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REGULAR ARTICLE

Soil microbial biomass, nutrient availability and nitrogen mineralization potential among vegetation-types in a low arctic tundra landscape

Haiyan Chu · Paul Grogan

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Abstract Arctic plant communities vary greatly over short distances due to heterogeneities in topography and hydrological conditions across the landscape. Recent evidence suggests substantial changes in vegetation including increasing shrub cover and density in the Arctic over the past three decades that may be in response to climate change. We investigated soil microbial biomass, nutrient availability, nitrogen (N) mineralization potential and nitrification potential in four of the principal vegetation-types across the low Arctic: dry heath, birch hummock, tall birch and wet sedge. Soil total carbon (C) and N contents, microbial biomass C, dissolved organic C (DOC) and N (DON), mineral N, and N mineralization potential differed considerably among vegetation-types. Tall birch and wet sedge soils had significantly higher DON, mineral N, and N mineralization potential than birch hummock or dry heath soils. Soil N mineralization potential across all soils was positively correlated with soil available C and N, and negatively correlated with soil total C:N ratios. Nitrification potential was negligible in all soils. These results demonstrate close relationships between soil biogeochemical properties, mineral N supply rates, and vegetation-types across an arctic landscape. Our soil N mineralization data suggest that climate warming may enhance N availability in tall birch soils more than in birch hummock soils, and therefore that increases in shrub densities across the landscape are most likely within and directly around current tall shrub patches.

Keywords Arctic tundra soils · Vegetation-type · Nutrient availability · Microbial biomass · Nitrification · Nitrogen mineralization

Introduction

Arctic ecosystems contain a variety of vegetation and associated soil-types that vary widely in biogeochemical properties (Giblin et al. 1991). Vegetation-types vary greatly across short distances due to heterogeneities in topography and hydrological conditions across the landscape (Bjork et al. 2007; Walker 2000). Soil carbon quality and microbiological activity also vary substantially among different vegetation-types (Cheng et al. 1998; Christensen et al. 1999; Nadelhoffer et al. 1991). Furthermore, soil nutrient contents and organic matter quality (Biasi et al. 2005; Cheng et al. 1998; Giblin et al. 1991), CO_2 and DON production (Grogan

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H. Chu (✉) · P. Grogan
Department of Biology, Queen's University,
Kingston, ON K7L 3N6, Canada
e-mail: chuh@queensu.ca

H. Chu
Institute of Soil Science, Chinese Academy of Sciences,
East Beijing Road 71,
Nanjing 210008, China

and Jonasson 2006; Neff and Hooper 2002), and net N mineralization rates (Bjork et al. 2007; Schmidt et al. 2002) all vary significantly among tundra vegetation-types. However, the biogeochemical relationships between vegetation-types and the soil properties that govern nutrient availability to those vegetation-types are not well characterized. These relationships are critical in understanding the functioning and distributions of individual vegetation-types across the arctic landscape.

Global warming is widely predicted to be largest and most rapid at high latitudes (IPCC 2007). Observational evidence over the past 30 years indicates that the warming is already under way in the Arctic (ACIA 2005; Chapin et al. 2005; Serreze et al. 2000). The impacts of climate change on arctic ecosystems are critical for the global C cycle because of the large amount of C stored in these cold regions (Billings et al. 1982; Oechel and Vourlitis 1994; Ping et al. 2008). Climate warming is expected to accelerate tundra soil organic matter (SOM) decomposition, resulting in ecosystems C losses to the atmosphere (Nadelhoffer et al. 1992). However, warming is also expected to increase nutrient mineralization, enhancing the rates of nutrient transformation to forms that are available to plants, thereby increasing plant biomass production, and promoting net C storage (Davidson et al. 2000; Kirschbaum 2000). Recent evidence suggests substantial increases in shrub cover and density in the Arctic over the past three decades that may be in response to climate change (Devi et al. 2008; Goetz et al. 2005; Sturm et al. 2001; Tape et al. 2006). Increased shrub cover and/or density results in enhanced absorption of solar radiation because of lower albedo and therefore localized atmospheric heating, providing a potentially significant positive feedback to climate warming (Chapin et al. 2005). By contrast, increased C uptake with shrub growth due to climate warming could exceed the enhanced CO_2 losses from soil organic matter decomposition, resulting in net carbon (C) storage and a negative feedback to climate warming (Shaver et al. 1992; Shaver et al. 2000).

It is generally believed that nutrient availability, especially N availability, is the most important factor that will determine vegetation dynamics and the rates, directions, and magnitudes of C fluxes in arctic ecosystems under a changing climate (Chapin et al. 1995; Cheng et al. 1998; Johnson et al. 2000; Jonasson et al. 1999; Leadley and Reynolds 1992; McKane et al. 1997; Shaver et al. 1992). Nutrient availability to plants in arctic ecosystems is controlled mainly by soil organic matter decomposition processes since most of the nutrients are stored in soils, and inputs are small (Shaver et al. 1992). Furthermore, plants may influence nutrient availability since vegetation-types differences in litter quality and soil microclimate regulate the decomposability of soil organic matter (Neff and Hooper 2002). Here, we characterize soil biogeochemical variables in a range of low arctic vegetation-types in order to understand the relationships between nutrient availability and the current distribution of vegetation-types across the landscape. Furthermore, we compare the potential for increases in nutrient availability among soils of these vegetation-types under warmer conditions.

Our study focuses on dry heath, mesic birch hummock, mesic tall birch and wet sedge vegetation-types, which are the principal ecosystems occurring along topographically determined moisture gradients within a common low arctic tundra landscape that extends thousands of kilometers across Canada from the MacKenzie River delta to the Hudson Bay (Porsild and Cody 1980). Our research addresses the following questions: (1) Can differences in soil biogeochemical variables be associated with differences in vegetation-types across a Canadian low arctic tundra landscape? (2) Are soil N mineralization potentials closely correlated with soil biogeochemical variables? (3) Does soil N mineralization potential differ among vegetation-types, and if so, what is the implication of climate warming?

Materials and methods

Study site characteristics

The study site was located near the Tundra Ecological Research Station (TERS) at Daring Lake (64°52′N, 111°35′W), in central Northwest Territories, Canada, approximately 300 km northeast of Yellowknife. Although designated as a southern arctic ecozone, this region is locally referred to as the ‘barrens’ because it lies approximately ~25 km north of the treeline. The region is underlain by continuous permafrost to a depth >160 m (Dredge et al. 1999) and has a shallow active layer developing during the thaw season, reaching a maximum of 0.3–1.2 m depending upon soil type and vegetation cover (Nobrega and Grogan 2008). The landscape is characterized by numerous Canadian Shield outcrops and occasional eskers that were formed toward the end of the most recent glacial period (Rampton 2000), and a large number of lakes covering ~30% of the surface (Lafleur and Humphreys 2008). Climate records from the Daring Lake Weather Station (1996–2008; Bob Reid, Indian and Northern Affairs Canada, unpublished data) indicate daily average temperatures as low as −41.8°C in the winter and as high as 22.2°C in the summer. An average of 123 days a year are above 0°C (May–September), and rainfall ranges from 70-220 mm.

Detailed vegetation mapping of the area as part of the Ecological Monitoring and Assessment Network indicates a hydrologically driven mosaic of tundra vegetation-types including dry heath, dwarf birch hummock, inundated wet sedge (Nobrega and Grogan 2008). Tall birch is generally in local patches near seeps and streams, or in topographic depressions that are protected from winds and where snow preferentially accumulates.

Dry heath vegetation consists of mat-forming evergreen shrubs (*Ledum decumbens* (Ait.), *Vaccinium vitis-idaea* (L.), *Empetrum nigrum* (L.), *Loiseleuria procumbens* (L.), and *Arctostaphylos alpina* (L.)), deciduous dwarf shrubs (*Betula glandulosa* (Michx.) and *Vaccinium uliginosum* (L.)), graminoids (mostly *Carex* spp.), significant lichen cover (*Cetra- ria nivalis* (L.), *Briocaulon divergens* (Ach.), *Cladina mitis* (Sandst.), *Cladina rangiferina* (L.)), and a moss layer that is not well-developed.

Mesic birch hummock vegetation is characterized by hummocks 10–30 cm high and deciduous dwarf birch (*B. glandulosa*) shrubs that are 10–40 cm tall and attain ~10–30% of the areal coverage. The remaining cover is a mixture of mostly ericaceous shrubs (*Andromeda polifolia* L., *V. vitis-idaea*, *V. uliginosum*, *L. decumbens*), sedges, mosses, lichens, and herbs (*Rubus chamaemorus* L.).

Tall birch vegetation is characterized by tall (50–150 cm high) dense *B. glandulosa* shrubs, and the understory generally consists of the same vegetation composition as the mesic birch hummock ecosystem (above). Occasional heavily-browsed *Salix* spp. shrubs are also present.

Wet sedge vegetation occurs in low-lying flat areas that are generally inundated with surface water for a substantial part of the growing season. Sedges (*Carex* and *Eriophorum* spp.) predominate above a thick moss layer composed largely of *Sphagnum* spp. and occasional *A. polifolia* (L.), *L. decumbens* (Ait.) and algae.

Experimental design and soil sampling

We surveyed the landscape near the TERS station, and located four similar well separated (300–3,000 m apart) patches (minimum size ~100 m^2) of each vegetation-type in the early summer of 2007 (June 23–26). In each patch (i.e. ‘plot’), sub-samples (~10 cm×10 cm) of the soil organic layer were collected (to 5 cm depth from the soil surface measured directly below the litter layer or from the green–brown moss transition) at 6 randomly located points using a sterile bread knife and composited together as a single replicate sample (i.e. $n=4$ for each vegetation-type). Samples were stored in a cooler with ice packs during transfer to the lab in Kingston, and processed within 7 days of collection. Aboveground plant material and living roots were removed prior to homogenizing the soil fraction of each sample.

Soil nutrients and microbial biomass analyses

Soil pH was determined using a fresh soil to water ratio of 1:5 (AB15 pH meter, Accumet, Fisher Scientific). Total soil C and N contents were determined by combustion (CNS-2000, LECO, St. Joseph, MI, USA) on soil samples that had been dried at 65°C for 48 h and ground with a ball mill (Retsch PM 200 Planetary Ball Mill, Haan, Germany). Soil mineral N, dissolved organic C (DOC) and dissolved total N (DTN) were extracted by adding 50 ml of 0.5 M K_2SO_4 to 10 g fresh soil, shaking for 1 h and then vacuum filtering through glass fiber filters (Fisher G4, 1.2 μm pore space). Ammonium (NH_4^+) and nitrate (NO_3^-) contents in the extracts were determined colourimetrically by automated segemented flow analysis (Bran+Luebbe AAIII, Germany) using the salicylate/dichloroisocyanuric acid and cadmium column/sulphanilamide reduction methods, respectively. DOC and DTN were determined using a TOC-TN analyzer (Shimadzu, Kyoto, Japan). Dissolved organic N (DON) was calculated as follows: $\left(\mathrm{DON} = \mathrm{DTN} - \mathrm{NH}_4^+\text{-N} - \mathrm{NO}_3^-\text{-N}\right)$. Soil available P was extracted by 0.5 M $NaHCO_3$ (pH 8.5) and the inorganic P (P_i) in the extracts was determined colourimetrically by automated segemented flow analysis (Bran+Luebbe AAIII, Germany) using the molybdenum blue method and a dialyzer to eliminate interference from the background color in the $NaHCO_3$ extract. The concentrations of nutrients in all extracts were corrected for moisture contents of the extracted soils.

Soil microbial biomass C and N were determined by the chloroform fumigation-direct extraction method (Brookes et al. 1985). Briefly, paired samples of moist soil (10 g) were placed in 120 ml plastic cups. One sample of each pair was extracted with 50 ml 0.5 M K_2SO_4 by shaking for 1 h, and the resulting suspension was filtered (Fisher G4 1.2 µm). The other sample of each pair was fumigated with ethanol-free chloroform for 24 h in darkness at 22°C, and then the chloroform was removed and the samples were extracted with 0.5 M K_2SO_4 as described above. Organic C in the extracts was determined using a TOC-TN analyzer (Shimadzu, Kyoto, Japan). Biomass C and N were calculated as the difference between the fumigated and non-fumigated extracts. We divided the microbial biomass values by 0.35 (k_C) and 0.4 (k_N), respectively, to account for C and N in the microbial cell walls that is not released by the chloroform (Jonasson et al. 1996).

Soil microbial biomass P was measured using a similar method as for biomass C and N except that the P_i was extracted by 0.5 M $NaHCO_3$ (pH 8.5). Some of the P_i released into solution can bind with the soil colloids during fumigation and extraction, and therefore cannot be recovered by 0.5 M $NaHCO_3$ (Brookes et al. 1982). To estimate the efficiency of P_i recovery, a known amount of orthophosphate (1.0 ml of a solution of KH_2PO_4 containing 250 µg P_i) was spiked into sub-samples (10 g) of the unfumigated soil and extracted by 0.5 M $NaHCO_3$ (pH 8.5). P_i in the extracts was determined colourimetrically as described before. Microbial biomass P was calculated as $\left(\left(P_{i\,(\mathrm{fumigated})} - P_{i\,(\mathrm{unfumigated})}\right) \times 100\right)/\left(K_p \times \%\ \mathrm{recovery}\right)$, where K_p is 0.4, accounting for the efficiency of extraction from lysed microbial cells (Brookes et al. 1982), and % recovery is the proportion of added P_i recovered from each spiked unfumigated soil sample.

Soil nitrogen mineralization and nitrification potential analyses

N mineralization potentials of the soils associated with each vegetation-type were determined by incubating multiple sub-samples of moist soil (30 g) in 120 ml sampling cups that were covered by polyvinyl-chloride cling film (to allow air exchange and restrict moisture loss) in darkness at 22°C for up to 10 weeks. We determined soil nitrification potentials using further sub-samples of moist soil (30 g) that was amended with ammonium sulfate solution (100 mg NH_4^+-N kg^{-1} fresh soil), and incubated in the same way as described above. Moisture contents differed among soils of the different vegetation-types (Table 1), and were maintained at original in situ levels during the incubations by gravimetrically determining moisture loss weekly and adding distilled water as necessary. Separate incubated soil sub-samples (n=4) were collected after 2, 4, 6, 8, and 10 weeks, and extracted by 0.5 M K_2SO_4 for NH_4^+ and NO_3^- determinations as described above.

Table 1 Soil moisture, pH and nutrient contents in the organic layer of the principal vegetation-types near Daring Lake in June 2007 (n=4)

Vegetation type	Gravimetric moisture (%)	pH (H_2O)	Soil C (%)	Soil N (%)	C:N ratio	DOC (mg kg^{-1})	DON (mg kg^{-1})	NH_4^+-N (mg kg^{-1})	NO_3^--N (mg kg^{-1})	PO_4^{3}-P (mg kg^{-1})
Dry heath	183 (46)^a	4.5 (0.2)^a	34.5 (7.8)^a	1.11 (0.19)^a	31.0 (2.0)^b	353 (73)^a	20.6 (6.7)^a	0.15 (0.10)^a	b.d.	11.0 (9.3)^a
Birch hummock	309 (15)^{bc}	4.3 (0.3)^a	46.5 (1.7)^b	1.58 (0.20)^b	29.8 (2.9)^b	577 (136)^{ab}	35.4 (14.0)^a	0.42 (0.53)^a	b.d.	5.2 (2.0)^a
Tall birch	275 (79)^b	4.6 (0.2)^a	36.2 (5.5)^a	1.79 (0.29)^b	20.3 (1.2)^a	789 (133)^b	65.0 (11.9)^b	9.04 (3.64)^b	b.d.	5.2 (2.8)^a
Wet sedge	382 (41)^c	5.2 (0.1)^b	35.0 (1.2)^a	1.97 (0.17)^b	17.9 (1.0)^a	532 (99)^a	61.8 (8.6)^b	12.5 (6.94)^b	1.20 (1.15)	5.9 (0.9)^a

Values within the same column that do not share the same superscript letter differ significantly (P<0.05). Standard deviations in parentheses (n=4)

DOC dissolved organic nitrogen; *DON* dissolved organic nitrogen; *b.d.* below detection

Table 2 Soil microbial biomass C, N and P in the organic layer of the principal vegetation-types near Daring Lake in June 2007 (n=4). Values within the same column that do not share the same superscript letter differ significantly (P<0.05). Standard deviations in parentheses (n=4)

Vegetation type	Biomass C (mg g^{-1})	Biomass N (mg g^{-1})	Biomass P (mg g^{-1})	Biomass C:N	Biomass C:P	Biomass N:P
Dry heath	8.6 (0.9)^{ab}	0.77 (0.07)^{a}	0.36 (0.01)^{a}	11.1 (0.4)^{b}	23.8 (3.3)^{ab}	2.14 (0.23)^{ab}
Birch hummock	12.4 (1.3)^{c}	0.96 (0.06)^{a}	0.37 (0.08)^{a}	12.9 (0.6)^{bc}	34.9 (8.1)^{b}	2.69 (0.53)^{b}
Tall birch	7.4 (0.5)^{a}	0.91 (0.19)^{a}	0.64 (0.31)^{a}	8.4 (1.6)^{a}	13.4 (5.5)^{a}	1.62 (0.65)^{a}
Wet sedge	11.3 (2.4)^{bc}	0.83 (0.24)^{a}	0.62 (0.23)^{a}	13.9 (1.6)^{c}	19.6 (6.1)^{a}	1.41 (0.42)^{a}

Statistical analyses

Vegetation-type effects on each of the biogeochemical variables were determined by separate one-way analyses of variance (ANOVAs) (JMP 7.0.2, 2008, SAS Institute, Cary, NC, USA), and Tukey Kramer HSD tests. Data were log transformed to meet the requirements of normality when necessary. All significant results are reported (P<0.05). Separate correlations between N mineralization potential and each possible controlling soil variable were determined by bivariate analyses (JMP 7.0.2, 2008, SAS Institute, Cary, NC, USA).

Results

Soil chemistry and nutrient availability among vegetation-types

Soil moisture contents differed greatly among vegetation-types at the beginning of the growing season ($F_{3,\ 12}$=16.9, P=0.0001). Dry heath and wet sedge soils had significantly lower and higher moisture contents respectively, than the mesic birch hummock and tall birch soils (Table 1). Soil pH was similar in dry heath, birch hummock and tall birch vegetation-types, but significantly higher in the wet sedge vegetation-type ($F_{3,\ 12}$=13.1, P=0.0004) (Table 1). Soil total organic C contents were significantly higher in birch hummock than the other three vegetation-types ($F_{3,\ 12}$=5.38, P=0.014), and total N contents were lowest in dry heath soil ($F_{3,\ 12}$=11.4, P=0.0008). Consequently, soil total C:N ratios in birch hummock and dry heath were ~50% higher than those in tall birch and wet sedge vegetation-types ($F_{3,\ 12}$= 47.6, P< 0.0001). Soil DOC contents differed significantly among vegetation-types, and were highest in tall birch and lowest in dry heath ($F_{3,\ 12}$=10.0, P=0.0014). Soil DON and NH_4^+-N contents were similar in tall birch and wet sedge, and were ~2 and ~80 times larger respectively than in birch hummock and dry heath (DON: $F_{3,\ 12}$=15.5, P=0.0002; NH_4^+-N: $F_{3,\ 12}$=10.2, P=0.0013). NO_3^--N content was below detection in almost all the soils except wet sedge. Soil available PO_4^{3-}-P did not differ significantly among vegetation-types. Together, these results indicate strong vegetation-types differences in soil organic matter N content, and the availability of soil C and N (but not P) to plants and microbes in early summer within the same arctic landscape.

Soil microbial biomass and nutrient contents among vegetation-types

Microbial biomass C was at least 30% higher in birch hummock and wet sedge than in dry heath and tall birch soils ($F_{3,\ 12}$=9.8, P=0.0015), while neither microbial biomass N nor P differed significantly among vegetation-types (Table 2). C:N, C:P and N:P ratios in the microbial biomass were significantly higher in the birch hummock soil than in the tall birch soil.

Soil N mineralization and nitrification potentials among vegetation-types

NH_4^+-N contents increased rapidly in the incubated tall birch and wet sedge soils, but increased much more slowly in the birch hummock soil, and changed little in the dry heath soil (Fig. 1a). NH_4^+-N contents in the tall birch soil were 9 and 55 times larger than in the birch hummock and dry heath soils, respectively at the end of the incubation. By contrast, NO_3^--N contents during the incubations were very low and changed little over 10 weeks in any of the vegetation-types (Fig. 1b). Furthermore, our tests of nitrification potential in the presence of excess NH_4^+-N yielded also indicated negligible nitrifier activity (Fig. 2). Together, these results and the very low in situ NO_3^- levels (Table 1) strongly suggest that nitrification is severely limited in the soils of this low arctic landscape.

Correlations between N mineralization potential and controlling variables

We calculated the correlations among soil N mineralization potential, moisture content, pH, nutrient content and microbial biomass across all soil samples from all vegetation-types (Table 3). N mineralization potential (calculated as the difference in soil NH_4^+ content between the beginning and the end of the incubation) was strongly positively correlated with soil total N ($r=0.72$; $P=0.0016$), DOC ($r=0.58$; $P=0.0179$), DON ($r=0.78$; $P=0.0004$), NH_4^+ ($r=0.78$; $P=0.0004$), and was negatively correlated with soil total C:N ratio ($r=-0.78$; $P=0.0004$). N mineralization potential also tended to be correlated positively with *in situ* soil gravimetric water content ($r=0.47$; $P<0.07$). Soil pH was negatively correlated with soil total C ($r=-0.61$; $P=0.0123$) and positively correlated with NH_4^+-N ($r=0.64$; $P=0.0074$). Soil total N was positively correlated with soil DOC ($r=0.66$; $P=0.0053$), DON ($r=0.83$; $P<0.0001$), and NH_4^+ ($r=0.61$; $P=0.0129$).

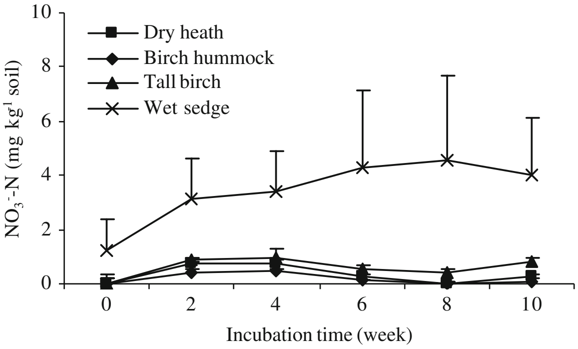

Fig. 2 Soil NO_3^- concentrations over time among vegetation-type in the nitrification potential incubations for each vegetation-type. 100 mg NH_4^+-N kg^{-1} fresh soil had been added initially to each sample. *Vertical bars* are standard deviations ($n=4$)

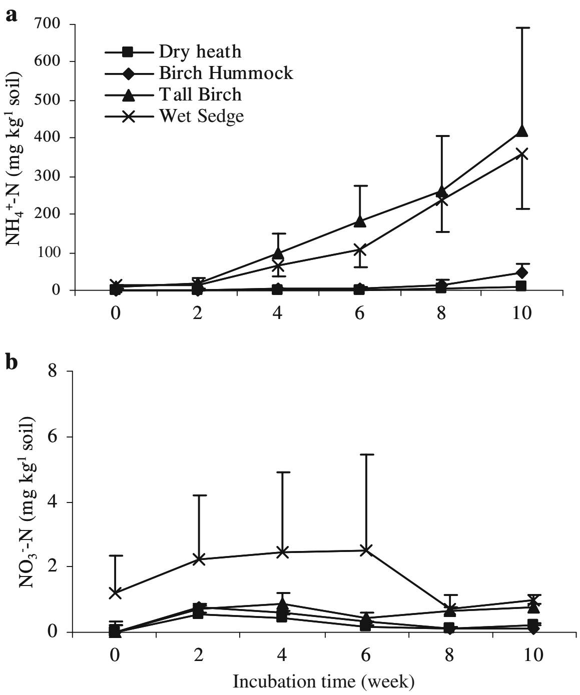

Fig. 1 Soil NH_4^+ (**a**) and NO_3^- (**b**) concentrations over time in the nitrogen mineralization potential incubations for each vegetation-type. *Vertical bars* are standard deviations ($n=4$)

Discussion

Soil biogeochemical variables among vegetation-types

Our results demonstrate strong differences in soil nutrient availability, microbial biomass and N mineralization potential among the principal vegetation-types that extend across the full soil moisture gradient of low arctic tundra. In particular, soil total C:N ratios were ~50% lower in the wet sedge and mesic tall birch as compared to the dry heath and mesic birch hummock ecosystems. Correspondingly, soil DON and NH_4^+ contents in early summer were ~2 and ~80 times higher, respectively in the tall birch and wet sedge than in the other two vegetation-types. Since lower soil total C:N ratios generally indicate relatively easily decomposable (high quality) soil organic matter (Paul and Clark 1996), and rates of ecosystem net C gain are generally largest in tall birch and wet sedge ecosystems (Johnson et al. 2000; Nobrega and Grogan 2008; Shaver and Chapin 1991), our results suggest a direct correlation between soil organic matter quality and ecosystem productivity across the low Arctic.

Table 3 Correlations between N mineralization potential and possible controlling variables for soils under all vegetation-types in the study (n=16)

Correlations	Soil Moist.	Soil C	Soil N	Soil C:N	DOC	DON	NH_4^+	Avail. P	MBC	MBN	MBP	N Mineral.
Soil pH	0.35	**−0.61**	0.34	**−0.70**	−0.23	0.30	**0.64**	−0.06	0.06	−0.18	**0.51**	0.37
Soil Moist.		0.37	**0.85**	**−0.58**	0.47	**0.69**	0.43	−0.40	0.45	0.10	0.21	0.47
Soil C			0.28	0.37	0.34	0.01	−0.32	−0.18	0.50	0.35	−0.27	−0.13
Soil N				**−0.73**	**0.66**	**0.83**	**0.61**	−0.44	0.19	0.17	0.44	**0.72**
Soil C:N					−0.47	**−0.83**	**−0.80**	0.36	0.15	0.04	**−0.60**	**−0.77**
DOC						**0.82**	0.29	−0.40	−0.24	0.23	0.19	**0.58**
DON							**0.69**	−0.40	−0.15	0.10	0.35	**0.77**
NH_4^+								−0.14	0.08	0.26	0.39	**0.78**
Avail. P									−0.09	0.00	−0.13	−0.30
MBC										**0.53**	−0.07	−0.14
MBN											0.29	0.01
MBP												0.20

Values in bold indicate significant correlations ($P<0.05$)

DOC dissolved organic carbon; *DON* dissolved organic nitrogen; *Avail. P* available P; *N mineral.* N mineralization potential

Our research addressing the inter-relationships between tundra vegetation-types and soil biogeochemistry is a true landscape-scale study. We have compared the full range of vegetation-types that typically occur along soil moisture gradients in arctic tundra. These vegetation-types and their associated soils have all experienced a common climate and glacial history. Previous studies have documented differences in soil total C and N, C:N ratio, mineral N, microbial biomass C, DOC and DON fluxes among low arctic vegetation-types in European, Alaskan and Siberian tundra (Biasi et al. 2005; Bjork et al. 2007; Cheng and Virginia 1993; Cheng et al. 1998; Giblin et al. 1991; Neff and Hooper 2002). In most of these studies, soil samples were collected from a single patch for a given vegetation-type, and the sub-samples within this patch were treated as replicates. In our study, soil samples were collected from four well separated patches across the landscape (300–3,000 m apart) for each vegetation-type and some of these patches were from different toposequences (or valleys), thereby avoiding pseudo-replication (Hurlbert 1984) and making our conclusions more robust at the landscape scale.

Soil microbial biomass C was 30% higher in the birch hummock and wet sedge soils compared to the other two vegetation-types. Since there were no differences in microbial N or P contents among vegetation-types, the microbial C:N was higher in the birch hummock and wet sedge, moderate in the dry heath and lowest in the tall birch. These results suggest higher fungal dominance within the soil microbial community in birch hummock than in tall birch vegetation-types, which is consistent with the epifluorescent microscopy studies of the site (Buckeridge and Grogan 2008; Buckeridge et al. 2009). We also observed that soil total C:N ratio was not significantly correlated with the microbial biomass C:N ratio, suggesting that variations in soil element ratios did not significantly affect soil microbial biomass element ratios, which contrasts with the observations by Cleveland and Liptzin (2007).

Soil nitrogen mineralization and nitrification potential among vegetation-types

Soil N mineralization potentials were much greater in both the tall birch and wet sedge soils than in the other two soils, and closely correlated with the differences in soil organic matter quality (inverse soil total C:N). Our room temperature incubations at original *in situ* moisture contents reflect differences in the capacities of these soils to supply NH_4^+ into the soil solution under relatively warm conditions. The birch hummock and tall birch soils had similar moisture contents but quite different N mineralization potentials, indicating that *in situ* moisture content was not a strong determinant of N mineralization patterns among vegetation-types across the landscape under warm conditions at least. Inverse relationships between field net N mineralization rates and soil C:N ratios have also been observed in other tundra soils (Bjork et al. 2007) and in the organic layer of coniferous forest soils (Gundersen et al. 1998; Ollinger et al. 2002). Together our incubation and these field results strongly suggest that soil C:N ratio is a critical inverse determinant of N mineralization rates in organic soils of temperate and high latitude ecosystems.

Differences in the quantity of litter inputs for decompositions may also contribute to variation in N mineralization rates among plant communities (Hobbie 1996; Hobbie et al. 2000; Shaver et al. 1997). Tall birch communities are highly productive, resulting in relatively large litter inputs to soils each year (Shaver and Chapin 1991), providing ample high quality organic matter for decomposition and mineralization. Our wet sedge soils also had high N mineralization potentials, which might be because of the combination of a high-quality organic matter input (dead sedges) and the very high soil moisture levels for much of the summer in sedge communities, preventing the decomposition of this high-quality organic matter. High N mineralization in wet sedge tundra was also observed in *in situ* buried bag studies (Schmidt et al. 2002; Shaver et al. 1998). Cheng et al. (1998) observed that differences in microbial mineralization rates among vegetation-types were correlated to differences in microbial biomass in Alaskan tussock tundra. However, we did not observe significant correlations between soil microbial biomass and N mineralization potential.

In the present study, the *in situ* soil NO_3^- contents were below detection or very low in all the vegetation-types, and NO_3^- did not increase significantly during 10-week incubations with/without NH_4^+-N addition. These results demonstrated that nitrification is not limited by NH_4^+ availability alone, and suggest that nitrification rates are very low in these arctic soils. Other factors such as low soil pH or low abundances of nitrifiers likely contribute to the very low nitrification potentials in these soils.

Recent shrub expansion in arctic tundra has been associated with climate warming (Devi et al. 2008; Sturm et al. 2001; Tape et al. 2006). In the present study, both the birch hummock and tall birch vegetation-types contained the same shrub species (*B. glandulosa*) albeit at differing levels of abundance and stature, and had similar vegetation composition, topography, soil pH and moisture contents. We observed that N mineralization potential in tall birch soil was ~9 times that in birch hummock soil. The high N mineralization potential in the tall birch soil may be partly attributed to higher nutrient availability in tall birch patches due to nutrient influxes in stream and seep flow (Chapin and Shaver 1996). Buckeridge et al. (2009) observed that N cycling rates were ~3 times faster in tall birch than in birch hummock ecosystems in late summer in an *in situ* incubation study, suggesting that differences in litter-induced microbial activity promoted rapid N cycling and enhanced birch growth in tall birch tundra. Birch shrub growth in Alaskan tundra similar to our site is strongly limited by nutrient availability (Bret-Harte et al. 2004; Chapin et al. 1995). Our soil N mineralization data suggest that climate warming will enhance N availability in tall birch soils more than in birch hummock soils, and therefore that increases in shrub densities across the landscape are most likely within and directly around current tall shrub patches.

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