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The effects of simulated spring goose grazing on the growth rate and protein content of *Phleum pratense* leaves

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Abstract The effects of simulated goose grazing on *Phleum pratense* plants were tested in an Iceland hayfield during the spring goose staging period (19 April–11 May 1997). Plants in an area excluded from the influence of grazing and the nutrient effects of goose faeces were subject to the removal of the youngest lamina once, three and four times during this period. Clipping three and four times resulted in 25–41% increases in cumulative elongation of youngest laminae compared with unclipped plants. Total cumulative lamina growth of entire plants showed no significant difference between unclipped plants and those clipped three and four times, hence no overcompensation occurred. Sequential clipping elevated the protein content of the youngest laminae from 20% to 27–33%, whereas there was no change amongst shoots clipped only once. Because geese only consume the youngest lamina of each *Phleum* plant, measurements from this experiment showed that regular physical removal of growing biomass doubled the biomass of preferred tissue available to geese and increased the potential protein intake 3.5 times at experimental clipping frequencies similar to levels of sequential harvesting observed amongst staging geese compared to less frequent harvesting. These increases were achieved without any fertilising effects of goose faeces implicated in such effects in previous studies.

Key words *Phleum pratense* · *Anser albifrons flavirostris* · Grazing · Overcompensation · Protein content

Introduction

The effects of grazing on plant production have attracted many studies concerning plant-herbivore interactions. Central to the concept of plant-herbivore interactions is the question of whether the physical removal of above-ground green material stimulates growth, so that plant production of grazed plants exceeds that of ungrazed plants (McNaughton 1979; termed “over-compensation” by Belsky 1986; Milchunas and Lauenroth 1993). In the study of the effects of grazing of monocotyledonous plants by arctic geese, overcompensation has been found in some situations (Cargill and Jefferies 1984; Kotanen and Jefferies 1987, 1989; Bazely and Jefferies 1989) explained in some circumstances by enhanced nutrient availability from deposition of goose faeces (Bazely and Jefferies 1985; Hik et al. 1991) but not in others (Kotanen and Jefferies 1989; Zellmer et al. 1993; Gauthier et al. 1995). In addition, there is evidence that grazed graminoids have significantly higher nitrogen concentrations than ungrazed plants (Dyer and Bokhari 1976; Mattson 1980; Cargill and Jefferies 1984; Gauthier et al. 1995). This is important since there is considerable evidence to suggest that the nitrogen content of plant organs is a major determinant of forage quality for geese (Kear 1966; Sedinger 1997). Some studies have suggested that the nitrogen content may be dependent upon goose faecal input, the number and timing of the grazing events and phenology of plant growth (Hik et al. 1991). Beaulieu et al. (1996) found that whilst addition of goose faeces had no effect on plant growth, clipping alone stimulated enhanced levels of nitrogen content, with highest levels at highest frequencies of clipping. However, none of these studies have focused upon the precise parts of plants consumed by the geese, and hence the particular

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effects of their physical removal, nor attempted to assess the benefit which accrues to feeding geese from enhancement of graminoid growth and protein content as a result of their foraging patterns.

Most recent studies of goose grazing have occurred during the reproductive period in summer on arctic systems, while few have been undertaken during spring migration (e.g. Black et al. 1991), when geese are more mobile and their exploitation of vegetation in the early stages of growth is likely to be determined by patterns of quality at large spatial scales. The prelude to breeding makes this period a crucial one for the accumulation of stores and reserves in preparation for reproduction, hence the potential for enhancing plant production and/or quality at this time may have implications for the reproductive output of individual geese (Alisauskas and Ankney 1992).

Icelandic spring-staging geese are highly selective in their diet, exploiting only the youngest lamina of timothy grass *Phleum pratense* shoots when feeding in hayfields, which exhibits the lowest fibre content, but the highest protein content, of all laminae present on the plant (Fox 1993). These youngest laminae are robust, in-rolled and erect (compared to older leaves which are reflexed and usually lying on the substrate), making their harvest by geese relatively simple and ensuring high intake rates. In this study, we conducted repeated clipping experiments on *Phleum* plants in Iceland to see if removal of green biomass in the form of these youngest laminae had an effect on the crude protein and lamina growth rate of only those grass leaves specifically selected by migrating geese staging in the general area. Hence, we considered that, in contrast to other systems where differences between hand-clipping and animal grazing have been found (e.g. Archer and Tieszen 1980), this specific clipping technique does effectively mimic the highly selective nature of goose grazing in its effect upon the plant. The experiment was carried out in the absence of goose faecal material which could have a compounding effect on lamina growth/regrowth and protein content. Observations show that geese sequentially harvest growing monocotyledonous plants (Prins et al. 1980; Rowcliffe et al. 1995), and observations from Iceland in previous springs suggested that hayfields, or parts of hayfields were generally exploited between three and four times in the course of the spring staging of geese (A.D. Fox, unpublished work). For this reason, we planned to mimic goose grazing in a trial plot at frequencies similar to those experienced by grass plants used by geese to assess its effect on lamina elongation and protein content as this relates to feeding geese.

Materials and methods

Study area

Fieldwork was conducted at the Hvanneyri Agricultural College, Borgarfjörður, in west Iceland (64°34'N 21°46'W) in spring 1997.

The area is the most important in Iceland for staging Greenland white-fronted geese *Anser albifrons flavirostris* migrating from the wintering areas in Ireland and Britain to breeding areas in West Greenland (Francis and Fox 1987; Fox et al. 1994). The first geese arrived at Hvanneyri on 16 April 1997, but the main arrival was on 18 April; most remained until a major departure on 10 May, and all were gone by 12 May. Up to 1000 geese used the College farm which comprises some 70 hayfields, used to grow winter keep for store animals (sheep, cattle and horses) kept indoors at the time of the study. Many geese staging in Iceland exploit the early growth of reseeded hayfields as these become snow free in the spring (Fox et al. 1991, 1992), and geese especially select those newly reseeded swards of *Phleum pratense* (Fox 1993) which are commonly cultivated for hay crop (Thorvaldsson 1997), although they do feed on *Poa pratense* and *Deschampsia caespitosa* hayfields as well.

Methods

To assess the contemporary use of the five pure sown *Phleum pratense* fields on the Hvanneyri farm (i.e. those where *P. pratense* comprised more than 50% of the green aboveground biomass present), we counted the numbers of geese present in each between two and five (but mostly three) times each day. On this basis, the cumulative percentage goose use of each field unit was calculated by summing the cumulative number of goose-days. To test for regular peaks in goose numbers using field units, lagged count time series were tested for autocorrelation (Royama 1992). Autocorrelation functions lying outside the 95% positive confidence interval indicates a significant autocorrelation corresponding to the cyclical return rate of geese to regraze the field unit. Regularly occurring sequential peaks in autocorrelation function with increasing time confirm a persistent cycle in field use.

To test our hypotheses that removal of green material (in a way which mimics goose grazing) would stimulate growth and protein content of the subsequent lamina, a 2 m × 1 m enclosure was established in a stand of almost pure *Phleum* in a hayfield (field no. 48) to eliminate the influence of goose grazing and defaecation. Within the enclosure, individual *Phleum* plants were marked with tags on cotton loops each bearing identification codes. In order to assess the effect of the clipping and the frequency of clipping, we established four treatments, each replicated by 25 randomly selected plants. These were (1) uncut plants, (2) plants cut once (on 19 April), (3) plants cut three times (19 April, 29 April and 6 May) and plants cut four times (19 April, 26 April, 2 May and 8 May). For each treatment, only the central youngest lamina was removed at each cut and all the youngest laminae were harvested on 11 May. The length of all laminae extant on the plants were measured on all individuals on 23, 26, 29 April and 2, 6, 8 and 11 May (that is including those laminae present at the start of the experiment and all laminae which developed subsequently). In presenting the results of lamina growth, length measurements are presented as cumulative growth from 19 April when the experiment commenced. In the case of all treatments, the birth of a new lamina resulted in the original youngest lamina being replaced by a new youngest lamina which was in turn clipped, this being the lamina which would have been taken by a feeding goose. Lamina lengths were converted to dry weight biomass on the basis of 300 clipped youngest laminae which were measured fresh, then dried and weighed. After harvest, all leaf material was dried at 60°C for at least 24 h and analysed for nitrogen content using a NA-1500 Nitrogen Analyser (Carlo Erba Instruments) with BBOT (C₂₆H₂₆N₂O₂S) as a standard. Crude protein was then expressed as 6.25 nitrogen content as a percentage of dry weight (Allen 1989).

We used repeated measures analysis of variance (ANOVA) to test for treatment effects using date of harvests for all of the measured parameters as the dependent variable. Where univariate tests of hypotheses for within-subject effects were significant for time and the interaction term time × treatment, we carried out ANOVA on the data for each time interval to determine significant differences in cumulative growth of (1) youngest laminae and (2) all laminae combined for each plant. In comparing the birth rates of

new lamina, the large proportion of zero values necessitated the use of non-parametric tests.

Results

Field use by geese

None of the five fields examined showed any cyclic pattern in regrazing, since none of the autocorrelation functions reached levels of significance within the staging period ($P > 0.05$). The birds did, however, show distinct patterns of sequential harvesting, insofar as all the fields were grazed for a period and were then left unexploited for a period before geese returned (Fig. 1). Most of these fields showed between two and four periods of intensive exploitation during the goose staging period, hence we have some confidence that the frequencies of clipping in the experiment reflected those experienced by the plants under field conditions of goose exploitation during the 1997 season.

Effects of clipping youngest laminae on elongation of *Phleum* laminae

Removal of the youngest lamina three and four times resulted in a significantly greater (25–41% increase) lamina elongation in this lamina (measured throughout the course of the goose staging period) than unclipped plants (i.e. including the removed fraction, Fig. 2). This was partly because unclipped plants were more likely to produce (and hence invest elongation in) new laminae than the plants clipped once by the end of the goose staging period (Fig. 3). Total cumulative lamina elongation (i.e. summing cumulative increment of all lami-

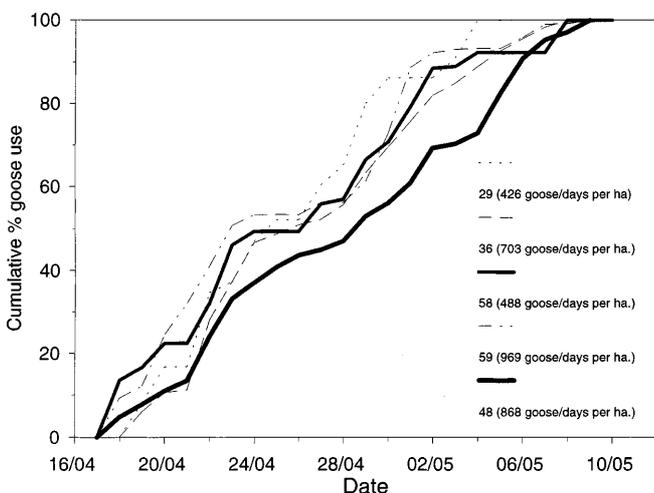


Fig. 1 Cumulative percentage total goose/days counted on each of the five *Phleum pratense* reseeded hayfields during the course of the spring staging period (19 April–11 May) of Greenland white-fronted geese at Hvanneyri in spring 1997. Different hayfields are identified by their farm number codes; values indicate total goose/day use throughout the spring staging period in relation to field size in each case

nae, including the material removed by clipping) showed that there was no significant difference between unclipped plants and the plants clipped 3 and 4 times, but that the plants that were clipped once showed significantly reduced cumulative lamina elongation (Fig. 4).

Effects of clipping youngest laminae on their subsequent protein content

Sequential clipping of *Phleum* resulted in significant increases in the protein content of the youngest laminae (i.e. those taken by geese) by the end of the goose spring staging period, but there was no statistically significant difference between the protein content between the start and end of the goose staging period amongst plants clipped only once (Fig. 5). There were, however, significant differences between the treatments on 11 May.

Effects of clipping on the potential biomass available for consumption by geese

Dry weight mass (D , mg) was related to lamina length (L , mm) based on the following formula: $D = 1.55L - 0.27$

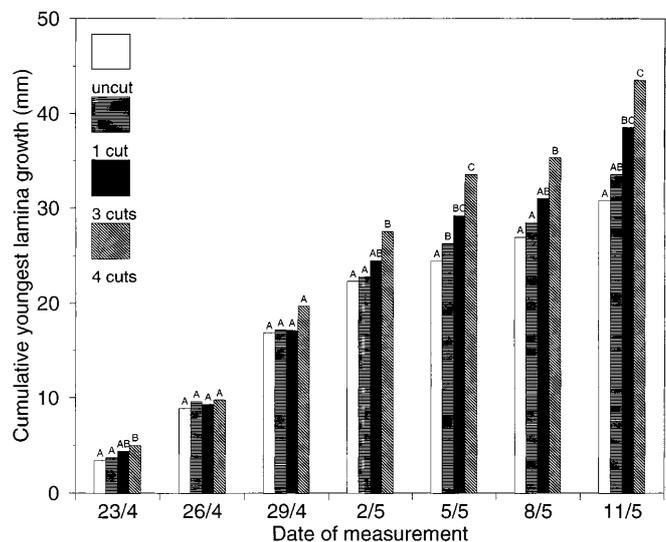


Fig. 2 Cumulative mean lamina length measurements of 25 tagged *P. pratense* plants subject to no clipping and those subject to the removal of the youngest lamina once, three and four times during the period 19 April–11 May 1997 in enclosed plots at Hvanneyri Agricultural College Farm, Iceland. All data relate to repeated measurements of the single lamina which was the youngest lamina at the start of the experimental period. Histogram plots indicate the mean cumulative lamina length based on 25 replicates for each treatment, and for the clipped plants includes removed material. Repeated measures ANOVA showed significant effects of time ($F_{6,576} = 1308.6$, $P < 0.001$) and time \times treatment ($F_{18,576} = 9.44$, $P < 0.001$), hence individual ANOVA tests were carried out as follows 23 April $F_{3,99} = 3.29$, $P = 0.024$; 26 April $F_{3,99} = 0.29$, $P = 0.839$; 29 April $F_{3,99} = 2.21$, $P = 0.092$; 2 May $F_{3,99} = 4.70$, $P = 0.004$; 5 May $F_{3,99} = 9.96$, $P < 0.001$; 8 May $F_{3,99} = 6.91$, $P < 0.001$; 11 May $F_{3,99} = 11.79$, $P < 0.001$. Similar letters indicate no significant difference between mean values at the point of each harvest, based on pairwise Tukey-Kramer tests at $P > 0.05$ where ANOVAS indicate significant differences between means

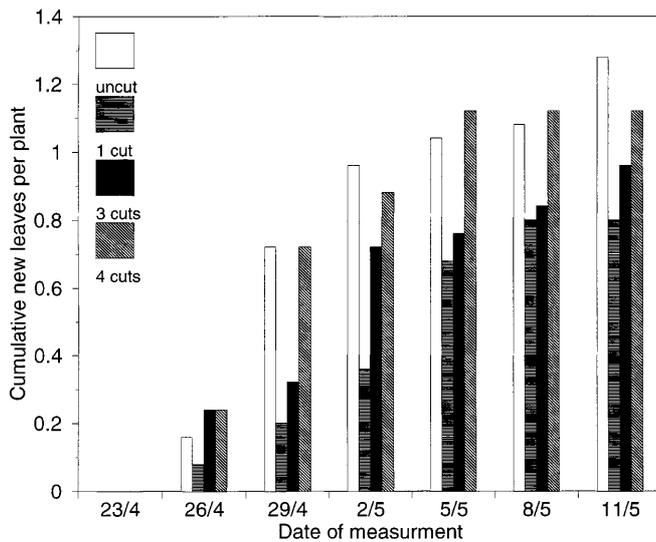


Fig. 3 Average cumulative generation of new youngest laminae per plant appearing on 25 tagged *P. pratense* plants subject to no clipping and those subject to the removal of the youngest lamina once, three and four times during the period 19 April–11 May 1997 in enclosed plots at Hvanneryi Agricultural College Farm, Iceland. Significantly fewer new youngest laminae were produced by the end of the trial in plants cut once than uncut plants ($\chi^2 = 19.1$, $df = 1$, $P < 0.001$), but there were no significant differences between the other treatments ($P > 0.05$)

($r = 0.93$, $n = 300$, $P < 0.001$). The cumulative biomass removed during the course of the staging period was greater amongst the clipped plants than unclipped (Table 1). The cumulative biomass of youngest laminae produced by plants clipped four times during the staging period was more than double that obtained from uncut plants (Table 1). Note that because only the youngest lamina was removed at each clipping event, the difference in cumulative biomass harvested was of greater magnitude than that of leaf elongation, because unclipped youngest laminae eventually became subtending at the birth of new youngest laminae, but nevertheless continued to grow (and therefore contribute to lamina elongation in Fig. 4). In the clipping experiments, this new younger lamina was harvested (since geese take these laminae), rather than the subtended (i.e. measured) lamina.

Effects of clipping on the potential amount of protein available for consumption by geese

Given the mass and quality of each harvested youngest lamina obtained from each treatment, it was possible to derive cumulative biomass and quality measures for each treatment derived by a theoretical goose exploiting *Phleum* through different frequencies of return harvests mimicked by each of the treatments. Because of the combined effects of enhanced cumulative biomass produced as young laminae and the elevation of protein levels in the regrowing laminae, the theoretical effects of

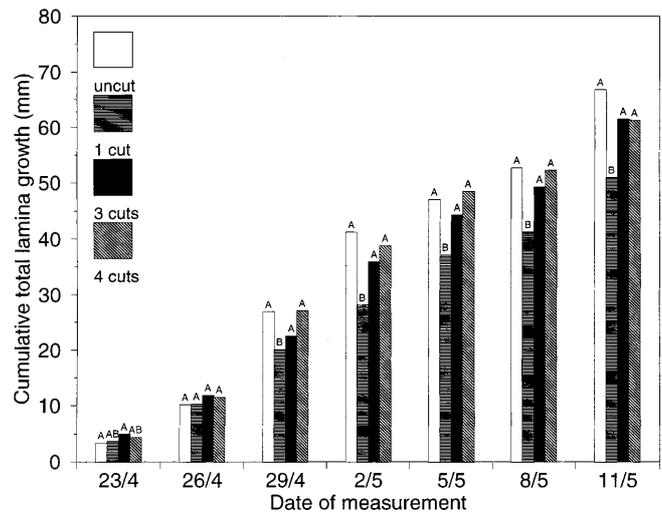


Fig. 4 Cumulative mean lamina length measurements of 25 tagged *P. pratense* plants subject to no clipping and those subject to the removal of the youngest lamina once, three and four times during the period 19 April–11 May 1997 in enclosed plots at Hvanneryi Agricultural College Farm, Iceland. All measurements relate to the measurement of total lamina length based on all laminae present on each plant throughout the experimental period. Histogram plots indicate the mean cumulative lamina length based on 25 replicates for each treatment, and for the clipped plants includes removed material. Repeated measures ANOVA showed significant effects of time ($F_{6,576} = 823.4$, $P < 0.001$) and time \times treatment ($F_{18,576} = 3.92$, $P < 0.001$), hence individual ANOVA tests were carried out as follows ANOVAS as follows 23 April $F_{3,99} = 3.31$, $P = 0.025$; 26 April $F_{3,99} = 0.64$, $P = 0.592$; 29 April $F_{3,99} = 4.84$, $P = 0.004$; 2 May $F_{3,99} = 8.00$, $P < 0.001$; 5 May $F_{3,99} = 3.80$, $P = 0.013$; 8 May $F_{3,99} = 3.44$, $P = 0.020$; 11 May $F_{3,99} = 3.79$, $P = 0.013$. Similar letters indicate no significant difference between mean values at the point of each harvest, based on pairwise Tukey-Kramer tests at $P > 0.05$ where ANOVAS indicate significant differences between means

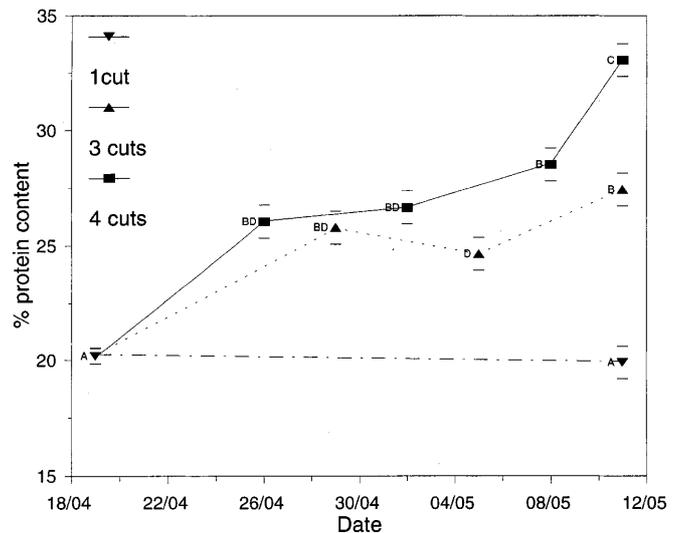


Fig. 5 Mean percentage dry weight protein content (\pm SE) of harvested youngest laminae cut from 25 tagged *Phleum pratense* plants subject to no clipping and those subject to the removal of the youngest lamina once, three and four times during the period 19 April–11 May 1997 in enclosed plots at Hvanneryi Agricultural College Farm, Iceland. Similar letters indicate no significant differences between mean values based on pairwise *t*-tests at $P > 0.05$

Table 1 Cumulative biomass and protein (mean dry weight per plant \pm SE, mg) obtained up to and including the harvest of 11 May 1997 from the removal of youngest laminae from 25 tagged *Phleum pratense* plants subject to no clipping and those subject to the removal of the youngest lamina once, three and four times during the period 19 April–11 May 1997 in enclosed plots at Hvanneyri Agricultural College Farm, Iceland

	Uncut	1 Cut	3 Cut	4 Cut
Biomass (mg)	3.50 \pm 1.78	5.00 \pm 1.84	7.08 \pm 1.97	8.85 \pm 1.73
Protein (mg)	0.70 \pm 0.35	0.94 \pm 0.37	1.49 \pm 0.44	2.02 \pm 0.45

more frequent harvesting by geese were to enhance the amount of protein that could be derived from sequential harvesting. Hence, the amount of protein (in terms of protein per unit dry weight of lamina material removed and in absolute terms) increased with the number of harvesting events, such that the potential goose intake of protein from plants with material removed on four occasions was 3.5 times that of plants only harvested once at the beginning and again at the very end of the study (Table 1).

Discussion

According to the habitat matching rule of optimal foraging theory, the use of any particular hayfield at Hvanneyri by geese will be determined by its internal state (the quality and availability of the feeding resource) and the relative attractiveness of other feeding resources in the vicinity. The lack of a regular cyclical patterns of exploitation of *Phleum* hayfields there, is therefore probably as much to do with the available food resources in the immediate vicinity and the increase in growth rate of the vegetation as the spring progressed. Nevertheless, as predicted on the basis of previous studies (Prins et al. 1980; Rowcliffe et al. 1995), geese did return to sequentially harvest a regrowing sward, exploiting individual field units for some days (generally *c.* 4 days) duration, before leaving them for other feeding resources (generally being absent for *c.* 2–3 days). Since the observed return rates to the same *Phleum*-dominated fields were between three and four times during the course of the spring staging period, it would appear that the experimental clipping frequencies did mimic those used by the geese in their foraging on *Phleum pratense* at Hvanneyri.

The effects of clipping the youngest lamina of *Phleum* plants three and four times during the staging period of the geese were to increase the total amount of youngest lamina tissue produced compared to uncut plants and those cut once. This was partly the result of the fact that repeatedly clipped lamellae never reached the point where they opened laterally to subtend the next generation of youngest laminae in the way that occurred amongst unclipped plants. However, the enhanced elongation of the youngest lamina did not correspond to “overcompensation” during the period of the study

(*sensu* McNaughton 1979; Belsky 1986), since the plants clipped three and four times showed no significant difference in total cumulative lamina incremental growth overall compared with the uncut control. As concluded by Gauthier et al. (1995) in their study of arctic graminoids, this could be because we are measuring lamina births and elongation over too short a time scale to detect any such effect. However, in this study, we are primarily concerned with the effects of grazing on an agricultural grass crop in terms of their potential feedback to goose grazing patterns, hence the absence of detectable overcompensation during the staging period is significant in terms of how the geese exploit these swards.

In most recent goose-graminoid interaction studies, attempts to detect overcompensation have relied upon measured changes in overall net above ground primary production and general nutrient content, and have not taken account of the growth, birth and death rates of individual leaves over sufficiently short periods (e.g. Kotanen and Jefferies 1987) to identify whether compensatory growth has taken place at the level where there are detectable consequences for the herbivorous waterbirds which feed upon these plants. In this study, the results suggest that *Phleum* shows a flexible response to defoliation by removal of the youngest lamina by reallocation of leaf elongation in more rapid regrowth of the growing tip (albeit at cost to the overall production of lamina tissue overall during the measured period). Increasing frequency of removal of youngest laminae apparently increased the regrowth rate, indicating overcompensation at the lamina growth level, but not at the plant level. However, because geese are so selective in their removal of youngest laminae, this mechanism has considerable implication for these herbivores. The results show that more frequent harvesting, combined with increased regrowth rate of the youngest laminae, increased the harvested biomass at frequencies which mimicked field observations of goose grazing frequencies.

Since the removal of the youngest lamina four times during the period elevated protein levels above those of plants cut three times and once, the geese benefit from (1) more frequent harvests, (2) enhanced biomass production of the youngest lamina (the only part of the *Phleum* plant removed by geese) and (3) the quality of those laminae, which increased up to the point of departure of the geese. In this way, the four-cut treatment produced double the biomass and almost four times the protein of the uncut treatment by the point of harvest at the end of the goose staging period. Although the finding that lamina removal elevates protein content of above-ground biomass in graminoids is not new (e.g. Beaulieu et al. 1996), this study is the first to quantify the variable response of this effect at different harvest intervals by mimicking the precise removal of plant parts by geese.

The significant reduction in total lamina growth (as a result of the reduction in generation of new laminae) in

shoots cut only once relative to uncut and more frequently cut plants is surprising, and is unlikely to be a random or sampling effect, since the differences became significant only after the second cuts in the other treatments. This may suggest a threshold response of growing shoots to grazing, with repeated removal of laminae stimulating growth in contrast to a differential response to a rare grazing event, although this clearly requires further investigation.

These results suggest that at this early stage in their spring growth, the grazed *Phleum* plants were able to compensate for the loss of their youngest laminae by their continued growth, apparently at rates of elongation in excess of those of unclipped plants. However, overall, this enhanced growth was probably at cost to the ultimate elongation of other laminae, since there were no significant differences between three- and four-cut treatments and uncut plants in the overall accumulation of green laminae on each plant. In other studies, it has been suggested that the lack of overcompensation is the result of bryophyte interception of soluble cations from goose faeces denying plants the benefit of nutrient leachate from droppings (e.g. Gauthier et al. 1995; Beaulieu et al. 1996). All the hayfields exploited by the geese at Hvanneyri are on mineral soils with virtually no bryophytes present in the sward. In any case, in the present study, the lack of overcompensation occurred in the absence of any nutrients supplied from goose faeces, suggesting that the plants may be able to tolerate at least such levels of grazing during this early growing period within one field season.

The benefit to the geese of the plant investing in youngest lamina elongation is clear, since they select almost exclusively for this lamina for the relatively short period they stage in the area (Fox 1993). Hence, in this study, repeated removal stimulated both (1) production of the very plant tissue targeted by geese for food and (2) enhanced protein content of that food, without the need to invoke nitrogen cycling through deposition of goose faeces.

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References

Alisauskas RT, Ankney CD (1992) The cost of egg-laying and its relationship to nutrient reserves in waterfowl. In: Batt BDJ, Afton AD, Anderson MG, Ankney CD, Johnson DH, Kadlec JA, Krapu GL (eds) Ecology and management of breeding waterfowl. University of Minnesota Press, Minneapolis, pp 30–61

- Allen SE (1989) Chemical Analysis of Ecological Materials. Blackwell, Oxford
- Archer A, Tieszen LL (1980) Growth and physiological responses of tundra plants to defoliation. *Arct Alp Res* 12:531–532
- Bazely DR, Jefferies RL (1985) Goose faeces: A source of nitrogen for plant growth in a grazed salt marsh. *J Appl Ecol* 22:693–703
- Bazely DR, Jefferies RL (1989) Leaf and shoot demography of an arctic stoloniferous grass, *Puccinellia phryganodes*, in response to grazing. *J Ecol* 77:811–822
- Belsky AJ (1986) Does herbivory benefit plants? A review of the evidence. *Am Nat* 127:870–892
- Beaulieu J, Gauthier G, Rochefort L (1996) The growth response of graminoid plants to goose grazing in a High Arctic environment. *J Ecol* 84:905–914
- Black JM, 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
- Cargill SM, Jefferies RL (1984) The effects of grazing by lesser snow geese on the vegetation of a sub-arctic salt marsh. *J Appl Ecol* 21:669–686
- Dyer MI, Bokhari UG (1976) Plant-animal interactions: studies of the effects of grasshopper grazing on blue grama grass. *Ecology* 57:762–772
- Fox AD (1993) Pre-nesting feeding selectivity of pink-footed geese *Anser brachyrhynchus* in artificial grassland. *Ibis* 135:417–422
- Fox AD, Gitay H, Boyd H, Tomlinson C (1991) Snow-patch foraging by pink-footed geese *Anser brachyrhynchus* in south Iceland. *Holarct Ecol* 14:81–84
- Fox AD, Boyd H, Warren SM (1992) The phenology of spring pre-nesting feeding in Iceland-nesting geese. *Ecography* 15:289–295
- Fox AD, Norriss DW, Stroud DA, Wilson HJ (1994) Greenland white-fronted geese in Britain and Ireland, 1982/83–1993/94. National Parks and Wildlife Service, Dublin and Greenland White-fronted Goose Study, Aberystwyth
- Francis IS, Fox AD (1987) Spring migration of Greenland white-fronted geese through Iceland. *Wildfowl* 38:7–12
- Gauthier G, Hughes RJ, Reed A, Beaulieu J, Rochfort L (1995) Effect of grazing by greater snow geese on the production of graminoids at an arctic site (Bylot Island, NWT, Canada) *J Ecol* 83:653–664
- Hik DS, Sadul HA, Jefferies RL (1991) Effects of the timing of multiple grazings by geese on net above ground primary production of swards of *Puccinellia phryganodes*. *J Ecol* 79:715–730
- Kear J (1966) The food of geese. *Int Zool Y B* 6:96–103
- Kotanan P, Jefferies RL (1987) The leaf and shoot demography of grazed and ungrazed plants of *Carex subspathacea*. *J Ecol* 75:961–975
- Kotanan P, Jefferies RL (1989) Response of arctic sedges to release from grazing: leaf elongation in two species of *Carex*. *Can J Bot* 67:1414–1419
- McNaughton SJ (1979) Grazing as an optimization process: grass-ungulate relationships in the Serengeti. *Am Nat* 113:691–703
- Mattson WJ (1980) Herbivory in relation to plant nitrogen content. *Annu Rev Ecol Syst* 11:119–161
- Milchaunas DG, Lauenroth WK (1993) Quantitative effects of grazing of vegetation and soils over a global range of environments. *Ecol Monogr* 63:327–366
- Prins HHT, Ydenberg RC, Drent RH (1980) The interaction of brent geese *Branta bernicla* and sea plantain *Plantago maritima* during spring staging. *Acta Bot Neerl* 29:585–596
- Rowcliffe JM, Walkinson AR, Sutherland WJ, Vickery JA (1995) Cyclic winter grazing patterns in brent geese and the regrowth of salt-marsh grass. *Funct Ecol* 9:931–941
- Royama T (1992) Analytical population dynamics. Chapman and Hall, London
- Sedinger JS (1997) Adaptations to and consequences of an herbivorous diet in grouse and waterfowl. *Condor* 99:314–326
- Thorvaldsson G (1997) The vegetation of Icelandic hayfields. *Náttúrufræðingurinn* 67:45–52 (In Icelandic)
- Zellmer ID, Claus MJ, Hik DS, Jefferies RL (1993) Growth responses of arctic graminoids following grazing by captive lesser snow geese. *Oecologia* 93:487–492