

grazing treatment ($F_{2,20}=34.01$, $p<0.001$), but no interaction. Post-hoc Tukey's test revealed that plants grazed for 5 hours had significantly lower final live length than the ungrazed plants. There was a difference between 1hr grazed and ungrazed plant length only in the warmed treatments. The final live length of *Dupontia* measured 17 days after grazing (Fig. 2b) showed significant negative effects due to OTC ($F_{1,20}=6.51$, $p=0.019$) and grazing treatment ($F_{2,20}=11.43$, $p<0.001$), and no interaction. Post-hoc Tukey's test revealed that plants grazed for 5 hours had a significantly lower final leaf length than either the plants grazed for 1 hour or the ungrazed plants.

On average, 64 mm (67%) of live *Alopecurus* was removed by grazing; this value
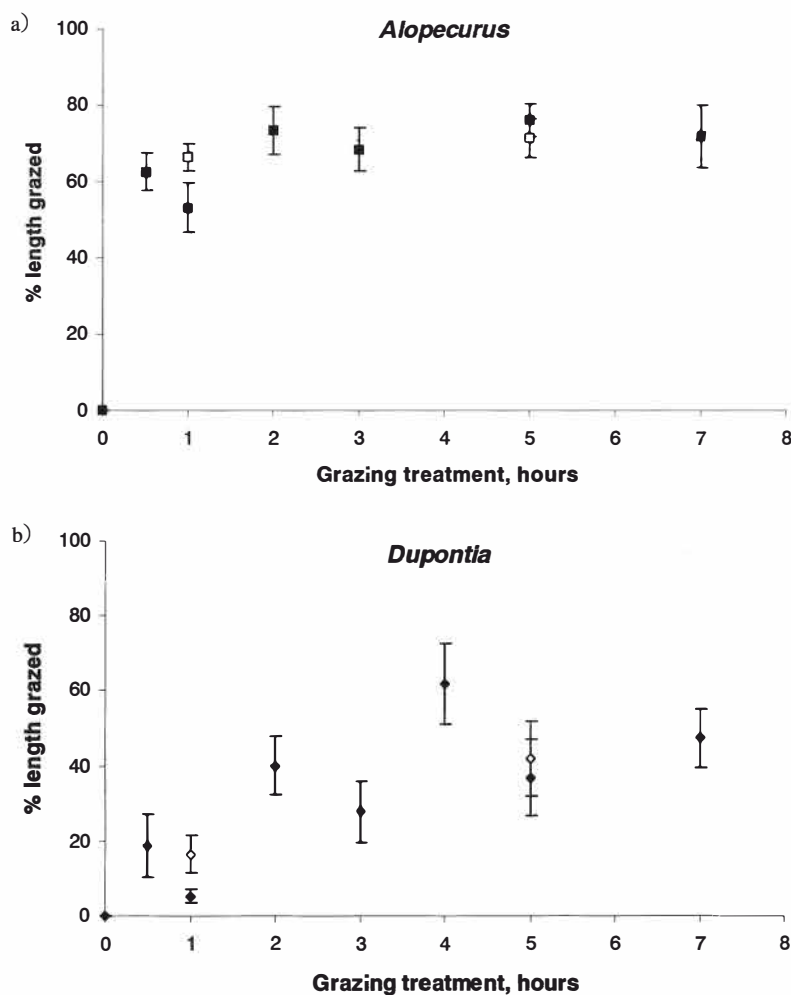

Fig. 3. *Percentage of live leaf length grazed by Barnacle geese in the grazing gradient in Adventdalen, Svalbard, 2003. Means and standard errors of 5 plots are presented (5 plants per plot) for 0, 1 and 5 hours of goose grazing and means of 10 plants are shown for a) 0.5, 2, 3, 7 hours grazing in Alopecurus borealis in the mesic site, and b) 0.5, 2, 3, 4, 7 hours grazing in Dupontia fisheri in the wet site. Filled symbols: plants in ambient plots, open symbols: plants in OTC plots.*

was not dependent on OTC or grazing treatment, and data from the grazing gradient showed only a weak positive relationship between the number of hours geese were on the plot and the amount grazed ($F_{1,68}$=9.73, p=0.003, R^2=0.13). There was a better relationship between percentage of leaf length grazed than absolute amount grazed in mm- and the hours of grazing ($F_{1,68}$=19.08, p<0.0001, R^2=0.22, Fig. 3a). For *Dupontia*, the length grazed was independent of OTC treatment but differed between grazing levels ($F_{1,12}$=11.11, p=0.006) so that significantly more was removed in 5 hours than in 1 hour (61 mm (39%) and 18 mm (11%), respectively). The length of leaf grazed was weakly related to hours of grazing ($F_{1,78}$=10.23, p=0.002, R^2=0.12), but there was a better fit between percentage of plant grazed and hours of grazing ($F_{1,78}$=28.62, p<0.0001, R^2=0.27, Fig. 3b).

The growth rate of *Alopecurus* (Fig. 4) was enhanced by grazing ($F_{2,20}$=16.71, p<0.001) but not by OTC and there were no significant interactions. There was no significant difference in growth rate between plants grazed for one or five hours, but data from the gradient showed a weak positive relationship between growth rate and hours of grazing ($F_{1,68}$=11.25, p=0.001 R^2=0.14). Using data from the grazing gradient we found that growth rates increased with increasing length grazed ($F_{1,68}$=79.88, p<0.0001, R^2=0.54). Figure 6a shows the growth rates of the grazed plants only from all ambient plots (n=85, $F_{1,83}$=40.02, p<0.0001, R^2=0.33).

There was no significant effect of either OTC or grazing treatment on the growth rate of *Dupontia* (Fig. 4), and no relationship with hours of grazing. Data from the grazing gradient showed no relationship with amount grazed ($F_{1,78}$=3.20, p=0.078, R^2=0.04). However, using grazed plants only from all ambient plots (n=66), a weak but significant positive relationship was found between growth rate and amount grazed ($F_{1,64}$=25.82, p<0.0001, R^2=0.29, Fig. 6b).
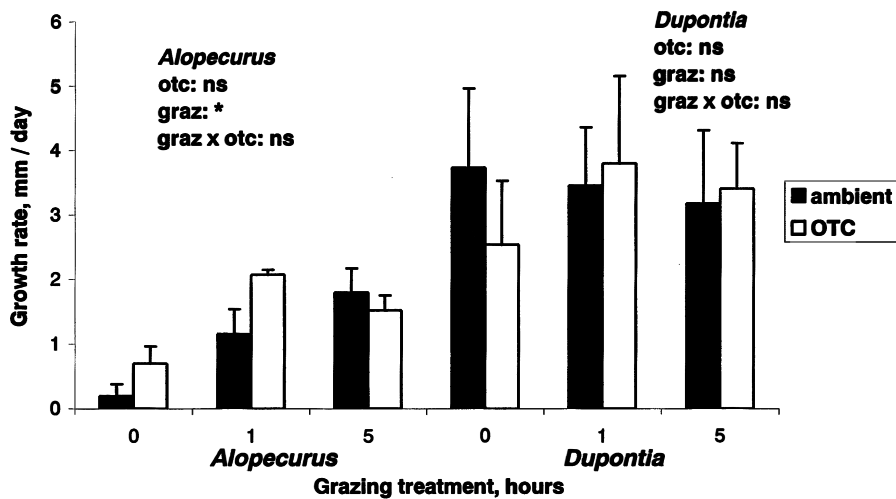

Fig. 4. Growth rate (mm/day) for Alopecurus borealis, mesic site and Dupontia fisheri, wet site, 2003. 0, 1, 5 refer to the duration of grazing treatment (hours). Means and standard errors of 5 plots are presented, 5 plants per plot.
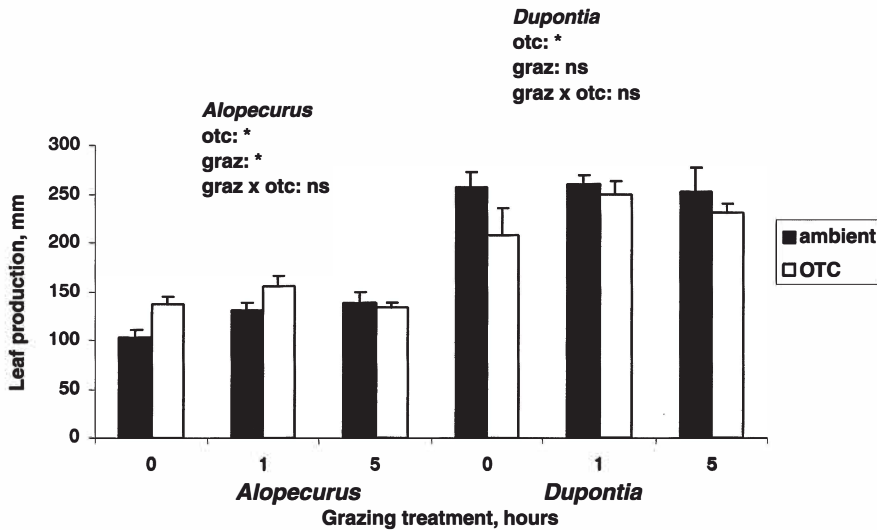
Fig. 5. *Cumulative leaf length production (mm) for Alopecurus borealis, mesic site and Dupontia fisheri, wet site. 0, 1, 5 refer to the duration of grazing treatment (hours). Means and standard error of 5 plots are presented, 5 plants per plot.*

The leaf length production of *Alopecurus* (Fig. 5) was enhanced by OTC ($F_{1,20}=$ 6.41, $p=0.020$) and grazing ($F_{2,20}=3.64$, $p=0.045$), and there were no significant interactions. Leaf length production had a weak positive relationship with hours of grazing ($F_{1,68}=5.06$, $p=0.03$, $R^2=0.07$) but a strong positive relationship with length grazed ($F_{1,68}=210$, $p<0.001$, $R^2=0.76$). Figure 7a shows the leaf length production of the grazed plants only from all ambient plots ($n=85$, $F_{1,83}=212$, $p<0.0001$, $R^2=0.72$).

Leaf length production of *Dupontia* (Fig. 5) was lower in the plots with OTCs ($F_{1,20}=4.75$, $p=0.041$) but there was no effect of grazing treatment and no interactions. Leaf production had a weak negative relationship with hours of grazing ($F_{1,78}=11.58$, $p=$ 0.001, $R^2=0.13$), and a weak but significant positive relationship with amount grazed ($F_{1,78}=16.18$, $p=0.0001$, $R^2=0.17$). Figure 7b shows the relationship with the grazed plants only from all ambient plots ($n=66$, $F_{1,64}=40.02$, $p<0.0001$, $R^2=0.43$).

In summary:

Alopecurus in OTCs were larger early in the season than plants in ambient plots, but growth rate was not further enhanced by warming in the rest of the season. Grazing stimulated *Alopecurus* growth rate resulting in increased leaf length production.

Dupontia grown in OTCs were smaller compared with plants from ambient plots early in the season, but thereafter OTCs did not affect the growth rate. The growth rate was slightly enhanced by grazing, resulting in increased production of the most heavily grazed plants.

4. Discussion

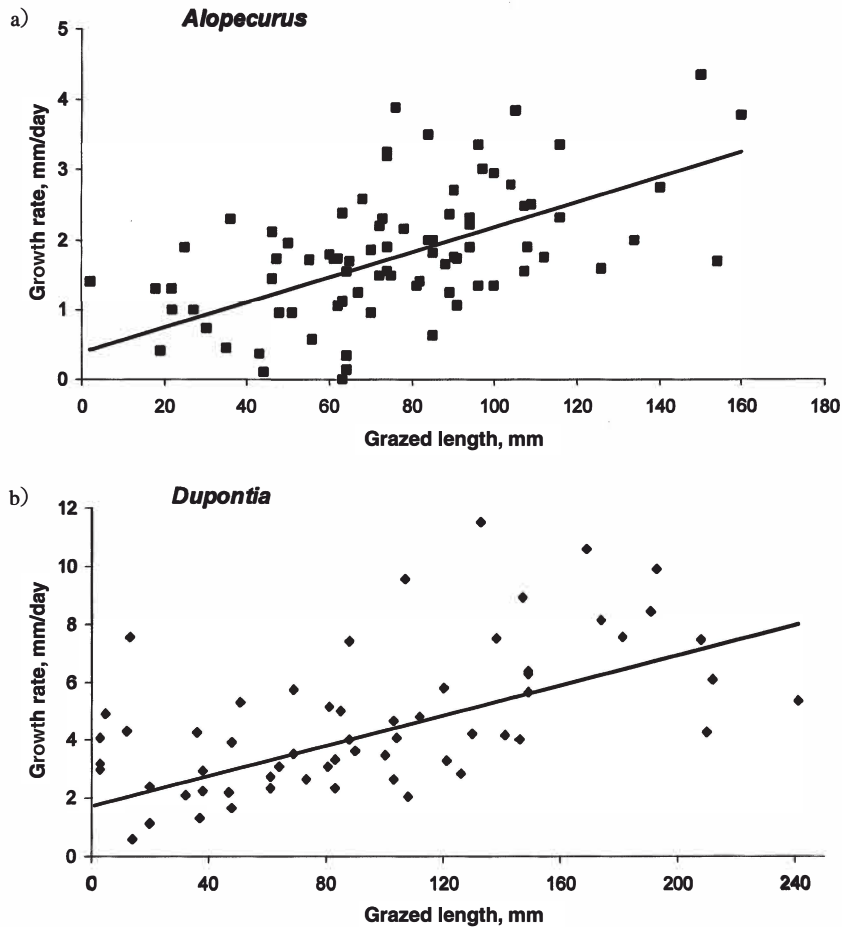This experiment is the first one in which experimental goose grazing has been

Fig. 6.   Relationship between growth rate (mm/day) and length of leaf grazed (mm) by Barnacle geese
for a) Alopecurus borealis, and b) Dupontia fisheri, 2003 in plots with ambient temperature.
a) $y=0.018x+0.40$, b) $y=0.026x+1.74$: NB note the different scales on the axes.

performed by captive wild adult geese in the field in the Arctic in combination with
temperature manipulations, and as such has enabled us to examine responses of tundra
plants in detail.   Inadvertently the OTCs in the wet habitat cooled the ground slightly;
since they were not ventilated at the base they may have functioned as a cold air trap.
Such OTC-induced belowground cooling has also been observed in mesic moss tundra in
Iceland where OTCs were ventilated (Jónsdóttir et al., 2005).   In our experiment this
resulted in plants with a lower total live leaf length and a lower cumulative leaf
production than in the ambient conditions.   However, in both habitats, we could
measure the effect of differential soil and surface temperature conditions on the growth
of plants in factorial combination with grazing of different intensities.   Within a month
following snowmelt, there were significant differences in total live leaf length in both
species due to OTC effect, and these differences were maintained throughout the
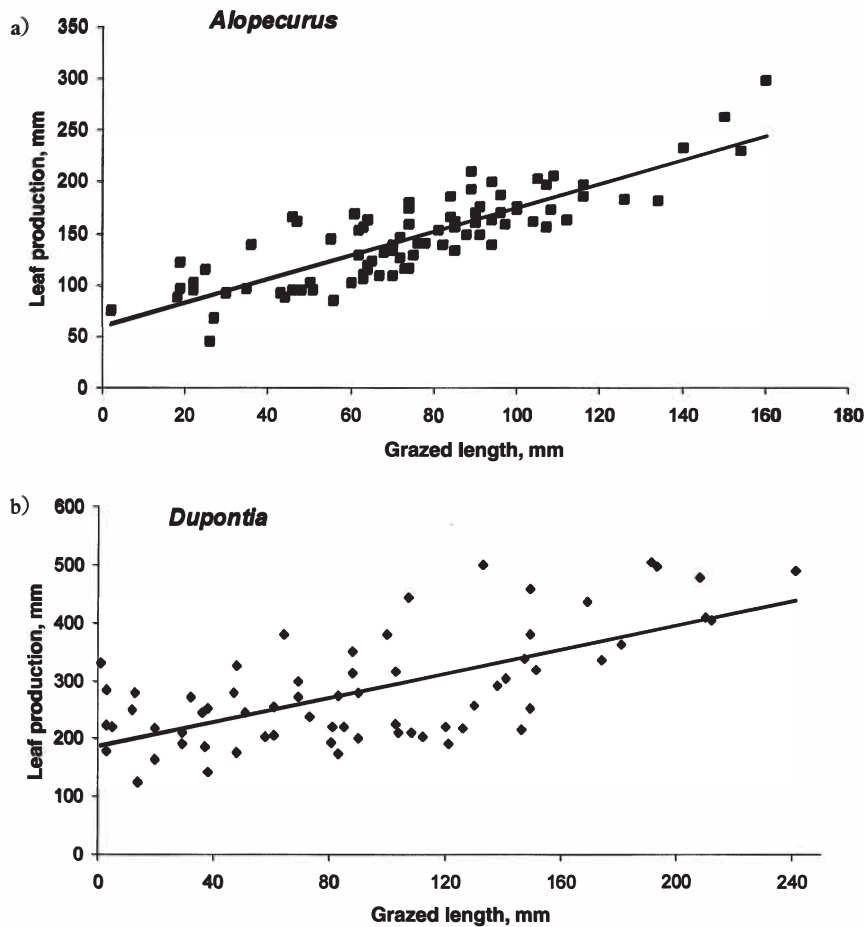
Fig. 7. Relationship between cumulative leaf length production (mm) and length of leaf grazed (mm) by Barnacle geese for a) Alopecurus borealis, and b) Dupontia fisheri, 2003 in plots with ambient temparature. a) $y = 1.153x + 60.48$, b) $y = 1.039x + 188.19$: NB note the different scales on the axes.

experimental period. In both cases the warmer belowground treatment produced larger plants. This is in keeping with findings elsewhere in the Arctic; warmer temperatures enhance metabolism and growth (Arft et al., 1999). At the end of the measurements (17–20 days after grazing), plants of both species grazed for 5 hours had significantly lower live leaf length than the ungrazed plants, and for Dupontia this was also lower than the plants in the 1 hour grazing treatment. Reductions in plant size brought about by the overgrazing treatment were therefore still evident 2–3 weeks after the time of grazing, which would have important implications for either the geese or other herbivores in the area. The plant growth response here did not show a regrowth to match or exceed the ungrazed plants as reported for Carex subspathacea or Puccinellia (respectively, measured 44 days after grazing) by Zellmer et al. (1993). The lack of

interactions between grazing intensity and warming treatment suggest no synergistic effects.

The differential lengths grazed in the 1 and 5 hour grazing treatments for the two species is at least partly explained by a higher shoot density, thus higher availability of *Dupontia* than *Alopecurus*. Counts of shoot densities before and after grazing (Cooper and Jónsdóttir, unpublished data) show that within 3 hours, 100% of the *Alopecurus* shoots present in a plot were grazed, but it took 7 hours before all *Dupontia* shoots were grazed.

The cumulative production was enhanced for both species by warmer belowground conditions (*i.e.* inside the OTC for *Alopecurus* and in the ambient plots for *Dupontia*). Grazing enhanced leaf growth rate and cumulative leaf production. *Alopecurus* was strongly stimulated by grazing and thus clearly overcompensated. Interpretation of our data on a treatment basis suggests that *Dupontia* had no growth rate or cumulative leaf production response to grazing treatment. However, availability and selective grazing by geese must also be considered. Individual plant responses showed growth and production were enhanced by grazing. Enhanced regrowth as a response to grazing has been classified by Belsky (1986) using the terms 'compensation, over- and under-compensation', so that overcompensation occurs when the production of grazed plants exceeds that of ungrazed plants. Herbivore-optimization models predict that the levels of overcompensation depends on the intensity of grazing (McNaughton, 1979; Hik and Jefferies, 1990). In our experiment, *Alopecurus* strongly overcompensated (grazed plants had higher production than ungrazed) and *Dupontia* showed some overcompensation.

Overcompensation was found in several goose grazing studies in the Arctic (Cargill and Jefferies, 1984a; Kotanen and Jefferies, 1987; Bazely and Jefferies 1989; Hik and Jefferies, 1990) although this may have been overestimated in some studies (Bakker and Loonen, 1998). Wegener and Odasz (1997) reported overcompensation in *Dupontia fisheri* following simulated grazing under laboratory conditions, and a high grazing tolerance was reported for this species in the Alaskan Arctic (Tieszen, 1978; Brown *et al.*, 1980). This positive effect of grazing was explained by take up of nutrients from faeces (Bazely and Jefferies, 1985), especially for shallow rooting plants (*e.g. Puccinellia phryganodes* roots in the top 4 cm of sediment, Hik and Jefferies, 1990). Nutrient availability is probably the main factor limiting vascular plant processes in arctic ecosystems (Cargill and Jefferies, 1984a) and studies have shown that increased nutrient availability increases plant production in the Arctic (Chapin, 1995; Chapin and Shaver, 1996). In contrast, Gauthier *et al.* (1995) and Beaulieu *et al.* (1996) found reduced aboveground production in *D. fisheri* following grazing by greater snow geese at Bylot Island in High Arctic Canada; Bakker and Loonen (1998) also found no overcompensation in *Poa arctica* following grazing by barnacle geese in Ny-Ålesund, Svalbard. In both of these systems, a thick moss layer absorbed nutrients before they could reach the deeper *Dupontia* and *Poa* grass roots. Without the input from added nutrients, some arctic graminoids may even take longer than one year to recover fully from grazing in previous years (Archer and Tieszen, 1980, 1983). We suggest that in our experiment *Alopecurus*, growing in shallow moss, was able to enhance growth rate and increase cumulative production in response to grazing by using increased nutrient availability

from faeces. In contrast, overcompensation was lower for *Dupontia*; the thick moss layer in the wet habitat may have prevented a large proportion of the nutrients from faeces reaching the deep roots of this species.

This experiment considered only the aboveground part of the plants. However, regrowth after grazing relies on the use of belowground resources. A clipping experiment on *Alopecurus* and *Dupontia* at the same site during the same experimental period (Chaput, 2003) indicated that simulated grazing by removal of leaf material leads to reductions in belowground resources which could threaten the survival and growth of these plants in subsequent years, as suggested by Mattheis *et al*. (1976), Chapin *et al*. (1980), Gauthier *et al*. (1995) and Beaulieu *et al*. (1996).

The results of this investigation imply that in a warmer climate, these tundra grasses are likely to grow larger and therefore provide more forage for geese or other herbivores. However growth responses to grazing may have a limit beyond which compensatory growth is not possible. Aboveground growth appears to be stimulated by grazing when the plants can take up nutrients supplied by goose faeces, but regrowth may be incomplete and at the expense of belowground reserves.

Acknowledgments

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