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Microtopography and Plant-Cover Controls on Nitrogen Dynamics in Hummock Tundra Ecosystems in Siberia

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Abstract

Earth hummocks constitute the most common surface structures of Arctic regions. In hummock tundra ecosystems, small mounds of earth alternate with depressions, the so-called interhummock areas. This study aimed at elucidating how differences in microtopography and associated variations in abiotic and biotic factors control biogeochemical cycles in hummock tundra soils. We assessed N pools and N transformation rates in hummocks and interhummock areas in the southern tundra subzone and along a soil-moisture gradient in the typical tundra subzone of the Taymyr Peninsula, Siberia, Russia. On a regional scale, N pools and transformation rates were positively related to latitude and therefore to temperature. Generally, wetter or waterlogged soil conditions tended to decrease gross mineralization rates and soil microbial N at least in interhummock areas. In contrast, at small spatial scales, soil microclimatic conditions were not the main determinant of the observed nitrogen cycling pattern. We found higher N pools and N gross mineralization rates at interhummock areas (wetter and cooler) compared to the hummocks (warmer and drier). The observed differences in N cycling between microsites of hummock tundra may be the consequence of different plant-cover and variable substrate inputs resulting from differences in microrelief.

Introduction

As a result of permafrost and active cryogenic processes, Arctic ecosystems exhibit a wide range of patterned-ground features including circles, polygons, nets, steps, and stripes (Washburn, 1956). Among the most widely distributed surface structures in the permafrost areas are earth hummocks (MacKay, 1980), which belong to the group of nonsorted nets according to the classification of patterned ground by Washburn (1956). Hummock tundra is characterized by small mounds of earth and intermediary depressions. Although hummocks are remarkably regular in their distribution, their size varies considerably. Usually, individual hummocks are 40–60 cm high and range from 110 to 160 cm in diameter (Tarnocai and Zoltai, 1978), but hummocks as much as 3 m in diameter may be found (Bliss, 1997). Earth hummocks differ from peat hummocks in that the latter develop in mires and consist of mosses and peat. In contrast to hummock tundra, the typical feature of tussock tundra is the presence of small grass mounds that are entirely built by the cotton-grass *Eriophorum vaginatum* (Schimel, 1995). Tussocks may be present on the hummocks, and peat hummocks may develop on earth hummocks, reflecting the high complexity of the system.

The genesis of hummocks is still not fully understood. Generally, it is thought that repeated frost heaving and cryoturbation contribute to the formation of this specific relief type (Quinton, 2000; Van Vliet-Lanoe, 1998; Washburn, 1956). However, the hummocky microtopography develops quickly, independent of soil texture, soil moisture, and temperature (Tarnocai and Zoltai, 1978). In Canada most earth hummocks developed between 3000 and 5000 yr BP during the cool climatic period (Tarnocai and Zoltai, 1978). Earth hummocks usually consist of mineral soil that may be exposed to the surface or only sparsely vegetated during an early stage of development. In later developmental stages and in the southern subzones of the Arctic, hummock tundra typically has a continuous but mosaic plant cover (Chernov and Matveyeva, 1997). Because the soils associated with hummocks and interhummock areas commonly differ in abiotic and biotic factors (Bliss, 1981; Klimowicz and Uziak, 1996), soil conditions may change dramatically across relatively short distances, resulting in relief-related differences in physicochemical properties, microclimate, and plant cover. Interhummock areas form the drainage network for subsurface water flow and are therefore moister than hummocks and exhibit shallower permafrost thawing depths (Quinton, 2000). The interhummock areas are usually dominated by mosses, which themselves act as heat insulators and decrease soil temperatures, thereby promoting further environmental heterogeneity (Longton, 1988). In contrast, hummocks are mainly vegetated by sedges, grasses, and dwarf shrubs and are usually drier and warmer than interhummock areas (Zoltai and Tarnocai, 1974).

Contrary to tussock tundra, only limited data exist on the nutrient status and biogeochemical processes of hummock tundra, although this type of tundra accounts for a substantial part of the Arctic. Arctic ecosystems generally exhibit a low net primary productivity (Knapp and Smith, 2001; Wookey, 2002) and slow litter decomposition and soil organic matter turnover (Hobbie and Gough, 2004). These characteristics are primarily due to low temperatures, high soil-moisture contents, and short thawing seasons—factors that directly affect plant growth, but also severely constrain microbial activities and nutrient mineralization (Marion and Black, 1987; Moorhead and Reynolds, 1993; Nadelhoffer et al., 1992). Climatic warming, which is predicted to be more pronounced in high latitudes than in other regions (Maxwell, 1997), is therefore likely to have a strong effect on Arctic ecosystems (Nadelhoffer et al., 1997; Shaver et al., 2000). The magnitude and consequences of such alterations remain unclear, in part because of our limited understanding of the patchiness and complexity of many types of Arctic ecosystems, including hummock tundra. The topography exerts an important influence not only on physical properties, but also on nutrient and carbon cycling rates, either directly through spatial patterns in climate or indirectly through variations in plant cover, litter quality, and quantity (Belyea, 1996; Fisk et al., 1998;

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FIGURE 1. Microtopography of a hummock tundra ecosystem in the typical tundra subzone of Arctic Russia during the early growing season (Taymyr Peninsula, Siberia). The average distance from one hummock center to the next is 90 cm. Hummocks are ~10–30 cm in height.

Luken and Billings, 1985; Mueller et al., 1999; Robinson, 2002; Sommerkorn et al., 1999). For example, mosses that mainly occur in the interhummock areas exhibit low growth rates with long nutrient turnover times (Hobbie, 1995). Further, their relatively high C/N ratios cause slow decomposition rates. In contrast, graminoids, which tend to dominate hummocks, are characterized by high growth rates and relatively lower C/N ratios, thereby facilitating rapid nutrient turnover (Chapin et al., 1995; Hobbie, 1995). It is likely that any effect of climate warming will be modulated by patterns in abiotic and biotic factors. The differential responses of diverse plant functional groups to warming imply that the heterogeneity of the hummock tundra plays a key role in understanding its response to climatic change. As part of a project on global warming and its biogeochemical feedbacks on Arctic ecosystems, we studied patterns of nitrogen cycling in hummock tundra soils in both the southern tundra subzone and the typical tundra subzone of Arctic Russia.

Because nitrogen cycling and availability are crucial to the responses to warming of N-limited northern ecosystems, our study aimed at elucidating controls on N dynamics in hummock tundra ecosystems. By studying hummock tundra soils we intended to close an existing gap in knowledge of nutrient-cycling processes and functioning of this important component of the Arctic landscape. We hypothesized that microclimatic variations associated with the microrelief cause higher N-mineralization rates and increased N availability in the warmer and drier hummocks compared to the cooler and wetter interhummock areas. Furthermore, we hypothesized that mosses in interhummock areas may slow down N-mineralization rates, whereas graminoids may accelerate nitrogen turnover. Toward this goal we determined forms of plant-available nitrogen and gross rates of nitrogen mineralization and microbial nitrogen immobilization in hummock and interhummock areas along a soil-moisture gradient and on a regional scale (southern tundra subzone compared to the typical tundra subzone).

Materials and Methods

SITE DESCRIPTION

The study was carried out during July 2000 on the Taymyr Peninsula. We sampled from two sites that represent (1) the southern tundra subzone and (2) the typical tundra subzone of the Russian Arctic, described by Chernov and Matveyeva (1997).

The sampling site in the typical tundra subzone was located near Lake Nyagamya (72°42′N, 88°26′E). The vegetation at the site may be classified as erect dwarf-shrub tundra (Walker, 2000) consisting of a moss layer ~8 cm high and a dwarf-shrub layer as high as 35 cm. At this site, three subsites were studied along a soil-moisture gradient from the shoreline of the lake (*wet site*) to a well-drained area on the top of a ridge (*mesic site*). The third subsite was established on a poorly drained, late-melting place at the foot of a hill, where interhummock areas were completely waterlogged during the study period (*waterlogged site*).

The sampling site in the southern tundra subzone was situated in the vicinity of River Pyasina (70°17′N, 88°31′E). The vegetation at the site may be classified as low-shrub tundra. Here, in addition to a moss and dwarf-shrub layer, some shrubs of up to 1 m height were present. The actual sampling site in the southern tundra subzone was a mesic zonal site on a gentle slope (~2°).

Both research sites were characterized by the presence of hummocks (Fig. 1). The earth hummocks ranged from 10 to 30 cm in height and from 30 to 50 cm in diameter. They accounted for between 40 and 60% of the soil surface. The main soil and vegetation characteristics of the research sites are summarized in Tables 1 and 2. Closed plant communities occurred on both hummocks and interhummock areas. The hummocks were dominated by grasses and sedges; *Carex bigelowii* and different *Eriophorum* species were most abundant. Dwarf shrubs, mostly *Dryas octopetala* and *D. punctata*, covered 20–30% of the surface of hummocks at the southern tundra site and at the mesic subsite of typical tundra, but were absent at the other two subsites of typical tundra. The vegetation of the interhummock areas was mainly composed of mosses, which formed a cover ranging from 60 to 100%. On drier sites, the mosses were associated with lichens, but the lichens formed a low overall cover (<5%). On the wetter plots of the typical tundra site and throughout the southern tundra site, deciduous shrubs, mainly *Salix* species, also rooted in the interhummock areas. Additionally, a range of forbs grew in both subzones of tundra, although most of them appeared with low frequency, and some were only locally abundant.

Gleyic Cryosols represented the major soil types at the southern tundra site, and Orthic Cryosols dominated at the typical tundra site. All soils had a thin organic layer of largely undecomposed plant material at the surface (1–3 cm thick). The soil showed no distinct horizons at the southern tundra site, but was divided into upper A-horizon (Ap in hummocks, Ah in interhummock areas) and lower Bg-horizon at the

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TABLE 1

Soil properties; data are means of five replicates; within each column and subzone, values followed by different letters are significantly different (ANOVA, LSD, $P < 0.05$).

Relief	Subsite	Soil type[1]	Moisture (% of DW[2])	Temperature (°C)	ALD[3] (cm)	Clay[4] (%)	Silt[5] (%)	Sand[6] (%)	pH_{H_2O}	C (%)	N (%)	C/N
Southern tundra subzone												
Hummocks	mesic	Gleyic Cryosols	66.3 a	6.5 a	30.3 a	14.1	40.0	45.9	5.86	7.22 a	0.46 a	15.7
Interhummock areas	mesic	Histi-Gleyic Cryosols	304 b	5.3 b	21.7 b	13.2	36.4	50.4	5.95	18.05 b	1.08 b	16.7
Typical tundra subzone												
Hummocks	mesic	Haplic Cryosols	41.9 a	2.8 a	19.2 a	41.1	48.7	10.2	6.61	2.66 a	0.21 a	12.7
Interhummock areas	mesic	Histic Cryosols	87.1 c	1.3 b	9.8 b	39.9	50.1	10.0	6.69	5.10 b	0.33 bc	15.5
Hummocks	wet	Haplic Cryosols	64.1 b	2.4 c	27.4 d	36.1	56.7	7.2	5.72	4.84 ab	0.34 c	14.2
Interhummock areas	wet	Histic Cryosols	107.6 c	1.0 b	21.4 c	35.9	54.6	9.5	5.89	9.29 c	0.59 d	15.7
Hummocks	waterlogged	Haplic Cryosols	45.1 a	6.2 d	28.8 d	21.3	26.3	52.4	6.07	2.96 ab	0.22 ab	13.5
Interhummock areas	waterlogged	Histic Cryosols	61.2 b	4.4 e	19.4 ab	22.5	31.7	45.8	6.17	3.45 ab	0.26 abc	13.3

[1] Soil classification according to WRB (World Reference Base for Soil Resources) soil classification (FAO, 1998).

[2] DW = dry weight.

[3] ALD indicates "active-layer depth."

[4] Refers to particles with size of <0.002 mm.

[5] Refers to particles with size of 0.002–0.059 mm.

[6] Refers to particles with size of 0.06–2 mm.

typical tundra site. The Ah-horizon averaged 23 cm thick (minimum, 17 cm), and the Ap horizon averaged 39 cm thick (minimum, 28 cm). The permafrost table was roughly parallel to (but slightly flattened in comparison with) the microtopography of the surface. The climate at each site is continental-Arctic, and the mean annual temperature of the Taymyr Peninsula is –14°C (Matveyeva, 1994).

SOIL SAMPLING

For each subsite in the typical tundra subzone and for the southern tundra site, five hummocks and five adjacent interhummock areas were sampled within an area of 300 × 300 m. After removing the layer of undecomposed organic material, soil samples were taken either to the permafrost table or to a depth of 15 cm, sieved (2 mm) and thoroughly mixed. Subsamples were oven-dried (at ~60°C), and total N and C and soil-moisture content were determined. Extracts were prepared from 1-g aliquots of fresh soil by shaking them for 1 h in 10 mL of 1 *M* KCl or deionized water followed by filtration. After addition of a microbial inhibitor, 10 μ*M* phenylmercuric acetate, the extracts were stored at field temperatures (0–5°C) until transport to laboratories in Vienna. The KCl extracts were used to measure exchangeable NH_4^+ and amino acids, whereas NO_3^- was determined in water extracts. The active-layer depth (ALD) was measured by means of a metal rod. Soil temperature was logged at a soil depth of 5 cm every 30 min throughout the 4 weeks of the study.

SOIL NITROGEN AND CARBON CONTENTS

Amino acids were analyzed colorimetrically as α-amino N by applying a modified ninhydrin assay of Amato and Ladd (1988). Briefly, aliquots of the extract (1 mL) were mixed with 10 mg MgO and shaken for 12 h in open vials at room temperature to remove NH_4^+. After centrifugation, the ninhydrin reagent (Sigma-Aldrich, Vienna, Austria) was added to an aliquot of the supernatant (1:1), and the mixture was heated to 100°C in a water bath for 15 min. After cooling, ethanol (50%) was added (1.25:1), and the absorbance was measured at 570 nm. NH_4^+ was analyzed by use of the salicylic acid assay as described by Kandeler and Gerber (1988). NO_3^- was determined by ion-chromatography and conductivity detection after chemical suppression (DX 500 and ASRS-Ultra, Dionex, Vienna, Austria) by using an anion-exchange column (AS11; 250 × 4 mm i.d., Dionex) and NaOH gradient elution (2–40 m*M* in 8 min). Total N and C were determined with an elemental analyzer (EA 1110, CE Instruments, Milan, Italy). Atropine was used as the elemental reference material.

GROSS NITROGEN-TRANSFORMATION

Rates of gross N transformation (gross N mineralization, N immobilization) were assessed by using the ^{15}N-pool-dilution method (Myrold and Tiedje, 1986; Schimel et al., 1986). To two subsamples each of 2-g sieved soil, 400-μL aliquots of 0.25 m*M* $(^{15}NH_4)SO_4$ were applied uniformly. The assays were mixed thoroughly and incubated at ambient soil temperature for periods of 4 and 24 h. Incubations were terminated by extracting the samples with 12 mL of 1 *M* KCl. Prior to analysis, $^{15}NH_4$ was recovered in acid traps after adding 100 mg of MgO over 5 days. The acid traps consisted of circular, ash-free filter papers containing 10 μL of 2.5 *M* $KHSO_4$ and were wrapped in Teflon-coated tapes. After drying, isotopic enrichment was measured by continuous-flow isotope-ratio mass spectrometry (IRMS) using an elemental analyzer coupled to a gas IRMS system (Delta^{PLUS}; Finnigan MAT, Bremen, Germany), as described in detail by Wania et al. (2002). Rates of gross N mineralization and N immobilization were calculated by using the equation provided by Barrett and Burke (2000). N immobilization was calculated with the assumption that gross N nitrification rates are negligible, because cold and wet conditions of Arctic soils are considered to largely inhibit nitrifiers (Nadelhoffer et al., 1992).

MICROBIAL-BIOMASS NITROGEN

Microbial biomass was measured by the fumigation-extraction method according to Amato and Ladd (1988) with the following modifications: a subsample of 2 g of fresh soil was fumigated with ethanol-free chloroform for 24 h and thereafter extracted with 15 mL of 1 *M* KCl. The amount of α-amino N released by chloroform fumigation was estimated as the difference between the ninhydrin-reactive N in the fumigated and the nonfumigated soil extracts. Soil microbial-biomass N was calculated by using the following equation: biomass

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TABLE 2

Dominant plant species and functional groups of the sampling sites (Taymyr Peninsula, Russia).

Relief	Subsite	Dominant plant species[1]	Cover[2] (%)	Functional group
Southern tundra subzone				
Hummocks	mesic	*Car big, Eri cal, Eri pol, Eri vag*	20	grasses and sedges
		Dry oct, Dry pun	20	evergreen shrubs
		Tof coc	5	forbs
Interhummock areas		*Dic con, Dic elo, Gym inf, Hyl spl, Onc wah, Pol str, Tom nit*	100	mosses
		Sal gla, Sal pul, Sal sax, Vac uli	20	deciduous shrubs
		Car big, Eri coc, Eri pol, Eri vag	5	grasses and sedges
Typical tundra subzone				
Hummocks	mesic	*Eri cal, Eri pol, Eri vag, Jun cas, Poa tur*	40	grasses and sedges
		Dry oct, Dry pun	30	evergreen shrubs
		Ast umb	10	forbs
Interhummock areas		*Abi abi, Aul tur, Dic con, Dic elo, Gym inf, Hyl spl, Pol pil, Pti cil, San unc, Sph gir, Tom nit*	60	mosses
		Car big, Eri cal, Eri pol, Eri vag	10	grasses and sedges
		Sal pol	10	deciduous shrubs
		Dry oct	5	evergreen shrubs
		Bis ell, Sax nel	5	forbs
Hummocks	wet	*Car big, Eri cal, Eri pol, Eri vag, Jun cas*	80	grasses and sedges
		Sal pol	5	deciduous shrubs
		Vac vi	5	evergreen shrubs
Interhummock areas		(3)	80	mosses
		Car big, Eri cal, Eri pol, Eri vag, Jun cas	10	grasses and sedges
		Sal pol	5	deciduous shrubs
		Rum arc	5	forbs
Hummocks	waterlogged	*Car big, Eri vag, Jun cas, Poa tur*	60	grasses and sedges
		Sal pol	5	deciduous shrubs
		Dry oct, Dry pun	5	evergreen shrubs
		Ast umb	5	forbs
Interhummock areas		(3)	60	mosses
		Sal gla, Sal pul, Sal rep, Sal sax	40	deciduous shrubs

[1] Species abbreviations in alphabetical order: *Abi abi* = *Abietinella abietina*, *Ast umb* = *Astragalus umbellatus*, *Aul tur* = *Aulacomnium turgidium*, *Bis ell* = *Bistorta elliptica*, *Car big* = *Carex bigelowii* subsp. *ensifolia*, *Dic con* = *Dicranium congestum*, *Dic elo* = *Dicranium elongatum*, *Dry oct* = *Dryas octopetala* subsp. *incisa*, *Dry pun* = *Dryas punctata*, *Eri cal* = *Eriophorum callitrix*, *Eri pol* = *Eriophorum polystachyon* subsp. *triste*, *Eri vag* = *Eriophorum vaginatum*, *Gym inf* = *Gymnocolea inflata*, *Hyl spl* = *Hylocomium splendens*, *Jun cas* = *Juncus castaneus*, *Onc wah* = *Oncophorus wahlenbergii*, *Poa tur* = *Poa turfosa*, *Pol pil* = *Polytrichum piliferum*, *Pol str* = *Polytrichum strictum*, *Pti cil* = *Ptilidium ciliare*, *Rum arc* = *Rumex arcticus*, *Sal gla* = *Salix glauca*, *Sax nel* = *Saxifraga nelsoniana*, *Sal pol* = *Salix polaris*, *Sal pul* = *Salix pulchra*, *Sal rep* = *Salix reptans*, *Sal sax* = *Salix saxatilis*, *San unc* = *Sanonia uncinata*, *Sph gir* = *Sphagnum girgensohnii*, *Tof coc* = *Tofieldia coccinera*, *Tom nit* = *Tomentyptum nitens*, *Vac uli Vaccinium uliginosum*, *Vac vit* = *Vaccinium vitis-ideae*.

[2] Cover (%) indicates the projective cover of the dominant higher plants in percent; only plant functional groups with cover $\geq 5\%$ are given.

[3] Composition of mosses as for mesic subsite of the typical tundra subzone.

N = 3.1 × ninhydrin-reactive N released from fumigated soil (Amato and Ladd, 1988).

STATISTICS

Data were analyzed by using Statgraphics 4.0 (Stats Incorporated). Significance of differences between means of the study sites and between hummocks and interhummock areas of the southern and typical tundra subzones were assessed by using one-way analysis of variance (ANOVA) and the least significant difference test (LSD). By including the three subsites of the typical tundra subzone in the analysis of differences between relief-related microsites, the combined effects of relief and subsite were examined. Means were considered significantly different at the $\alpha = 0.05$ level.

Results

SOIL CHARACTERISTICS

Soil temperature was significantly lower in interhummock areas than in hummocks (Table 1). This difference was also reflected by shallower active-layer depths (ALDs) in the depressions. Soil-moisture contents were significantly higher for interhummock soils than for hummocks. However, the difference was least pronounced for the waterlogged subsite of the typical tundra subzone (Table 1). Although the soils at the latter subsite were apparently waterlogged, this interpretation was not reflected in data on soil-moisture content. The content of clay (particles < 0.002 mm), known to hold more water than larger particles, was relatively low at this typical tundra subsite (Table 1), most likely leading to a reduced water-holding capacity of these soils. The pH values of water in the soils were between 5.7 and 6.7 and showed no marked differences between hummocks and interhummock areas of either site (Table 1).

The soils differed in organic C and total N levels (Table 1). The contents of C and N were higher at the southern tundra site than in typical tundra. The interhummock areas always exhibited higher C and N contents than hummocks, with the exception of the waterlogged subsite in the typical tundra, where the contents were similar at both microsites. No significant differences were observed in C/N ratios, although they tended to be higher in interhummock areas compared to hummocks and in soils of the southern tundra compared to the typical tundra subzone.

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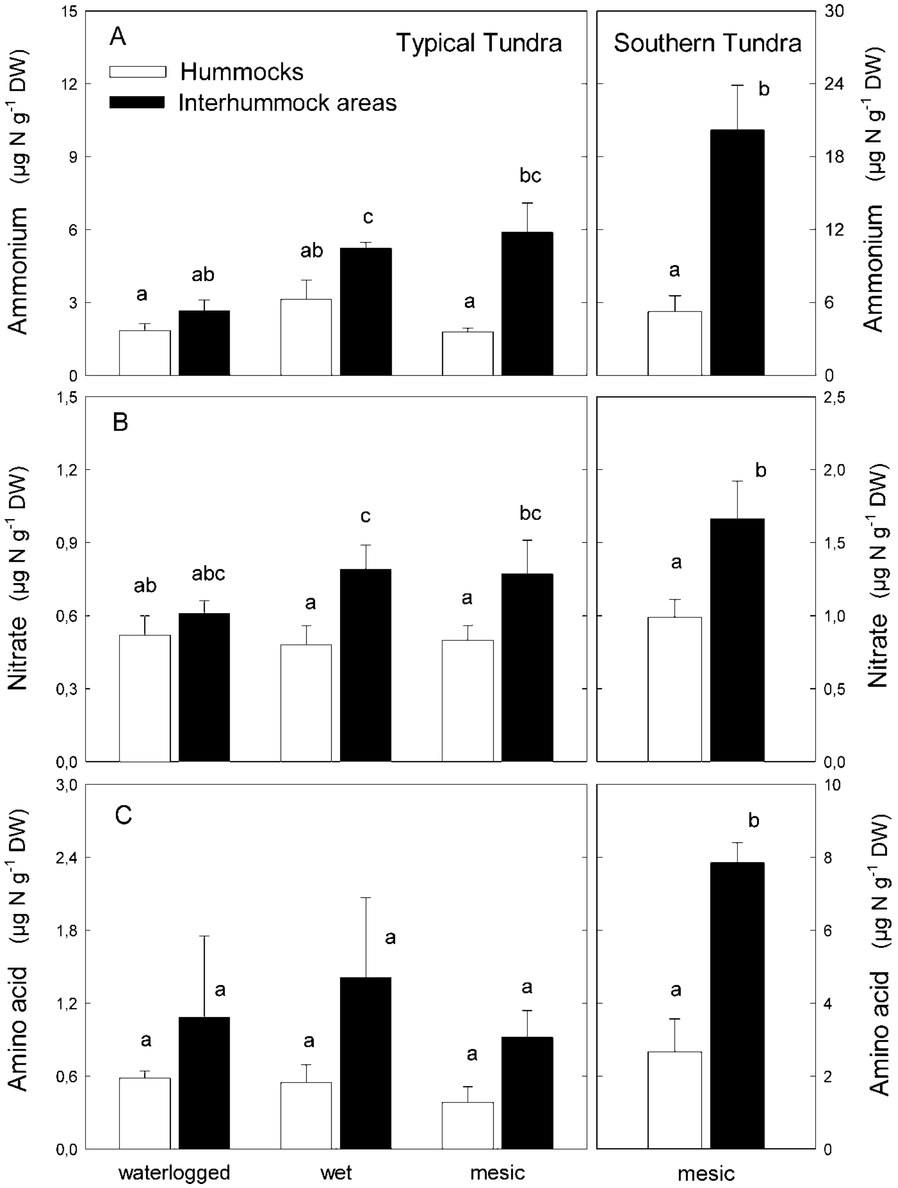

FIGURE 2. Concentrations of extractable NH_4^+ (A), NO_3^- (B), and amino acids (C) in soils of hummocks and interhummock areas of a southern tundra subzone ecosystem and three subsites of a typical tundra subzone ecosystem at the Taymyr Peninsula, Russia. Bars represent means plus one standard error ($n = 4$–5). Within each site, bars with different letters are significantly different (ANOVA, LSD, $P < 0.05$).

NITROGEN POOLS

NH_4^+ dominated the pool of soluble N in all habitats (2–20 µg N g^{-1} dry weight [DW]), followed by amino acids (0.4–8 µg N g^{-1} DW) and NO_3^- (0.5–1.7 µg N g^{-1} DW; Fig. 2). Levels of microbial-biomass N ranged from 3.5 to 150 µg g^{-1} DW (Fig. 3) and were, thus, relatively high compared to levels of KCl-extractable N. Microbial-biomass N represented on average 130% of the concentration of available N in typical tundra and 440% at the southern tundra site and accounted for 0.3% and 1.4% of total N at the sites, respectively. Soils at the southern tundra site exhibited significantly greater N-pool sizes than soils of typical tundra. The difference was most pronounced in microbial-biomass N, with a 10-fold higher N concentration at the southern tundra site compared to the typical tundra site.

Considerable variations in N concentrations were also observed between soils of hummocks and interhummock areas. All sites showed a strong tendency toward higher N concentrations in the interhummock soils, with statistically significant differences for NO_3^- and NH_4^+ at the wet and the mesic subsites of the typical tundra site ($P < 0.05$, ANOVA, LSD) and for all N pools of the southern tundra site ($P < 0.01$). Only the waterlogged subsite of the typical tundra site, where generally the lowest N availabilities were detected, did not show any differences in N pools. Microbial-biomass N was also higher in interhummock soils compared to hummock soils at the southern tundra site ($P < 0.05$). Total N, extractable N, and microbial-biomass N were similar in hummock soils of the waterlogged, wet, and mesic subsite. Inorganic N decreased with increasing soil-moisture content in soils of interhummock areas.

NITROGEN-TRANSFORMATION PROCESSES

The general patterns of gross N mineralization were similar to that of N pools. The highest rates of gross mineralization were observed in interhummock soils of the southern tundra site, and the lowest were seen in soils at the waterlogged subsite of the typical tundra site (Fig. 4). Again, no differences between the hummocks of waterlogged, wet, and mesic sites in typical tundra could be found, whereas in interhummock areas, the lowest N-mineralization rates were observed in the waterlogged soils. Mean rates of gross mineralization were fivefold higher at the southern tundra site than in typical tundra. Except for the typical-tundra waterlogged subsite, where no differences between hummocks and interhummock areas were observed, rates of gross mineralization were on average threefold higher in interhummock areas. However, these higher rates were only significant for soils

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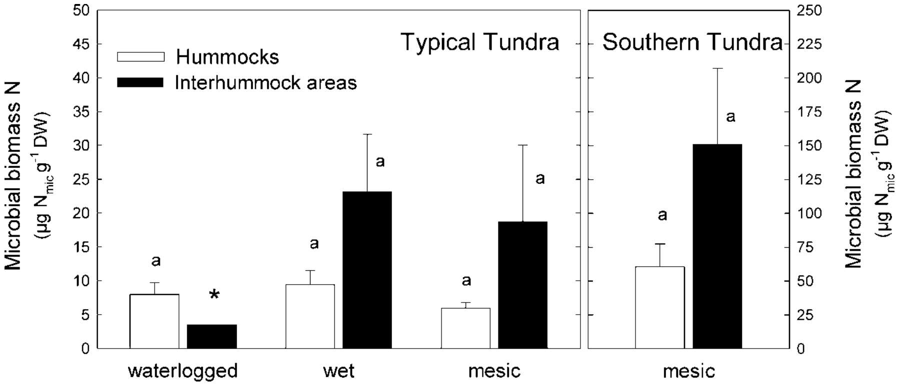

FIGURE 3. Microbial nitrogen in soils of hummocks and interhummock areas of the southern tundra subzone and three subsites of the typical tundra subzone, Taymyr Peninsula, Russia. Bars represent means plus one standard error ($n = 3$–5; asterisk denotes single value). Within each site, bars with different letters are significantly different (ANOVA, LSD, $P < 0.05$).

of the southern tundra ($P < 0.01$). No differences between hummocks and interhummock areas were found for N immobilization (Fig. 5). The rates were higher in southern tundra compared to typical tundra.

Discussion

Although levels of total soil N and C were generally within the range reported for Arctic ecosystems (Cheng et al., 1998; Lipson and Nasholm, 2001; Post and Pastor, 1985), N availability, microbial-biomass N, and N gross mineralization rates were clearly not homogeneously distributed between the different microrelief forms of hummock tundra (Figs. 2–4) and across the studied sites (southern vs. typical tundra). On a local scale, soils of the interhummock areas of almost all sites showed higher N pools and N-mineralization rates compared to hummocks. This was not only true for soils along a moisture gradient in the typical tundra subzone, but also for soils in the southern tundra subzone, where available N pools and turnover rates were generally higher. Two factors may explain the differences in nutrient dynamics between microhabitats of hummock tundra: first, the microtopography and associated physicochemical properties and, second, the plant species through their specific functional traits.

EFFECTS OF MICRORELIEF AND SOIL CONDITIONS

In hummock tundra, a lateral flow of water from elevated hummocks to lower-situated interhummock areas occurs (Quinton, 2000). Because higher N pools were found in interhummock soils compared to hummock soils, it is likely that dissolved organic and inorganic N forms accumulate in the depressions of the interhummock areas as a result of their lower microtopographic position in the relief. Both surface as well as subsurface runoff along the permafrost table, which was roughly similarly shaped as the surface, may contribute to the accumulation of nutrients in interhummock areas. A similar flow of nutrients has frequently been demonstrated along several topographic sequences (Giblin et al., 1991; Högberg, 2001; Kummerow et al., 1987). In tussock tundra—a system that is structured similarly to hummock tundra—higher concentrations of mineral nutrients have also been found in intertussock compared to tussock soils (Cheng et al., 1998).

The relief may not only promote flow of water and nutrients away from the hummocks, but may also promote litter redistribution by wind and snow from exposed to lower-situated parts of the relief (Fahnestock et al., 2000). At the sites studied here, the litter of the majority of the species accumulated in interhummock areas, providing organic matter input to the soil (data not shown). This redistribution may have led to the considerably higher amounts of organic N and C observed in soils of interhummock areas (Table 1). Higher organic N and C, in turn, may have favored higher N mineralization in interhummock soils, as evidenced by faster N-mineralization rates (Fig. 4). Soil C and N have been shown to be primary drivers for gross N-mineralization rates (Booth et al., 2003). In our study, both higher organic matter contents and greater N availabilities due to water inflow possibly contributed to faster N-mineralization rates of interhummock areas, although the relative contribution of the two processes to the observed pattern cannot be determined by our data. However, the differences in microbial-mineralization rates and soil-nutrient status were accompanied by differences in microbial biomass, a pattern that was also found in tussock tundra (Cheng et al., 1998). N-immobilization rates were lower than gross N-mineralization rates, indicating net N mineralization in Arctic soils. The rates were similar between hummocks and interhummock areas, which is consistent with the higher N availability in interhummock soils.

Several physicochemical parameters such as water content and temperature may also vary with microrelief. Within this generally wet ecosystem (Christensen et al., 1998), interhummock areas of each subzone and subsite were always wetter than hummocks, if not waterlogged, and mean temperatures were lower. Both factors—low

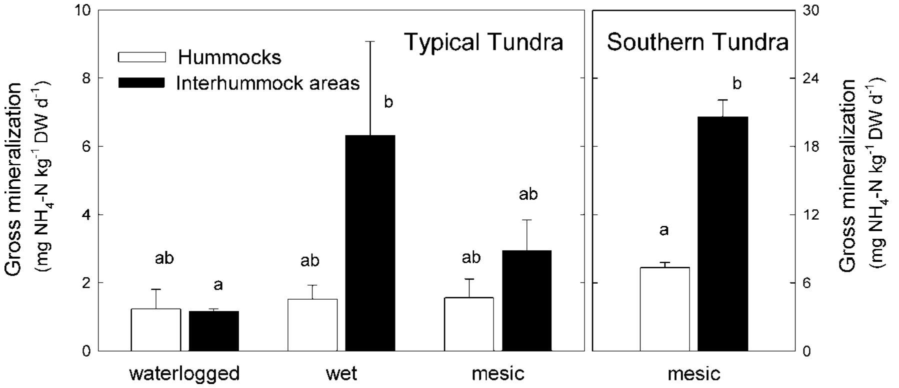

FIGURE 4. Rates of gross N mineralization in soils of hummocks and interhummock areas of a southern tundra subzone ecosystem and three subsites of a typical tundra subzone ecosystem at Taymyr Peninsula, Russia. Bars represent means plus one standard error ($n =$ 3–5). Within each site, bars with different letters are significantly different (ANOVA, LSD, $P < 0.05$).

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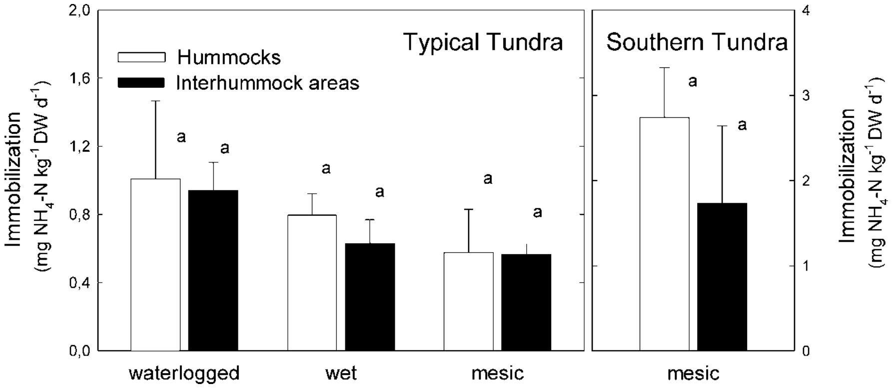

FIGURE 5. Rates of N immobilization in soils of hummocks and interhummock areas of a southern tundra subzone ecosystem and three subsites of a typical tundra subzone ecosystem at Taymyr Peninsula, Russia. Bars represent means plus one standard error (n = 3–5). Within each site, bars with different letters are significantly different (ANOVA, LSD, $P < 0.05$).

temperatures and high water contents—generally restrict microbial activity (Christensen et al., 1998; Flanagan and Veum, 1974; Johnson et al., 1996). The inhibiting effect of waterlogging on microbial activity was shown in the typical tundra subsites by the lower inorganic N availability and N-mineralization rates of waterlogged soils in the interhummock areas. This effect even overruled the effect of temperature, because the waterlogged site was the warmest of the three subsites of typical tundra. Nevertheless, compared to hummocks, we found higher N-mineralization rates and microbial N pools at interhummock areas, which were wetter and cooler than the hummocks. This result suggests that both effects—soil-moisture content and temperature—were overruled by other factors at the small spatial scale considered here.

Although many studies, especially those utilizing experimental approaches, have demonstrated that temperature (Hartley et al., 1999; Hobbie, 1996; Oberbauer et al., 1991) and soil-moisture content (Johnson et al., 1996) are major determinants on nutrient-cycling rates of Arctic soils, increasing evidence also indicates that other topographic patterns are controlling nutrient turnover. For example, an incubation study with Arctic soils at different sites along a toposequence revealed that the overall effect of quality of soil organic matter was more important in controlling C- and N-mineralization rates than temperature (Nadelhoffer et al., 1991). Environmental factors such as substrate quantity (Fahnestock et al., 2000; Giblin et al., 1991) or quality (Johnson and Damman, 1991; Moore, 1991) often appear to overrule effects of temperature or soil humidity in the field. As a result of greater water saturation of soils, Fisk et al. (1998) suggested that plant-mediated factors may have greater influence on nutrient-mineralization rates in Arctic (as compared to, e.g., alpine) ecosystems than soil climate. This situation may lead to an adaptation of Arctic microorganisms to anaerobic soil conditions (Schmidt, 1999; Schmidt and Bolter, 2002). Our data add support to this possibility, because the observed differences in N pools and N-mineralization rates between hummocks and interhummock areas were not related to differences in temperature and soil-moisture content, but may be attributed to differences in dissolved nutrients and substrate input in the form of litter. Thus, our primary hypothesis was not confirmed by our data. However, whenever plant composition and structure are similar between Arctic sites with different climatic regimes, the temperatures and soil-moisture contents may control nutrient dynamics. In our study, this was evident by (1) higher N pools and turnover rates at the lower-latitude site (southern tundra subzone) compared to the site in the typical tundra subzone and (2) the negative effect of waterlogging on N mineralization in interhummock areas along the moisture gradient in the typical tundra subzone.

EFFECTS OF PLANT FUNCTIONAL TYPES

As mentioned already, plant species and, thus, substrate quality and quantity may also be a crucial determinant of biogeochemical cycles in Arctic soils (Hobbie, 1995; Shaver et al., 1998). In hummock tundra the dominant plant species of hummocks are sedges and dwarf shrubs, whereas the interhummock areas are predominantly colonized by mosses (Table 2). Mosses are generally thought to slow down nutrient turnover and decomposition, because of their recalcitrant litter and abundant antimicrobial substances (Aerts et al., 1999; Banerjee and Sen, 1979; Basile et al., 1999; Turetsky, 2003; Malmer et al., 2003). However, we found significantly higher N-mineralization rates in interhummock areas under mosses. A closer look into the literature revealed that higher rates of N mineralization may occur together with lower decomposition rates in Arctic and boreal regions and temperate bogs and fens (Hobbie, 1996; Aerts et al., 1999; Verhoeven et al., 1990; Scheffer and Aerts, 2000; Fisk et al., 2003; Wardle et al., 2003). Possible reasons for these observations include a low N-immobilization potential of microbes at moss-dominated sites (Hobbie, 1996; Verhoeven et al., 1990) or different microbial communities (Scheffer and Aerts, 2000). This possibility suggests that under such circumstances, decomposition is more limited by carbon than by nitrogen, leading to a net N mineralization (Hobbie, 1996; Schimel and Weintraub, 2003).

It is interesting to note that we also found higher microbial biomass under mosses, and thus, another mechanism may have been of importance. Mosses access nutrients mainly from wet and dry deposition, with a low uptake of nutrients from the soil (Bates, 2000; Marion et al., 1982). Hence, in interhummock soils, microorganisms may experience only low competition from plants for nutrients in soil and litter, thus promoting microbial biomass and high net mineralization rates. In contrast to mosses, sedges and grasses that dominate hummocks are characterized by dense and deep root systems (Eissenstat et al., 2000; Gebauer et al., 1995), thereby effectively acquiring both inorganic and organic N. Hence, vascular plants may efficiently compete with microorganisms for nutrients, thereby controlling microbial biomass and activity (Wang and Bakken, 1997; Marion et al., 1982; Schimel and Bennett, 2004). However, patterns of competition between microorganisms and plants may change during the course of the season (Bardgett et al., 2002; Jaeger et al., 1999).

Summary

This study demonstrates that biogeochemical cycles and nutrient pools of hummock tundra are strongly affected by microrelief and vegetation. On a regional scale, temperature seems to control nutrient dynamics of hummock soils with similar plant composition and structure. However, on a smaller spatial scale, the different N cycling rates and N pools of hummocks and interhummock areas most likely result from both the occurrence of different plant functional types and the nutrient redistribution. Together these effects seem to override the effect of the cooler and wetter microclimate that dominates the interhummock soils. Thus, plant cover and redistribution of nutrients as

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a result of microtopography were more important in controlling N mineralization than temperature and soil-moisture content alone.

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