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REGULAR ARTICLE

Soil nitrogen cycling rates in low arctic shrub tundra are enhanced by litter feedbacks

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Abstract Shrub growth has increased across the Arctic in recent decades and is strongly limited by soil nitrogen (N) availability. In order to understand the role of N in controlling shrub growth, we compared N-cycling in tall birch (*Betula glandulosa*) and surrounding dwarf birch hummock vegetation on similar soils in a Canadian low arctic site. Stable isotope tracer analysis revealed N pools and cycling rates were ~3 times larger and faster in the tall birch ecosystem in the late growing season, just prior to leaf senescence. Gross NH_4^+-N production rates in these ecosystems correlated positively with larger pools and production rates of dissolved soil C and N, higher quality litter inputs and lower soil C. Analyses of the soil microbial community in both ecosystems indicated similar fungal dominance (epifluorescence microscopy) and similar compositions of the principal fungal or bacterial phylotypes (denaturing gradient gel electrophoresis). Together, these results strongly suggest that vegetation feedbacks associated with larger inputs of higher quality litter promote rapid soil N-cycling and enhanced shrub growth in tall birch tundra. We conclude that these litter-related feedbacks during summer may be as important as snow-shrub feedbacks in maintaining and promoting differences in shrub growth across the arctic landscape.

Keywords ^{15}Nitrogen · Gross N mineralization · Arctic tundra · Litter · Soil microbial community · *Betula*

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Introduction

Arctic research has detected climate warming impacts over the past 20–30 years and recent evidence indicates substantial vegetation change is occurring across the tundra (IPCC 2007). For example, remote sensing studies have characterized an increase in peak-season biomass across the Arctic over the past three decades (Goetz et al. 2005; Myneni et al. 1997). Time-series aerial photography and plot-level investigations have linked this biomass change to an increase in abundance and density of shrubs across

the circumpolar tundra (Devi et al. 2008; Sturm et al. 2001a; Tape et al. 2006), and this association between warming and shrub expansion is supported by several experimental warming studies of tundra shrub apical growth (Chapin et al. 1995; Jonasson et al. 1999; Walker et al. 2006). Increased shrub cover results in enhanced absorption of solar radiation and therefore localized atmospheric heating, providing a potentially very significant positive feedback to climate warming (Chapin et al. 2005). By contrast, increased woody growth by shrubs stores carbon (C), which may promote a negative feedback by mitigating some of the CO_2 released as a result of enhanced organic matter decomposition from warmer soils (Shaver et al. 1992, 2000).

Primary productivity in both tall shrub and tussock tundra ecosystems is limited by N availability (Shaver and Chapin 1980). Although shrub expansion is most prevalent in floodplain habitats, moderate increases in shrub growth and cover have been documented on plateaus and slopes (Tape et al. 2006) where preferential pathways for surface water flow are not apparent. Riparian sites are often seasonally flooded suggesting that water flow and occasional flooding disturbance enhance N availability adjacent to streams and rivers (Chapin and Shaver 1981), and N cycling rates are faster in riparian tall shrub soils than in tussock tundra (Giblin et al. 1991). By contrast, in laboratory incubations at a constant temperature non-riparian shrub soils can have either slower (Hobbie 1996; Kielland 1995) or faster (Weintraub and Schimel 2003) rates of net N mineralization, and reduced amino acid immobilization (Kielland 1995), relative to tussock soils. Soil N cycling is controlled by soil microbes and soil microbial communities differ between shrub and tussock tundra soils in Alaska (Wallenstein et al. 2007), suggesting the microbial community structure may be an important control on soil N cycling and N availability to plants. In particular, fungal:bacterial ratios may differ under enhanced shrub growth if litter and root exudate quality and quantity differs, as soil fungi and bacteria utilize different soil C substrates (Rinnan and Baath 2009). This may in turn alter N cycling rates if soil organic matter decomposition, N mineralization rates and trophic interactions in fungal-dominated communities are slow relative to bacterial-dominated communities (Moore et al. 2005; Wardle et al. 2004). Investigation of in situ N cycling field rates and potential microbial controls on N availability in tall shrub and low shrub tundra areas where surface water is not a confounding control is essential to understanding current differences in shrub growth across the landscape and predicting patterns of shrub expansion.

Current theories about tundra ecosystem succession have suggested that a positive feedback exists between shrubs and snow, whereby deeper snow around shrubs promotes warmer soil temperatures and increased N availability at spring thaw (Sturm et al. 2005). The positive contribution of winter shrub dynamics for annual ecosystem N budgets may be countered by summer constraints on N cycling, such as cooling of soils via increased canopy shading and an associated shallower active layer (Chapin et al. 2005; McFadden et al. 1998; Sturm et al. 2001a; Wookey et al. 2009). In addition, rates of litter decomposition may be reduced by a greater proportion of more recalcitrant woody litter in *Betula*-dominated tundra (Hobbie 1996; Weintraub and Schimel 2005a; Wookey et al. 2009). At present, it is believed that positive winter effects of tall shrubs on N availability exceed negative summer effects, promoting shrub expansion, although these potential negative summer feedbacks involving soil temperature and litter quality effects on N-cycling have not yet been investigated (Sturm et al. 2005).

In this study we present a field investigation of gross and net N cycling rates under tall birch tundra and birch hummock tundra in the Canadian Low Arctic in late summer. Our goal was to characterize ecosystem differences in substrate and the soil microbial community during the growing season, and to investigate the influence of these two factors on N cycling rates and N availability as potential mechanisms for enhanced shrub growth. In particular, our aim was to address the following research questions: (1) Are N pool sizes in the soil organic matter and microbial biomass larger, and N-cycling rates faster, in tall birch tundra relative to birch hummock tundra? (2) Does the quality (C:N) of soil and litter differ between tall shrub and birch hummock tundra? (3) Do the soil fungal:bacterial ratios or the dominant soil microbial phylotypes differ between tall shrub and birch hummock tundra? (4) Are N-cycling rates correlated with the quality of soil organic matter and litter, and the soil microbial community in these tundra ecosystems?

Methods

General site description

This study was conducted on mesic birch hummock and tall birch ecosystems at the Tundra Ecosystem Research Station (TERS) at Daring Lake (64º52′ N, 111º33′W), approximately 300 km north of Yellowknife in the Northwest Territories, Canada, at the end of the 2006 growing season (August 20-September 1). The valley in which we carried out this study (~4 km^2) is bordered by an esker and outcroppings of Canadian Shield bedrock. Both ecosystem types are circumpolar in distribution (Bliss and Matveyeva 1992) and occur in the middle of a toposequence that extends from dry heath vegetation at the top of the esker to wet sedge vegetation at the base of the valley. The soils in the two ecosystem types are Orthic Dystric Turbic Cryosols (Soil Classification Working Group 1998) and consist of an organic horizon ~3–20 cm deep above cryoturbated silt-sand mineral horizons.

The birch hummock ecosystem (Fig. 1a) used in this study and others (Buckeridge and Grogan 2008; Lafleur and Humphreys 2008; Nobrega and Grogan 2007; 2008) occurred as frequent patches in the valley and is characterized by hummocks 10–30 cm high and deciduous dwarf birch shrubs (*Betula glandulosa*) that are 10–40 cm tall and attain ~10–30% of the areal coverage. The remaining cover is a mixture of mostly ericaceous shrubs (bog rosemary (*Andromeda polifolia* L.), mountain cranberry (*Vaccinium vitis-idaea* L.), bog blueberry (*V. uliginosum* L.), and labrador tea (*Ledum decumbens* (Ait.))), sedges (*Eriophorum vaginatum* L. and *Carex* spp. (L.)), mosses (*Aulacomnium turgidum* (Wahlenb.) and *Sphagnum* spp.), lichens, and cloudberry (*Rubus chamaemorus* L.).

The tall birch ecosystem (Fig. 1b) used in this study occurred as a large patch (~40×130 m) of dense (~90% areal coverage), tall (~50–100 cm high) *B. glandulosa* shrubs, on a gentle slope in the valley. Surface stream water preferential flow patterns were not evident at this site; similar tall birch patches occurred at several other locations across the valley but these other patches were either closely associated with definite stream or river flows, or in wind-protected, deep snow accumulation areas, such as the lee of eskers. We focused on this mesic large tall birch patch because we were interested in interpreting our results in the context of the potential for increases in shrub density in landscape areas without obvious hydrological or topographical influences. The understory, found directly beneath shrubs as well as lining and within the caribou trails between shrubs, consists of the same vegetation composition as described for the mesic birch hummock ecosystem above.

Soil nutrient pools and net cycling rates

Plots (~0.5 m diameter, $n=5$) centered on a birch shrub within each ecosystem type were selected arbitrarily and without preconceived bias (McCune and Grace 2002). Net nitrogen (N) and dissolved organic C (DOC) cycling rates were determined using a modification of the buried bag technique (Eno 1960). Four cores were taken within each plot to the full depth of the organic layer (range: 6 to 11 cm in

Fig. 1 Birch hummock (**a**) and tall birch (**b**) ecosystems at Daring Lake, NWT, Canada, in August. Photo credit: Ian McCormick

the birch hummock plots; 8 to 10 cm in the tall birch plots) and no mineral soil was included. Live plant and lichen material was removed from the core surfaces, but any surface litter was retained. Two cores were designated as 'final' cores and placed intact into separate gas-permeable polyethylene bags which were sealed and then inserted back into the ground before replacing the live plant material that had been removed on top. The two 'initial' cores were returned to the field lab and were processed within a few hours of sampling. The two initial cores from under each shrub were composited and homogenized by hand, which include removal of large roots (>2 mm). The mixed cores were immediately sub-sampled (~10 g fresh weight soil) for soil solution extraction, microbial biomass estimation and soil moisture calculations. Extraction was achieved by adding 50 mL of 0.5 M K_2SO_4, shaking the sample cups intermittently over one hour and then filtering through glass fiber filters (Fisher G4, 1.2 μm pore space) using a vacuum. Soil microbial biomass C and N contents were determined by the chloroform-fumigation direct-extraction (CFE) technique (Brookes et al. 1985). Fumigation lasted 24 h in a darkened vacuum desiccator jar at field lab temperature (~10–15°C). Extraction of fumigated soil was as described above, and all extracts were frozen until analysis at Queen's University in Kingston, Ontario. After 10 days of in situ incubation, the final cores were retrieved and extracted as described above. Net cycling rates were calculated from the change in extractable soil solution NH_4^+-N, dissolved organic nitrogen (DON) or dissolved organic carbon (DOC) concentrations, during the field incubations. NH_4^+-N and NO_3^--N in the extracts were determined colourimetrically, using automated flow analysis (Bran-Leubbe Autoanalyzer III, Norderstadt, Germany) and the indophenol and sulphanilamide methods (Mulvaney 1996). NO_3^--N was below our detection level for these samples (common in these soils) and was assumed to be negligible in these ecosystems. Dissolved organic carbon (DOC) and dissolved total nitrogen (DTN) contents in the extracts from fumigated and non-fumigated soils were determined by oxidative combustion and infrared (Nelson and Sommers 1996) or chemiluminesence analyses, respectively (TOC-TN autoanalyzer, Shimadzu, Kyoto, Japan). DON was calculated as the difference between DTN and NH_4^+-N. Microbial biomass C and N contents (MBC and MBN) were calculated as the difference between initial fumigated and non-fumigated C and N samples, and no correction factor (k_C or k_N) was applied. All C and N concentrations in the extracts were corrected for the dilution associated with the moisture content of each soil sample. Soil moisture content was calculated after complete oven drying at 65°C.

^{15}N injections ('Isotope pool dilution') and sample processing

To estimate gross cycling rates, two additional soil cores from each of the five plots at the two ecosystem types were sampled as described above. The cores were injected with 99 atom% $^{15}NH_4Cl$ (0.9 mg ^{15}N/L or ~0.0029 μg ^{15}N cm^{-3} or ~0.16 μg ^{15}N g dw $soil^{-1}$; Cambridge Isotope Laboratories, Andover, MA), which increased the extractable NH_4^+ pool by ~0.1–3% and the soil moisture by ~8–30%. Initial ^{15}N cores were then mixed and sub-sampled as described above. The remaining final ^{15}N cores were placed intact in PVC tubes sealed on both ends by polyethylene and incubated in the same holes from which they came. After 24-hour incubation, these cores were mixed and sub-sampled as described above.

Surface litter and total soil C and N pools

To assess surface litter quantity and quality differences between the two ecosystems, soil turves (top organic layer with tightly rooted organic soil and vegetation, mean area = 80 cm^2) were cut from each plot. The cores were first upturned and gently shaken to remove most of the surface leaf and any small twig litter, then the live plant shoots were removed and not included, so that the remaining surface litter could be collected by hand picking. Leaf senescence had not yet begun or was just beginning, implying that our litter measures did not include the current year's production. Our purpose was to sample the surface leaf litter pool that had senesced in recent years and had not yet been consolidated or incorporated into humified organic matter. Dried initial soil and litter were oven-dried (65°C) and ground (Retsch ZM 200 Ultra Centrifugal Mill (litter) or Retsch PM 200 Planetary Ball Mill (soil), Haan, Germany) and then analyzed for total carbon and nitrogen (LECO CNS 2000, St. Joseph, USA). All C:N ratios are atomic.

Gross mineralization (diffusion procedure) and gross immobilization (salt dry-down procedure)

A modified version of the diffusion technique described by Stark and Hart (1996) was used to prepare soil solution extracts from the gross mineralization cores for ^{15}N analysis. Aliquots of 0.5 M K_2SO_4 extract from each birch hummock and tall birch initial and final core were spiked with a $^{14}NH_4Cl$ solution in 125 mL mason jars. $^{14+15}NH_4^+$ in the extract + spike solution was volatilized to NH_3 by the addition of 0.2 g of MgO to the extract solution. $^{14+15}NH_3$ was subsequently captured over six days on acid traps made by sealing two acidified (10 μL 0.5 M $KHSO_4$) quartz filter discs (CAT No. 1851-047, QMA grade Whatman filters) in Teflon tape. After the six day diffusion, the traps were removed from the jars and dried discs were sent to the Environmental Isotope Laboratory (University of Waterloo) for ^{15}N analysis using an Isochrom Continuous Flow Stable Isotope Ratio Mass Spectrometer (GVInstruments/ Micromass-UK) coupled to a Carlo Erba Elemental Analyzer (CHNS-O EA1108, Italy).

To determine ^{15}N in soil microbes, a modified salt dry-down procedure was used on the fumigated extracts of the initial and final ^{15}N injected cores (Dijkstra et al. 2006). The salt extracts were dried in an oven at 65°C, ground to a fine powder and analyzed for their δ ^{15}N ratios and total N content at the Colorado Plateau Stable Isotope Laboratory (North Arizona State University) using a Delta Plus Advantage Gas Isotope-Ratio Mass Spectrometer (Thermo Electron, Bremen) coupled to a Carlo Erba Elemental Analyzer (NC2100, Italy).

Isotope dilution calculations

Rates of gross mineralization (dilution of the $^{14+15}NH_4^+$-N pool with $^{14}NH_4^+$-N over time; an estimate of new mineralization of organic material to NH_4^+-N), gross consumption (gross mineralization minus the change in the $^{14+15}NH_4^+$-N pool over time; an estimate of the total removal of ^{15}N from the soil solution, due to uptake of ^{15}N by plants, microbes and/or abiotic fixation) and gross immobilization (^{15}N enrichment in the MBN over time; an indicator of the microbial N uptake portion of gross consumption) were calculated using the isotope dilution equations, and following the assumptions of the Kirkham and Bartholomew model (1954) as cited in Hart et al. (1994): a) no isotopic fractionation occurs during microbial transformations of soil N; b) added ^{15}N may be immobilized by microbes, but is not re-mineralized during the in situ incubation; and c) rates of microbial transformations of N are constant during the incubation period. The relatively short incubation time (24 h) used in the present study makes violations of these assumptions unlikely (Hart et al. 1994). All results were calculated using ^{15}N excess in soil and microbial pools adjusted relative to (in situ) background levels of ^{15}N excess in soil and microbial pools.

Microbial community analysis

To test for differences in the soil microbial community between the two ecosystem types, we used epifluorescent microscopy to count fungal hyphae and bacterial cells and to estimate fungal and bacterial volumes, and we used denaturing gradient gel electrophoresis (DGGE) of amplified DNA extracts to compare community fingerprints of dominant bacteria and fungi. Cores were collected from the same plots as net and gross cycling cores to the bottom of the organic layer. One sample was collected for total counts, and two composites were collected for molecular analysis. Surface plants and large roots were removed and soils designated for nucleic acid analysis were well-mixed and frozen for return to the lab at Queen's University. Soil samples for total counts (10 g) were blended with 90 mL of water at 13,000 rpm for 5 min, and then 9 mL of the suspension was fixed with 1 mL of formalin prior to transport to Queen's University for slide preparation.

Microscopy slide preparation was according to Bloem et al. (1995) with some modifications, as described in Buckeridge and Grogan (2008) using the polysaccharide stain fluorescent brightener 28 (FB 28) to stain total fungi (i.e. live plus dead fungal mass), and the nucleic acid stain DTAF to stain total bacteria (i.e. live plus dead bacterial mass). All samples were viewed with an epifluorescent microscope (Nikon E600W), and photographed with a cooled 16-bit digital colour camera (QICAM 1394, QImaging, Burnaby, B.C.). Bacterial cell counts and volume were based upon the average of ten fields-of-view per slide and fungal hyphal analyses were the average of 20 fields-of-view per slide. Enumeration of bacteria and fungi was done semi-automatically using

the software program SimplePCI (version 5.3.1, Compix, Cranberry Township, PA), which quantifies the length (L) and breadth (B) of each user-selected organism in a field-of-view. Length collected in this manner was used to calculate fungal hyphal length. Bacterial and fungal volume per cell (V) were calculated as $V = \pi/4 \times B^2 \times (L - B/3)$ (Bloem et al. 1995). Volumes were converted to mass of C assuming a mean fungal C content of 3.1×10^{-13} g C mm^{-3} and a mean bacterial C content of 1.3×10^{-13} g C mm^{-3} (Bloem et al. 1995).

Soil DNA was extracted from 0.25 g of soil using the Power Soil extraction kit (MOBIO, Carlsbad, CA), which uses a combination of bead-beating and proprietary solvents to remove excess humic acids and extract DNA. DNA was frozen before analysis (−20°C) and then diluted ten times for use as PCR template. The primer pair GC-338f (forward) and 907r (reverse) was used for the amplification of eubacterial 16S rRNA gene (Chu et al. 2007) and the primer pair FF390 (forward) and FR1-GC (reverse) was used for the amplification of the fungal 18S rRNA gene (Vainio and Hantula 2000) with a nested PCR (FF390 and FR1 for the 1st PCR, FF390 and FR1-GC for the 2nd PCR). PCR amplification was performed with a Techne TC-3000 thermocycler (Barloworld, USA). PCR mixtures were prepared with a 0.2 mM concentration of each deoxynucleoside triphosphate, 5 μl of 10× PCR buffer, 2.0 mM $MgCl_2$, 0.4 μM of each primer, 1.25 U (1.0 U for fungal PCR) of *Taq* polymerase (Fermentas), and 1 μl of soil DNA template, in a final volume of 50 μl. Amplification was always started by placing the PCR tubes into the preheated (95°C) thermal block of the thermocycler. The thermal profile for amplification was as follows: 10 min at 95°C; 35 cycles of 1 min at 95°C, 1 min at 50°C, and 1 min at 72°C (or 1.5 min for fungal PCR); and 5 min at 72°C (or 10 min for fungal PCR). The PCR products were electrophoresed on 1% agarose to ascertain their size and quality, and were then separated using DGGE with a D-Code universal mutation detection system (Bio-Rad Laboratories) according to the instruction manual. The bacterial PCR products were loaded on 6% (*wt/vol*) polyacrylamide gels with a denaturing gradient of 40% to 60% (100% denaturant contains 7 M urea and 40% formamide). The fungal PCR products were loaded on 8% (*wt/vol*) polyacrylamide gels with a denaturing gradient of 25% to 55%. The gels were run in 1× Tris-acetate-EDTA buffer at 60°C and 65 V for 20 h (16 h for the fungal gel), with the first 12 min at 200 V. After DGGE, the gels were stained with 1:10,000 SYBR green I (Invitrogen, Molecular Probes, Eugene, OR) and scanned with a ChemiGenius scanner (Syngene, Cambridge, UK).

Statistical analyses

Differences between the birch hummock and tall birch ecosystems were determined by one-way analyses of variance (ANOVAs) (JMP 7.0.2, 2008, SAS Institute, Cary, NC, USA). Data were log transformed to meet the requirements of normality when necessary. Variation in gross mineralization rates among all birch hummock and tall birch plots was related to all factors not directly involved in the calculation of the nitrogen cycling rate, using bivariate fits (n=9, one soil diffusion value was not recovered). All significant results are reported (P<0.05).

Results

Ecosystem N and C pools and stoichiometry

The surface litter N pool just prior to leaf senescence late in the growing season was ~2.5 times larger in the tall birch ecosystem than in the birch hummock ecosystem due to more litter mass as well as significantly higher litter N concentrations (Table 1). By contrast, litter C concentrations did not differ significantly resulting in significantly lower C:N in litter at the tall birch site (Table 1). Total N in the soil organic layer beneath the surface litter did not differ significantly between the ecosystem types (Table 1). Soil C concentrations, however, were ~50% lower in the tall birch ecosystem (Table 1), resulting in significantly lower soil C:N ratios (Table 1).

NH_4^+-N, dissolved organic N (DON) and dissolved organic C (DOC) pools were 2.8, 3.3 and 2.7 times larger, respectively, in the soil solution of the tall birch ecosystem (Fig. 2, Table 2). In addition, there were 1.5 times more C and N stored in the microbial biomass pool in the tall birch soil (Fig. 2, Table 2). Most (>90%) of this microbial C was stored in the fungal rather than the bacterial biomass in both of these ecosystems, and the fungal C and fungal: bacterial ratio was larger (P≤0.1) in the tall birch

Table 1 Litter and soil properties in the organic layer of birch hummock and tall birch tundra ecosystems in late summer (n=5). Properties that are significantly different (P<0.05) between vegetation types are in bold font (s.e. = standard error)

			Birch hummock		Tall birch		$F_{1,8}$	P
			mean	(se)	mean	(se)		
Litter	Mass	g m^{-2}	473	(58)	900	(205)	4	0.08
	C concentration	%	52	(0.3)	49.4	(1.9)	1.8[a]	0.2
	N concentration	%	**1.04**	(0.03)	**1.35**	(0.06)	22.2	**0.002**
	C/N		**50.4**	(1.3)	**36.7**	(1.9)	34.9	**0.0004**
	Total C	g m^{-2}	246	(30)	456	(112)	3.3	0.1
	Total N	g m^{-2}	**4.9**	(0.7)	**12.6**	(3.3)	6.6[a]	**0.03**
Soil organic layer	C concentration	%	**45.4**	(1.9)	**30.7**	(4.4)	9.5	**0.02**
	N concentration	%	1.27	(0.07)	1.13	(0.2)	0.4	0.5
	C/N		**35.9**	(1.1)	**27.7**	(1.1)	27.9	**0.0007**
	Total C	kg m^{-2}	5.3	(0.8)	4.0	(0.8)	1.3	0.3
	Total N	kg m^{-2}	0.15	(0.02)	0.15	(0.04)	0.001	0.9
	Soil water content	g g dw $soil^{-1}$	**2.28**	(0.23)	**0.64**	(0.04)	50.3	**0.0001**

[a] log transformed to meet expectations of normality, for statistical analysis

system (Table 2). The mean soil C: microbial C: soil solution C ratio in birch hummock tundra was 403:4:1, and 109:2:1 in tall birch tundra. Similarly, the soil N: microbial N: soil solution N ratio was 193:6:1 in birch hummock tundra, and 58:3:1 in the tall birch ecosystem. Larger relative amounts of C and N in the microbial and soil solution pools are probably a good indicator of enhanced availability of these elements to microbes and plants, therefore our stoichiometric results together with our soil solution results are indicative of higher plant-available N in the tall birch ecosystem.

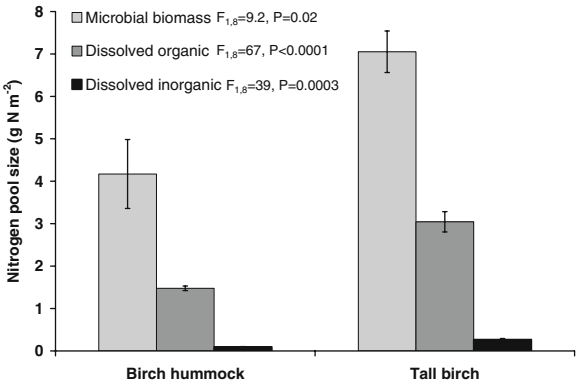

Fig. 2 Nitrogen contents in the soil microbial biomass and in the dissolved organic and inorganic (NH_4^+-N) pools of the soil solution in the birch hummock (n=5) and tall birch (n=5) ecosystems in late summer. *Error bars* indicate +/− one standard error

Soil N cycling

N cycling was much faster in the tall birch than in the birch hummock ecosystem in late summer. Gross N mineralization rates (i.e. ammonification) and gross N consumption rates were 3 and 6 times faster in the tall birch ecosystem, respectively (Fig. 3) and daily rates in both ecosystems were substantially larger than pool sizes or net mineralization rates. The mean residency time for $^{15}NH_4^+$-N in the soil solution (pool size/gross mineralization rate) was 5.5 h in tall birch tundra and 14 h in birch hummock tundra ($F_{1,7}$=5.6, P=0.0006). Gross mineralization rates across both ecosystems were particularly strongly and positively correlated with DOC pools (Fig. 4a). In addition, gross mineralization rates were significantly and positively correlated with DON pools (Fig. 4b), net ammonium mineralization (R^2=0.85, P=0.0004), net DON production (R^2=0.66, P=0.008) and net DOC production (R^2=0.57, P=0.02). By contrast, gross mineralization rates were negatively correlated with litter C:N (Fig. 4c), soil water (R^2=0.51, P=0.03), and soil C concentration (R^2=0.52, P=0.03), and were not significantly correlated with any of the measured microbial properties. However, the correlation with

Table 2 Soil solution and soil microbial properties in the organic layer of birch hummock and tall birch tundra ecosystems in late summer (n=5). Net rates were determined with the buried bag technique. Properties that are significantly different (P<0.05) between vegetation types are in bold font (s.e. = standard error)

			Birch hummock		Tall birch		$F_{1,8}$	P
			mean	(s.e.)	mean	(s.e.)		
Soil solution	Net NH_4^+-N mineralization	mg m^{-2} d^{-1}	**−7.1**	(0.8)	**−19.9**	(2.8)	19.7	**0.002**
	Net DON production	g m^{-2} d^{-1}	**−0.04**	(0.01)	**−0.11**	(0.02)	5.9	**0.04**
	Dissolved organic carbon (DOC)	g m^{-2}	**13.0**	(1.4)	**35.5**	(4.4)	23.9	**0.001**
	Net DOC production	g m^{-2} d^{-1}	**−0.7**	(0.3)	**−2.4**	(0.7)	5.7	**0.04**
Soil microbes	Microbial biomass carbon (MBC)	g m^{-2}	**54**	(10)	**84**	(6)	7.0	**0.03**
	MBC/N		11.2	(0.4)	10.2	(0.4)	3.2	0.1
	Fungal carbon	g m^{-2}	15.7	(2.8)	24.3	(4.7)	3.4[a]	0.1
	Bacterial carbon	g m^{-2}	1.7	(0.2)	1.4	(0.3)	0.4	0.5
	Fungal hyphal length	10^3 km m^{-2}	63.3	(8.7)	44.0	(3.8)	4.1	0.08
	Bacterial cell count	10^{13} cells m^{-2}	10.4	(1.7)	7.7	(1.3)	1.5	0.3
	Fungal/bacterial carbon		9.7	(2.1)	20.5	(6.5)	3.2[a]	0.1

[a] log transformed to meet expectations of normality for statistical analysis

fungal length approached significance (R^2=0.41, P=0.06).

Negative net production rates, calculated with the buried bag method, for NH_4^+-N, DON and DOC imply that consumption of these C and N pools from the soil solution exceeded microbial mobilization (organic C and N production) and mineralization (ammonium production) and were 2.8, 2.8 and 3.4 times faster (more negative), respectively, in the tall birch ecosystem (Table 2). Initial pool sizes and net production rates of DOC and DON calculated from final and initial gross mineralization cores revealed similar patterns between ecosystems, although immobilization was 2-10× as strong in this one-day incubation as compared to daily rates calculated from the ten-day incubation (data not shown). However, net mineralization rates calculated with the isotope dilution method (differences between gross mineralization rates and gross consumption rates (Fig. 3)) were slightly positive in both ecosystems and not significantly different between ecosystems, averaging 187 (±79) mg NH_4^+-N m^{-2} d^{-1} in the birch hummock tundra and 91(±209) NH_4^+-N mg m^{-2} d^{-1} in the tall birch ecosystem. Gross rates of $^{15}NH_4^+$-N immobilization by microbes did not significantly differ between the two ecosystems (Fig. 3), however the difference between gross consumption and gross microbial immobilization was negative in the birch hummock and positive in the tall birch ecosystem ($F_{1,7}$=6.05, P=0.04). These data generated with the isotope dilution method imply that NH_4^+-N is produced and consumed at a faster rate in the tall birch system, and this faster consumption in the tall birch ecosystem is not the result of faster microbial immobilization, but due to some other form of consumption (nitrate was below detection in all samples, so this may include acquisition by plant roots or fixation to soil surfaces). Estimates of the mean residency time for the ^{15}N in the microbial biomass (MBN/immobilization rate) ranged between 22 and 231 days, and did not differ between ecosystem types ($F_{1,7}$=0.5, P=0.5).

Microbial community structure and fingerprinting

The proportions of fungal and bacterial biomass determined with epifluorescent microscopy were quite similar between the two ecosystem types (Table 2). Fungi were more strongly dominant with shorter hyphal length in the tall birch ecosystem (P<0.1; Table 2). The resulting larger hyphal C:length ratio (0.49 mg C km^{-1} (tall birch) vs 0.22 mg C km^{-1} (birch hummock), $F_{1,8}$=14.9, P=0.005) suggests fungal community differences between the two ecosystems, or fungal morphological plasticity to C availability. Indeed, hyphal C:length ratio was signif-

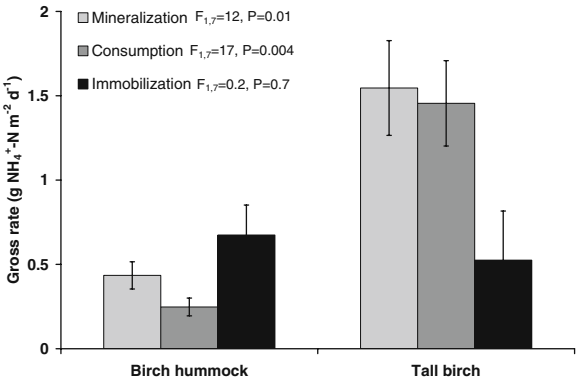

Fig. 3 Soil N-cycling rates, as gross mineralization, gross consumption, and gross microbial immobilization, in the birch hummock (n=4) and tall birch (n=5) ecosystems in late summer. *Error bars* indicate +/− one standard error

icantly correlated with DOC pools (R^2=0.43, P=0.04). By contrast, neither bacterial cell counts nor bacterial cell volume (bacterial C/bacterial counts) differed significantly between ecosystems (Table 2).

Community fingerprinting revealed several obvious matches in the dominant fungal and bacterial bands between these two ecosystem types, indicating substantial community similarity, despite strong differences in soil biogeochemical pools and cycling rates and plant species relative abundances. More than half the bands in the fungal (9/11) and bacterial (12/17) DGGE gels were shared by both ecosystems, either consistently or with variation in intensity between or within ecosystems (labeled a, b and c, Fig. 5a and b). One fungal band was unique to each of the ecosystems (d and e, Fig. 5a) and there was one bacterial band unique to the birch hummock ecosystem (d, Fig. 5b) and four to the tall birch (e, Fig. 5b) bacterial communities.

Ecosystem microclimate and edaphic properties

Soil organic layer moisture content was 3.5 times higher in the birch hummock ecosystem than in the tall birch ecosystem (Table 1), yet soils from both ecosystems were dry relative to earlier stages in the growing season. For example, typical mid-summer soil moistures are ~2.5 and 4 g water [g soil dry weight]$^{-1}$ for the tall shrub and birch hummock ecosystems, respectively (K. Buckeridge, *personal observation*). Neither mean bulk density (0.14 g cm^{-3}) nor depth of the organic layer (9 cm) differed significantly between ecosystem types. Soil temperatures at 2.5, 5.0, and 10.0 cm depth did not different between the ecosystems on the last day of the buried bag incubations and were 11, 9, and 6 °C at the respective depths.

Discussion

Our study demonstrates that N cycling rates were ~3 times faster in a tall birch tundra site as compared to nearby birch hummock tundra in late summer. Correlative factors strongly suggest that the faster N cycling was directly driven by higher levels of dissolved organic C available to soil microorganisms, and indirectly by lower litter C:N. The high daily inorganic N turnover rates in this study are equivalent to 67% and 26% of the annual new N uptake required to support aboveground net primary productivity for shrub (2.33 g N yr^{-1}) and tussock (1.72 g N yr^{-1}) ecosystems respectively (Shaver and Chapin 1991). Our results suggest that N cycling in the late growing season may be very important for understanding shrub expansion across the arctic tundra.

Litter and soil quality effects on N cycling

Meta-analyses indicate that high soil C concentrations generally promote faster gross mineralization rates across all ecosystems, including tundra soils (Booth et al. 2005). The results from our tundra organic soils with globally high soil C concentrations support this model because we found correspondingly high rates of gross N mineralization (350 to 2,600 mg NH_4^+-N m^{-2} d^{-1}, or 12–90 mg NH_4^+-N kg^{-1} dry soil d^{-1}, n=9). Nevertheless, the tall birch soils in our study had lower soil C concentrations relative to birch hummock soils and yet faster gross N mineralization rates. Our results suggest that it is not just the quantity of soil C that drives mineralization of dissolved organic N to NH_4^+-N, but also the quality. In particular, there were larger amounts of dissolved organic and presumably labile C in the tall birch soil solution, larger proportions of total belowground C in the microbial biomass and the soil solution pools of the tall birch soils, and there was a very strong correlation between gross N mineralization rates and soil DOC pools in both ecosystems (R^2=0.95, Fig. 4a). The marked decline in C concentration between the litter and underlying organic layer in the tall birch ecosystem strongly suggests more rapid

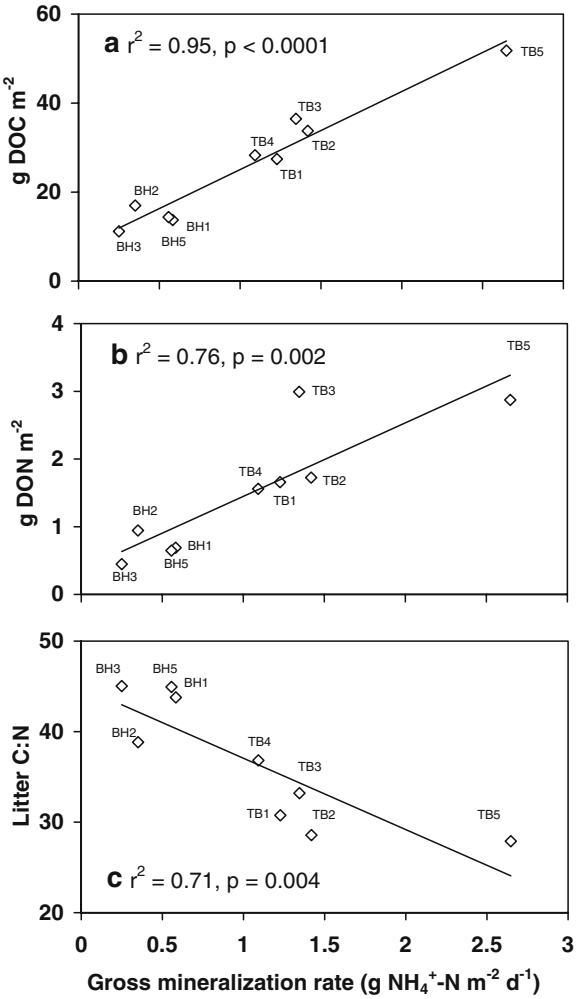

Fig. 4 Bivariate fits of gross N mineralization rate and soil dissolved organic carbon (**a**); soil dissolved organic nitrogen (**b**); and litter C:N (**c**), for all birch hummock (BH; n=4) and tall birch plots (TB; n=5)

surface decomposition rates through the growing season. Furthermore, these data suggest that lower C concentrations in the tall birch soils may be the result of faster surface decomposition rates due to larger inputs of relatively high N concentrations in the litter from the tall birch shrubs (Fig. 4c). Together, these results imply that tall birch shrubs may promote their own growth through positive vegetation feedbacks that enhance N cycling during the late growing season.

Our results suggest that litter decomposition is faster when mesic tundra is dominated by tall birch shrubs. By contrast, other studies indicate litter decomposition of *Betula* is slow relative to most other species in tussock tundra (Hobbie 1996; Weintraub and Schimel 2005a). In support of our findings, circumpolar decomposition studies have found that litter C:N content is a good inverse predictor of decomposition rates, and deciduous shrub litter loses mass faster than graminoid or evergreen shrub litter (Aerts and Chapin 2000; Aerts et al. 2006; Cornwell et al. 2008; Quested et al. 2003; Taylor et al. 1989). Higher litter C:N ratios in our birch hummock tundra may be explained by the larger proportions of mosses, graminoids and low evergreen shrubs relative to birch shrubs. In addition, the effectiveness of litter C:N as a predictor of decomposition rates is tempered by the quality of litter C; in particular, higher concentrations of plant phenolics and lignin can slow decomposition (Hobbie 1996; Taylor et al. 1989). Concentrations of secondary plant compounds can vary among genera and species geographically (Bryant et al. 1994; Graglia et al. 2001; Pennings et al. 2001), as can rates of litter decomposition (Cornwell et al. 2008). Our study site is dominated by *B. glandulosa*, which may produce less recalcitrant litter than the common Alaskan tussock tundra shrub *B. nana*, thereby resulting in faster decomposition and DOC production.

N-cycling rates and N supply to plants

Plant growth in mesic tundra is generally N-limited (Shaver and Chapin 1980) and plants compete poorly for N with soil microbes, at least over an annual time scale (Buckeridge and Jefferies 2007; Grogan and Jonasson 2003; Marion et al. 1982; Schimel and Chapin 1996; Sorensen et al. 2008). The present N paradigm hypothesizes that tundra plant N uptake is primarily limited to recently depolymerized organic N, because microbial N mineralization rates are believed to be low in N-limited tundra soils, resulting in little opportunity for mineralized N diffusion to plant roots (Schimel and Bennett 2004). However, rapid rates of gross N mineralization in these soils suggest that tundra plant access to microsite pools of inorganic N are greater than previously believed. For instance, it has been suggested that the isotope pool dilution procedure for determining gross N cycling rates may be recording microbial recycling of small pools of labile N, and thus may not be a good indication of soil organic matter decomposition processes (Fierer et al. 2001). However, the large inputs of

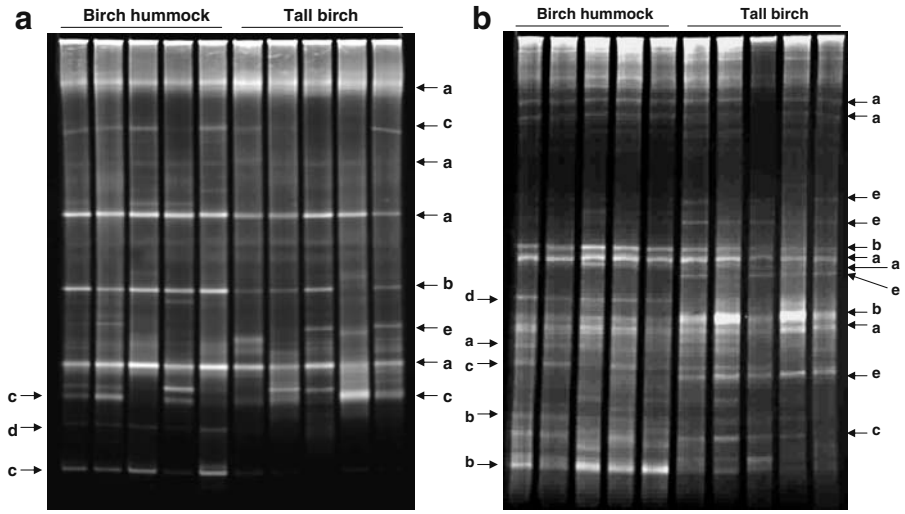

Fig. 5 Soil fungal (**a**) and bacterial (**b**) community composition as determined by denaturing gel gradient electrophoresis (DGGE) for birch hummock and tall birch ecosystems in late summer (n=5). Bands (i.e. phylotypes) common to both birch hummock and tall birch are indicated by '*a*' if of similar intensity, by '*b*' if different intensity between ecotypes, by '*c*' if different intensity within ecotypes. Bands that are specific to the ecosystem types are indicated by '*d*' (birch hummock) and '*e*' (tall birch)

^{14}N diluting the small soil solution $^{14+15}NH_4^+$-N pool, and the significant positive correlations between gross N mineralization rates and DON pools as well as DON production rates, indicate that new mineralization of DON occurred in these two ecosystems. Furthermore, the rate of this N mineralization, not just the pool size, determines the potential for inorganic N mobilization between microsites and possible N uptake by plants (Schimel and Bennett 2004). Therefore, if plants access inorganic (or organic) N as occasional fortunate bystanders of microbial N mobilization, faster N mineralization rates under tall birch shrubs are a potential positive feedback mechanism, promoting further plant growth and consequent litter production. Indeed, experimental NP-additions to tundra enhance total above-ground biomass (Jonasson et al. 1999) and increase shrub dominance (Chapin et al. 1995), strongly suggesting that positive shrub apical growth responses to experimental warming are due to faster soil N cycling (Chapin et al. 1995; Walker et al. 2006).

Plant and microbial demands for inorganic and organic N appear to be similar in tundra soils. For instance, the rapid rates of inorganic N pool turnover found in these birch hummock and tall birch ecosystems (5.5 to 14 h) are of the same magnitude as the rapid rates of potential amino acid turnover in early and late-successional Alaskan taiga (3 to 6 h; Kielland et al. 2007). Similar rates for both inorganic N and amino acid turnover have been recorded in arctic salt marsh soils (Henry and Jefferies 2003). Since tundra shrubs appear to take up organic N and inorganic N in roughly equal proportions (Kielland et al. 2006; Nordin et al. 2004) and organic N pools are 6.5 to 8 times larger than inorganic N pools in birch hummock and tall birch tundra (Fig. 2), a substantial portion of the organic N pool must be in forms that are not readily accessible to plants. Total free amino acids (TFAA) are possibly a better indicator of plant-available organic N, and TFAA and NH_4^+-N concentrations are similar in tundra soils (Weintraub and Schimel 2005b). So, although tundra plants can 'short-circuit' the N-cycle by taking up organic N (Kaye and Hart 1997; Kielland 1994; Schimel and Bennett 2004), it is evident that tundra plant uptake of inorganic N is also critical to meeting annual plant N demands. Therefore, the very high N mineralization rates relative to N pools in these soils, and three times higher N mineralization rates in tall birch compared to birch hummock soils may be an important component of tundra plant N availability in general, and shrub dominance in particular.

Methodological considerations

Net N mineralization rates calculated as the difference between gross N mineralization and gross N con-

sumption are slightly larger than rates calculated by the buried bag technique and probably reflect differences inherent in the techniques. For instance, nutrient mobilization from soil organic matter may not respond linearly to core incubation time. We have reported daily NH_4^+-N, DON and DOC production/immobilization rates with the buried bag method (Table 2), that are averages over a 10-day incubation period. Rates measured over the one day incubation (gross mineralization cores) indicate that production and immobilization of C and N was stronger (2–10×) on the first day of incubation relative to the average daily rate over ten days. This implies that the cumulative production and consumption rate over ten days was not linear, and that microbial depolymerization and mineralization of organic matter may have been stimulated on the first day by the immediate effects of soil handling and substrate addition (0–3% of background) (Schimel and Bennett 2004), with a lag in consumption rates. Therefore, soil handling and incubation time may be exaggerating N mineralization as calculated with the isotope dilution method, but these methodological issues do not detract from the large differences found between ecosystem types in this study.

Equal rates of gross immobilization in the birch hummock and tall birch ecosystems together with faster mineralization and consumption in the tall birch ecosystem suggest that much more of the added ^{15}N (~1 g $^{15}NH_4^+$-N m^{-2} d^{-1}) is not accounted for by microbial uptake in the tall birch ecosystem (Fig. 3). The ^{15}N consumed from the soil solution pool but not accounted for in the microbial biomass may reflect stronger isotopic N fractionation by soil microbes in the tall birch ecosystem, as a result of a larger N flux. Alternatively, it may represent enhanced N adsorption to soil surfaces or *very rapid* NO_3^--N cycling and denitrification (as nitrate pools were not detected in these soils) that could be available for plant uptake under normal conditions (i.e. in the absence of an isolating soil core). In summary, the ^{15}N dynamics within the soil solution indicate that rapid soil N supply exceeds microbial demand for N in tall birch tundra in the late growing season, and may provide a mechanism explaining enhanced shrub growth in this ecosystem.

Tundra microorganisms

Despite differences in nitrogen cycling rates, soil and litter quality, and plant species relative abundances between these two ecosystems, there was relatively little difference between the two soil microbial communities at the scale we analyzed. The chloroform-fumigation technique indicated that more C and N were stored in the microbial community under tall birch shrubs. Since there were few differences in the dominant bacterial and fungal DGGE bands in these two ecosystems, and total fungal and bacterial counts and volume estimates were similar, our analyses suggest a broadly similar soil microbial community composition and structure, with the exception of changes in the physiological form of the fungal hyphae. These results are consistent with a finer-scale analysis of tall shrub and tussock soils in Alaska, which only found large differences between microbial communities at the sub-phyla level (Wallenstein et al. 2007). Preliminary investigations by our lab using DGGE analyses in this and other low arctic sites indicate substantial differences between soil microbial community compositions among vegetation sites that differ in soil moisture regime (i.e. wet sedge meadow, mesic tundra and dry heath; H. Chu, *unpublished data*). The lack of major differences between tall birch and birch hummock microbial communities may reflect a similar mesic soil, and perhaps a common history, whereby our tall birch site was once a birch hummock ecosystem. In any event, we can conclude that the tall birch vegetation feedbacks that accelerated N cycling may be in part a result of a larger microbial biomass, but were not caused by major differences in the dominant components of the soil microbial community.

The summer side of the snow-shrub hypothesis

The snow-shrub hypothesis (Sturm et al. 2001a, b; Sturm et al. 2005) is a climate-driven biotic feedback that has been proposed to explain the maintenance and increased density of shrubs across the tundra. This hypothesis is focused on the winter season, proposing that deep snow accumulation around shrubs restricts winter soil temperature declines, thereby facilitating winter microbial breakdown of soil organic matter and nutrient release, thus increasing the winter production of N (Sturm et al. 2001a). This N becomes available to plants in spring and may be preferentially accessed by deciduous shrubs, resulting in increased growth and greater snow accumulation in subsequent years. This preferential

spring uptake of N by shrubs has been inferred from fertilization studies which show eventual domination by deciduous shrubs after several years of chronic fertilizer addition (Bret-Harte et al. 2002; Chapin et al. 1995). However, since the fertilizer was added after spring thaw each year, the shrub growth responses are most likely due to enhanced N uptake during the growing season, consistent with our late summer results that found larger pools of available N and faster rates of N cycling under tall shrubs. Furthermore, these fertilization studies demonstrate stronger photosynthetic responses to excess N addition, rather than greater shrub competitive abilities leading to preferential uptake of N when it is present only as a limiting resource. Since N availability generally limits both plant and soil microbial N uptake in mesic tundra (Schimel and Weintraub 2003; Shaver and Chapin 1980), the capacity of shrubs to promote and preferentially-acquire this growth-limiting nutrient under normal (i.e. low fertility) conditions is critical to understanding potential shrub expansion. Our results suggest that at ambient soil fertility levels during the growing season, tall birch ecosystems supply more N into plant-available pools, and therefore shrubs should benefit if they are able to outcompete the rest of the assembled vegetation to acquire this N.

This study was conducted at the end of the plant growing season, at the beginning of N resorption from leaves to stems and fine roots to rhizomes (Chapin 1980), and prior to fresh inputs of leaf litter. Tundra soil solution nutrient pools are larger in late summer as compared to peak growing season in some tundra ecosystems, including tall shrub (Giblin et al. 1991; Weintraub and Schimel 2005b). This seasonal variation in soil nutrient pools presumably reflects seasonal differences in plant nutrient uptake, but may not reflect seasonal differences in gross soil N cycling rates, which can be lower in some tundra soils in autumn (Buckeridge and Jefferies 2007). Tussock tundra soil microbes switch from net immobilization of N to net mineralization of N at the end of the growing season (Schimel et al. 2004); it is not known whether this switch occurs in other tundra ecosystems, and if it does, this switch had not yet occurred in the two ecosystems that we investigated. Cooler summer temperatures as a result of shading under Alaskan shrub tundra are predicted to reduce summer N mineralization rates (McFadden et al. 1998; Sturm et al. 2001b; Wookey et al. 2009). Although there were no differences in temperature during our sample period, tall birch soils tended to be slightly cooler than birch hummock soils in mid-summer (<4 °C, P. Grogan*, personal observation*), presumably due to shading. However, lab incubation studies of Alaskan tundra soils of varying soil organic matter quality suggest that decomposition and microbial N cycling rates are much more sensitive to litter quality differences than to such small differences in temperature (Nadelhoffer et al. 1991). Therefore, our results do not support the idea that shrub litter quality and canopy shading in the growing season period restrict N cycling and plant growth thereby countering positive winter feedback processes (Chapin et al. 2005; Sturm et al. 2001a; Wookey et al. 2009). In fact, our study demonstrates that the potential exists for positive vegetation feedback processes during the growing season to be a strong factor maintaining differences in shrub growth across the landscape and potentially promoting climate change-induced increases in shrub density, if shrubs can access the large and rapidly cycling pools of inorganic and organic N in tundra soils at this time.

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