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# Vegetation loss alters soil nitrogen dynamics in an Arctic salt marsh

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**Summary**

**1** Plant and microbial nitrogen (N) dynamics were examined in soils of an Arctic salt marsh beneath goose-grazed swards and in degraded soils. The degraded soils are the outcome of intensive destructive foraging by geese, which results in vegetation loss and near-irreversible changes in soil properties. The objective of the study was to determine whether vegetation loss led to a decline in microbial activity and a redistribution of N amongst the different soil N pools that potentially could adversely affect plant regrowth.

**2** *In situ* N allocation between plants, microbes and soil was determined based on injection of $^{15}NH_4Cl$ into soil cores; changes in isotopic ratios and N concentrations in the different pools were measured after 24 h. Degraded soils, in contrast to vegetated soils, were characterized by a decline in microbial biomass, reduced microbial $^{15}N$ excess, reduced rates of gross N immobilization and an increased microbial residency time of $^{15}N$. In vegetated soils, both microbes and the forage grass, *Puccinellia phryganodes*, accumulated $^{15}N$ such that little remained in the soil abiotic phase after 24 h, unlike in degraded soils.

**3** The decline in microbial activity in degraded soils may be linked to a low availability of soil carbon in the absence of plants and to deteriorating abiotic conditions, including the occurrence of hypersalinity in summer.

**4** Not all biotic processes respond similarly to the change in ecosystem state. Unlike vascular plant productivity and goose foraging which are absent in degraded soils, soil microbial activity is maintained, albeit at a lower level. In spite of this activity, the greater proportion of $^{15}N$ in degraded soils is in the abiotic pool rather than in microbial biomass with an increased potential for soil N loss from leaching and soil erosion.

**5** Disturbance linked to herbivory often triggers catastrophic shifts in ecosystem properties resulting in vegetation loss and changes in soil biogeochemical cycling that are irreversible, at least on a decadal time scale, and lead to the loss of N and other nutrients required for plant growth. These results clearly illustrate that microbial activity does not compensate for the effects of plant removal on soil N retention.

*Key-words*: gross nitrogen mineralization, isotope dilution assay, microbial biomass, $^{15}N$ allocation, *Puccinellia phryganodes*

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## Introduction

Different plant species can have important effects on N cycling and microbial activity in soil that in turn affect plant function in different ecosystems (Binkley 1996; Van der Krift & Berendse 2001; Lovett *et al*. 2004; Chapman *et al*. 2006), including those in the Arctic (Giblin *et al*. 1991; Nadelhoffer *et al*. 1991; Shaver & Chapin 1991; Zak & Kling 2006). Catastrophic shifts in community assemblages and processes often accompany intense herbivory resulting in desertification of landscapes in northern biomes and elsewhere (Schlesinger *et al*. 1990; Hik *et al*. 1992; Srivastava & Jefferies 1996;



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Van de Koppel *et al*. 1997). The total loss of vegetation associated with a catastrophic shift also may be expected to affect N cycling (Van de Koppel *et al*. 1997; Walker *et al*. 2003), but the extent to which soil microbial activity *per se* is altered is poorly known, at least in Arctic ecosystems. When plants are removed from soils, erosion and leaching can lead to loss of total N (Vitousek & Matson 1985). In a N-limited system, soil microbes may compensate for the lack of plant uptake by immobilizing greater amounts of N. Alternatively, loss of plants may lead to slower microbial activity and reduced N mineralization because of the dependency of soil microorganisms on carbon (C) sources from root exudates and plant litter during different seasons, including winter (Bardgett *et al*. 1998, 2005).

Temperature, water availability and snow depth are also important controls on microbial activity and plant growth in soils of cold regions (Brooks *et al*. 1998; Schimel *et al*. 2004). When air temperatures are well below the freezing point, snow insulates soil so that soil temperatures are often between 0 °C and −8 °C. Decomposition of litter and net mineralization of N can occur at these subzero temperatures (Giblin *et al*. 1991; Lipson *et al*. 1999; Schmidt *et al*. 1999). Lipson *et al*. (2000) suggested, however, that soil microbial activity becomes C-limited in late winter as supplies of labile soil C from senesced plant tissue produced the previous autumn decline. This limitation, together with the effects of freeze–thaw cycles and faunal predation, contribute to the death and lysis of microbial biomass and the release of soluble inorganic and organic N in soils at thaw (Lipson *et al*. 2000; Schmidt & Lipson 2004; Edwards *et al*. 2006). These nutrients may be an important contributor to plant and microbial N budgets in summer, as N released from frozen soils at thaw is immobilized by microbes and plants. However, processes controlling the utilization are unclear, especially in degraded soils in cold regions where inputs of plant necromass are minimal.

Catastrophic shifts in vegetation have occurred in the coastal marshes of the Hudson Bay Lowlands on the Arctic–sub-Arctic boundary where increasing numbers of migratory lesser snow geese, *Chen caerulescens caerulescens* A.O.U., breed in summer and extensively grub roots and rhizomes of the dominant graminoids, *Puccinellia phryganodes* and *Carex subspathacea*, in early spring (Jefferies *et al*. 2004). Their foraging activities result in a positive feedback leading to exposed hypersaline soils in most years in which the vegetation is unable to re-establish (Srivastava & Jefferies 1996; Chang *et al*. 2001; Handa *et al*. 2002). Over time the number and size of remaining vegetated patches have declined commensurate with the increase in the area of exposed soils (Hik *et al*. 1992; McLaren & Jefferies 2004).

The effect of loss of plants on microbial activity and N dynamics in soils of these goose-degraded marshes is uncertain, but it is likely to affect the ability of the system to return to its original vegetated state because of the known influence of plants on soil N cycling. In this study, the partitioning of $^{15}N$ between microbial and plant biomass and abiotic soil components was compared among soils to see if microbial activity was reduced in exposed soils compared to that of vegetated soils, presumably due to a dependence of soil microorganisms on plant C.

In order to monitor short-term N allocations between plants, microbes and soils in both vegetated and grubbed sites, $^{15}NH_4Cl$ was injected into soil cores, and changes in isotope ratios and N concentrations in these compartments were measured at the start of the experiment and 24 h later. The approach involved collecting shoots and roots from cores at these two times to measure their $^{15}N$ enrichment, and the use of the chloroform-fumigation incubation technique (Witt *et al*. 2000) to lyse microbial cells in order to measure $^{15}N$ enrichment and total C and N in microbial biomass following soil extractions. In addition, soils were extracted to determine amounts of exchangeable inorganic N. The overall data not only provided estimates of amounts and relative proportions of $^{15}N$ distributed between plants, microbial biomass and soils, but also amounts of N and C in microbial biomass and the soil pool sizes of exchangeable inorganic N and dissolved organic N. Based on these results, a comparison was made of the N dynamics in vegetated and exposed soils in the different marshes in order to determine whether the proportional distribution of $^{15}N$ differs between vegetated and exposed sediments. Lastly, we calculated gross rates of N mineralization and rates of gross microbial N immobilization which are better methods for estimating the potential amount of inorganic N available to plants and for microbial storage, respectively, compared to measures of net N mineralization. The latter often show values close to zero in Arctic soils due to the confounding of microbial N mineralization and N accumulation (Hobbie & Chapin 1996; Schimel *et al*. 2004).

## Materials and methods

### STUDY SITE AND SAMPLE COLLECTION

This study was conducted at La Pérouse Bay (58°04′ N, 94°03′ W), located on the south-west coast of Hudson Bay, approximately 30 km east of Churchill, MB, Canada. The intertidal zone is inundated daily with tides in late summer and autumn, while the supratidal section is covered by tides approximately once every two years. The soils are classified as Regosolic Static Cryosols (Agriculture Canada 1987). In vegetated soils, a shallow humified organic soil (< 10.0 cm in depth) is present in the older supratidal marsh, but the younger intertidal sites have only a very thin layer of organic-rich material at the surface (< 3.0 cm). The grubbed areas, which are termed 'degraded' in each section of the marsh, are missing rhizomes and roots of graminoids, most of which occur in the upper 3 cm. The thin organic layer has been lost in degraded areas in the intertidal zone

**Table 1** Values (± SE) ($n$ = 3–5) for moisture, salinity, redox potential, soil C : N ratio and microbial C : N ratio of the soil samples used in the experiments at La Pérouse Bay, Manitoba, Canada, for the spring, summer, and early and late winter (soil moisture only) of 2003/4, and as an annual mean. MBC and MBN refer to microbial carbon and nitrogen, respectively

| Site and treatment | Time of year | Moisture† (% of dry weight) | Salinity† (g dissolved solids $L^{-1}$) | Redox‡ (mean mV at 2 cm depth) | C:N (atomic ratio) | MBC : MBN†‡ (atomic ratio) |
|---|---|---|---|---|---|---|
| Supratidal intact | 8 June | 91 ± 7 | 18 ± 3 | 314 ± 27 | 20 ± 2 | 21 ± 2 |
| | 26 June | 121 ± 25 | 27 ± 4 | 194 ± 13 | 19 ± 2 | 14 ± 3 |
| | 11 July | 115 ± 10 | 27 ± 4 | 351 ± 9 | 19 ± 1 | 13 ± 0 |
| | 30 October | 139 ± 11 | 22 ± 3 | – | 17 ± 2 | 15 ± 3 |
| | 29 April | 115 ± 2 | – | – | – | – |
| | Mean | 116 ± 8 | 24 ± 2 | 284 ± 13 | 19 ± 1 | 15 ± 1 |
| Supratidal degraded | 8 June | 92 ± 10 | 41 ± 7 | 140 ± 17 | 27 ± 7 | 52 ± 3 |
| | 26 June | 103 ± 10 | 60 ± 6 | 115 ± 12 | 21 ± 1 | 29 ± 14 |
| | 11 July | 93 ± 12 | 47 ± 0.4 | 319 ± 14 | 24 ± 3 | 5 ± 3 |
| | 30 October | 77 ± 6 | 56 ± 3 | – | 27 ± 1 | 26 ± 1 |
| | 29 April | 183 ± 6 | – | – | – | – |
| | Mean | 110 ± 19 | 52 ± 3 | 196 ± 15 | 25 ± 2 | 26 ± 5 |
| Intertidal intact | 8 June | 63 ± 3 | 8 ± 0.3 | 300 ± 8 | 30 ± 1 | 6 ± 0.4 |
| | 26 June | 62 ± 7 | 8 ± 1 | 153 ± 13 | 37 ± 4 | 9 ± 1 |
| | 11 July | 64 ± 1 | 8 ± 0.4 | 407 ± 12 | 35 ± 1 | 7 ± 3 |
| | 30 October | 92 ± 12 | 15 ± 1 | – | 27 ± 2 | 13 ± 3 |
| | 29 April | 70 ± 2 | – | – | – | – |
| | Mean | 70 ± 6 | 10 ± 1 | 285 ± 16 | 32 ± 2 | 9 ± 1 |
| Intertidal degraded | 8 June | 58 ± 6 | 13 ± 3 | 242 ± 31 | 25 ± 0.5 | 2 ± 1 |
| | 26 June | 63 ± 2 | 10 ± 1 | 112 ± 24 | 33 ± 0.5 | 9 ± 3 |
| | 11 July | 57 ± 2 | 10 ± 2 | 346 ± 14 | 40 ± 1 | 5 ± 2 |
| | 30 October | 71 ± 7 | 17 ± 2 | – | 39 ± 4 | 42 ± 12 |
| | 29 April | 65 ± 3 | – | – | – | – |
| | Mean | 63 ± 3 | 13 ± 1 | 232 ± 19 | 35 ± 2 | 15 ± 5 |
| Site | | *** | *** | ** | *** | ** |
| Treatment | | NS | *** | *** | NS | NS |
| Time | | NS | * | *** | NS | ** |
| Site × treatment | | NS | NS | * | NS | NS |
| Site × time | | NS | NS | NS | * | * |
| Treatment × time | | NS | * | * | NS | * |
| Site × treatment × time | | NS | NS | NS | NS | NS |

†Data were log transformed for statistical analysis.
‡Degrees of freedom and F-score adjusted according to Huyhn-Feldt ε to meet sphericity.
Levels of significance are shown as $*P < 0.05$, $**P < 0.01$, $***P < 0.001$ where $\alpha = 0.05$. For time interactions $\alpha = 0.0125$ or 0.01 and NS = not significant.

resulting in exposure of mineral sediments, but in the supratidal marsh much of the surface organic layer is still present. In the absence of plant cover, degraded organic and mineral sediments frequently become hypersaline, especially in dry summers, and are typically more compacted than vegetated soils, with lower redox potentials and a higher C : N ratio (Table 1).

### SAMPLE PROCESSING

Processing of samples took place in the field laboratory at La Pérouse Bay, except that early and late winter samples were processed at the University of Toronto. On each sampling date, soil blocks were removed to characterize soil properties, including redox potential and salinity, in both vegetated and degraded sites in the intertidal and supratidal zones following established procedures (Srivastava & Jefferies 1995, 1996; Wilson & Jefferies 1996).

In order to monitor short-term partitioning of $^{15}N$ between plants, microbes and soils, very low concentrations of highly enriched $^{15}NH_4Cl$ were injected into soil cores, and changes in isotope ratios and N concentrations in the different soil compartments were measured after 24 h. In June, July (spring and summer) and October (early winter) of 2003, and in April of 2004 (late winter), pairs of soil cores ($n$ = 3–5) were removed from two sites, each 200 × 200 m, in the intertidal and supratidal zones, respectively. Soils from the two sites were sampled beneath patches of *P. phryganodes*. In addition, samples were taken from exposed mineral sediment in the intertidal zone (missing the surface 2–3 cm organic-rich layer) and in grubbed soils in the supratidal zone where the surface organic layer was still intact, using a 7.3-cm diameter polyethylene tube cut to a depth of 6.5 cm. The resulting soil cores were wrapped in plastic film. At each site, each pair of cores was taken at least 30 m apart from other cores within a treatment.

The spring and summer cores were placed overnight in the ground adjacent to the marsh and field laboratory during the isotopic incubation, whereas frozen winter samples were flown to Toronto surrounded by ice packs in a cooler, and incubated the following day at 3–4 °C after thawing.

Core processing follows the method of Hart *et al*. (1994). On each sample date, cores were injected with $^{15}NH_4Cl$ (99% $^{15}N$) at a concentration that was approximately equivalent to the background concentration of soluble $NH_4^+$ ($10^{-4}$–$10^{-3}$ M; Henry & Jefferies 2003) and soil moisture increased by < 6%. One core was returned to the storage site to incubate *in situ* for 24 h, and the other core was used as a control at time zero. The cores were incubated for only 24 h to minimize the possibility that the $^{15}N$ assimilated was not re-mineralized (Kirkham & Bartholomew 1954; Davidson *et al*. 1991). Previous studies of these soils indicated half-lives of $^{15}N$ turnover of 5–35 h (Henry & Jefferies 2003).

Roots were collected from the upper 5 cm of each vegetated core, together with shoots (0 and 24 h incubation) and the living, fine white roots were teased from a subsection of the core top and rinsed in deionized water. Subsequently, roots were rinsed in 5 mM $CaCl_2$ for 5 min to remove any isotope present in the Donnan free space (Epstein *et al*. 1963), before all plant material was dried at 50 °C for a week and stored for isotopic analysis. The remainder of each core was thoroughly hand-mixed to minimize heterogeneity and microsite variation (Davidson *et al*. 1991), then subsampled for moisture content (*c.* 10 g fresh wt. soil), analysis of exchangeable inorganic nitrogen (15 g fresh wt. soil extracted in 75 mL 2 M KCl) (Hart *et al*. 1994), and for estimation of dissolved total nitrogen and microbial biomass (2 × 70 g fresh wt. soil extracted in 140 mL of 0.5 M $K_2SO_4$) using a modified chloroform-fumigation-extraction (Witt *et al*. 2000; Henry & Jefferies 2003).

## SAMPLE ANALYSES

### *Exchangeable inorganic nitrogen and total carbon and nitrogen in soils*

The exchangeable inorganic N ($NH_4^+$ and $NO_3^-$) was measured in filtered (8-μm pore size) 2 M KCl soil extracts with the use of an auto-analyser (Technicon AA II, Tarrytown, NY) (Edwards *et al*. 2006). Soil C : N ratios were determined on ground, oven-dried soil (50 °C) using an Elemental Combustion System 4010 CHN Analyser (COSTECH International, Valencia, CA).

### *Microbial nitrogen and carbon and dissolved organic nitrogen in soils*

To estimate microbial N and dissolved total N in soil (DTN), the total extractable nitrogen in filtered (1.6-μm pore size) 0.5 M $K_2SO_4$ fumigated and unfumigated soil extracts were oxidized with alkaline persulphate (Cabrera & Beare 1993) and the nitrate produced was measured with the use of the auto-analyser. The difference in N between oxidized extracts of fumigated and unfumigated soils, gave an estimate of microbial N (corrected by a factor of 2.5, $k_N = 0.4$ to allow for incomplete oxidation; Jonasson *et al*. 1996). This pool is assumed to represent the N used for microbial structure as well as cytoplasmic storage and thus may vary relative to microbial C according to N availability. Soluble organic N (DON) was calculated as the difference between DTN in unfumigated samples and exchangeable (KCl extracts) inorganic N ($NH_4^+$ and $NO_3^-$). Microbial carbon in oxidized extracts was determined as the difference between unfumigated and fumigated samples using the dichromate titration method to measure carbon (Nelson & Sommers 1996); the value was corrected by a factor of 2.85 ($k_C = 0.35$ for incomplete oxidation; Jonasson *et al*. 1996). This pool is assumed to represent the C used for microbial structure and thus is equivalent to the size of the microbial biomass. Interference with C estimations from soil $Fe^{2+}$ at this site has been shown to be insignificant (Henry & Jefferies 2003).

### *Recovery of $^{15}N$ ammonium in samples*

$^{15}N$ was recovered from aliquots of the $K_2SO_4$ and KCl extracts (0 and 24 h) using a modified diffusion technique (Stark & Hart 1996), incorporating acidified, pre-leached filter paper discs (7 mm; Whatman no. 1) sealed in PTFE (Polytetrafluroethylene) tape. To recover $^{15}N$-ammonium in the extracts, acid traps were made by pipetting 5 μL of 2.5 M $KHSO_4$ onto duplicate discs and then folding and sealing a piece of PTFE tape over these discs (the tape is permeable to gases but not liquids). The sample extract, the acid trap which floated on the surface of the liquid, and MgO (0.2 g) were sealed in a plastic specimen container for 6 days. The containers were agitated gently each day. In the presence of the oxide, which made the extract solution alkaline, soluble $NH_4^+$ inorganic N was converted to $NH_3$ that volatilized and was trapped on the acidified filter paper discs which were then analysed for their $^{15}N$ content. Due to the low expected concentration of $^{14}N$ in the samples and the presence of highly enriched tracer, 8 mL of KCl-extracted sample were added to 20 mL of 0.14 mM $^{14}NH_4Cl$ in 2 M KCl carrier solution before a sample was pipetted into a container.

### *Recovery of $^{15}N$ nitrate in samples*

Nitrate was recovered from the alkaline persulphate-oxidized $K_2SO_4$ samples in order to estimate the amount of N taken up by soil microbes during the incubation. For this procedure, 2 mL of oxidized sample plus 2 mL of the persulphate reagent were autoclaved and placed in 250 mL Mason jars (Bernardin, Rye, New York) with 20 mL of 0.18 mM $K^{14}NO_3$, then 2 mL of 10 M NaOH was added to maintain alkalinity during the diffusion process (Stark & Hart 1996). The jars were left open for 3 days to remove $NH_3$ in the extracts. Subsequently,

replacement water, an acid trap, 0.4 g of Devarda's alloy (to convert $NO_3$ to $NH_4$), and an additional 0.3 mL of 10 m NaOH were added and the jar sealed for 6 days. $^{15}N$ enrichments were blank-corrected using a calculated blank that does not assume complete recovery (Stark & Hart 1996). The mass of the N in the blank was calculated by comparing diffused and non-diffused isotope standards, where the non-diffused standard was prepared by pipetting $^{15}N$ as $^{15}NH_4Cl$ directly onto filter paper discs. Blanks, N standards and diffused and non-diffused $^{15}N$ standards were included in all diffusion analyses.

### *Measurement of $^{15}$nitrogen*

The samples were analysed for their $^{15}N/^{14}N$ ratios and N content using an Isochrom continuous flow stable isotope mass spectrometer (Micromass, G. V. Instruments, Manchester, UK) coupled to a Carlo Erba elemental analyser (CHNS-O EA1108, Thermo Fisher Scientific, Milan, Italy) at the Environmental Isotope Laboratory, University of Waterloo, Ontario.

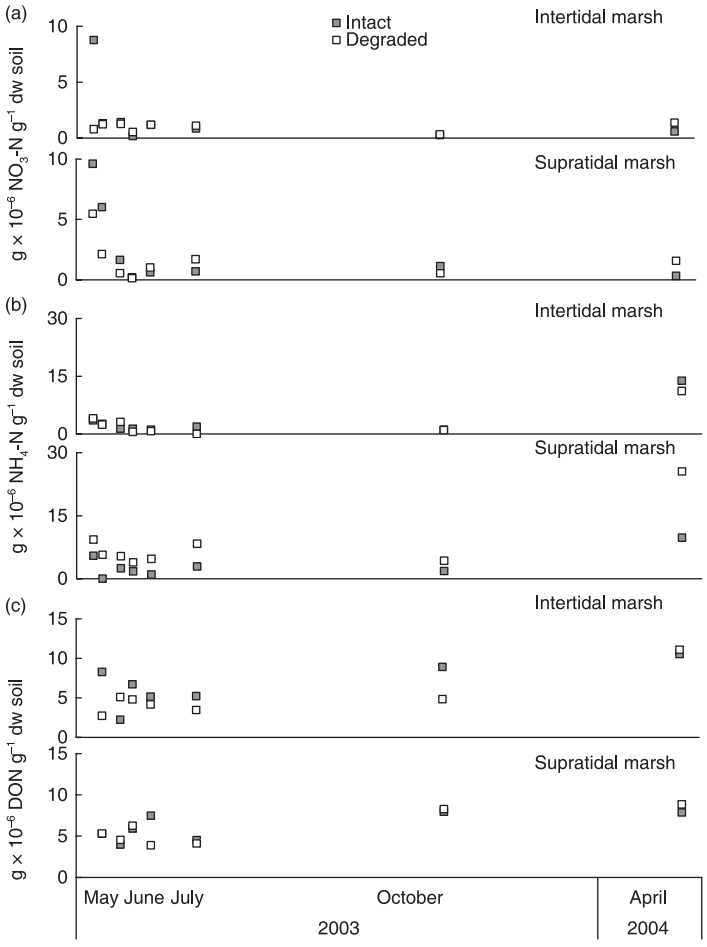


**Fig. 1** (a) Mean exchangeable nitrate concentrations (2 M KCl-extractable) ($n$ = 3–5) per g dry wt. soil; (b) mean exchangeable ammonium concentrations (2 M KCl-extractable) ($n$ = 3–5) per g dry wt. soil; (c) mean exchangeable dissolved organic nitrogen (DON) concentrations ((2 M $K_2SO_4$-extractable DTN) – (2 M KCl-extractable inorganic N)) ($n$ = 3–5) per g dry wt. soil. Soils are from vegetated (intact) and unvegetated (degraded) sites in intertidal and supratidal salt marshes at La Pérouse Bay, Manitoba, Canada.

#### CALCULATION OF DATA

Data of $^{15}N/^{14}N$ ratios were used to determine gross rates of mineralization, in order to estimate the potential amount of inorganic N available to plants independent of microbial N immobilization. Gross rates of mineralization, together with immobilization, were measured after 24 h based upon the isotope dilution calculation (Kirkham & Bartholomew 1954; Davidson *et al*. 1991; Hart *et al*. 1994). As the calculation depends upon a number of assumptions (Kirkham & Bartholomew 1954; Davidson *et al*. 1991) which may not be fully met, the results were calculated as $^{15}N$ excess in soil, microbial and plant pools relative to background levels, as an indicator of the relative activities of the different pools.

#### STATISTICAL ANALYSES

Results were compared using a multivariate analysis of variance (MANOVA) in order to account for any loss of independence between repeatedly sampled sites and treatments across time. Most models which were used incorporated a one-between, four-within model (Winer *et al*. 1991), with the source of variation measured between means of the intertidal or supratidal marsh sites, and between the vegetated state or the degraded states and their interactions, across five dates. The exceptions were soil inorganic and organic N, which were compared between marsh sites and treatments, but across eight and seven dates, respectively. For all response variables, variation within treatment means across dates were considered repeated measures, and the assumption of sphericity was confirmed with Mauchley's $W$, with the degrees of freedom and $F$-score reduced according to the Huyhn-Feldt epsilon correction when required (Scheiner & Gurevitch 1993). Since univariate tests were used to analyse within-subject effects, the Bonferroni adjustment was made where $\alpha$ (0.05) was divided by the number of repeated measures to decide significance. Some data were log-transformed to meet the requirements of normality. Only significant results are presented and all analyses were performed with JMP 5.1 (SAS Institute 1989–2003, Cary, NC).

## Results

#### SOIL AND PLANT CHARACTERISTICS

The intertidal and supratidal marshes differed significantly in all soil variables that were measured (Table 1). Soils of the supratidal marsh had lower C : N ratios and redox values, and higher salinities and moisture contents compared with the intertidal soils. Salinity and redox potential differed significantly between treatments, with degraded soils having higher salinities and lower redox potentials than vegetated soils. In all soils, the amounts of exchangeable ammonium and nitrate ions (Fig. 1a,b) either decreased from early spring to summer and remained low, or were low

throughout the entire period. In contrast, values for exchangeable $NH_4^+$ were high in all soils in late winter 2004 but after thaw at the end of May 2003 (the previous year), $NO_3^-$ concentrations in soil extracts were high, with the exception of degraded soils in the intertidal marsh. Nitrification of ammonium pool may create a transient pulse of nitrate that is rapidly utilized. Within both marshes, degraded soils tended to have higher amounts of exchangeable ammonium ions (treatment effect: $F_{1,8} = 7.5$; $P = 0.03$), especially in the supratidal marsh, creating a significant difference between marshes (site effect: $F_{1,8} = 42.1$; $P = 0.0002$) and a significant interaction (site × treatment effect: $F_{1,8} = 41.6$; $P = 0.0002$). Amounts of soil DON (Fig. 1c) were broadly similar between marsh sites, with values generally higher than those for ammonium on most sampling dates; peak values occurred in early and late winter at all sites (time effect: $F_{6,48} = 12.4$, $P < 0.0001$).

The amount of $^{15}N$ in the total dissolved N pool in incubated degraded soils was much greater than that in vegetated soils ($F_{1,8} = 117.7$; $P < 0.0001$) (Fig. 2a), and there were significant accumulations of isotope in this pool in degraded soils in early spring (2003) and in late winter (2004) in all soils (time: $F_{4,32} = 61.1$; $P < 0.0001$, time × treatment: $F_{4,32} = 16.3$; $P < 0.0001$). Where the sediments were vegetated, the primary forage grass, *Puccinellia phryganodes*, had a greater $^{15}N$ tissue concentration in shoots (site effect: $F_{1,4} = 221.4$, $P = 0.0001$) and roots (site effect: $F_{1,4} = 13.1$, $P = 0.02$) in the intertidal marsh compared with values for the supratidal marsh (Fig. 2b). Net uptake of $^{15}N$ into plant tissues over 24 h increased from spring to summer, but decreased from early to late winter, especially in intertidal sites (roots, time effect: $F_{4,16} = 14.2$, $P < 0.0001$, time × site: $F_{4,16} = 19.1$, $P < 0.0001$; shoots, time effect: $F_{4,16} = 11.5$, $P = 0.0001$, time × site: $F_{4,16} = 7.3$, $P = 0.002$). Note that there was still a substantial amount of plant uptake in early winter cores (October 2003) over a 1-day incubation at 3–4 °C, after the ground had been frozen and snow-covered for 3 weeks (Fig. 2b).

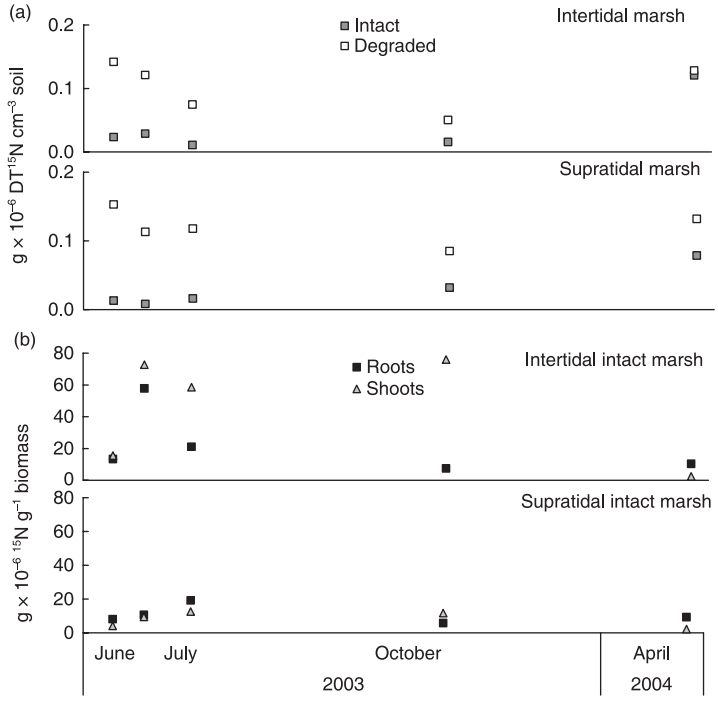


**Fig. 2** (a) Mean $^{15}N$ excess after 24 h incubation in the dissolved total soil nitrogen pool (DTN) ($n = 3$–5) per unit volume of soil (μg $^{15}N$ $cm^{-3}$); (b) mean $^{15}N$ excess after 24 h into tillers of *Puccinellia phryganodes* ($n = 3$–5), per g dry wt. biomass from intact vegetated marshes. In each case $^{15}N$ excess refers to the amount of $^{15}N$ measured in soil extracts and plant biomass, respectively, relative to the background natural abundance. Soil types as indicated in the legend of Figure 1.

## SOIL MICROBIAL BIOMASS

Microbial biomass carbon (MBC) per unit volume of soil (Fig. 3a) differed between marshes ($F_{1,8} = 23.3$; $P = 0.001$) and between treatments ($F_{1,8} = 11.0$; $P = 0.01$), such that it was highest in the supratidal intact soils, and lowest in supratidal degraded soils, with less of a treatment effect in the intertidal soils. MBC did not vary significantly from spring to early winter, and late winter values for MBC were not measured. Values of microbial biomass nitrogen (MBN) (Fig. 3b) did not differ between the two marshes per unit volume of soil, although MBN was significantly greater in vegetated compared to degraded soils ($F_{1,8} = 21.4$; $P = 0.002$). There was a substantial rise in MBN in late winter (time effect: $F_{6,48} = 8.6$, $P < 0.0001$).

The mean MBC : N ratio for spring, summer and early winter at both marshes (Table 1) varied between 2 and 52 and it was highly variable across all sampling dates. This variability was associated with changes in values of MBC across dates, especially in degraded areas (Fig. 3a), suggesting N availability may not be the primary control on the size of the microbial biomass at an annual time scale. Overall, supratidal soils had a higher MBC : N ratio than intertidal soils (site effect: $F_{1,7} = 10.8$; $P = 0.01$, treatment effect NS). The MBC : N ratio decreased slightly from spring to summer, then increased in early winter which was more pronounced at the intertidal site and in degraded soils (time effect: $F_{2.3,16.2} = 8.9$; $P = 0.002$; time × site: $F_{2.3,16.2} = 7.3$; $P = 0.004$; time × treatment: $F_{2.3,16.2} = 5.5$; $P = 0.01$).

## SOIL MICROBIAL ACTIVITY

The amount of $^{15}N$ in microbial biomass per unit volume of soil after 24 h of incubation ($MB^{15}N$ excess) (Fig. 3c) was lower in degraded soils compared with vegetated soils (treatment effect: $F_{1,8} = 85.2$; $P < 0.0001$). Although the microbial biomass in supratidal soil samples accumulated more $^{15}N$ than that in intertidal soil cores in mid-summer, there was no significant difference in values between sites. Appreciable accumulation of $^{15}N$ in microbial biomass occurred in late winter, although generally amounts were less than detected in summer.

There were no significant differences between marshes or treatments in rates of gross mineralization, based on the isotope dilution method (Fig. 4a). Rates of gross

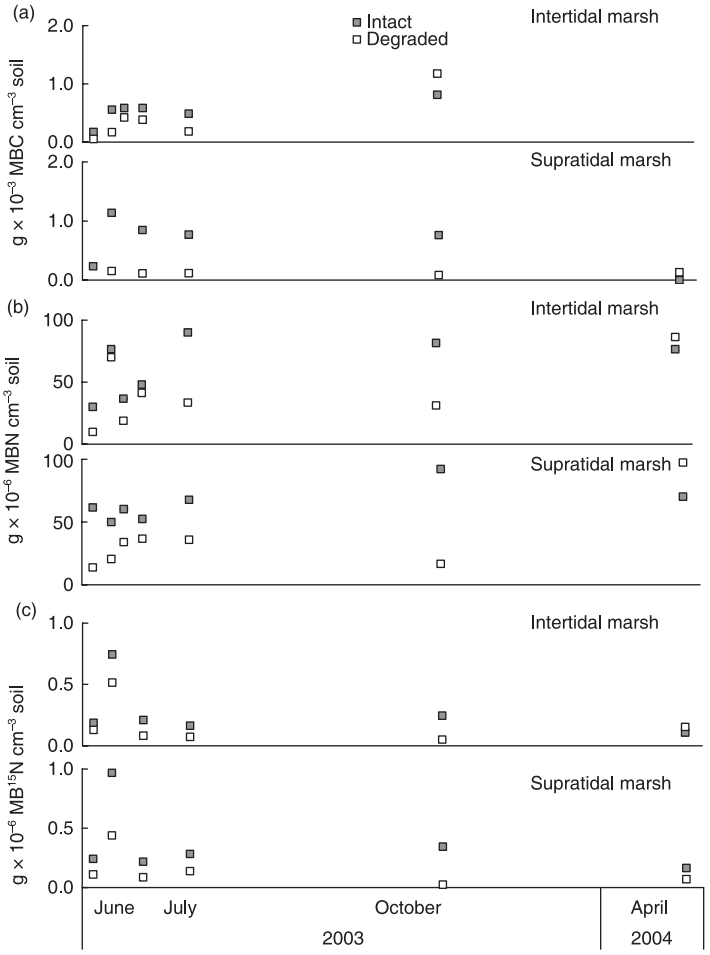


**Fig. 3** (a) Mean microbial biomass carbon ($n$ = 3–5) per unit volume of soil (mg C cm$^{-3}$); (b) mean microbial biomass nitrogen ($n$ = 3–5) per unit volume of soil (μg N cm$^{-3}$); (c) mean $^{15}$N excess ($n$ = 3–5) after 24 h incubation into the microbial biomass nitrogen per unit volume of soil (μg $^{15}$N cm$^{-3}$). $^{15}$N excess refers to the amount of $^{15}$N measured in the corrected ($k_N$ = 0.4) extractable microbial N, relative to the background natural abundance. Soil types as indicated in the legend of Fig. 1.

mineralization were very low in late winter (April 2004) when relatively large amounts of $NH_4^+$ and DON were present in marsh soils (Fig. 1a,c) (time effect: $F_{4,32} = 3.7$; $P = 0.01$). Rates of microbial immobilization also were low at this time (Fig. 4b) (time effect: $F_{4,24} = 8.2$; $P = 0.0003$). Seasonal variability in microbial immobilization of $^{15}$N was sensitive to the presence of actively growing vegetation (time × treatment: $F_{4,24} = 4.6$; $P = 0.007$). Although there was no difference between soils in rates of gross mineralization, microbial N immobilization was much lower in degraded soils ($F_{1,6} = 37.3$; $P = 0.0009$) than comparable values for vegetated soils, except in late winter (April 2004).

Marsh site had no effect on the time that $^{15}$N resided in the microbial biomass (Fig. 4c), unlike the treatment effect, with a greater $^{15}$N microbial residency time in degraded soils (treatment effect: $F_{1,8} = 21.9$; $P = 0.002$). Note that the residency times reached maximum values in late winter in all soils, and this seasonal increase was greatest in vegetated soils (time effect: $F_{4,32} = 25.3$; $P < 0.0001$; time × treatment: $F_{4,32} = 2.6$; $P = 0.05$).




### $^{15}$N DISTRIBUTION AMONG SOIL POOLS

The proportional distribution of added $^{15}$N label within soils (Fig. 5) indicates that treatments affected the distribution of $^{15}$N in the different pools as microbes dominated $^{15}$N uptake in vegetated soils overall. In contrast to vegetated soils, there was less $^{15}$N uptake by microbes in degraded plots, and more $^{15}$N remained in the abiotic phase, resulting in similar amount of $^{15}$N in each of these two pools, and an interaction with treatments (pool effect: $F_{1,14} = 47.0$; $P < 0.0001$, treatment × pool: $F_{1,14} = 49.5$; $P < 0.0001$). In both marshes, the proportional distribution of $^{15}$N in the different pools was sensitive to the interaction with sampling time (time effect: $F_{4,56} = 8.8$; $P < 0.0001$, time × pool: $F_{4,56} = 10.7$; $P < 0.0001$). Among vegetated sites in the intertidal marsh, the proportion of $^{15}$N present in plants and microbes was broadly similar in summer. In late winter, a substantial proportion of the $^{15}$N recovered remained in the abiotic phase of the soil.

## Discussion

Exposure of mineral soil in this Arctic coastal marsh is triggered by the grubbing activities of geese leading to changes in soil properties including hypersalinity in most summers and the loss of total soil N (Table 1) (Srivastava & Jefferies 1996; Wilson & Jefferies 1996; Wilson *et al*. 1999; Walker *et al*. 2003; McLaren & Jefferies 2004). This state is characterized by a decline in microbial growth compared with that in soils beneath graminoid swards, as indicated by reduced microbial biomass $^{15}$N excess, reduced immobilization without reduced gross mineralization, and by longer microbial $^{15}$N residency times (Figs 3c and 4a–c). These changes are similar in both the organic-rich and mineral soils, despite differences in salinity and organic matter content (Table 1) (Srivastava & Jefferies 1996; Wilson & Jefferies 1996; McLaren & Jefferies 2004). Large amounts of $^{15}$N in the soil abiotic pool of both degraded marsh soils (Figs 2a and 5) suggest that microbial demand for N is less than the supply rate. In the absence of plants, inorganic N and DON accumulate in the abiotic phase of these degraded soils compared to vegetated soils, and much of this N may be lost ultimately in drainage water or from other causes. Both types of degraded soil become increasingly depleted in total N, as reported by McLaren & Jefferies (2004).

Plant removal by geese may lead to C limitation of soil microbes, particularly in the supratidal marsh, as low inputs of allochthonous materials from infrequent tidal immersion cannot compensate for loss of inputs of organic C from root exudates and plant litter. Notably, microbial C declines steeply in exposed organic-rich supratidal soils in the summer, and it is also low in exposed intertidal soils at this time, coincident with the absence of tidal cover in summer (Fig. 3a). The rise in microbial C in late October at the latter site may be linked to allochthonous tidal inputs in autumn. In

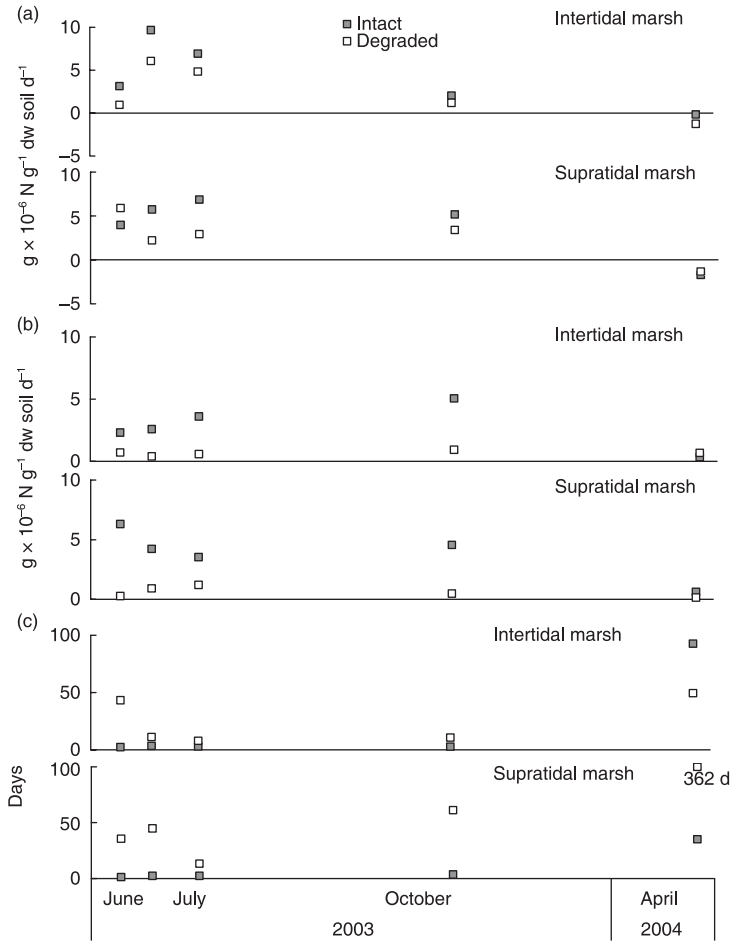


**Fig. 4** (a) Mean rates of gross mineralization ($n$ = 3–5) per g dry wt. soil per day, as calculated by the isotope dilution equation; (b) mean rates of gross immobilization ($n$ = 3–5) per g dry wt. soil per day, as calculated by the isotope dilution equation and assuming an exponential decline of the $^{15}$N pool; (c) mean rates ($n$ = 3–5) of microbial $^{15}$N residency time in days, as calculated by the isotope dilution equation and assuming an exponential decline of the $^{15}$N pool. Soil types as indicated in the legend of Fig. 1.

addition, the declining proportion of $^{15}$N in summer recovered in microbial biomass in samples from degraded soils (Fig. 5) and the continued gross mineralization without immobilization indicate possible C-limitation for the growth of microorganisms. Much of the isotope not taken up by microorganisms remained in the soil phase (Fig. 5). Results of recent studies of experimental additions of glucose to plots in these coastal soils have shown increased microbial activity in early spring and summer (Hargreaves 2005; K. Edwards, pers. comm.). In addition, amounts of microbial C showed a substantial autumnal rise in vegetated plots receiving N in early June and the first part of July, in contrast to the remainder of the summer (Hargreaves 2005). The results support the hypothesis that the rate of C loss from plants in the snow-free period, either as surface litter, or as root exudates or turnover, strongly regulates soil microbial activity (Bardgett *et al*. 1998; Hamilton & Frank 2001; Bardgett *et al*. 2005).

The seasonal record of $^{15}$N allocation indicates little overall change in the incorporation of the isotope in microbial biomass in vegetated sites from June to October (Figs 3c and 5). Unlike the seasonal demands of plants, soil microorganisms took up a similar proportion of the total injected $^{15}$N. During summer much of the $^{15}$N was immobilized in plant and microbial biomass in vegetated soils, and little remained in the soil solution (Fig. 5). An earlier study showed that in summer there was little net N mineralization in these soils (Wilson & Jefferies 1996), similar to Alaskan results (Giblin *et al*. 1991).

In spite of low air temperatures, soil microbial activity is known to continue during the early winter because of the insulating effect of snow (Giblin *et al*. 1991; Oechel *et al*. 1997; Brooks *et al*. 1998). Snow-cover maintains soil temperatures above or just below 0 °C on the Churchill Peninsula until late November in most years (P. Kershaw, pers. comm.). At these temperatures mineralization of soil N may be expected to occur (Schmidt *et al*. 1999; Schmidt & Lipson 2004). By late winter considerable amounts of soluble inorganic and organic N were present in soils, representing cumulative net mineralization of N over the winter season and possibly some nutrient recycling following faunal predation (Sjursen *et al*. 2005) during short-lived thaw cycles. Values of gross mineralization and immobilization (Fig. 4a,b), however, were low in late winter when the availability of soil N was high (Fig. 1). Microbial biomass, unlike vascular plants, accumulated high amounts of total N and $^{15}$N, but residency time was very long (Fig. 4c) indicating little microbial turnover of N in late winter. During the winter, microbial activity is uncoupled from plant growth, except for the dependency on carbon released from senescing plant tissue produced the previous summer (Bardgett *et al*. 2005).

The proportional allocation of $^{15}$N to plants in vegetated soils is high relative to values for other Arctic ecosystems (Grogan & Jonasson 2003; Grogan *et al*. 2004; Nordin *et al*. 2004), but the result is consistent with previous studies at La Pérouse Bay (Henry & Jefferies 2003). During the plant growing season average microbe : plant $^{15}$N uptake ratios are approximately 3.5 : 1 and 1.5 : 1 for the supratidal and intertidal marsh, respectively. This can be compared to $^{15}$N uptake ratios of approximately 50 : 1 in another short-term Arctic study (Nordin *et al*. 2004). In the latter study, as well as in longer term studies, many of the tundra plants examined were slow-growing Ericaceous species and not species with a higher intrinsic growth rate, such as *P. phryganodes*, with a high nutrient demand. Individual tillers of this grass in swards at La Pérouse Bay produce a new leaf on average once every 11 days and leaf life span is between 28 and 33 days during the growing season (Bazely & Jefferies 1989; Srivastava & Jefferies 1996).

The higher proportion of isotope allocated to plants in these soil cores also may be a grazing effect of geese, as a common response associated with herbivory is an increase in shoot N (Guitian & Bardgett 2000), including shoots of *P. phryganodes* (Hik & Jefferies 1990). The mechanisms accounting for this increase are typically

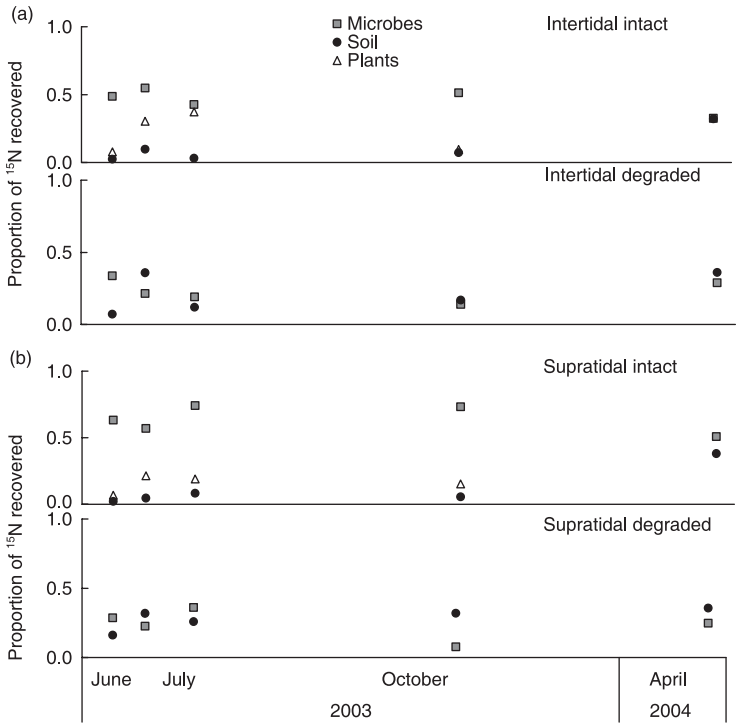


**Fig. 5** Mean distribution of $^{15}$N after 24 h ($n$ = 3–5), as a proportion of the original amount of $^{15}$N injected, amongst the microbial biomass, the plant biomass and the ($K_2SO_4$-extractable) soil solution in cores from (a) the intertidal marsh and (b) the supratidal marsh. Soil types as indicated in the legend of Fig. 1.

linked to adequate sources of labile C in the rhizosphere derived from an elevated translocation of carbon to the roots of defoliated plants and an increase in root exudates where soil carbon availability is low (Bardgett *et al*. 1998). This results in an increase in microbial turnover and N mineralization. At La Pérouse Bay, however, the positive feedback leading to increased net primary production and new shoots that are rich in nitrogen is dependent upon the input of goose faeces which contain soluble inorganic N and amino acids (Henry & Jefferies 2002), and in their absence net annual primary productivity does not increase in grazed swards (Bazely & Jefferies 1985; Hik & Jefferies 1990). Aside from potential root exudations of organic carbon, faecal inputs also provide a source of soluble organic carbon for soil microorganisms that may alleviate carbon limitation in these soils.

## Conclusions

Arctic landscapes possess a diversity of ecosystems where steep gradients in physical conditions are evident over short distances (Giblin *et al*. 1991; Nadelhofer *et al*. 1991; Shaver & Chapin 1991). The organic substrates in litter and the exudates from plant species characteristic of the different ecosystems largely structure both the composition and the function of the soil microbial communities within these systems (Zak & Kling 2006). Although the composition of the microbial communities has not been determined in this study, large differences across short distances occur in plant litter inputs, environmental conditions and rates of microbial activity between vegetated and disturbed sites. There were declines in microbial biomass, rates of microbial immobilization, and in microbial activity in degraded sites compared with results from vegetated soils, despite the absence of plant competition and the differences in soil properties. Loss of vegetation and the absence of grazing appear to reduce, but not eliminate, microbial activity, which is dampened probably by the absence of plant inputs to soils. Thus, as soon as vegetative cover is removed, the system moves irrevocably towards the degraded state, where the soils are hypersaline in most years, but the decline in microbial activity is not dramatic, unlike the decline in vascular plant growth and grazing by snow geese. The vegetated state and the exposed mineral soil represent two alternate stable states (Hik *et al*. 1992; Handa *et al*. 2002) and the transient surface organic layer in grubbed (degraded) supratidal soils can be considered an unstable state. The presence of a large fraction of $^{15}$N in the abiotic phase of degraded soils, rather than the biotic phase, indicates this pool is likely to decline and be lost when soils are leached at thaw and during tidal immersions. The outcome is a shift in the proportional distribution of N from the biotic to the abiotic phase in degraded soils and an increased potential for loss of soluble and exchangeable N, consistent with the loss of total N in these soils reported earlier (McLaren & Jefferies 2004).

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