Moss carpets constrain the fertilizing effects of herbivores on graminoid plants in arctic polygon fens

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Abstract: We conducted a fertilization experiment in polygon fens that were grazed by Greater Snow Geese on Bylot Island (Canadian Arctic) to determine whether mosses can interfere with nutrient cycling and thereby prevent a direct fertilizing effect of herbivore faeces on vascular plants. We measured the effects of nitrogen (N), phosphorus (P), and faecal addition on growth parameters and nutrient content of graminoids and mosses over a 2 year period. Growth and nutrient content of graminoids were enhanced only for high levels of N addition (5 $g \cdot m^{-2}$ per season), and showed little response to P addition. Although the growth of mosses showed a slight response to N or P addition, it is primarily nutrient content that was generally enhanced at all levels of fertilization. In many cases, stronger responses were detected when N and P were applied in combination, rather than singly. Addition of goose droppings had no effect on any measured parameters. Our results suggest that bryophytes act as a natural barrier by absorbing nutrients from external additions, thus blocking the access of highly assimilable nutrients to graminoid plant roots. At increased levels of N addition, bryophytes were apparently saturated so the nutrient surplus leached down to roots and was thus available for graminoid plant growth. The presence of a thick moss layer likely explains why the deposition of faeces by herbivores such as geese has no effect on graminoid growth in arctic polygon fens.

Key words: fertilization, moss carpet layer, nutrient cycling, plant–herbivore interactions, polygon fens, Snow Goose.

Résumé : Nous avons réalisé une expérience de fertilisation dans les polygones de tourbe broutés par la Grande oie des neiges sur l'Île Bylot (arctique canadien) pour déterminer si les mousses peuvent modifier le cycle des nutriments et ainsi empêcher un effet fertilisant des herbivores sur les plantes vasculaires. Nous avons mesuré les effets d'ajouts d'azote, de phosphore et de fèces d'oie sur les paramètres de croissance et le contenu en nutriments des graminoïdes et des mousses après 2 années de fertilisation. La croissance et le contenu en nutriments des graminoïdes ont augmenté seulement en réponse aux ajouts élevés d'azote (5 $g \cdot m^{-2}$ par saison) et ont montré une faible réponse aux ajouts de phosphore. Même si la croissance des mousses a été légèrement influencée par les ajouts d'azote ou de phosphore, c'est surtout leur contenu en nutriments qui a généralement augmenté sous tous les niveaux de fertilisation. Souvent, une réponse plus importante a été détectée lorsque l'azote et le phosphore étaient ajoutés en combinaison. L'addition de fèces n'a eu d'effet sur aucun paramètre. Nos résultats suggèrent que les bryophytes agissent comme une barrière naturelle en absorbant les nutriments provenant de la fertilisation, bloquant ainsi l'accès des racines des plantes vasculaires à des nutriments très assimilables. Sous des ajouts élevés d'azote, les bryophytes sont apparemment saturées et le surplus de nutriments peut être lessivé jusqu'aux racines et devenir disponible pour la croissance des graminoïdes. La présence d'un épais tapis de mousses peut expliquer pourquoi la déposition de fèces par des herbivores comme les oies n'a pas d'effet sur la croissance des graminoïdes dans les polygones de tourbe de l'Arctique.

Mots-clés : fertilisation, tapis de mousses, cycle des nutriments, interactions plantes–herbivores, polygones de tourbe, Oie des neiges.

Introduction

Plant growth in the Arctic is constrained by low radiation, precipitation, and nutrient availability, and by the short duration of the snow-free period. In turn, the low nutrient availability of arctic systems is largely explained by low soil temperatures, which inhibit microbial activity that is essential to decomposition and turnover processes (Henry and Jefferies 2003). Thus, productivity of tundra vegetation is strongly and consistently limited by mineral nutrient availability (Shaver and Chapin 1995). Nitrogen (N) is often the primary limiting nutrient in tundra plant communities, usually followed by phosphorus (P) (Haag 1974; Chapin et al. 1975; McKendrick et al. 1978; Henry et al. 1986).

Herbivores can also locally modify the structure and species composition of the tundra (Kerbes et al. 1990; Jefferies et al. 1994). Grazing can either lead to an enhancement or a reduction of plant production via a series of negative or pos-

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itive feedbacks (McNaughton 1979). An enhancement of vegetative growth occurs under very specific conditions; low soil nutrients and a high grazing pressure can lead to a rapid turnover of nutrients in the soil (Jefferies et al. 1994). Faeces and urine contain a high proportion of soluble nutrients that can be readily taken up and assimilated by plants, and hence enrich the soil. According to Bazely and Jefferies (1985), 60% of the N from goose faeces is available within 48 h, and can be a major source of nutrients for arctic plants. The passage of plants through the digestive system of herbivores can therefore bypass the limiting step of nutrient release from litter decomposition in cold environments (Ruess et al. 1989; Gauthier et al. 1996). A positive feedback on plant growth following grazing was observed in the subarctic salt marsh at La Pérouse Bay, Manitoba, Canada. Moderate grazing by Lesser Snow Geese (*Anser caerulescens caerulescens* L.) enhanced net aboveground primary production (Cargill and Jefferies 1984), mostly owing to the fertilizing effect of goose faeces (Bazely and Jefferies 1985; Hik and Jefferies 1990). Another example is provided by reindeer (*Rangifer tarandus platyrhynchus* Vrolik) faeces, which positively influence the growth of vascular plants by stimulating soil nutrient recycling in a subarctic environment (Olofsson et al. 2004; van der Wal et al. 2004). However, such positive feedbacks are not ubiquitous. In the wetlands of Bylot Island in the Canadian High Arctic, plants grazed by Greater Snow Geese (*Anser caerulescens atlanticus* Kennard) are able to produce new foliage, but grazing does not enhance net aboveground primary production (Gauthier et al. 1995; Beaulieu et al. 1996). In contrast with the salt marshes and mineral soil of La Pérouse Bay, the polygon fens and freshwater wetlands of Bylot Island produce an organic, peaty soil that is composed of a dense carpet of bryophytes (Gauthier et al. 2006).

Bryophytes are a major component of tundra wetlands (Vitt and Pakarinen 1977). Mosses affect several ecosystem functions such as soil stabilization, soil and permafrost insulation, soil moisture regime, pollutant interception, and enhancement of N fixation (Press et al. 1998). Even though it is well known that mosses interfere with nutrient cycling for vascular plants in peatlands (Malmer et al. 1994, 2003; Li and Vitt 1997), this interaction has rarely been considered in tundra ecosystems until recently (Longton 1984; Kotanen 2002; van der Wal et al. 2003). Nutrient absorption in mosses occurs directly through the cellular surface and is enhanced by a single-celled leaf structure and a high exchange capacity of cell walls (Clymo 1963; Craigie and Maass 1966). The absence of a positive response of graminoid plants to surface nutrient addition in some arctic wetlands may thus be due to the moss carpet that absorbs or retains these nutrients on their cell walls (Gauthier et al. 1996; Pineau 1999; Kotanen 2002). However, the amount and nature of nutrients (N or P) released from herbivore faeces that can be absorbed by mosses, and the subsequent effects of this sequestration on graminoid plant growth, remains poorly understood.

Several moss-removal experiments have been conducted in arctic, alpine, and boreal systems, but their effects on vascular plant communities have been variable. In tussock tundras, the growth of graminoid plants or deciduous shrubs was enhanced by moss removal (Hobbie et al. 1999; Bret-Harte et al. 2004), but little effect was found on the growth of *Eriophorum vaginatum* (Fetcher 1985). In a High-Arctic meadow, growth of small vascular plants increased after moss removal (Sohlberg and Bliss 1987). However, moss-removal is an invasive experiment that can result in serious side-effects. For instance, moss removal affected the fine scale structure of a mountain grassland (Herben and Wagnerová 2004) and resulted in changes in temperature regimes in various ecosystems, which could alter decomposition processes (Sohlberg and Bliss 1987; Startsev et al. 2007). In an oligotrophic wet meadow, seedling recruitment of some species was negatively affected by moss removal because of increased desiccation (Špačková et al. 1998). Thus, both positive and negative effects of moss removal treatment could complicate comparisons with treatment without moss removal.

We conducted a fertilization experiment in the polygon fens on Bylot Island that are grazed by Greater Snow Geese to determine whether mosses can act as a barrier to surface nutrients for vascular plants, and the threshold above which this barrier can be overcome. We measured the effects of variable nutrient addition (both in terms of amount and composition, i.e., N or P) on growth parameters (tiller and flower densities and net aboveground primary production) and nutrient content of graminoid plants and mosses. We wished to clarify the role of bryophytes in trophic interactions between herbivores, graminoid plants, and bryophytes, and to estimate the fertilizing effects of goose droppings in these fens. Plant nomenclature follows the United States Department of Agriculture Natural Resources Conservation Service (2009) plant database.

Materials and methods

Study area

The experiments were carried out in a glacial valley (50 km^2) located on the southwest plain of Bylot Island, Nunavut, Canada (73°08′N, 80°00′W). The site is characterized by a mosaic of freshwater wetland habitats composed of polygon fens, small lakes, and aggregations of ponds, surrounded by upland tundra (Massé et al. 2001; Ellis and Rochefort 2004). Fens and pond margins are covered by a low density of graminoids, such as *Dupontia fisheri* R. Br., *Eriophorum scheuchzeri* Hoppe, and *Carex aquatilis* Wahlenb. var. *stans* (Drejer) Boott, growing through a dense and continuous carpet of brown mosses that are dominated by the genus *Drepanocladus* (see Appendix A, Table A1). This area is the main breeding site of the Greater Snow Goose in the Arctic (Reed et al. 2002) and about 105 800 geese (adults and goslings) were present in 2003 (A. Reed, unpublished data). *Dupontia fisheri* and *E. scheuchzeri* are the prefered food of geese in the wet habitats on Bylot Island (Gauthier 1993; Manseau and Gauthier 1993; Gauthier et al. 1995).

Experimental design

A randomized block design with six blocks and nine treatments was used. Locations of the blocks were selected to encompass a range of polygon wetness within the valley where our camp was situated. A given block needed to be homogeneous and large enough to receive all treatments,

Table 1. Description of fertilization treatments according to dose and concentration used of nitrogen (N) and phosphorus (P).

	Dose		Concentration		
	($g \cdot m^{-2} \cdot year^{-1}$)		($mol \cdot L^{-1}$)		
Treatment	N	P	N	P	Abbreviation
1. Water-only control	—	—	—	—	—
2. Faeces*	0.6 to 1	0.03 to 0.06	—	—	—
3. N	1	0	0.036	0	N_L
4. N	3	0	0.107	0	N_I
5. N	5	0	0.179	0	N_H
6. P	0	1	0	0.016	P_I
7. P	0	3	0	0.048	P_H
8. N + P	3	0.5	0.107	0.008	N_IP_L
9. N + P	5	1	0.179	0.016	N_HP_I

Note: Nutrients were applied once in late June 2003 and 2004.

*The faecal treatment corresponded to 40 $faeces \cdot m^{-2}$.

and separated by at least 500 m from another block. Within blocks, experimental units (metallic exclosure) of 2 m × 2 m were placed the year before sampling on a well-developed and homogeneous moss carpet (cover close to 100%) with a good cover of graminoid plants typically grazed by geese (*D. fisheri* and *E. scheuchzeri*). Units were protected from goose grazing by a chicken-wire fence that was 50 cm high with ropes criss-crossing the top and located at least 5 m apart to prevent cross contamination by treatment application. Treatments were randomly assigned to units and maintained for 2 years (2003 and 2004). We determined that the polygon fens are N-limited on Bylot Island because N:P ratios in water were < 9 for five blocks and < 12 for one block, as measured in a hole at least 5 m away from all experimental units in each block (see Güsewell 2004).

A previous fertilization experiment had shown that graminoid plants in polygon fens are influenced by a single addition of 10 $g \cdot m^{-2}$ but not by 1 $g \cdot m^{-2}$ of N (Pineau 1999). We thus determined our low ($N_L = 1\ g \cdot m^{-2}$), intermediate ($N_I = 3\ g \cdot m^{-2}$), and high ($N_H = 5\ g \cdot m^{-2}$) annual doses of N. For P, we applied the same high dose ($P_H = 3\ g \cdot m^{-2}$) that had been used by Pineau (1999), as well as an intermediate dose ($P_I = 1\ g \cdot m^{-2}$). We also added N and P in combination to examine the synergistic effect of these nutrients, using the same doses as in the high N and intermediate P treatments ($N_HP_I = 5\ g \cdot m^{-2}$ of N + 1 $g \cdot m^{-2}$ of P). In addition, we applied a N + P treatment with lower doses ($N_IP_L = 3\ g \cdot m^{-2}$ of N + 0.5 $g \cdot m^{-2}$ of P), because we suspected that the synergistic effect of these nutrients could elicit a plant response at lower concentrations. Lastly, we added fresh goose faeces at a level of 40 $faeces \cdot m^{-2}$ every year (see Table 1 for doses and concentrations of treatments). Geese deposit on average 6.9 $faeces \cdot m^{-2}$ throughout the summer (annual range: 3.6–11.4 $faeces \cdot m^{-2}$) over the 1991–2006 period (Gauthier et al. 1995; G. Gauthier, unpublished data). The faecal density used in this experiment thus represented approximately 3 to 10 times the mean amount of faeces naturally deposited by geese, but was similar to the maximum recorded on individual experimental units (29 $faeces \cdot m^{-2}$). Although the density of faeces added was high, we estimated that it was equivalent to the addition of 0.6–1.0 $g \cdot m^{-2}$ of N and 0.03–0.06 $g \cdot m^{-2}$ of P, which is comparable with the amount of N added in the low N treatment (Table 1; dried droppings weigh 1 g on average and contain 1.5%–2.5% of total N and 0.07%–0.15% of total P; Beaulieu 1995; R. Pouliot unpublished data). Since Pineau (1999) had shown that graminoid plants did not respond to the addition of 1 $g \cdot m^{-2}$ of N, we decided that the use of a lower density of faeces would be ineffective.

An obvious way to test whether mosses constrain access to nutrients by graminoid plants would be to remove mosses, but such a manipulation would lead to several biases. Removing mosses in our polygon fen systems would often mean exposing the roots of the vascular plants, as the main root mass is located on average at 5 cm below the living moss but ranging from 2 to 10 cm (Pineau 1999). It is almost impossible to remove the moss carpet without damaging the vascular plants growing through this layer, especially at our study site where tillers are small and very dense. Removal manipulation would create a depression where standing water would accumulate within the continuous moss carpet, likely to change the ecophysiological relationship (Startsev et al. 2007). Also, with the removal of the upper moss layer, the well-preserved lower peat would still exhibit active cation exchange properties, since polyuronic acids persist in the holocellulose of dead cell walls (Craigie and Maass 1966; Clymo 1967). As numerous studies that have used moss removal experiments indicated several limitations on this approach (Sohlberg and Bliss 1987; Špačková et al. 1998; Herben and Wagnerová 2004; Startsev et al. 2007; see also Introduction), we discarded this treatment in our experiment.

Almost all fertilization treatments were applied in one dose in late June (some faecal treatments were applied in early July), at the emergence of vascular plants and as soon as standing water from spring snow-melt had receded from the experimental units. N fertilizer (34–0–0) was applied as ammonium nitrate (NH_4NO_3) and P fertilizer was added as superphosphate phosphoric acid (H_3PO_4, 0–46–0). Goose faeces were collected fresh in the field, less than 1 h following defecation (mainly from adults). For consistency, we

Table 2. Results of two-way ANOVAs and a-priori contrasts to evaluate the effect of nutrient additions on growth parameters of graminoids plants and mosses after two growing seasons.

	Tiller density		Flower density		Primary production			
	Graminoid		Graminoid		Graminoid		Moss	
Source of variation	df	*P*	df	*P*	df	*P*	df	*P*
Block	5		5		5		5	
Treatment	8	**<0.01**	8	0.08	8	**<0.01**	8	**<0.01**
Error	40		40		40		33	
Total	53		53		53		46	
Contrasts								
C1: Control (1) vs. Other treatments (2 to 9)	1	0.10	1	0.22	1	0.36	1	**<0.01**
C2: Control (1) vs. Faeces (2)	1	0.65	1	0.10	1	0.72	1	0.70
C3: N (4, 5) vs. N + P (8, 9)	1	0.20	1	0.06	1	**0.02**	1	**0.01**
C4: P (6) vs. P + N (9)	1	0.92	1	0.71	1	0.58	1	0.12
C5: N linear effect	1	**<0.01**	1	0.25	1	**<0.01**	1	0.19
C6: N quadratic effect	1	0.09	1	0.14	1	**0.02**	1	0.27
C7: P linear effect	1	0.42	1	0.55	1	0.87	1	0.36
C8: P quadratic effect	1	0.52	1	0.24	1	0.84	1	0.08

Note: Numbers in parentheses refer to treatments in Table 1; degrees of freedom (df) are adjusted for missing values; values in bold emphasize significant differences ($P < 0.05$).

used 500 g of fresh faeces as the equivalent of 40 faeces. The N fertilizer was dissolved in 2 L of water before application. Faeces were conserved whole and scattered uniformly, as well as the P fertilizer, on the moss surface before watering (2 L by experimental unit). To be consistent, control units also received 2 L of water. The water was obtained from open water between polygon fens near experimental units.

Vegetation sampling

Aboveground mass of vascular plants was sampled during the peak of aboveground biomass (early August) at the end of the second year of treatments by taking three 10 cm × 10 cm × 10 cm subsamples of turf, including vascular and nonvascular plant species, in each experimental unit (subsamples were pooled). Aboveground phytomass is a good approximation of net aboveground primary production in this ecosystem (Gauthier et al. 1995). We only considered live aboveground phytomass of graminoids (i.e., *D. fisheri*, *Eriophorum* spp. and *C. aquatilis*) because other vascular plants were scarce (<0.5% cover). Aboveground parts included green leaves and green and white parts of the tiller above the last leafing node. Numbers of individual tillers and number of flowering stems were counted to obtain tiller and flower densities. Plant material was dried at 45 °C to constant weight, and reported as dry mass.

Moss annual net primary production (MAPP, in g·m^{-2}) was estimated with the following equation (Vitt and Pakarinen 1977):

$$[1] \qquad \mathrm{MAPP} = [W \times G]/[S \times H]$$

where W = dry biomass of live moss (g), G = mean annual increment of moss (m), S = sample surface area (m^2), and H = mean height of live moss (m; see below). Several moss species demonstrate visible annual growth in the Arctic (Vitt and Pakarinen 1977). On Bylot Island, *Polytrichum swartzii* Hartm. and *Meesia triquetra* (L. ex Jolycl.) Ångstr. show clear seasonal differences in leaf size and spacing between leaves, and those species were used as natural markers to estimate moss net primary production (see Pouliot 2006). Whenever possible, we collected ≥15 stems of *P. swartzii* or *M. triquetra* in each experimental unit near the end of growing season (mid-August) to measure annual growth increments (G). We cored four turf subsamples of 22.5 cm^2 each, 10 cm deep, and pooled results within experimental units (S). Living moss is composed of two parts, an upper green portion (the photosynthetic, active layer) and a lower brown portion (the less active layer, which extends down to the beginning of vascular plant rhizome systems). The mean height of the green moss layer (H) was measured around each core at 10 different places. The green portion of moss was cut and dried at 45 °C to constant weight (W).

To examine nutrient leaching through the peat column, peat was put in 10 decomposition bags and placed, the year before sampling, down to the level of vascular plant roots (approximately 5 cm deep) under each experimental unit. Bags were 5.5 cm × 6 cm, made of 1 mm nylon mesh, and filled with approximately 1.5 g of dried materiel collected at the same time of the year than vegetation sampling.

Chemical analyses

Total N and P concentration were measured in all graminoid and moss samples and in the peat samples coming from decomposition bags (hereinafter referred to as peat). Subsamples within experimental units were pooled and then ground before analyses. Total N was assessed with flow injection analysis (FIA; Quikchem 8000 of Lachat Instrument, Milwaukee, Wisconsin, USA) and total P was measured with an inductively coupled plasma analysis (ICP; model OPTIMA 4300 DV of Perkin-Elmer, Waltham, Massachusetts, USA) following the digestion method described in Parkinson and Allen (1975). Ratios of N/P concentration in graminoids, mosses, and peat were then calculated, as well as the N and P content in plant tissues (primary production × N or P concentration; g·m^{-2} of N or P) of graminoids and mosses.

Table 3. Results of two-way ANOVAs and a-priori contrasts to evaluate the effect of nutrient additions on total N and P concentration and N/P concentration ratios of graminoid plants, mosses, and peat after two growing seasons.

	Total N concentration						Total P concentration						N/P ratio					
	Graminoid		Moss		Peat		Graminoid		Moss		Peat		Graminoid		Moss		Peat	
Source of variation	df	*P*	df	*P*	df	*P*	df	*P*	df	*P*	df	*P*	df	*P*	df	*P*	df	*P*
Block	5		5		5		5		5		5		5		5		5	
Treatment	8	0.19	8	**<0.01**	8	0.22	8	**0.02**	8	**<0.01**	8	0.82	8	**0.03**	8	**<0.01**	8	0.45
Error	40		40		40		38		40		40		38		40		40	
Total	53		53		53		51		53		53		51		53		53	
Contrasts																		
C1: Control (1) vs. Other treatments (2 to 9)	1	0.64	1	**<0.01**	1	0.60	1	**0.05**	1	**<0.01**	1	0.77	1	0.22	1	0.94	1	0.93
C2: Control (1) vs. Faeces (2)	1	0.91	1	0.12	1	0.41	1	0.84	1	0.36	1	0.46	1	0.94	1	0.93	1	0.64
C3: N (4, 5) vs. N + P (8, 9)	1	0.28	1	0.73	1	0.06	1	0.28	1	**<0.01**	1	0.56	1	0.26	1	**<0.01**	1	0.60
C4: P (6) vs. P + N (9)	1	0.16	1	**<0.01**	1	0.98	1	0.15	1	0.54	1	0.37	1	**0.03**	1	**0.05**	1	0.14
C5: N linear effect	1	0.20	1	**<0.01**	1	**0.02**	1	**<0.01**	1	0.97	1	0.91	1	**<0.01**	1	**<0.01**	1	0.21
C6: N quadratic effect	1	0.85	1	0.26	1	0.15	1	0.42	1	0.79	1	0.95	1	0.70	1	0.08	1	0.16
C7: P linear effect	1	0.31	1	**<0.01**	1	0.31	1	0.99	1	**<0.01**	1	0.37	1	0.73	1	**<0.01**	1	0.70
C8: P quadratic effect	1	0.28	1	0.49	1	0.86	1	0.28	1	0.19	1	0.94	1	0.93	1	0.06	1	0.46

Note: Numbers in parentheses refer to treatments in Table 1; degrees of freedom (df) are adjusted for missing values; values in bold emphasize significant differences ($P < 0.05$).

Statistical analyses

Two-way ANOVAs for complete randomized block design were performed to analyze the effect of fertilization on net aboveground primary production, total N and P concentration, N/P ratios, and N and P content in plant tissues for graminoids and mosses. We also evaluated the effect of fertilization on N and P concentration and N/P ratios in peat and on tiller and flower densities of graminoid plants. Eight a-priori contrasts (called C1 to C8) were run (see Tables 2 to 4). Significant probability levels were set to $\alpha = 0.05$. Data were tested for homogeneity and normality and transformed when necessary. All analyses were conducted using the general linear model procedure of SAS Software (SAS Institute Inc. 2003).

Results

Single nutrient effect

Addition of N at levels ranging from 1 to 5 g·m^{-2} caused an increase in net aboveground primary production and tiller density of graminoid plants (C5 and C6 in Table 2; Fig. 1). Increases in primary production and tiller density were noticeable only when N_H was applied, and both values were about twice as high as in the controls. Addition of P had no effect on net aboveground primary production of graminoids (C7 and C8 in Table 2; Fig. 1). Net primary production of mosses was not affected by specific N and P additions (C5 to C8 in Table 2; Fig. 1), but a slight trend was noted for increased moss production under all N additions. This trend was confirmed by the finding that overall moss production was generally higher in experimental units that received nutrients compared with the control (C1 in Table 2). Nutrient additions had no effect on flower density of graminoids (Table 2).

The total N concentration of graminoids did not increase when N was applied (treatment effect, $P = 0.19$; Table 3; Fig. 2). However, total P concentration of graminoids was lower in nutrient-addition treatments than in the control (C1 and C5 in Table 3; Fig. 2; 26% lower in N_H than in the control). Overall, N and P concentration of mosses were significantly higher in the nutrient-addition treatments than in control units (C1 in Table 3). N concentration of mosses increased linearly with addition of N (C5 in Table 3; Fig. 2; 56% higher under N_H compared with the control), and concentrations of both N and P in mosses increased linearly with the level of P addition (C7 in Table 3; Fig. 2; increases of 33% and 281%, respectively, for P_H compared with the control). Finally, nutrient concentration of peat increased linearly with addition of N (C5 in Table 3; 17% higher in N_H compared with the control). N/P ratios of graminoids and mosses changed significantly under N addition (increase of 98% for graminoids and 58% for mosses in N_H compared with the control; C5 in Table 3; Fig. 2) and P addition (only for mosses, 3 times lower in P_H compared with the control; C7 in Table 3; Fig. 2), but no change was found for N/P ratios of peat (C5 to C8 in Table 3).

When combining information on nutrient concentration and primary production, we found that the N content in plant tissues was 2 times higher for both graminoids and mosses (N_H compared with the control; C5 and C6 in Table 4; Fig. 3). However, the effect of N addition was mainly

Table 4. Results of two-way ANOVAs and *a-priori* contrasts to evaluate the effect of nutrient additions on N and P content in plant tissues of graminoid plants and mosses after two growing seasons.

	N content				P content			
	Graminoid		Moss		Graminoid		Moss	
Source of variation	df	*P*	df	*P*	df	*P*	df	*P*
Block	5		5		5		5	
Treatment	8	**<0.01**	8	**<0.01**	8	0.25	8	**<0.01**
Error	40		33		38		33	
Total	53		46		51		46	
Contrasts								
C1: Control (1) vs. Other treatments (2 to 9)	1	0.38	1	**<0.01**	1	0.82	1	**<0.01**
C2: Control (1) vs. Faeces (2)	1	0.74	1	0.34	1	0.89	1	0.31
C3: N (4, 5) vs. N + P (8, 9)	1	**<0.01**	1	**<0.01**	1	0.28	1	**<0.01**
C4: P (6) vs. P + N (9)	1	0.30	1	**<0.01**	1	0.84	1	**0.04**
C5: N linear effect	1	**<0.01**	1	**<0.01**	1	0.06	1	0.44
C6: N quadratic effect	1	**0.02**	1	**0.05**	1	0.07	1	0.45
C7: P linear effect	1	0.63	1	**0.03**	1	0.88	1	**<0.01**
C8: P quadratic effect	1	0.63	1	0.12	1	0.75	1	**0.02**

Note: Numbers in parentheses refer to treatments in Table 1; degrees of freedom (df) are adjusted for missing values; values in bold emphasize significant differences ($P < 0.05$).

seen under N_H for graminoids. Under P addition, P content in plant tissues changed only for mosses (over 4 times higher in P_H compared with the control; C7 and C8 in Table 4; Fig. 3).

Addition of faeces had no effect on primary production of graminoid plants and mosses, nor on tiller and flower densities of graminoids (C2 in Table 2; Fig. 1). Also, addition of faeces did not cause any increase in total N nor P concentration or N/P ratios of graminoid plants, mosses and peat (C2 in Table 3; Fig. 2).

Synergistic effect of combined N + P additions

A synergistic effect of N + P addition on the primary production of graminoid plants was detected compared with N added alone, but not for P (C3 and C4 in Table 2; Fig. 1); production decreased by 45% under N_HP_I by comparison with N_H. In contrast, moss production was higher in combined N + P addition than when N was added singly (C3 in Table 2; Fig. 1); it was 55% higher for N_IP_L and 21% higher for N_HP_I. However, no synergistic effect on moss production was found compared with single P addition (C4 in Table 2; Fig. 1).

N + P addition had no effect on total N or P concentration in graminoid plants compared with single N or P addition (C3 and C4 in Table 3; Fig. 2). In contrast, total N concentration of mosses was 45% higher when N and P were added together (N_HP_I) than when P was added singly (C4 in Table 3; Fig. 2). Phosphorus concentration of mosses was also higher when P was applied with N than when N was added alone (C3 in Table 3; Fig. 2); it was 46% higher under N_IP_L and 107% higher when added at N_HP_I. The consequence was that for mosses, the N/P ratio decreased significantly under combined N + P addition compared with N added singly, but increased compared with P added singly (C3 and C4 in Table 3; Fig. 2). Similarly, the N/P ratio of graminoids also increased under combined N+P addition compared with P added singly, but did not change compared with N added singly (C3 and C4 in Table 3; Fig. 2).

Combining information on nutrient concentration and primary production revealed that the N content of mosses increased under a combined N + P addition compared with N alone, whereas the P content showed the opposite trend compared with P alone (C3 and C4 in Table 4; Fig. 3). For graminoids, the N content in plant tissues decreased under combined N + P addition compared with N added alone, but did not change compared with P added alone (C3 and C4 in Table 4; Fig. 3).

Discussion

We found that graminoid plants in polygon fens of Bylot Island are N-limited, whereas mosses show no N or P limitations (see also Pineau 1999). Nonetheless, our experimental results showed that the aboveground primary production of vascular plants was not promoted by a low level of N addition, and that a N level of 5 $g \cdot m^{-2}$ was required to have a positive effect on graminoid production. Phosphorus additions varying from 1 to 3 $g \cdot m^{-2}$ had no effect on graminoid growth. Both N and P addition had a marginal effect on the growth of the moss layer, but most noticeably, bryophytic tissues showed increased N and P concentration, suggesting that these nutrients were absorbed by leaves. The absence of a growth response by arctic graminoids under low N addition is therefore likely explained by the presence of a moss carpet.

Because nutrients in arctic polygon fens are deposited on the moss carpet, bryophytes are the first organisms to capture nutrients. Owing to the high exchange capacity of moss cell walls (Clymo 1963) and their ability to absorb nutrients directly through the cellular surface, mosses act like a natural barrier by sequestering added nutrients and constraining movement down the soil profile to the roots of vascular plants. As the level of N addition increased in our experiment, bryophytes absorbed an increasing amount of N up to a saturation point. Our results suggest that when N addition reached 5 $g \cdot m^{-2}$, the absorption capacity of mosses was exceeded. Moreover, modest but sustained nutrient addition, such as that used in our experiment, can significantly alter the nutrient recycling behaviour of bryophytes (Phuyal et al. 2008). Under such conditions, a surplus of nutrients can seep down to the rooting zone of graminoids, as shown by the increased N concentration of peat. Consequently, additional N then becomes available for vascular plants, which resulted in an increase in production, tiller density, N content in tissues, and N/P ratio of graminoids.

Moss constraints on nutrient cycling in arctic wetlands

Several fertilization experiments have been conducted in arctic freshwater wetlands over the last 30 years. Henry et al. (1986) showed that graminoids responded weakly to fertilization in wet sedge meadows with a moss layer on Ellesmere Island, and moderately at a site dominated by *Cassiope tetragona* (L.) D. Don, where a thin organic layer was present, despite moderately high level of fertilization (N and P ranged from 5 to 25 g·m^{-2}). However, a strong response by graminoids and forbs was found at all levels of fertilization in a site dominated by *Dryas integrifolia* Vahl, where organic layers were absent. The results of Henry et al. (1986) thus support the hypothesis that the response of graminoid plants to fertilization in tundra wetlands is modulated by the presence of a moss layer. Similarly, most fertilization experiments conducted in wetlands dominated by mosses found no effect on graminoid growth or nutrient concentration when N was applied at a level below 5 g·m^{-2}, either alone or with P (see Appendix A, Table A2). Haag (1974), however, observed a positive response with a N dose of 3.4 g·m^{-2}, based on two replicates only 1.5 m apart. In a rich Norwegian fen dominated by brown mosses, N addition of 20.7 g·m^{-2} were still not sufficient to promote growth of graminoids (Øien 2004). In addition, a positive response to P addition was only reported at levels above 3 g·m^{-2}, either when applied alone or with N (see Appendix A, Table A2).

Experiments with ^{15}N have provided additional evidence for the role of mosses in the absorption of nutrients in these ecosystems. In a tussock tundra of northern Alaska, ^{15}N was immediately taken up by mosses following application, but absorption rate declined over time. In contrast, vascular plants showed a slow, steady increase in ^{15}N uptake throughout the 2 months of the experiment, mostly owing to weak absorption by the brown moss compartment (Marion et al. 1982). Kotanen (2002) showed that bryophytes absorbed the majority of ^{15}N when added to the soil surface of polygon fens, whereas graminoids absorbed more ^{15}N than bryophytes when nutrients were applied below the growing layer of mosses. In a moist tussock tundra, the growth response of graminoids and *Betula nana* L. was greater in a moss removal treatment with and without fertilization compared with the control (Hobbie et al. 1999; Bret-Harte et al. 2004). An increase of soil nutrient availability was also found in plots without mosses. Collectively, these studies provide strong evidence that mosses benefit more readily than vascular plants from surface addition of N, which is consistent with our results from arctic polygon fens.

In contrast, mosses in our study system were apparently not saturated by P addition at the levels tested because P concentration in plant tissue of graminoids showed little increase, and no enhancement of P concentration was found in

Fig. 1. Effect of annual N and P additions on primary production of graminoid plants and mosses, and effect of annual N additions on tiller density of graminoid plants after two growing seasons. Each data point is a mean value and pooled SEs of treatments are presented. Linear or quadratic effects of N additions are shown by solid (graminoids) or broken (mosses) lines when significant. See Table 2 for *P* values (*n* = 24 in all cases).

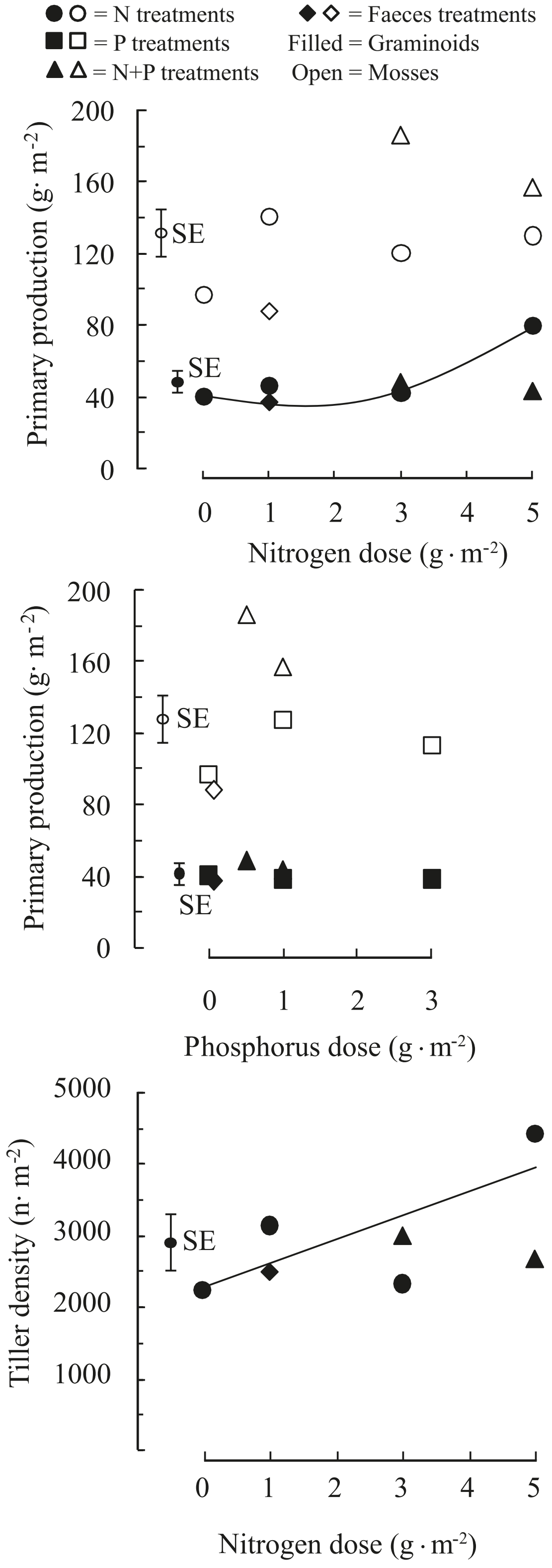
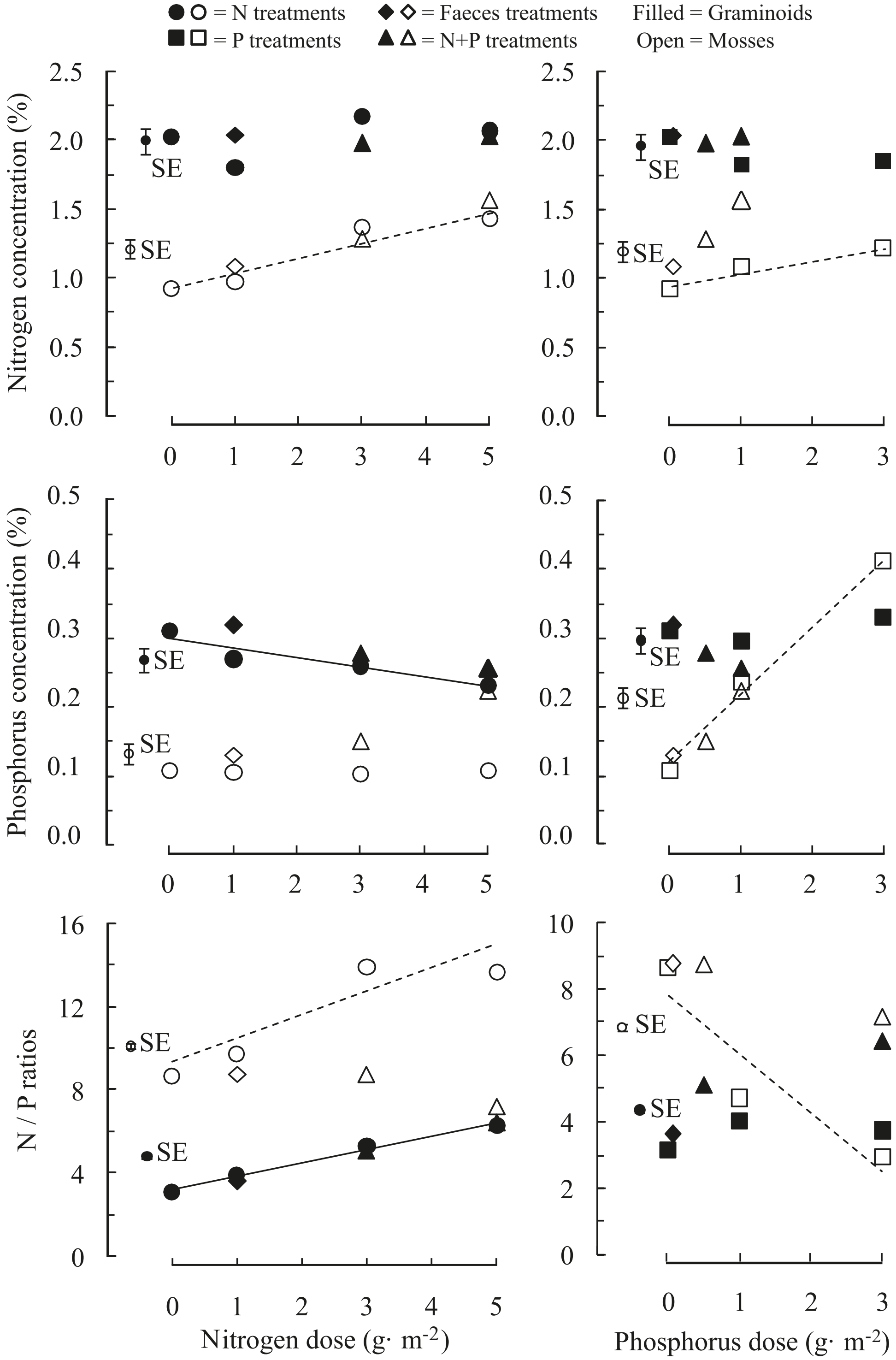
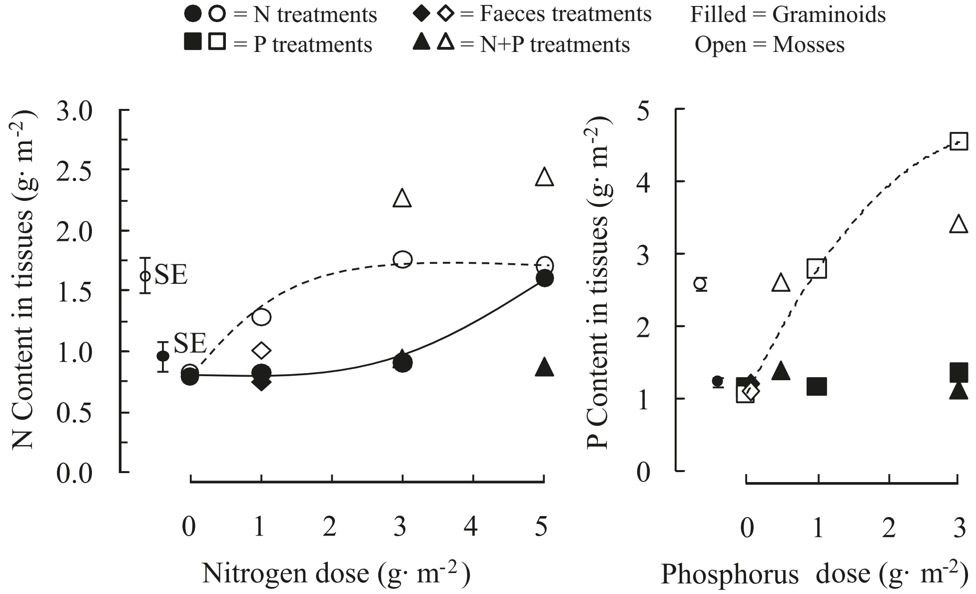


Fig. 2. Effect of annual nutrient additions on total N and P concentration, and on N/P concentration ratios of graminoid plants and mosses after two growing seasons. Each data point is a mean value, and pooled SEs of treatments are presented. Linear effects of N and P additions are shown by solid (graminoids) or broken (mosses) lines when significant. See Table 3 for *P* values (*n* = 24 in all cases).



peat. Phosphorus concentration and content in moss tissues showed an important increase, but no plateau was reached as we showed for N concentration or content. Consequently, no extra P was available in peat for graminoid growth. Except for nutrient concentrations in moss tissues, no direct effect of P was detected on mosses or graminoids, but this nutrient may still have indirectly enhanced the growth of graminoids via processes that promote the uptake and assimilation of N. We did find that moss primary production increased more when N was added in combination with P than when it was added alone. Indeed, P addition can improve N acquisition and retention in plants of floating fens (Güsewell et al. 2002, 2003; Reed et al. 2007) and increase interception of atmospheric N (Lamers et al. 2000). Phos-

Fig. 3. Effect of annual nutrient additions on N and P content in plant tissues for graminoid plants and mosses after two growing seasons. Each data point is a mean value and pooled SEs of treatments are presented. Linear or quadratic effects of N and P additions are shown by solid (graminoids) or broken (mosses) lines when significant. See Table 4 for *P* values (*n* = 24 in all cases).



phorus may be rapidly immobilized, to be released slowly when plants need additional inputs of P to maintain growth under increasing N depositions (van der Hoek et al. 2004). However, the decrease in graminoid primary production when N was added with P is difficult to explain, as perhaps another nutrient limitation appeared. Also, in other ecosytems, fertilization increased competition (Berendse 1983), changed plant interactions (Levine et al. 1998), or decreased species richness (Rajaniemi 2002), and these processes may have contributed to the decline in graminoid production.

The role of mosses in plant–herbivore interactions

Nutrient leaching from herbivore faeces is a natural surface addition that occurs frequently in ecosystems. Some studies have reported a fertilizing effect of faeces on vascular plants in arctic environments, but not always (Gauthier et al. 2006). Bazely and Jefferies (1985) reported a positive effect of goose faeces on graminoid production in the salt marshes of La Pérouse Bay (Manitoba, Canada), where plants grow directly on mineral soil without a moss layer. However, studies carried out in mossy polygon fens at our study site showed no response of graminoids to additions of goose faeces (Beaulieu et al. 1996; Pineau 1999; this study). A lack of response may occur simply because the faecal density was too low. In an Alaskan salt marsh, Zacheis et al. (2002) concluded that a density of 1.8 faeces·m^{-2} was too low to promote plant growth. However, the density used in our experiment was relatively high, since it represented 6 times the mean density recorded at our study site over the 1991–2006 period (6.9 faeces·m^{-2}, Gauthier et al. 1995; G. Gauthier, unpublished. data). Therefore, it appears unlikely that faecal density alone could explain the lack of response of graminoid plants to this treatment. Although we cannot rule out the possibility that the effect of faeces was too localized to be detected by our sampling method, the absence of an effect of faeces is consistent with the results of our fertilization experiment at a similar nutrient level. We therefore suggest that goose faeces, as nutrient additions, did not stimulate the growth of graminoids in our experiment because of the presence of a moss layer in the freshwater wetlands. Unlike mineral soil found in tidal flats, mosses can restrict the uptake of mineralized N by vascular plants.

Greater Snow Geese grazing in polygon fens of Bylot Island remove a significant amount of the annual plant production (Gauthier et al. 1995; Massé et al. 2001;[2]) and have a considerable impact on the species composition of this community (Gauthier et al. 2004, 2006). Even though goose faeces can provide a significant amount of nutrients, this level is apparently not sufficient to enhance vascular plant growth. Based on the mean faecal density (see above), geese add approximately 0.18 g·m^{-2} of N and 0.01 g·m^{-2} of P per year on Bylot Island, which is far below the levels at which graminoids showed a positive response (5 g·m^{-2} of N). Thus, the moss constraint on nutrient recycling appears a key factor to explain why grazed plants in polygon fens showed only a compensatory response (Gauthier et al. 1995), rather than an overcompensatory response, as found in grazed salt marshes (Cargill and Jefferies 1984; Hik and Jefferies 1990). In polygon fens, graminoid plants are able to develop new tillers after goose grazing, but production never surpasses that of ungrazed plants (Beaulieu et al. 1996). To explain the lack of overcompensatory growth in this ecosystem, it has been suggested that either grazing occurs too late in the season, when the regrowth capacity of graminoid plants is

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[2] See also L.Valéry, M.-C. Cadieux, and G. Gauthier. Spatial heterogeneity of primary production in wetland tundra as both cause and consequence of foraging patterns of an expanding Greater Snow Goose breeding colony (Bylot Island, NU, Canada). Submitted for publication in Ecoscience.

low, or the moss carpet sequestered nutrients released from goose faeces over an extended period (Gauthier et al. 1995; Beaulieu et al. 1996). Our study supports the second hypothesis. Grazed plants must draw upon reserves to regrow and do not have immediate access to nutrients released by goose faeces, which are easy to assimilate.

In conclusion, the two-level trophic model developed for geese and graminoid plants in arctic salt marshes does not appear directly applicable to freshwater wetlands with a dense carpet of bryophytes (Gauthier et al. 2006). Bryophyte communities modify the two-level interaction into a more complex, three-level trophic interaction where mosses sequester the nutrients added by goose faeces, to the detriment of grazed vascular plants. Nutrient additions thus benefit bryophytes in the short-term and promote accumulation of nutrients in their tissues. Eventually, nutrients should be slowly released from below the moss compartment through decomposition and gradually transferred to the roots of graminoid plants, as suggested for other moss-dominated communities (Marion et al. 1982; Li and Vitt 1997). However, the rate and time frame at which this transfer occurs remains unknown. Longer-term experiments are required to explore the effects of sustained nutrient addition on production and decomposition of both bryophytes and graminoid plants to elucidate nutrient turnover in arctic polygon fens.

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Appendix A

Appendix A, Table A2 appears on the following pages.

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Table A1. List of species and mean percentage cover in experimental units with control treatment after one growing season during the vegetation peak (measured in four 25 cm × 25 cm quadrats in each unit, *n* = 24).

Vascular plants	Cover (%)	Bryophytes	Cover (%)
Graminoids	$\sim$9	**Brown mosses**	$\sim$93
Arctagrostis latifolia (R. Br.) Griseb.	+	*Aulacomnium palustre* (Hedw.) Schwägr.	+
Carex aquatilis Wahlenb. var. *stans* (Drejer) Boott	1	*Aulacomnium turgidum* (Wahlenb.) Schwägr.	1
Dupontia fisheri R. Br.	6	*Brachythecium turgidum* (Hartm.) Kindb.	1
Eriophorum scheuchzeri Hoppe	2	*Bryum algovicum* Sendtn. ex Müll. Hal. var. *algovicum*	1
Non-graminoids	+	*Bryum cryophilum* (Schwägr.) Bruch & Schimp.	+
Cardamine pratensis L.	+	*Calliergon giganteum* (Schimp.) Kindb.	+
Pedicularis sudetica Willd. subsp. *albolabiata* Hultén	+	*Campylium stellatum* (Hedw.) C.E.O. Jensen var. *arcticum* (R.S. Williams) Sav.-Ljub.	2
Ranunculus hyperboreus Rottb.	+	*Cinclidium arcticum* Bruch & Schimp.	13
Salix arctica Pall.	+	*Drepanocladus* sp.	73
Saxifraga cernua L.	+	*Meesia triquetra* (L. ex Jolycl.) Ångstr.	1
Stellaria longipes Goldie	+	*Oncophorus wahlenbergii* Brid.	+
		Polytrichum swartzii Hartm.	1
		Sphagnum sp.	+
		Hepatics	+

Note: Cover of < 1% is indicated by +.

Table A2. Synthesis of nutrient addition experiments carried out on graminoid plants in tundra wetlands that clearly indicated the presence of a dominant mossy ground layer or a well-developed organic soil.

			Treatments				
Author(s), habitat(s), and study site(s)	Parameters measured after *t* growing seasons	Graminoid plants	N	P	NP	NPK	Faeces
Bazely and Jefferies (1985)[a]	Production (*t* = 1)	*Puccinellia phryganodes* (Trin.) Scribn. & Merr., *Carex subspathacea* Wormsk. ex Hornem.	●	●	●	●	+
Tidal flat; (*n* = 5), La Pérouse Bay, Manitoba	N content (*t* = 1)		●	●	●	●	+
Beaulieu et al. (1996)[b]	Production (*t* = 1)	*Dupontia fisheri* R. Br., *Eriophorum scheuchzeri* Hoppe	●	●	●	●	ns
Low polygon fen; (*n* = 4), Bylot Island, Nunavut	N concentration (*t* = 1)		●	●	●	●	ns
Chapin et al. (1975)[c,d]	Production (*t* = 1)	*D. fisheri, Eriophorum angustifolium* Honck., *Carex aquatilis* Wahlenb.	●	●	●	ns	●
Low polygon fen; (*n* = 2), Barrow, Alaska			●	●	●	+	●
	N concentration (*t* = 1)		●	●	●	ns	●
	P concentration (*t* = 1)		●	●	●	+	●
Gough and Hobbie (2003)[e]	Production (*t* = 4)	All graminoid plants	+	ns	+	●	●
Moist, non-acidic tundra; (*n* = 3), Toolik Lake, Alaska	Cover (*t* = 4)		+	ns	+	●	●
Haag (1974)[f]	Production (*t* = 1)	*Carex rariflora* (Wahlenb.) Sm., *Carex chordorrhiza* Ehrh. ex L. f., *E. scheuchzeri, E. angustifolium*	+	–	+	●	●
Low polygon fens; (*n* = 2), Tuktoyaktuk, Northwest Territories							
Henry et al. (1986)[g,h]	Production (*t* = 3)	*Carex membranacea* Hook., *E. angustifolium*	ns	●	●	ns	●
Wet sedge meadow; (*n* = 2), Alexandra fjord, Nunavut		*C membranacea*	ns	●	●	+	●
Mack et al. (2004)[i]	Production (*t* = 20)	Vascular plants	●	●	+	●	●
Moist, acidic tundra; (*n* = 4), Toolik Lake, Alaska	N content (shoot) (*t* = 20)		●	●	+	●	●
	N content (root) (*t* = 20)		●	●	+	●	●
McKendrick et al. (1978)[j]	Leaf mass·tiller^{-1} (*t* = 1)	*D. fisheri*	+	ns	+	●	●
Moist tundra; (*n* = 1), Footprint Creek, Alaska	N concentration (*t* = 1)		+	ns	+	●	●
	P concentration (*t* = 1)		ns	+	+	●	●
Øien (2004)[k]	Production (site 1 and 2) (*t* = 2)	All graminoid plants	ns	ns	ns	●	●
Rich fen; (*n* = 3), Sølendet Nature Reserve, Norway	Production (site 3) (*t* = 2)		ns	ns	+	●	●
	Tiller density (site 1 and 2) (*t* = 2)		ns	ns	ns	●	●
	Tiller density (site 3) (*t* = 2)		ns	ns	+	●	●
Shaver and Chapin (1995)[j]	Leaf mass·tiller^{-1} (*t* = 2, 3, 4)	*E. angustifolium, C. aquatilis*	+	ns	ns	●	●
Wet sedge tundra; (*n* = 4)	N concentration (*t* = 2)		+	●	ns	●	●
Atigun River, Alaska	P concentration (*t* = 2)		●	+	+	●	●

Table A2 (*concluded*).

Author(s), habitat(s), and study site(s)	Parameters measured after *t* growing seasons	Graminoid plants	Treatments				
			N	P	NP	NPK	Faeces
Shaver and Chapin (1995)[o]	Leaf mass·tiller^{-1}(t = 3)	*E. angustifolium*	+	+	+	●	●
Wet sedge tundra; (n = 4), Franklin Bluffs, Alaska	Leaf mass·tiller^{-1} (t = 2, 3, 4)	*C. aquatilis*	ns	+	+	●	●
	N concentration (t = 2)	*C. aquatilis*	+	●	ns	●	●
	P concentration (t = 2)	*C. aquatilis*	●	+	+	●	●
Shaver and Chapin (1995)[o]	Leaf mass·tiller^{-1} (t = 1)	*E. angustifolium*	ns	ns	ns	●	●
Wet sedge tundra; (n = 4), Slope Mountain, Alaska	Leaf mass·tiller^{-1} (t = 2, 3, 4)		ns	+	+	●	●
Shaver and Chapin (1995)[o]	Leaf mass·tiller^{-1} (t = 1)	*E. angustifolium*	ns	ns	ns	●	●
Wet sedge tundra; (n = 4), Pump 2, Alaska	Leaf mass·tiller^{-1} (t = 2, 3, 4)		+	+	+	●	●
	N concentration (t = 2)		ns	●	ns	●	●
	P concentration (t = 2)		●	+	+	●	●
van Heerwaarden et al. (2003)[o]	N concentration (t = 4)	*Eriophorum vaginatum* L.	+	●	●	●	●
Ombrotrophic part of bog (n = 8), Stordalen, Sweden	P concentration (t = 4)		–	●	●	●	●
Pineau (1999)[o]	Production (t = 2)	*C. aquatilis, D. fisheri, E. scheuchzeri*	+	ns	+	●	ns
Low polygon fen; (n = 5), Bylot Island, Nunavut	Tiller density (t = 1)		+	ns	+	●	ns
	N concentration (t = 2)		+	●	+	●	ns
	P concentration (t = 2)		●	+	ns	●	ns
This study[o]	Production (t = 2)	*D. fisheri, E. scheuchzeri*	+	ns	–	●	ns
Low polygon fen; (n = 6), Bylot Island, Nunavut	Tiller density (t = 2)		+	ns	ns	●	ns
	N concentration (t = 2)		ns	ns	ns	●	ns
	P concentration (t = 2)		+	ns	ns	●	ns

Note: The site in Bazely and Jefferies (1985) study had no mossy ground layer or well-developed organic soil, but is included for faecal treatment comparisons. ●, no data; ns, no significant effect; +, positive effect; –, negative effect.

[a] Positive response for treatments of ca. 100, 300, or 575 g·m^{-2} of faeces.

[b] Faeces added 3 times throughout the growing season by goslings grazing in experimental enclosures.

[c] Treatment NPK = 9 g·m^{-2} of N + 4.5 g·m^{-2} of P + 7.2 g·m^{-2} of K.

[d] Treatment NPK = 3.6 g·m^{-2} of N + 14.4 g·m^{-2} of P + 4.5 g·m^{-2} of K.

[e] Treatment N = 10 g·m^{-2}; treatment P = 5 g·m^{-2}; treatment NP = 10 g·m^{-2} of N + 5 g·m^{-2} of P.

[f] Treatment N = 3.4 g·m^{-2}; treatment P = 2 g·m^{-2}; treatment NP = 3.4 g·m^{-2} of N + 2 g·m^{-2} of P.

[g] Treatment N = 5 g·m^{-2}; treatment NPK = 5 g·m^{-2} of N + 5 g·m^{-2} of P + 5 g·m^{-2} of K; aboveground phytomass for green parts only.

[h] Treatment N = 25 g·m^{-2}; treatment NPK = 25 g·m^{-2} of N + 25 g·m^{-2} of P + 25 g·m^{-2} of K; aboveground phytomass for green parts only.

[i] Treatment NP = 10 g·m^{-2} of N + 5 g·m^{-2} of P.

[j] Treatment N = 20.7 g·m^{-2}; treatment P = 14.7 g·m^{-2}; treatment NP = 20.7 g·m^{-2} of N + 14.7 g·m^{-2} of P.

[k] Treatment N = 12 g·m^{-2}; treatment P = 3 g·m^{-2}; treatment NP = 12 g·m^{-2} of N + 3 g·m^{-2} of P.

[l] Treatment N = 25 g·m^{-2}; treatment P = 25 g·m^{-2}; treatment NP = 25 g·m^{-2} of N + 25 g·m^{-2} of P.

[m] Treatment N = 10 g·m^{-2} of N.

[n] Treatment N = 10 g·m^{-2}; treatment P = 3 g·m^{-2}; treatment NP = 10 g·m^{-2} of N + 0.6 g·m^{-2} of P; treatment faeces = ca. 500 g·m^{-2}; treatments of 1 g·m^{-2} of N and 0.6 g m^{-2} of P were also tested but induced no response.

[o] Treatment N = 5 g·m^{-2}; treatment P = 3 g·m^{-2}; treatments NP = 3 g·m^{-2} of N + 0.5 g·m^{-2} of P or 5 g·m^{-2} of N + 1 g·m^{-2} of P; treatment faeces = ca. 500 g·m^{-2}; treatments of 1 and 3 g·m^{-2} of N and 1 g·m^{-2} of P were also tested but induced no response.