

# Fates of Added Nitrogen in Freshwater Arctic Wetlands Grazed by Snow Geese: The Role of Mosses

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## Abstract

Previous studies have shown that the growth of freshwater grasses and sedges eaten by breeding colonies of Snow Geese responds weakly to nitrogen additions, and also is poorly able to compensate within the same season for tissues lost to geese. These results contrast with the rapid responses to grazing and fertilization that have been observed in salt-marsh species. A possible explanation is that the mosses prominent in freshwater wetlands rapidly sequester added nitrogen, preventing access by forage species to the fecal inputs provided by foraging geese. To investigate this hypothesis, I added ecologically realistic amounts of ammonium and nitrate labelled with  $^{15}\text{N}$  to the surface and rooting zone of experimental plots in freshwater wetland vegetation at two Snow Goose colonies. Results indicate that the presence of mosses did not prevent forage species from rapidly taking up ammonium and nitrate added either at or below the moss surface. Nonetheless, most of the added  $^{15}\text{N}$  was absorbed by the moss layer; consequently, mosses tend to divert nitrogen away from forage species and into long-lasting peat. In the long term, this may reduce the ability of freshwater forage plants to recover from damage by increasing populations of Snow Geese.

## Introduction

The effects of foraging by Snow Geese (*Chen caerulescens* L.) on the vegetation close to their arctic breeding colonies depend upon the habitat considered. In northern salt-marshes, plant growth tends to be N-limited (Cargill and Jefferies, 1984a; Bazely and Jefferies, 1985; Nadelhoffer et al., 1992), but goose feces provide a rich source of available nitrogen (Bazely and Jefferies, 1985; Ruess et al., 1989; Hik and Jefferies, 1990). This fecal N enables forage plants (primarily grasses and sedges) to promptly replace the tissues that are consumed; if grazing intensity is moderate, the result can be increased primary production relative to ungrazed vegetation (Cargill and Jefferies, 1984b; Hik and Jefferies, 1990; Hik et al., 1991). This model contrasts with goose-plant interactions in arctic freshwater wetlands, which respond weakly to both foraging geese and nutrient additions. In the Snow Goose colony at Bylot Island, Nunavut Territory, foraging by geese fails to increase growth of freshwater grasses and sedges (Gauthier et al., 1995, 1996; Beaulieu et al., 1996), and consistent growth responses were not observed when droppings (Beaulieu et al., 1996) or inorganic N (Pineau, 1999) were added at 1 to 2 times natural rates of availability. Similarly, at La Pérouse Bay, Manitoba, foraging by geese increases leaf production of freshwater sedges (Kotanen and Jefferies, 1989a, 1989b), but this increase is small compared to that observed for salt-marsh sedges (Kotanen and Jefferies, 1987). Rapid responses to fertilization can occur in freshwater species, but only when nutrients are added at rates far above natural values. Pineau (1999) detected significant within-season growth responses of sedge fen species when inorganic N was added at 20 times the natural rate of N addition by geese in preferred habitats. Similarly, Manseau and Gauthier (1993) demonstrated enhanced within-season growth when nitrogen was added as NPK fertilizer at 5.5 times the natural rate.

Mosses are scarce in salt-marshes, but frequently are the

dominant ground cover in other northern ecosystems including boreal forests and peatlands, where they rapidly absorb and sequester inorganic nitrogen (Van Cleve and Alexander, 1981; Oechel and Van Cleve, 1986; Longton, 1988; Bonan and Shugart, 1989; Jonasson and Shaver, 1999) and probably some organic nitrogen as well (Kielland, 1997). Mosses are abundant in freshwater wetlands exploited by Snow Geese, and form dense carpets in heavily used areas (Kerbes et al., 1990; Jefferies, 1988a, 1988b; Kotanen and Jefferies, 1997), probably in response to increased light and reduced competition with forage plants (Jonasson, 1992). It has been suggested that freshwater grasses and sedges may be poorly able to respond to geese because nutrients released from goose feces are taken up instead by the surface layer of mosses (Gauthier et al., 1995, 1996; Beaulieu et al., 1996; Pineau, 1999), which either outcompete forage species or simply act as nutrient sinks. In freshwater wetlands with dense moss layers, the net result may be that nutrients are available to forage species only when they are added at rates far above natural values. These amounts may saturate the moss layer, and also may reduce the soil C:N ratio, promoting mineralization of organic N (Binkley and Hart, 1989; Li and Vitt, 1997).

This study is a first step towards describing the nutrient dynamics of freshwater wetlands exploited by Snow Geese. I used experimental tracer additions of  $^{15}\text{N}$  (Schimel, 1993; Lajtha and Michener, 1994; Robinson, 2001) at two widely separated locations (Bylot Island and La Pérouse Bay) to investigate whether mosses may prevent forage species from accessing the nitrogen made available by geese. The principal question I addressed was whether forage species can access inorganic nitrogen when it is added to the moss surface at concentrations reasonable in grazed communities. In addition, I investigated whether injecting inorganic nitrogen beneath the moss surface improves uptake by forage species, as might be expected if liv-

ing mosses normally absorb surface-added nutrients before they penetrate as deeply as the roots of forage plants.

## Materials and Methods

### STUDY SITES

#### Bylot Island

A 50-km<sup>2</sup> valley on the western coastal plain of Bylot Island (73°08'N, 80°00'W—hereafter "Bylot") is a major brood-rearing area for the largest breeding colony of Greater Snow Geese (*Chen caerulescens atlanticus*), currently numbering more than 69,000 nesting adults (Gauthier et al., 1996). Low-lying regions are dominated by wet low-center polygons, typically 10 to 20 m in diameter, which frequently contain mossy freshwater fens. These fens and polygon margins support a variety of graminoids (*Dupontia fisheri* R. Br., *Carex aquatilis* Wahlenb. var. *stans* Drej., *E. scheuchzeri* Hoppe, and other *Eriophorum* spp.), set in a dense carpet of mosses (mainly *Drepanocladus revolvens* (Sw.) Warnst. but also *Drepanocladus brevifolius* (Lindb.) Warnst., *Calliergon giganteum* (Schimp.) Kindb., and *Sphagnum subsecundum* Nees in Sturn.). These habitats are intensively grazed by Snow Geese, primarily after hatch; the most important food plants are *D. fisheri* and *E. scheuchzeri* (Gauthier, 1993; Manseau and Gauthier, 1993; Hughes et al., 1994a, 1994b; Gauthier et al., 1995, 1996). The exact location of this colony differs from year to year, as the main nesting area shifts to different areas of the coastal plain (Lepage et al., 1996); however, the same posthatch foraging habitats are exploited each year.

#### La Pérouse Bay

La Pérouse Bay (58°04'N, 94°03'W—hereafter "LPB") is located on the Hudson Bay coast about 25 km east of Churchill, Manitoba. This site is in the core of a colony of Lesser Snow Geese (*Chen caerulescens caerulescens*) which has increased from just under 2000 pairs in 1968 (Cooke et al., 1995) to an estimated 44,500 pairs in 1994 (K. Abraham, R. F. Rockwell, and K. Ross, unpublished survey). Coastal areas are dominated by *Puccinellia phryganodes* (Trin.) Scribn. & Merr.—*Carex subspathacea* Wormskj. salt-marshes which gradually have been converted to mudflats as the colony has grown and geese have increasingly overexploited their foraging areas (Cooch et al., 1991, 1993; Williams et al., 1993; Srivastava and Jefferies, 1996; Abraham and Jefferies, 1997; Jano et al., 1998). Inland, much of the landscape consists of shrubby *Salix-Betula-Myrica* vegetation containing a mosaic of freshwater ponds and carpets of saturated moss (mostly *Drepanocladus uncinatus* (Hedw.) Warnst. and *Aulacomnium* spp.) supporting *Carex* spp. together with small amounts of *Dupontia*, *Eriophorum* spp., and other graminoids (Jefferies, 1988a, 1988b; Kotanen and Jefferies, 1989a, 1997). Traditionally, breeding birds relied on salt-marsh species for forage during most of the summer, though both breeders and staging migrants used freshwater sedge meadows as a source of forage in spring and late summer (Jefferies, 1988a, 1988b; Kotanen and Jefferies, 1989a, 1989b, 1997). However, as the colony has grown and intertidal marshes have been degraded, geese increasingly have nested and foraged in freshwater wetlands. Many *Carex* spp. are consumed, but *C. aquatilis* is the principal freshwater forage species.

### EXPERIMENTAL METHODS

I established five experimental plots at Bylot on 23–24 June 1997, each located in a different low-center polygon. Each plot

was positioned in an area containing a saturated moss carpet with populations of *D. fisheri* and *E. scheuchzeri*. I created a similar set of five experimental plots at LPB on 10–11 August, 1997 in depressions containing sparse populations of *C. aquatilis* set in similar but shallower moss carpets. At both sites, each plot contained 10 saturated moss-peat monoliths separated from one another by 50 to 100 cm. These monoliths were created by confining existing peat and vegetation in situ with an open-ended aluminum sheeting cylinder measuring 250 cm<sup>2</sup> in area × 20 cm in height. Each cylinder was sunk into the ground to a 15 cm depth, leaving a 5-cm-high elevated rim around the monolith. Each cylinder was then covered with chicken wire to exclude geese.

The stable isotope <sup>15</sup>N often is used as a tracer, since it has low natural abundance: 0.3663% of naturally occurring nitrogen atoms are <sup>15</sup>N; almost all of the remainder are <sup>14</sup>N (Schimel, 1993; Lajtha and Michener, 1994; Robinson, 1994). I applied <sup>15</sup>N additions and control treatments to my experimental plots on 24 June (Bylot) and 10–11 August (LPB). I added a single pulse of 0.1 g N m<sup>-2</sup> labelled with 98% <sup>15</sup>N as (<sup>15</sup>NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub> to the moss/grass/sedge surface of two cylinders per site; I applied this nitrogen as thirteen 7.5-ml aqueous surface additions in a hexagonal template. I also similarly added an equal amount of <sup>15</sup>N as K<sup>15</sup>NO<sub>3</sub> to the surface of a second pair of cylinders. I then repeated these treatments in two additional pairs of cylinders per site, except that I injected the solutions beneath the living moss layer (5 cm depth). This nitrogen application rate is approximately equal to the total soluble nitrogen content of 10 droppings m<sup>-2</sup> (Cargill and Jefferies, 1984b; Bazely and Jefferies, 1985; Ruess et al., 1989), which is close to the annual mean of 2 to 10 droppings m<sup>-2</sup> yr<sup>-1</sup> reported for Bylot by Gauthier et al. (1995), and less than the annual input in preferred habitats at either LPB (currently ca. 75 droppings m<sup>-2</sup> yr<sup>-1</sup>; R. L. Jefferies, unpubl.) or Bylot (20 droppings m<sup>-2</sup> yr<sup>-1</sup>; Pineau (1999). Finally, I added equivalent volumes of deionized water to the surface of 2 unlabelled controls per site. The amount of water or solution added to each plot was equivalent to a 4-mm rainfall event.

### SAMPLING AND ANALYSIS

At each site, samples were collected destructively on two dates. At Bylot, sampling was performed 1 d and 33 d after <sup>15</sup>N addition (25 June and 27 July). At LPB, the first set of samples was collected after 2 to 5 d (13–15 August); because of limitations of time, the second set was taken after 8 to 10 d (19–20 August). At each sampling, live moss (green, near-surface), dead moss/peat (brown, subsurface), and forage plants (separated into roots and shoots) were removed from the experimental monoliths, rinsed in 0.5 M KCl, and dried. This procedure was intended to remove readily exchangeable surface N, leaving behind only the fraction of N which had been absorbed by plants and was therefore unavailable for further uptake. The forage species sampled at Bylot were *D. fisheri* and *E. scheuchzeri*; at LPB, the dominant sedge, *C. aquatilis*, was sampled.

Samples were dried, ground in a Wiley Mill (20 mesh), and analyzed by the University of Waterloo Environmental Isotope Lab on an Isochrom Continuous Flow Stable Isotope Mass Spectrometer (Micromass UK, Manchester), coupled to a Carlo Erba Elemental Analyzer (CE Instruments, Milan). Results primarily have been reported as <sup>15</sup>N values, which are the parts-per-thousand difference in ‰<sup>15</sup>N between atmospheric N and the sample N; higher <sup>15</sup>N values indicate higher levels of <sup>15</sup>N enrichment (Lajtha and Michener, 1994; Robinson, 2001). Reliable pool sizes (Binkley and Hart, 1989; Schimel, 1993; Robinson, 2001) are

TABLE 1

Values of  $\delta^{15}\text{N}$  ( $\%$  difference from standard), total N ( $\%$  of biomass) and C:N ratio in control plots. Values are mean  $\pm$  SEM; n = 5

Site	Fraction	First sampling			Second sampling <sup>a</sup>		
		$\delta^{15}\text{N}$	%N	C:N	$\delta^{15}\text{N}$	%N	C:N
Bylot	<i>Eriophorum</i> shoots	8.462 $\pm$ 1.892	2.157 $\pm$ 0.317	17.256 $\pm$ 2.616	2.640 $\pm$ 0.683	—	—
	<i>Eriophorum</i> roots	12.854 $\pm$ 2.448	1.523 $\pm$ 0.261	23.461 $\pm$ 2.881	6.476 $\pm$ 2.562	—	—
	<i>Dupontia</i> shoots	14.664 $\pm$ 5.697	1.626 $\pm$ 0.139	23.083 $\pm$ 1.839	2.396 $\pm$ 0.610	—	—
	<i>Dupontia</i> roots	34.002 $\pm$ 12.865	0.980 $\pm$ 0.077	34.280 $\pm$ 3.791	5.262 $\pm$ 2.014	—	—
	Live moss	14.174 $\pm$ 5.634	0.882 $\pm$ 0.125	35.208 $\pm$ 6.277	9.078 $\pm$ 7.007	—	—
	Dead moss	30.786 $\pm$ 5.643	0.804 $\pm$ 0.070	33.677 $\pm$ 3.442	6.000 $\pm$ 0.682	—	—
LPB	<i>Carex</i> shoots	3.044 $\pm$ 0.214	1.576 $\pm$ 0.111	28.990 $\pm$ 2.371	3.148 $\pm$ 0.442	1.470 $\pm$ 0.237	34.907 $\pm$ 6.930
	<i>Carex</i> roots	4.460 $\pm$ 0.672	0.624 $\pm$ 0.033	73.410 $\pm$ 4.068	2.894 $\pm$ 0.673	0.868 $\pm$ 0.102	52.993 $\pm$ 6.642
	Live moss	0.844 $\pm$ 0.580	1.576 $\pm$ 0.051	26.266 $\pm$ 1.425	0.498 $\pm$ 0.276	1.504 $\pm$ 0.108	29.191 $\pm$ 2.747
	Dead moss	1.772 $\pm$ 0.204	1.584 $\pm$ 0.144	26.345 $\pm$ 2.629	3.384 $\pm$ 1.303	1.621 $\pm$ 0.211	27.089 $\pm$ 3.490

<sup>a</sup> %N and C:N not estimated for the second Bylot sampling; see Methods for details.

not available due to difficulties in defining the total size of some of the labelled compartments. In particular, living moss graded into dead moss, dead moss graded into both organic soil and the permafrost zone, and the complete recovery and identification of root tissue was impractical. This did not prevent the selection of unambiguous subsamples for  $^{15}\text{N}$  analysis.

Total nitrogen content and C:N ratio also were obtained

using the mass spectrometers/elemental analyzer. For total N content and C:N ratios, values are not available for the first set of samples analyzed (Bylot, second sampling data) because large samples which saturated the elemental analyzer had to be excluded from analyses; this problem subsequently was avoided by analyzing smaller amounts of biomass. This problem does not affect  $\delta^{15}\text{N}$  estimates.

Results were analyzed using randomized block ANOVAs, with plot as a random blocking factor (Kirk, 1982). To meet homogeneity of variance assumptions,  $\delta^{15}\text{N}$  values were  $\log(x + 1)$  transformed before analysis ( $F_{\max}$  probabilities uncorrected for multiple tests:  $P > 0.05$  in 14 tests;  $P > 0.01$  in 5 tests;  $P < 0.01$  for LPB *Carex* shoots, first sampling date). Because sampling schedules differed between sites, each set of results was analyzed separately for each sampling date, rather than combined into a single analysis; combining both dates in a single analysis did not alter overall patterns of significance, and made very minor differences to between-treatment contrasts. A posteriori analyses used the Games-Howell procedure, which is robust against both unequal variances and unequal sample sizes (Day and Quinn, 1989). Means are reported  $\pm$  standard error.

## Results

### BYLOT ISLAND

Exchange of  $^{15}\text{N}$  among cylinders occurred but was greatly limited by the cylinder walls, as indicated by the control samples (Table 1). Values of  $\delta^{15}\text{N}$  for moist tundra plants and soils naturally lie close to 0, and vary by only about 10‰ (Nadelhoffer et al., 1996). Control  $\delta^{15}\text{N}$  values were larger than these expected values (Table 1), but generally were very small relative to the  $^{15}\text{N}$  addition treatments (Fig. 1).

Levels of enrichment in  $^{15}\text{N}$  addition treatments were very high (often  $>1000\%$ ; Fig. 1); these  $\delta^{15}\text{N}$  values would be impossibly large for a natural abundance study, but not for a tracer addition study in which  $^{15}\text{N}$  is added in very pure form. Enrichment was greater for *Dupontia* than for *Eriophorum* (Fig. 1), but for both species,  $^{15}\text{N}$  was greatly enriched in nearly all of the addition treatments, relative to the controls (Fig. 1); these effects were highly significant (Table 2). For both species, enrichment generally was similar between the first and second samplings (Fig. 1). On both sampling dates, there were no detectable differences among  $^{15}\text{N}$  addition treatments for *Eriophorum* shoots or roots (Fig. 1). *Dupontia* showed a similar response, although

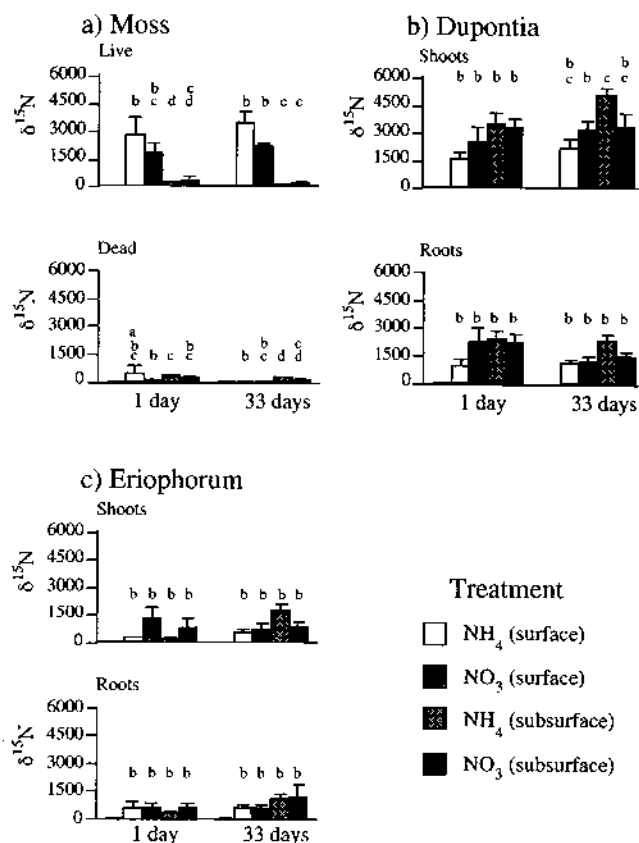


FIGURE 1. Bylot Island. Effects of experimental  $^{15}\text{N}$  addition treatments on  $\delta^{15}\text{N}$  values ( $\%$  difference from standard) after 1 d and 33 d. Controls are too small to appear at this scale; see Table 1 for values. Bars indicate mean  $\pm$  1 SEM; average sample size = 4.9 (range: 3–5). For each set of four bars, those sharing the same letter do not differ significantly; bars marked "a" do not differ significantly from controls ( $P > 0.05$ ; a posteriori tests).

TABLE 2

Bylot Island. Results of analyses of variance comparing effects of experimental  $^{15}\text{N}$  additions and controls on  $\delta^{15}\text{N}$  values. Treatments are treated as fixed; plots are treated as random blocks. Data were  $\log(x + 1)$  transformed before analysis

Variable	First sampling				Second sampling			
	Treatment		Plot		Treatment		Plot	
	F	df	F	df	F	df	F	df
Live moss	25.453***	4,16	0.639	4,16	71.873***	4,16	1.561	4,16
Dead moss	5.481**	4,15	0.268	4,15	25.778***	4,16	0.590	4,16
<i>Dupontia</i> shoots	170.035***	4,16	3.794*	4,16	234.045***	4,16	0.356	4,16
<i>Dupontia</i> roots	26.107***	4,16	1.024	4,16	84.724***	4,15	0.652	4,15
<i>Eriophorum</i> shoots	11.383***	4,16	0.857	4,16	41.174***	4,13	1.250	4,13
<i>Eriophorum</i> roots	10.405***	4,16	0.588	4,16	24.497***	4,15	0.660	4,15

\*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ .

there was a tendency for subsurface additions to lead to greater enrichment, and by the second date, the  $\text{NH}_4^+$  subsurface additions had significantly higher  $\delta^{15}\text{N}$  values than the  $\text{NO}_3^-$  surface additions (Fig. 1).

For mosses,  $^{15}\text{N}$  addition treatments were enriched relative to controls, and these levels of enrichment did not greatly change between samplings (Table 2; Fig. 1); however,  $\delta^{15}\text{N}$  values differed among addition treatments on both sampling dates (Fig. 1). For living mosses,  $\text{NH}_4^+$  and  $\text{NO}_3^-$  additions produced similar results, but  $\delta^{15}\text{N}$  values generally were much higher for surface additions than for subsurface additions (Fig. 1). Enrichment resulting from surface  $^{15}\text{N}$  additions was much greater in live than in dead mosses (Fig. 1). Values for live mosses were comparable to values for *Dupontia* shoots or roots, and much higher than values for *Eriophorum* shoots or roots (Fig. 1). Patterns for dead mosses were less pronounced, but some subsurface addition treatments did have higher  $\delta^{15}\text{N}$  values than did surface additions (Fig. 1).

Elemental analysis indicated total nitrogen content gener-

ally was higher for *Eriophorum* than for *Dupontia*, and higher for shoots than for roots (Table 1). Live mosses had lower values; dead mosses had the lowest values (Table 1). Nitrogen contents did not differ among treatments and controls ( $P > 0.18$  in all ANOVAs), as might be expected given the small amounts of N added to experimental plots. C:N ratios reflected patterns of nitrogen content: C:N ratios tended to be higher for mosses, and lower for leaves of forage species (Table 1). Mosses greatly outweighed forage plants (live moss:  $1741 \pm 179 \text{ g m}^{-2}$ ,  $n = 6$ ; graminoid shoots:  $24.67 \pm 3.70 \text{ g m}^{-2}$ ,  $n = 13$ ).

#### LA PÉROUSE BAY

Control  $\delta^{15}\text{N}$  values (Table 1) were very small relative to  $^{15}\text{N}$  addition treatments (Fig. 2): all control means were  $< 5\%$  at both samplings, which is within the naturally expected range of variation (Nadelhoffer et al., 1996). For *Carex*,  $\delta^{15}\text{N}$  was increased in nearly all of the addition treatments, relative to the controls (Fig. 2; Table 3). Levels of enrichment were less than those for *Eriophorum*, and much less than those for *Dupontia*, both from Bylot (Fig. 1). On both sampling dates, *Carex* shoots and roots showed no detectable differences among different  $^{15}\text{N}$  addition treatments (Fig. 2). Enrichment did not change substantially between the first and second sampling (Fig. 2).

For dead mosses,  $^{15}\text{N}$  addition treatments had higher levels of enrichment than controls, but there were no significant differences among different addition treatments, and no large changes in enrichment between sampling dates (Table 3; Fig. 2). Live mosses exhibited a more complex pattern. While  $^{15}\text{N}$  additions produced greater levels of enrichment than controls (Table 3; Fig. 2), there were numerous among-treatment differences: surface additions generally had much higher  $\delta^{15}\text{N}$  values than subsurface additions, and much higher values than dead mosses, or *Carex* shoots or roots (Fig. 2). Again, enrichment did not change substantially between sampling dates (Fig. 2).

Elemental analysis indicated that the nitrogen content of *Carex* shoots resembled that of both live and dead mosses (Table 1). Shoots were richer in nitrogen than roots (Table 1). C:N ratios were similar for mosses and *Carex* shoots (Table 1). Nitrogen contents did not differ among treatments and controls ( $P > 0.19$  in all ANOVAs). Mosses greatly outweighed forage plants (live moss:  $516 \pm 49 \text{ g m}^{-2}$ ,  $n = 6$ ; graminoid shoots:  $9.16 \pm 0.98 \text{ g m}^{-2}$ ,  $n = 6$ ).

#### Discussion

Growth of the forage plants that I considered in this study can rapidly respond to inorganic nitrogen when it is added at

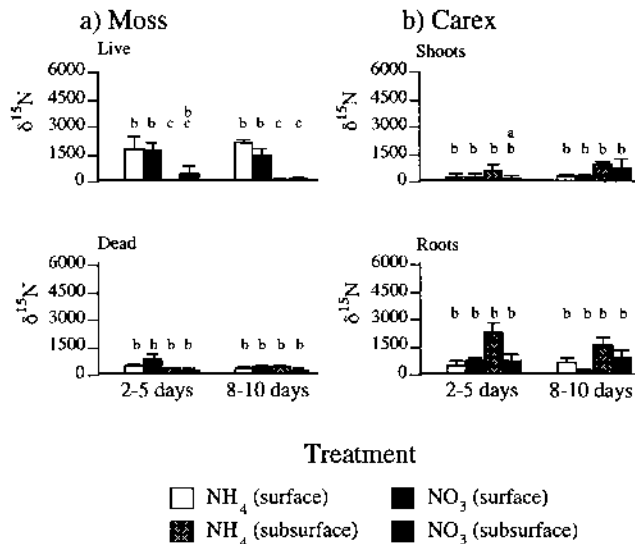


FIGURE 2. LPB. Effects of experimental  $^{15}\text{N}$  addition treatments on  $\delta^{15}\text{N}$  values (‰ difference from standard) after 2–5 d and 8–10 d. Controls are too small to appear at this scale; see Table 1 for values. Bars indicate mean + 1 SEM; average sample size = 4.8 (range: 4–5). For each set of four bars, those sharing the same letter do not differ significantly; bars marked "a" do not differ significantly from controls ( $P > 0.05$ ; a posteriori tests).

TABLE 3

La Pérouse Bay. Results of analyses of variance comparing effects of experimental  $^{15}\text{N}$  additions and controls on  $\delta^{15}\text{N}$  values. Treatments are treated as fixed; plots are treated as a random blocks. Data were  $\log(x + 1)$  transformed before analysis

Variable	First sampling				Second sampling			
	Treatment		Plot		Treatment		Plot	
	F	df	F	df	F	df	F	df
Live moss	22.313***	4,14	0.287	4,14	94.910***	4,15	3.055*	4,15
Dead moss	38.612***	4,14	0.359	4,14	39.417***	4,16	0.633	4,16
Carex shoots	10.007***	4,14	1.878	4,14	17.429***	4,16	3.328*	4,16
Carex roots	54.853***	4,13	2.238	4,13	22.236***	4,16	1.349	4,16

\*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ .

high concentrations (Manseau and Gauthier, 1993; Pineau, 1999). My study extends this work by demonstrating uptake also occurs when mineral N is added in amounts comparable to natural inputs. Most inorganic nitrogen in arctic soils (Van Cleve and Alexander, 1981; Chapin and Shaver, 1985; Kielland and Chapin, 1992) and goose droppings (Bazely and Jefferies, 1985; Ruess et al., 1989) occurs as ammonium ions, and while mosses can use both  $\text{NH}_4^+$  and  $\text{NO}_3^-$  (Brown, 1982; Bates, 2000), many arctic vascular plants show a preference for ammonium over nitrate (Chapin and Shaver, 1985; Kielland and Chapin, 1992). Despite this, rapid uptake by forage species occurred whether  $^{15}\text{N}$  was added as  $\text{NO}_3^-$  or  $\text{NH}_4^+$ , regardless of site, plant community, or sampling date. Thus, the presence of a dense moss carpet did not exclude forage plants from rapid access to either form of nitrogen: large amounts of  $^{15}\text{N}$  generally reached these plants within a few days, or hours.

Despite these results, there still are at least two ways that mosses could divert substantial amounts of N away from forage plants. First, mosses might be better competitors for inorganic N, either because of higher affinity or simply because they intercepted surface-added nitrogen before it reached plants' roots. If this were the case, forage species might be expected to have low levels of  $^{15}\text{N}$  enrichment relative to mosses, especially when nitrogen was added to the moss surface. Second, even if mosses did not outcompete forage species, they still could divert the fraction of added N that they were able to take up away from forage plants and instead sequester it in slow-cycling moss/peat pools. In this case, vascular plants would not necessarily have lower levels of enrichment than mosses, nor would subsurface injections necessarily increase uptake by forage species; however, if mosses represented a sufficiently large pool, the net result still would be to reduce the amount of inorganic N available to forage plants. Results of this experiment tend to favor this second possibility.

At least one experimental study has found evidence that mosses can outcompete arctic graminoids for surface-added N. Working in an Icelandic moss-heath community, Jónsdóttir et al. (1995) found that uptake of  $\text{NO}_3^-$  (and to a lesser extent  $\text{NH}_4^+$ ) by *Carex bigelowii* was increased when N was injected into the soil, rather than added to the surface of the moss (*Racomitrium lanuginosum*) layer. In contrast, in the present study, evidence that mosses outcompeted forage species is weak. The surface layer of living mosses captured substantial amounts of  $^{15}\text{N}$ ; nonetheless, large amounts of  $^{15}\text{N}$  generally reached forage species whether it was added to the moss surface or beneath it. The ability of forage plants to rapidly access both surface and subsurface nitrogen suggests that some uptake might occur via near-surface roots or leaf surfaces, as well as by deeper root systems. This also may explain why enrichment was much greater in *Du-*

*ponia* than in either *Eriophorum* or especially *Carex*: since the root system of *Du-ponia* is much more strongly concentrated near the ground surface than is true for the other two species (Chapin et al., 1980), it may gain an advantage in intercepting surface-added and near-surface nutrients. Alternatively, *Carex* may have had lower uptake because N was applied later in the season, when annual growth was beginning to decline; however, tundra graminoids often retain the capacity to rapidly take up nutrients late in the season, or even after aboveground tissue has senesced (Chapin et al., 1980; Chapin and Shaver, 1985; Kielland and Chapin, 1992).

This study does suggest, however, that mosses divert substantial amounts of added nutrients away from forage species. The nitrogen in goose droppings originates in forage plants, and primarily in leaf and shoot tissues; in salt-marsh systems, much of this nitrogen ultimately is recycled from droppings back into the aboveground tissues of food plants (Bazely and Jefferies, 1985). In my study, generously assuming an aboveground biomass of  $30 \text{ g m}^{-2}$  for both sites (Gauthier et al., 1995; Lepage et al., 1998; R. L. Jefferies, unpubl.),  $\delta^{15}\text{N}$  values suggest that the fraction of added nitrogen subsequently recovered from leaves of forage plants would roughly range from 2.7% (*Carex*) to 7.1% (pure stand of *Eriophorum*) to 19.9% (pure stand of *Du-ponia*) (final sampling date—all addition treatments pooled). These estimates of uptake by forage species are conservative, since they neglect roots, which were very difficult to sample. Nonetheless, biomass of living mosses alone outweighed shoots of forage species by more than 50:1 at both sites, while their levels of enrichment in surface N addition treatments were comparable to or greater than enrichment of both roots and shoots of forage species. These numbers must be treated with caution, but they suggest that the living moss layer rapidly immobilized most surface-added N.

Other studies of northern systems tend to agree with this conclusion. For example, Li and Vitt (1997) used  $^{15}\text{N}$  tracers to follow movements of surface-added  $\text{NH}_4^+$  in boreal bog and fen systems. Their results indicated that almost all of this nitrogen was rapidly sequestered in the moss-peat layer, particularly in near-surface horizons, and that even after two growing seasons >98% of recovered nitrogen still occurred in this layer while <2% had reached co-occurring shrubs. Similarly, Jónsdóttir et al. (1995) found that only 0.2% of  $^{15}\text{N}$  added to a moss-heath reached the dominant vascular plant, *Carex bigelowii*, within a week of application; instead, most added N was retained within the moss layer. In the long term, decomposition of mosses may release nitrogen into the rooting zone, but slow rates of decay should delay the transfer of nutrients from mosses to forage plants (Vitt, 2000). Thus, in freshwater wetlands the ultimate effect of geese may be to divert N from forage plants into long-

lived belowground sinks. Much of this nitrogen may be permanently lost from actively-cycling pools by being trapped in peat or permafrost (Van Cleve and Alexander, 1981; Oechel and Van Cleve, 1986; Bonan and Shugart, 1989; Jonasson and Shaver, 1999).

In summary, this study suggests that the nitrogen dynamics of freshwater wetlands exploited by Snow Geese may differ substantially from the model previously developed in salt-marshes. In freshwater wetlands, forage species rapidly can access a fraction of added nitrogen, but this fraction is small; in the longer term, inedible mosses may divert nutrients away from this goose-forage system, implying that freshwater forage species may be prone to long-term declines. Rapid population growth of Snow Geese (Abraham and Jefferies, 1997; Reed et al., 1998) already has resulted in severe reductions in populations of forage species in freshwater sedge meadows at sites including the McConnell River, Nunavut Territory (Kerbes et al., 1990) and La Pérouse Bay (Kotanen and Jefferies, 1997; Jano et al., 1998). Extensive areas of freshwater sedgelands ultimately may be at risk as Snow Goose populations continue to grow.

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