

DIVISION S-3—SOIL BIOLOGY & BIOCHEMISTRY

Soil Nitrogen, Microbial Biomass, and Respiration along an Arctic Toposequence

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ABSTRACT

To investigate the interactions among mineral N, C availability, microbial biomass, and respiration in arctic soils, we sampled soils five times during a growing season from a toposequence on a slope in northern Alaska. The toposequence consisted of six vegetative types from the ridge top to the stream bank: lichen heath, dry cassiope, moist carex (*Carex* spp.), water track, tussock tundra (intertussock), and riparian. The spatial distribution and temporal variation of soil mineral N, microbial biomass, soil C availability, and C turnover were soil type dependent. During the growing season, the concentration of soil $\text{NH}_4\text{-N}$ decreased in tussock tundra soils but increased in lichen heath soils. Soil C availability at all locations was the highest at the beginning of the growing season and declined thereafter. The C availability index (CAI) and the potential C turnover rate increased as soils became wetter. Tussock-forming tundra soil was generally colder than other sites and had high C/N ratios, low amounts of mineral N, and a low potential C turnover index, and therefore, was the least biologically active type. In contrast, water track was the most biologically active site in the sequence and had the highest C and N availability, the highest potential C turnover index, and the highest microbial biomass C and N. The mosaic of diverse plant communities and soil types that comprise arctic landscapes necessitates that accurate estimates of large-scale C or N budget can only be made by integration of all types of plant communities and soils.

ARCTIC TUNDRA in northern Alaska forms a rich landscape mosaic of diverse soil, topography, lakes, creeks, and vegetation types. The vegetation is represented by an array of different plant growth forms (vascular, nonvascular, woody, and herbaceous), which may change dramatically across relatively short distances (Bliss, 1981; Chapin and Shaver, 1985). This topographic variation is strongly related to moisture gradients (e.g., Bliss et al., 1984; Chapin et al., 1988) and the associated chemical, physical, and biological variables, e.g., depth of permafrost, nutrient availability, soil anoxia, and heat input (Hastings et al., 1989; Shaver and Chapin, 1991; Gebauer et al., 1995; Johnson et al., 1996). Thus, belowground processes, such as soil respiration, microbial activity, and nutrient mobilization and immobilization, are key elements that control ecosystem function in these ecosystems (Chapin and Shaver, 1989, 1996).

Several modeling studies predict that climate change in the near future will affect high latitude regions more

than other regions of the world (Mitchell et al., 1990; Maxwell, 1992). Summer air temperatures in northern Alaska are predicted to increase 3 to 6°C over current levels, whereas precipitation during the growing season is predicted to increase 20 to 30% (Maxwell, 1992). The impacts of these potential climate changes 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). It is generally believed that nutrient availability, especially N availability, is the most important factor that will determine the rates, directions, and magnitudes of C fluxes and the dynamics of arctic ecosystems under a changing climate (e.g., Leadley and Reynolds, 1992; Oechel and Billings, 1992; McKane et al., 1997a). Nutrient availability in arctic ecosystems is controlled mainly by decomposition processes, as most of the nutrients are stored in soil organic matter.

Many factors influence organic matter decomposition. Recent studies on tundra ecosystems suggest that the most important factors influencing tundra soil organic matter decomposition are the quality of the organic matter (Nadelhoffer et al., 1991), water conditions, temperature (Oberbauer et al., 1992; Hobbie, 1996), and their interactions (Bridgman et al., 1995). It is well known that microbial biomass is the main biological component of most biogeochemical processes in terrestrial ecosystems (Paul and Voroney, 1980). Microbial biomass interacts with ecosystem productivity and nutrient cycling by regulating nutrient availability. Microbial biomass also determines soil C storage and contributes to atmospheric CO_2 via respiration. However, studies of microbial biomass in arctic ecosystems have been scarce (Cheng and Virginia, 1993).

Understanding the potential impacts of climate change on arctic ecosystems is critical because large amounts of C are stored below ground in the arctic and other cold regions of the world. Much current research in the Arctic is directed toward developing models for predicting landscape patterns of water discharge, N availability, vegetation types, C flux, and net primary productivity (e.g., Reynolds and Leadley, 1992; Leadley et al., 1996; Shaver, 1996), particularly in relation to the potential impacts of climate change (Starfield and Chapin, 1996; McKane et al., 1997a,b). In order for these models to be successful, it is essential that we understand the extent of spatial and temporal heterogeneity of soil processes. At present, such data are lacking. Toward this end, we initiated a study to elucidate patterns of soil mineral N, microbial biomass C, soil respiration, and microclimatic conditions in six arctic communities

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Table 1. Site description.

Name	Plant community	Typical site
Lichen heath	<i>Dryas octopetala</i> <i>Selaginella sibirica</i> <i>Arctostaphylos alpina</i> (L.) K. Spreng	Windblown south-facing slopes on sandstone
Dry cassiope	<i>Cassiope tetragona</i> L. <i>Calamagrostis inexpansa</i>	Nonsorted stone stripes
Moist carex	<i>Carex bigelowii</i> <i>Sphagnum</i> spp.	Mesic sites on steeper slopes, some solifluction or cryoturbation
Water track	<i>Salix planifolia</i> Pursh <i>Sphagnum</i> spp. <i>Eriophorum angustifolium</i> L.	Water tracks, wet, mid-slopes
Tussock tundra (on tussock)	<i>Eriophorum vaginatum</i> L.	Stable mesic sites on flat or gentle slopes
Inter tussock	<i>Sphagnum</i> spp.	Above, but in between tussocks
Riparian carex	<i>Carex aquatilis</i> <i>Sphagnum</i>	Stream channels with a deep peat layer and moss covers

along an elevational toposequence in a small arctic watershed. Our objectives were to examine: (i) the relationships between mineral N, microbial biomass, and respiration in arctic soils within both spatial and temporal dimensions; and (ii) soil temperature, moisture, and slope position as controlling factors in determining soil organic matter decomposition and nutrient availability.

MATERIALS AND METHODS

Site Description

This study was conducted at the U.S. Department of Energy R4D study site in the Imnavait Creek watershed in the northern foothills of the Philip Smith Mountains in arctic Alaska (68°38' N, 149°25' W). Sampling was carried out on a southwest-exposed slope in six different tundra ecosystems forming a toposequence at which three types (lichen heath, dry cassiope dwarf-shrub tundra, and moist carex dwarf-shrub tundra) are located on the top of the ridge, two types (tussock tundra and water track) are distributed in the midslope, and one type (riparian) is at the slope bottom located along Imnavait Creek. Plant communities, topography, and soils at the R4D site have been described in detail by Walker et al. (1989) and are summarized in Table 1 (site description) and Table 2 (soil properties).

Lichen heath is found on the well-drained and most exposed areas on the top of the ridge. The plant community consists mainly of lichens and ericaceous shrubs such as alpine bearberry [*Arctostaphylos alpina* (L.) K. Spreng]. Soils in lichen heath are Pergelic Cryochrepts with a thin surface organic horizon and a relatively high bulk density. Bare areas are common in lichen heath.

The dry cassiope dwarf-shrub tundra consists of lichens, grasses, and evergreen shrubs such as *Cassiope tetragona* (L.) D. Don. Areas of frost boils are common, and the soils are wetter than those in the lichen heath and often have high clay content. A well-developed moss cover is common in dry cassiope dwarf-shrub tundra.

The vegetation in moist carex shrub tundra is dominated by carex in association with *Salix reticulata* L. and occasionally cotton grass (*Eriophorum vaginatum* L.). Mosses (*Sphagnum*, *Dicranum*, and others) provide a continuous cover in moist carex-shrub tundra. Soils in moist carex-shrub tundra are predominantly organic, and peat layers can reach a thickness of >30 cm.

Tussock tundra found in most of the midslope areas is dominated by graminoids, mainly cotton grass and *Carex bigelowii*, in association with the deciduous shrubs, *Betula nana* L. and *Salix pulchra* Cham., and the evergreens, wild rosemary (*Ledum palustre* L.) and cranberry (*Vaccinium vitis-idaea* L.).

Cotton grass forms tussocks that can be elevated 10 to 15 cm above the intertussock areas that are covered mainly by sphagnum mosses.

Soil from water tracks is found in small drainage-ways of intermittent water flow in the midslope areas (see Chapin et al., 1988; Hastings et al., 1989; Oberbauer et al., 1989, 1991, for detailed descriptions of water tracks). The vegetation in water tracks consists mainly of two deciduous shrubs, *Betula nana* L. and *Salix pulchra* L., with extensive undercover of sphagnum mosses. Soils in water tracks are predominantly organic with some minor mixing of clay materials carried by the water flow through the track from the upslope systems.

Riparian tundra is located along the Imnavait Creek at the bottom of the slope. The riparian vegetation is dominated by graminoids, mainly *Carex aquatilis* Whalenb., with a thick moss cover (see Oberbauer et al., 1992, for detailed site descriptions).

Soil Sampling and Measurements

The experimental design of this study consisted of the six different tundra types described above and six replicate plots within each type. In the tussock tundra, two types of samples were taken, one on the tussock and the other between tussock areas. These two types of samples from tussock tundra were treated as different tundra types in the following analysis and discussion. Surface soils were sampled five times during the growing season of 1990. Samples of 0- to 5-cm depth below the live moss layer (or soil surface where no green layer existed) were taken from six replicate plots under each plant community type using a 10-cm-diam. soil corer (at the three ridge-top areas) or by cutting of a 10 by 10 by 5 cm volume.

Table 2. Soil properties. Soils were taken from the 0- to 5-cm depth below the green moss layer. Numbers are means of six replicates. Values in parentheses are standard errors.

Name	N	C	C/N	BD†
				g cm ⁻³
Lichen heath	9.3 (1.71)	168 (34.2)	19.4 (2.59)	0.38 (0.031)
Dry cassiope	5.0 (2.25)	115 (42.3)	25.6 (5.76)	0.31 (0.049)
Moist carex	16.6 (1.39)	351 (11.0)	22.0 (2.23)	0.11 (0.011)
Water track	14.3 (1.66)	346 (21.0)	26.7 (4.70)	0.09 (0.003)
Tussock tundra	4.8 (0.27)	431 (1.9)	91.5 (5.55)	0.11 (0.005)
Inter tussock	6.9 (0.79)	390 (7.8)	60.7 (6.21)	0.06 (0.006)
Riparian carex	10.6 (1.11)	298 (28.4)	31.1 (5.65)	0.08 (0.005)

† BD is bulk density.

Samples were returned to the laboratory at Toolik Lake Field Station (within 20 km of the study site) and immediately stored at 4°C. Dimensions of each soil sample were recorded at the time of sampling and were used to calculate soil bulk density. Care was taken to minimize the effect of compression on the actual dimensions recorded. All subsequent analyses were done within 2 wk after soil collection. Major live plant materials (roots and shoots) and pebbles (size > 3 by 3 by 3 mm) in each sample were separated by hand and discarded. Coarse organic materials were cut into smaller pieces (<2 cm). Each sample was homogenized by hand mixing. We restricted our sampling to the 5-cm soil layer on the assumption that most biological activity occurs in this layer due to the high temperature and the high quality of the organic matter. Microbial biomass C content in the surface layer is nearly double that in the next soil layer (i.e., 5–10 cm) (Cheng et al., 1996, unpublished data).

A subsample of ≈10 g of fresh soil from each site described above was oven dried (60°C, >48 h) for gravimetric soil water content. Soil bulk density was calculated using the sample volume measured at the time of sampling, total fresh weight of the sample, and the water content. Bulked, oven-dried soils were analyzed for: (i) total C using the wet digestion procedure of Yeomans and Bremner (1988), (ii) total organic N by a micro-Kjeldahl digestion method followed by colorimetric analysis of NH_4^+ on a Technicon II Autoanalyzer (Technicon Industrial Systems, Tarrytown, NY), and (iii) organic matter by combustion (500°C, 4 h).

In situ soil temperatures at 1 and 5 cm below the moss surface were measured continuously at a single site in each community type with the exception of the lichen heath. Thermocouple sensors were read using a Campbell 21X micrologger (Campbell Scientific, Logan, UT) operating with 5-min scans and storing data as hourly averages. In addition to the continuous monitoring, soil temperature data were also obtained at 1- and 5-cm depths seven times during the season using 24-gauge copper-constantan thermocouples threaded through 4-mm-diam. wooden dowels inserted into the soil. Thermocouples were installed several days in advance of the measurements and read with a Campbell 21X micrologger using the internal panel reference.

Twenty grams of fresh, homogenized subsamples were weighed into 250-mL plastic bottles and 100 mL of 2 M KCl was added. The bottles were then shaken for 2 h on an orbital shaker. The shaken mixtures were filtered through Whatman no. 40 filter paper. The extracts were acidified by adding one drop of 12 M HCl and were then stored frozen in 50-mL plastic bottles. Concentrations of NH_4^+ and NO_3^- in each extract were analyzed colorimetrically on a Technicon auto-analyzer.

Basal and substrate-induced respiration (SIR) were measured using a soil respiration system with continuous gas flows. The soil respiration system consisted of a LI-COR CO_2 analyzer (LI-6251, LI-COR Inc., Lincoln, NE), a water bath for controlling the incubation temperature, and an air flow controlling and measuring unit (Cheng and Virginia, 1993). Briefly, after a 15-g fresh, homogenized subsample was placed into a 125-mL Erlenmeyer flask, the flask was connected to the respiration measuring system and after ≈40 min of incubation at 22°C at an air flow rate of 180 mL min^{-1} , the rate of CO_2 evolution from the soil sample became constant. At this point, the CO_2 evolution rate was recorded as the basal respiration rate of that sample. Glucose solution (60 mg L^{-1}) was then added with a syringe to the flask containing the same soil sample to bring the soil water content to near its holding capacity (no free-standing solution). Substrate-induced (glu-

case) CO_2 evolution from the sample was measured in the same way as the basal respiration mentioned above.

The SIR of each sample was converted to microbial biomass C using the equation developed by Anderson and Domsch (1978). Microbial biomass, estimated by the fumigation-extraction procedure, was highly correlated with substrate-induced respiration measurements ($P < 0.001$) across all habitats (Cheng and Virginia, 1993). There are some indications that the fumigation-extraction procedure may overestimate microbial biomass C in organic soils (Jenkinson, 1988; Cheng and Virginia, 1993). In this study, all microbial biomass C values were measured by SIR method.

Data Analysis

Studies of tundra ecosystems have reported high variation in soil characteristics among soils under different plant community types (Giblin et al., 1991; Nadelhoffer et al., 1991). This high variation, especially in organic C content, makes cross-type comparisons nearly meaningless if soil parameters are expressed only on a per gram soil basis, as is usually the case in the general soil literature. Therefore, we report our results in three types of units, i.e., per kilogram, per gram of soil C, and per unit of soil or solution volume. Virtually all primary measurements were per gram soil based. The other two units are conversions using soil bulk density and soil C content data. Per-gram-soil-based units were used in analyses concerning within-ecosystem phenomena such as temporal dynamics. The other two types of units were employed where cross-type comparisons, landscape patterns, and correlation between measurements were the primary concerns. All statistical comparisons between means were carried out using Fisher's least significant difference (LSD) method.

RESULTS

The soils of the study sites differed considerably in bulk density, organic C, and total N (Table 2). Lichen heath and dry cassiope shrub tundra soils from the upper ridge had higher bulk density and contained more mineral materials than the other sites. The midslope tussock tundra and intertussock tundra soils were highly organic (431 and 390 g C kg^{-1}) and had high C/N ratios (91.5 and 60.7). Water-track and moist carex dwarf-shrub tundra soils were also organic (346 g C kg^{-1}) but contained higher amounts of N (14 and 17 g N kg^{-1}), resulting in much lower C/N ratios (26.7 and 22.0) than for the tussock soils.

Precipitation was frequent during the early part of the season (Fig. 1). Soil moisture contents of the surface layer generally decreased during the season except for the ridge-top lichen heath soil, which remained low throughout the study period (Fig. 2). The soils formed a wet-to-dry sequence: riparian, water track, intertussock, tussock, moist carex, dry cassiope, and lichen heath.

Daily mean soil temperature of the surface layer (mean of temperatures at 1 and 5 cm for the five soil types) was lowest at the beginning of the growing season, highest at the beginning of July, and briefly decreased due to a snowfall during early July (Fig. 3a). Soil temperatures among the sites consistently differed during the growing season. Soil temperature at the surface layer of dry cassiope dwarf-shrub tundra was the highest among the five soil types, and tussock tundra

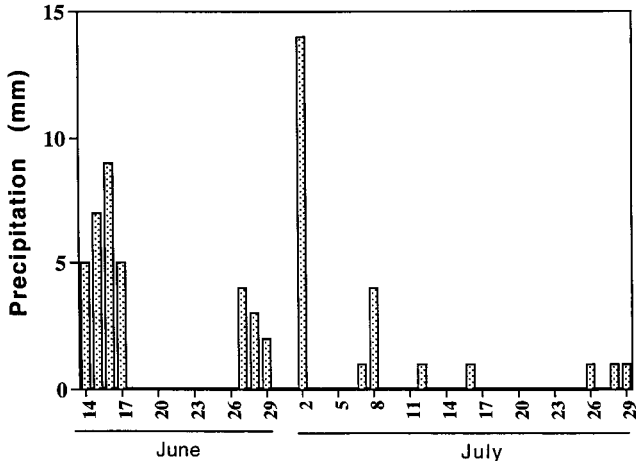


Fig. 1. Precipitation during the growing season.

was the lowest (Fig. 3b). Supplemental temperature measurements revealed that among the three soil types located near the ridge top, lichen heath soil had the highest soil temperature and moist carex the lowest (Fig. 4).

During the growing season, the concentration of extractable $\text{NH}_4^+\text{-N}$ (per gram soil) decreased in tussock and intertussock soils, increased in lichen heath soils, and changed significantly, but not unidirectionally, in moist carex shrub tundra and water-track soils (Table 3). No significant changes of $\text{NH}_4^+\text{-N}$ concentrations occurred through the growing season in dry cassiope shrub tundra and riparian soils. The concentration of soil $\text{NO}_3^-\text{-N}$ increased significantly in two drier sites, lichen heath and dry cassiope shrub tundra, as the growing season progressed, with the highest concentration found at the last sampling date (Table 4). In contrast, soil $\text{NO}_3^-\text{-N}$ peaked at the midsampling for water track and riparian.

Seasonal averages of $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$ (mg N kg^{-1}

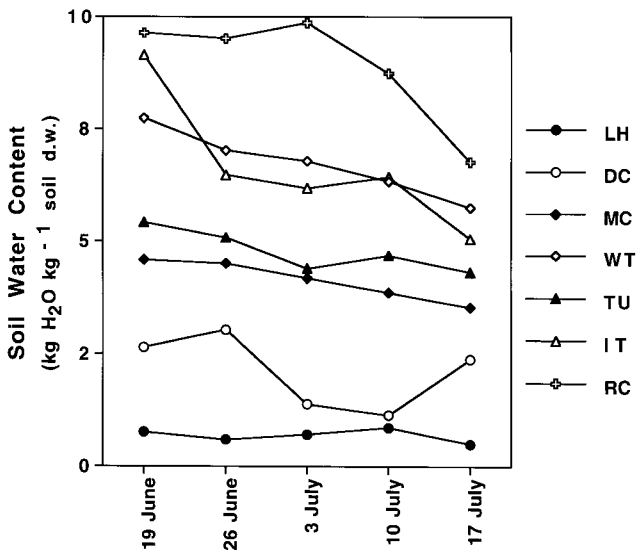


Fig. 2. Seasonal soil moisture in the 0- to 5-cm layer. IT: intertussock tundra; TU: tussock tundra; LH: lichen heath; MC: Moist carex shrub tundra; RC: riparian tundra; DC: dry cassiope dwarf-shrub tundra; WT: water track.

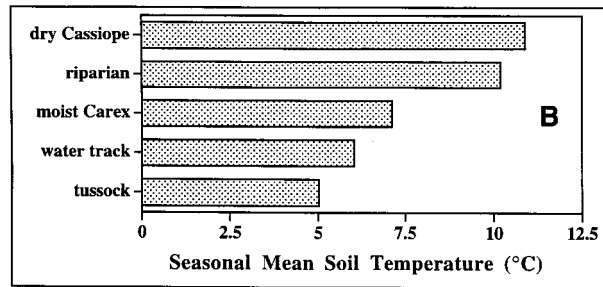
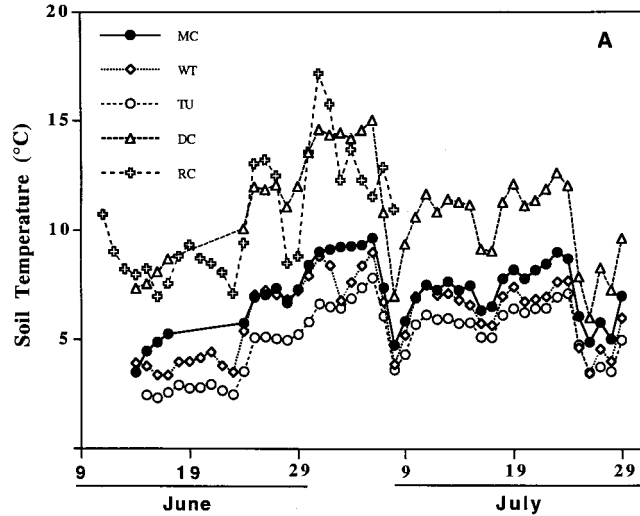


Fig. 3. Soil temperature (continuous): average of 1- and 5-cm depths for (A) seasonal changes and (B) average across the whole season. MC: moist carex shrub tundra; WT: water track; TU: tussock tundra; DC: dry cassiope shrub tundra; RC: riparian.

soil) for each soil type indicated that $\text{NH}_4^+\text{-N}$ was the dominant form in all habitats (Tables 3 and 4). Nitrate N existed at low levels and probably played a lesser role in supplying N for plants in these arctic systems except

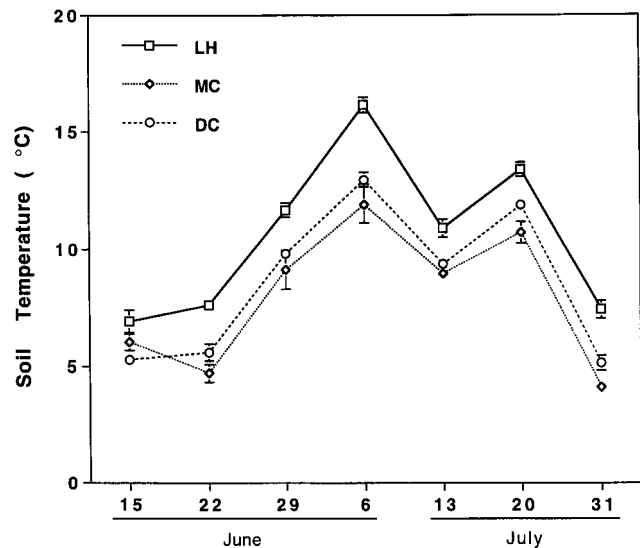


Fig. 4. Soil temperature (discontinuous). Average of 1- and 5-cm depths. Bar is ± 1 standard error. LH: lichen heath; MC: moist carex shrub tundra; DC: dry cassiope shrub tundra.

Table 3. Ammonium nitrogen. Numbers are means of six replicates. Numbers in each column with the same letter are not significantly ($P < 0.05$, LSD) different among sampling dates. Numbers of seasonal means with the same letter are not significantly ($P < 0.05$, LSD) different among topo-locations. See Table 1 for the descriptions of all locations.

Date	Topo-locations						
	Lichen heath	Dry cassiope	Moist carex	Tussock tundra	Inter tussock	Riparian carex	Water track
	$\mu\text{g NH}_4\text{-N g}^{-1}$ soil d.w.						
19 June	1.94bd	4.75a	12.14ab	8.86a	24.73a	12.02a	7.84b
26 June	2.59cd	6.99a	16.18a	8.68ab	7.87b	10.56a	9.86b
3 July	1.99bd	3.24a	6.86b	6.44ab	6.66b	11.70a	16.56a
10 July	3.67ac	4.17a	9.61b	5.06ab	6.02b	9.09a	10.12b
17 July	4.75a	6.44a	13.11ab	4.79b	7.40b	9.68a	17.48a
	$\mu\text{ NH}_4\text{-N g}^{-1}$ soil-C						
Seasonal mean	27.26AB	34.07B	34.47B	20.28A	25.53AB	29.09AB	34.90B

for the soils of dry cassiope shrub tundra and lichen heath where NO_3^- levels were considerably higher. Mean concentration of $\text{NH}_4^+\text{-N}$ (mg N kg^{-1} soil C) during the whole growing season was significantly lower in tussock soils than in water-track, moist carex shrub tundra, and dry cassiope shrub tundra soils.

Seasonal changes of basal respiration at 22°C ($\text{mg CO}_2 \text{ kg}^{-1}$ soil h^{-1}) declined as the growing season progressed for most of the soil types (Table 5). Basal respiration significantly decreased between the first and the second sampling dates in tussock, intertussock, and riparian soils, and between the first and the third sampling dates in dry cassiope shrub tundra soils, and between the second and the third sampling dates in dry cassiope shrub tundra soils and moist carex shrub tundra soils. However, no significant change in basal respiration between sampling dates was found in lichen heath soils.

Seasonal averages of basal respiration at 22°C ($\text{mg CO}_2 \text{ kg}^{-1}$ soil C h^{-1}) were the highest for water-track soils and the lowest for the lichen heath soils (Table 5). These basal respiration ($\text{mg CO}_2 \text{ kg}^{-1}$ soil C h^{-1}) rates represent C turnover rates under standard conditions (i.e., potential C turnover rates). These turnover rates tended to correspond to the landscape position of the soil types. Higher potential C turnover rates occurred at wetter sites while lower values were found in relatively drier sites.

Microbial biomass C ($\text{g biomass C kg}^{-1}$ soil C) in the 0- to 5-cm layer did not change significantly through the growing season for intertussock and riparian carex soils (Table 6). There was a noticeable increase of microbial biomass C at the last sampling date in dry cassiope shrub tundra and moist carex soils as well as at the

midsummer sampling date in lichen heath and water-track soils.

Seasonal averages of microbial biomass C (mg C g^{-1} soil C) indicated that water track and lichen heath soils had the highest microbial biomass C, whereas tussock, dry cassiope, and riparian soil had the lowest microbial biomass C (Table 6).

The ratio of basal respiration to SIR has been considered as a CAI (Parkinson and Coleman, 1991). The CAI showed a general decreasing trend across all soil types through the growing season (Table 7). The CAI in the water track significantly decreased from the first sampling date to the third sampling date and then remained fairly constant until the last sampling. A similar pattern existed in moist carex shrub tundra.

Seasonal averages of the CAI in the 0- to 5-cm layer were related to slope positions. The lowest CAI occurred in the dry mineral lichen heath soil on the top of the hill, the highest CAI in the wet organic soils (i.e., riparian and water track), and intermediate values in midslope moist soils (Table 7).

Many measurements in this study were significantly correlated with each other (Table 8). One important result was that NH_4^+ and NO_3^- contents were negatively and significantly correlated with soil C content. In contrast, basal respiration was positively and significantly correlated with soil C content. Soil water content (both kg kg^{-1} and g cm^{-3}) was positively correlated with CAI. Soil water content (both g g^{-1} and g cm^{-3}) was also positively correlated with per gram C based basal respiration or potential C turnover rate. Microbial biomass C was positively correlated with NH_4^+ and NO_3^- contents. Ammonium content was positively correlated with NO_3^- content.

Table 4. Nitrate nitrogen. Numbers are means of six replicates. Numbers in each column with the same letter are not significantly ($P < 0.05$, LSD) different among sampling dates. Numbers of seasonal means with the same letter are not significantly ($P < 0.05$, LSD) different among topo-locations. See Table 1 for the descriptions of all locations. BDL is below detectable level.

Date	Topo-locations						
	Lichen heath	Dry cassiope	Moist carex	Tussock tundra	Inter tussock	Riparian carex	Water track
	$\text{mg NO}_3\text{-N m}^{-2}$						
19 June	1.14b	0.74c	1.23a	1.07a	0.66a	0.55a	BDL
26 June	0.30b	0.48c	0.46a	0.65a	0.41a	0.83a	0.84a
3 July	1.38b	1.11c	0.89a	1.45a	0.70a	4.41b	3.60b
10 July	1.10b	3.93b	0.47a	0.68a	1.32a	BDL	0.66a
17 July	8.01a	11.63a	1.01a	BDL	BDL	BDL	1.45a
	$\mu\text{g NO}_3\text{-N g}^{-1}$ soil-C						
Seasonal mean	1.29A	1.99C	0.55B	0.44B	0.51B	0.93AB	0.83B

Table 5. Soil basal respiration at 22°C. Numbers are means of six replicates. Numbers in each column with the same letter are not significantly ($P < 0.05$, LSD) different among sampling dates. Numbers of seasonal means with the same letter are not significantly ($P < 0.05$, LSD) different among topo-locations. See Table 1 for the descriptions of all locations.

Date	Topo-locations						
	Lichen heath	Dry cassiope	Moist carex	Tussock tundra	Inter tussock	Riparian carex	Water track
	$\mu\text{g CO}_2 \text{ g}^{-1} \text{ soil h}^{-1}$						
19 June	46a	120a	254a	198a	335a	314a	347a
26 June	39a	95a	249a	140b	225b	198b	305a
3 July	34a	41b	104b	127bc	205b	205b	291a
10 July	44a	34b	114b	102c	163b	184b	244a
17 July	35a	77ab	155b	138b	173b	206b	317a
Seasonal mean	89.3A	116.0AB	135.7AB	114.0BD	146.3BD	157.0BD	223.1C

DISCUSSION

Temporal Dynamics

Carbon availability to microbes in these arctic ecosystems was generally high at the beginning of the growing season when the CAI of all sites was the highest (Table 7). These results tend to support the hypothesis that freeze-thaw processes during late fall and early spring periods produce more C available to the microbes from the rupture of microorganisms and release of soluble-C substrates (Skogland et al., 1988). Among the study sites, soil basal respiration under standard temperature and moisture conditions showed a trend similar to the CAI in terms of seasonal changes, highest at the first sampling date and decreasing afterward (Table 5).

The decreasing trend in NH_4^+ concentration in tussock soils indicated that either N immobilization, plant uptake, or both were dominant throughout the growing season and that most N mineralization occurred during the late fall and early spring (Table 3). This result agrees well with those of Giblin et al. (1991), who showed, using the buried-bag technique, that net N mineralization only occurred during the nongrowing season in tussock tundra soils at another arctic site. The trend of increasing NH_4^+ concentration through the growing season in lichen heath soil may mean that net N mineralization took place during the growing season. This result supports one of the findings of Giblin et al. (1991) that net N mineralization occurred in their hilltop heath soils only during the growing season. Many factors may be causing the fluctuation in NH_4^+ concentration observed in both water-track and moist carex shrub tundra soils, such as N transport due to water flows (Chapin et al., 1988; Oberbauer et al. 1989), changes in the depth to the water table (Oberbauer et al., 1992), and changes

in C availability (Table 7). The exact causes of the fluctuation in NH_4^+ concentration in water-track soil and moist carex shrub tundra soil need further investigation.

Severalfold increases in NO_3^- concentrations occurred in lichen heath and dry cassiope shrub tundra soils during the later part of the growing season (Table 4). In contrast, the levels of NO_3^- in the other soils were generally low. The presence of NO_3^- in these arctic ecosystems has also been reported by Giblin et al. (1991). Nitrate concentrations in water-track and riparian soils significantly increased at the midsummer sampling date and returned to the previous level at the next sampling date. The exact cause of this midsummer increase in NO_3^- -N in these two soils is unknown. The increase could represent in situ production or perhaps it is more likely that NO_3^- was transported from the hilltop ecosystems since this midsummer increase in NO_3^- -N coincided with a relatively heavy rainfall event and water movement downslope (see Fig. 1). This mechanism of N transport along the toposequence has been demonstrated to operate in rolling arctic landscapes (Chapin et al., 1988; Oberbauer et al., 1989). Giblin et al. (1991) reported that a considerable amount of NO_3^- accumulated in their resin bags in lichen heath soil.

In general, little temporal variation in microbial biomass C was found in these arctic soils during this growing season. Two exceptions included the noticeable increase at the last sampling for dry cassiope shrub tundra and moist carex tundra soils and at the midsummer sampling date for lichen heath and water-track soils. These results do not support the commonly postulated idea that microbial biomass is the lowest at the beginning of the growing season due to winter freezing kill (e.g., Skogland et al., 1988). One reason for these relatively constant microbial biomass C results might be that the first

Table 6. Microbial biomass C. Numbers are means of six replicates. Numbers in each column with the same letter are not significantly ($P < 0.05$, LSD) different among sampling dates. Numbers of seasonal means with the same letter are not significantly ($P < 0.05$, LSD) different among topo-locations. See Table 1 for the descriptions of all locations.

Date	Topo-locations						
	Lichen heath	Dry cassiope	Moist carex	Tussock tundra	Inter tussock	Riparian carex	Water track
	$\text{mg C g}^{-1} \text{ soil-C}$						
19 June	22.4ab	23.5ab	23.2ab	24.7a	31.7a	21.5a	28.4b
26 June	20.2b	19.0b	32.1a	20.0b	27.8a	20.3a	27.9b
3 July	41.8a	24.0ab	26.2ab	24.9a	31.5a	21.7a	43.7a
10 July	33.3ab	17.4b	21.4b	19.5b	25.1a	19.5a	34.0ab
17 July	32.2ab	29.1a	29.0ab	23.9ab	24.0a	23.5a	40.2ab
Seasonal mean	30.0BC	22.6A	26.4B	22.6A	28.0B	21.3A	34.8C

Table 7. Carbon availability index (Basal/SIR). Numbers are means of six replicates. Numbers in each column with the same letter are not significantly ($P < 0.05$, LSD) different among sampling dates. Numbers of seasonal means with the same letter are not significantly ($P < 0.05$, LSD) different among topo-locations. See Table 1 for the descriptions of all locations.

Date	Topo-locations						
	Lichen heath	Dry cassiope	Moist carex	Tussock tundra	Inter tussock	Riparian carex	Water track
19 June	0.397a	0.479a	0.650a	0.452a	0.496a	0.759a	0.698a
26 June	0.208b	0.369ab	0.410b	0.443a	0.407ab	0.530b	0.617a
3 July	0.230b	0.426ab	0.271c	0.317b	0.348b	0.529b	0.395b
10 July	0.189b	0.397ab	0.328bc	0.329b	0.335b	0.548b	0.401b
17 July	0.173b	0.299b	0.337bc	0.360b	0.448ab	0.505b	0.428b
Seasonal mean	0.239A	0.394B	0.399B	0.380B	0.407B	0.574C	0.508C

sampling date was not early enough to detect the lowest point. Early sampling before the start of spring thaw would be required to test this possibility. The increase in microbial biomass at the last sampling date might have been caused by the relatively warmer and drier conditions prevalent before and at the time of sampling (see Fig. 1 and 2). The increase in microbial biomass C at the midsummer sampling date in water-track soil might have been caused by transported substrates due to heavy rains recorded a few days before the sampling date. This was the same period when NO_3^- also peaked in this system.

Spatial Variation

The spatial variation in basic properties of these soils was extremely large and is typical of arctic soils (Nadelhoffer et al., 1992). Carbon content ranged from 115 to 431 g C kg⁻¹. Total N content ranged from 5 to 16.6 g N kg⁻¹, with the resulting C/N ratio varying from 19.4 to 91.5. Bulk density ranged from 0.06 to 0.38 g cm⁻³, typical for organic soils. Soil moisture increased systematically from the ridge top to the stream bank. Soil temperature at the surface also significantly differed among these soils (Fig. 3 and 4).

Carbon availability indexes in the 0- to 5-cm layer were related to slope position. The lowest value occurred in the dry mineral lichen heath soil on the ridge top, the highest values in the wet organic soils (i.e., riparian and water track), and intermediate values in midslope moist soils. The CAI was positively correlated with both per-gram-soil-based and per-volume-based soil water contents. In the wetter soils, available C might

have been preserved and accumulated since soil saturation and inundation would lead to anoxia and low microbial respiration. Oberbauer et al. (1992) reported that CO_2 efflux from riparian tundra systems was strongly influenced by depth to water table. Other studies reported that wetter sites tended to have larger accumulations of soil organic matter (Walker et al., 1989). Water undoubtedly plays a very important role in soil organic matter accumulation and losses in these arctic ecosystems (Funk et al., 1994). These results imply that any climatic changes that alter soil water conditions will have profound effects on C accumulations or losses in these tundra ecosystems. Draining of those wetter sites will result in a pulse of C losses due to the initially higher C availability at those sites.

Soil moisture conditions in these arctic soils also strongly affected potential C turnover rates (i.e., per gram soil C based basal respiration rates). Higher potential C turnover rates occurred at wetter sites while lower potential rates were found at drier sites. These results imply that soils at the wetter sites have a higher potential for losing C, whereas soils at the drier sites have lower C loss potential. This pattern agrees well with the above-discussed pattern for CAI.

Tussock soils had low potential C turnover rates but had a CAI that was similar to the other midslope soils. This finding indicates that factors other than C availability, such as temperature and N availability, could be important in determining the C turnover rate of tussock soil C. Seasonal mean soil temperature at the 1- and 5-cm depths was the lowest at the tussock tundra site (Fig. 3). Nitrogen may be highly limiting in tussock

Table 8. Correlation matrix. Numbers are correlation coefficients (r). Number of observation (n) = 220. $P(|r| > r_{0.05}) = 0.195$, $P(|r| > r_{0.01}) = 0.254$. Variables: D^b = bulk density, H_2O = water content (w/w), %C = carbon content (w/w), Basal/SIR = ratio of basal respiration to substrate-induced respiration (SIR), basal/gC = basal respiration rate per gram soil C, SIR/gC = substrate-induced respiration per gram of soil C, $\text{NH}_4^+/\text{gC} = \mu\text{g NH}_4^+-\text{N per gram of soil C}$, $\text{NO}_3^-/\text{gC} = \mu\text{g NO}_3^--\text{N per gram of soil C}$, $\text{NH}_4^+/\text{cc} = \mu\text{g NH}_4^+-\text{N per mL of soil volume}$, $\text{NO}_3^-/\text{cc} = \mu\text{g NO}_3^--\text{N per mL of soil volume}$, Basal/cc = basal respiration per mL of soil volume, SIR/cc = substrate-induced respiration per mL of soil volume.

	D^b	H_2O	C	Basal/SIR	basal/gC	SIR/gC	NH_4^+/gC	NO_3^-/gC	NH_4^+/cc	NO_3^-/cc	Basal/cc	SIR/cc
H_2O	-0.66											
C	-0.83	0.79										
Basal/SIR	-0.21	0.40	0.25									
basal/gC	-0.16	0.47	0.33	0.53								
SIR/gC	0.17	0.02	-0.02	-0.33	0.54							
NH_4^+/gC	0.34	-0.09	-0.23	0.15	0.36	0.30						
NO_3^-/gC	0.25	-0.13	-0.24	-0.17	0.01	0.22	0.33					
NH_4^+/cc	0.29	-0.31	-0.38	0.08	0.07	0.08	0.81	0.34				
NO_3^-/cc	0.24	-0.23	-0.30	-0.22	-0.09	0.17	0.28	0.94	0.40			
Basal/cc	-0.07	0.03	-0.03	0.47	0.66	0.27	0.26	0.04	0.41	0.07		
SIR/cc	0.22	-0.40	-0.36	-0.46	0.10	0.63	0.14	0.27	0.36	0.37	0.47	
$\text{H}_2\text{O}/\text{cc}$	-0.14	0.32	0.05	0.41	0.22	-0.16	0.09	-0.04	0.27	-0.01	0.54	0.06

tundra. Mineral N contents of both tussock and intertussock soils were low compared with other soils (Tables 3 and 4). These results are consistent with other reports in the literature (Chapin and Shaver, 1985; Shaver et al., 1986; Marion et al., 1987). The short-circuit in N cycling due to direct uptake of organic N by cotton grass may play an important role in this low-N-availability environment (Chapin et al., 1993; Kielland, 1994). Nitrogen limitation in tussock soils may also cause higher C/N ratio of microbial biomass (Cheng and Virginia, 1993) and decoupling of N mineralization from C mineralization (Marion and Black, 1987; Giblin et al., 1991; Nadelhoffer et al., 1991). Nitrogen availability in tussock tundra has been a focal point in several recent studies of potential effects of climatic change on chemical cycling in arctic ecosystems (Leadley and Reynolds, 1992; Moorhead and Reynolds, 1993).

Microbial biomass C averaged for five sampling dates during the growing season did not correspond to the toposequence of the sampling sites. Higher proportions of soil C were found as microbial biomass C in water-track and lichen heath soils whereas the lower values were found in riparian, tussock tundra, and dry cassiope shrub tundra.

Microbial biomass values (g C kg^{-1} soil C) in these arctic sites were within the range ($10\text{--}50 \text{ g C kg}^{-1}$ soil C) reported for forest and agricultural soils taken from temperate regions (Anderson and Domsch, 1986, 1989; Insam et al., 1989; Sparling, 1992). The ratio of microbial biomass C to total soil organic C in a soil was influenced by management regimes (Anderson and Domsch, 1989) and climatic conditions (Insam et al., 1989). Our results suggest that landscape topography may also strongly affect the ratio of microbial biomass C to total soil organic C.

Soils in the arctic tundra differed from each other with regard to soil properties, microbial biomass C, available C and N, and potential C turnover rate. Among these ecosystem types, tussock tundra soils had low N availability and low potential C turnover indexes, shallow thaw depth due to low temperature, and high C/N ratio. Therefore, the tussock tundra soil is the most biologically inactive type in the arctic landscape but occupies the largest area along the toposequence typical of this region (Stow et al., 1989). Water-track soils had the highest C and N availability, the highest potential C turnover index, and the highest microbial biomass C. Therefore, water tracks are the most biologically active areas of the arctic landscape but represent only a small relative area of this toposequence. Several other studies have shown similar results, e.g., Oberbauer et al. (1991). This mosaic of diverse plant communities and soil types determines that accurate estimates of a large-scale C or N budget in this arctic landscape can only be made by integration of all types.

Interactions

Mineral N content was negatively correlated with soil organic C content, whereas potential C turnover rate was positively correlated with soil organic C content.

This result may be explained by the higher organic C content normally associated with more fresh plant material with lower C/N ratio in the surface soils, which have a higher amount of available C and higher N immobilization potential. This may also indicate that net N mineralization is partially decoupled from C mineralization in soils having more fresh plant materials.

We have found that the amounts of the microbial biomass C are significantly correlated with the amounts of mineral N in the toposequence. It is widely known that microbial biomass is the main agent for most biogeochemical processes, including N mineralization and immobilization (Paul and Voroney, 1980), and that microbial biomass often comprises a major portion of the active nutrient pool. Nadelhoffer et al. (1991) and Giblin et al. (1991) found no correlation between N mineralization and soil respiration. Moorhead and Reynolds (1993) found no constant relationship between mineral N pool size and either CO_2 efflux or net N immobilization in simulations. Based on these observations, we suggest that microbial biomass may have overall control on N availability in this arctic toposequence even though the N cycle may be decoupled from the C cycle.

ACKNOWLEDGMENTS

This research was supported by a grant from the United States Department of Energy OHER/ERD as part of the R4D program. Logistical support was provided by the Institute of Arctic Biology, University of Alaska, Fairbanks. We thank Dr. F.S. Chapin III and Dr. G.R. Shaver, who critically read the manuscript and provided many valuable comments and suggestions. Field assistance by Marcy Darby and Bertram Ostendorf is appreciated. Robin McBride, Laura Knot, Qiangli Zhang, and Joe Verfaillie helped with laboratory analyses.

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