

# Soil carbon and nitrogen dynamics along a latitudinal transect in Western Siberia, Russia

H. Meyer · C. Kaiser · C. Biasi · R. Hämmerle ·  
O. Rusalimova · N. Lashchinsky · C. Baranyi ·  
H. Daims · P. Barsukov · A. Richter

Received: 4 February 2005 / Accepted: 8 June 2006 / Published online: 23 August 2006  
© Springer Science+Business Media B.V. 2006

**Abstract** An 1800-km South to North transect (N 53°43' to 69°43') through Western Siberia was established to study the interaction of nitrogen and carbon cycles. The transect comprised all major vegetation zones from steppe, through taiga to tundra and corresponded to a natural temperature gradient of 9.5°C mean annual temperature (MAT). In order to elucidate changes in the control of C and N cycling along this transect, we analyzed physical and chemical properties of soils and microbial structure and activity in the organic and in the mineral horizons, respectively. The impact of vegetation and climate exerted major controls on soil C and N pools (e.g., soil

organic matter, total C and dissolved inorganic nitrogen) and process rates (gross N mineralization and heterotrophic respiration) in the organic horizons. In the mineral horizons, however, the impact of climate and vegetation was less pronounced. Gross N mineralization rates decreased in the organic horizons from south to north, while remaining nearly constant in the mineral horizons. Especially, in the northern taiga and southern tundra gross nitrogen mineralization rates were higher in the mineral compared to organic horizons, pointing to strong N limitation in these biomes. Heterotrophic respiration rates did not exhibit a clear trend along the transect, but were generally higher in the organic horizon compared to mineral horizons. Therefore, C and N mineralization were spatially decoupled at the northern taiga and tundra. The climate change implications of these findings (specifically for the Arctic) are discussed.

**Keywords** Decomposition · Gross N mineralization · Microbial respiration · Nitrogen cycling · Transect study

---

H. Meyer · C. Kaiser · C. Biasi · R. Hämmerle ·  
A. Richter (✉)  
Department of Chemical Ecology and Ecosystem  
Research, University of Vienna, Althanstrasse 14,  
A-1090 Vienna, Austria  
e-mail: andreas.richter@univie.ac.at

O. Rusalimova · P. Barsukov  
Institute of Soil Science and Agrochemistry, Street  
Sovetskaya 18, Novosibirsk 630099, Russia

N. Lashchinsky  
Central Siberian Botanical Garden, Street  
Zolotodolinskaja 101, Novosibirsk 630090, Russia

C. Baranyi · H. Daims · R. Hämmerle  
Department of Microbial Ecology, University of  
Vienna, Althanstrasse 14, A-1090 Vienna, Austria

## Introduction

The carbon sequestration of terrestrial ecosystems is determined by the balance between net primary production (NPP) and heterotrophic

respiration (decomposition of dead organic material). In addition to environmental factors, such as temperature and soil moisture, that control both production and decomposition processes, the latter are also controlled by the quality and quantity of available substrates (litter and soil organic matter) and by the structure and composition of the microbial community (Swift et al. 1979). Controls on microbial decomposition differ from ecosystem to ecosystem. For example, low nutrient availability (Priha and Smolander 1999) and litter quality (Berg et al. 2000) are thought to constrain microbial activities in boreal forests; even in arctic ecosystems decomposition is thought to be restricted by nutrient limitation (Mack et al. 2004), in addition to high soil moisture, low temperatures, and a short growing season (Oechel et al. 1993). Climate change may therefore alter decomposition processes directly and indirectly (via effects on nutrient turnover), depending on initial state of the ecosystems (Shaver et al. 2000).

Siberia covers some of the dominant biomes on Earth, encompassing both treeless (steppe, forest steppe and southern tundra) and forested ecosystems (forest steppe, southern and northern taiga). These biomes contain vast pools of organic carbon and play an important role in the global carbon cycle (Jonasson et al. 2001). Understanding the controls over element cycling in these biomes is important to predict changes in C and N dynamics due to climate change. Climate change effects, especially those of increasing temperatures on ecosystem structure and function have been addressed by numerous laboratory studies and field-based experiments (for review see Shaver et al. 2000). In general, there are strong positive correlations between temperature and soil respiration (Peterjohn et al. 1994), soil net N mineralization (Lükewille and Wright 1997; Schmidt et al. 2002) and plant productivity (Jonasson et al. 1999), at least initially. In the longer term, however, many of the processes return to pre-disturbance levels, indicating that short-term reactions to warming may be different from long-term effects (Arft et al. 1999; Shaw and Harte 2001).

We here report the establishment of an 1800-km latitudinal transect through Western Siberia. The transect was organized along a mean annual

temperature (MAT) gradient of 9.5°C and covered all major vegetation types of Siberia. We used this transect to compare biomes along environmental gradients in order to understand the effect of warming and other environmental changes, as well as vegetation type, on decomposition processes and nutrient cycling. Our work specifically aimed at elucidating controls and constraints on carbon and nitrogen turnover in each of these biomes. Towards this goal we analyzed carbon and nitrogen pools, and microbial community composition together with microbial processes (gross nitrogen mineralization and heterotrophic respiration) in organic and mineral soil horizons, and used multivariate statistics to elucidate major constraints on microbial processes at current conditions.

## Materials and methods

### Study sites

The study was performed with soils collected from six sites along an 1800-km transect in Russia during the first half of July 2001 and July 2002. The sampling started in the south and proceeded to the north, so that phenologically similar situations were sampled (early summer aspects). The sites ranged from the border of Kazakhstan through Western Siberia to the estuary of the river Ob (Table 1). All sites were relatively flat and at elevations between 144 m in the south and 33 m in the north. Mean annual temperature (MAT) decreased from 1.6°C in the south to -7.9°C in the north. Mean July soil temperatures were measured by temperature loggers (TidBits, Onset) at 5 cm under soil surface at each site (Table 1). Mean annual precipitation was generally low and ranged between 270 mm at the steppe site and 408 mm at the northern taiga site (Table 1). The soils along the transect are formed on loess-like Aeolian sediments at the southern sites (steppe, forest steppe) and on sandy fluvio-glacial depositions of the river Ob and its numerous tributaries at the northern sites (taiga, tundra). The soils of the two northern most sites were characterized by permafrost and cryoturbation processes (Table 2).

**Table 1** Sampling sites along the latitudinal transect through Western Siberia

Biome	Position	MAT (°C) <sup>a</sup>	Mean soil temp. July 2002 (°C) <sup>b</sup>	MAP (mm) <sup>a</sup>	Vegetation subzone	Dominant plant species	Ecosystem NPP <sup>c</sup> (g C m <sup>-2</sup> a <sup>-1</sup> )
Steppe	53°43' N 73°43' E	1.60	20.6	270	True Steppe	<i>Festuca pseudovina</i> , <i>F. valesiaca</i> , <i>Artemisia austriaca</i> , <i>Phlomis tuberosa</i> , <i>Elytrigia repens</i> , <i>Seseli strictum</i>	175
Forest Steppe Meadow	55°12' N 72°24' E	0.75	18.2	319	Dry meadow	Meadow: <i>Festuca pseudovina</i> , <i>Poa angustifolia</i> , <i>Fragaria viridis</i> .	479–755
Forest			14.6		Aspen-birch forest	Forest: <i>Betula pendula</i> , <i>Populus tremula</i> , <i>Rosa majalis</i> , <i>Rubus saxatilis</i>	351
Southern Taiga	58°18' N 68°37' E	-0.50	12.4	395	Dark coniferous forest	<i>Abies sibirica</i> , <i>Populus tremula</i> , <i>Pinus sibirica</i> ,	362
Northern Taiga	65°55' N 78°08' E	-6.83	11.3	408	Larch-pine forest	<i>Picea obovata</i> , <i>Carex macroura</i> , <i>Oxalis actosella</i> <i>Larix sibirica</i> , <i>Pinus sibirica</i> , <i>Vaccinium vitis-idaea</i> ,	209
Southern Tundra	67°55' N 74°58' E	-7.91	8.2	341	Moss-lichen southern tundra	<i>Cladina stellaris</i> , <i>Pleurozium schreberi</i> <i>Betula nana</i> , <i>Salix sp.</i> , <i>Carex arcticisibirica</i> , <i>Vaccinium vitis-idaea</i> , <i>Cladina stellaris</i> , <i>Cladina rangiferina</i> , <i>Hylacomium splendens</i> , <i>Aulacomium turgidum</i>	88–150

<sup>a</sup> For the nearest available climate stations; according to Stolbovoi and McCallum 2002

<sup>b</sup> Soil temperatures were measured at the experimental sites at a depth of 5 cm

<sup>c</sup> NPP values from Bazilevich (1993)

## Soil sampling and soil properties

Five soil cores (25 × 25 cm to the depth of the upper mineral horizons) were collected at each site along an approximately 30-m transect. The soil samples were divided into organic and upper mineral soil horizons, and the whole horizon was sieved (< 2 mm) and thoroughly mixed (except for the Ah horizons of the Chernozems of steppe and forest steppe meadow, of which the horizons were sampled to a depth of 10 cm). Sub-samples were oven dried (app. 105°C) to determine the soil water content. After homogenization in a ball mill total C and N were measured (see below). Aliquots of fresh soil (1 g) were extracted with either 10 ml of 1 M KCl or deionized water by shaking for 2 h and subsequent filtration through ash free filters (Schleicher & Schüll, Germany). HgCl<sub>2</sub> was added to a final concentration of 10 μM to the extracts to inhibit post-sampling microbial growth. Approximately 300 mg of the soil mixture were immediately submersed in RNA-later (Ambion Europe Ltd) to prevent the degradation of nucleic acids. All extracts were stored below 10°C until transport to the laboratory. The KCl extracts were used to measure exchangeable NH<sub>4</sub><sup>+</sup> and dissolved organic nitrogen (DON); NO<sub>3</sub><sup>-</sup> was determined in the water extracts. The soil organic matter (SOM) content was determined by loss-on-ignition in a muffle furnace at 450°C for 4 h. Soil bulk density was determined by weighing soil cores of known volume after drying at 105°C. The pH was measured in suspension of soil in water at a ratio of 1:2.5.

## Soil C and N

Total soil C and N were determined by elemental analysis (EA 1110, CE Instruments, Milan, Italy). The concentration of NH<sub>4</sub><sup>+</sup> in soil was measured in KCl extracts by a salicylic acid assay (Kandeler and Gerber 1988). Nitrate was determined by ion-chromatography and conductivity detection after chemical suppression (ASRS-Ultra, Dionex, Vienna, Austria) using an anion exchange column (AS11, 250 × 4 mm in diameter, Dionex) and NaOH gradient elution (2–40 mM in 8 min). Dissolved organic nitrogen was determined as nitrate (see above) after an alkaline persulfate

digestion of the water extracts (Sollins et al. 1999).

## Microbial biomass

Microbial biomass was estimated by the fumigation-extraction method according to Amato and Ladd (1988). About 1.5 g of fresh soil was fumigated with ethanol-free chloroform for 48 h and extracted with 15 ml of 0.5 M K<sub>2</sub>SO<sub>4</sub> for 2 h and then filtered. The extracts were digested with alkaline persulfate and the nitrate produced was measured by ion-chromatography as described above. Microbial N flush was calculated as the difference of the chloroform-fumigated and non-fumigated samples.

## DNA isolation, PCR amplification and microbial community fingerprints (DGGE)

The microbial community structures in the different soil samples were analyzed through comparisons of community fingerprints obtained by denaturing gradient gel electrophoresis (DGGE; Muyzer et al. 1993). Total DNA was extracted from soil using the FastDNA kit (Bio101, Irvine, USA) and was quantified with the Picogreen DNA quantification kit (Molecular Probes, Eugene, USA). A fragment of DNA (566 bp) from the 16s rRNA gene was PCR-amplified using the forward Primer 341f with attached GC clamp: cgc ccg cgc ccc gcg ccc gtc ccg ccg ccc ccc gCC TAC GGG AGG CAG CAG and a reverse Primer 907r: CCG TCA ATT CMT TTG AGT TT (Muyzer et al. 1995). PCR amplification (initial denaturation step of 94°C for 4 min and 30 cycles of denaturation at 94°C for 40 s, annealing at 58°C for 40 s, elongation at 72°C for 1 min and a final elongation at 72°C for 30 min) was carried out in 50 μl volumes (Janse et al. 2004). Each reaction mix contained 1 U RedTaq-Polymerase (Sigma, Germany), 5 μl 10 × PCR buffer (Sigma, Germany), 1 μl BSA (2.5 mg/ml) (Fermentas Life Sciences), 5 μl of dNTP-mix (2 mM/dNTP) (Fermentas Life Sciences), 2 μl of MgCl<sub>2</sub> (25 mM), 50 pmol of each primer and 1 μl of template DNA.

DGGE analysis was performed with a Dcode Universal Mutation Detection System (Bio-Rad,

Herculis, CA) under the following conditions: 1-mm thick 6% polyacrylamide gels, a denaturant gradient of 42–65% urea-formamide (where 100% denaturant contained 7 M urea and 40% formamide) at 60°C, 100 V for 16 h. The software Primer 5.2.2 (Primer-E Ltd., UK) was used for determining the band pattern similarities (Bray–Curtis similarity matrix) among DGGE fingerprints of microbial communities based on the presence/absence of particular bands and for subsequent cluster analysis and dendrogram reconstruction (group average linking method).

### C and N mineralization

Soil respiration rates were determined in the field by a modified alkaline CO<sub>2</sub> trapping method (Öhlinger 1995). Approximately 10 g of soil were incubated with 5 ml 0.25 M NaOH in a closed vessel at ambient soil temperature over 3 days. The absorbed CO<sub>2</sub> was precipitated as barium carbonate by adding 10 ml of 1 M BaCl<sub>2</sub>. The remaining NaOH was titrated with 0.1 M HCl using phenolphthalein as an indicator.

We measured gross N mineralization instead of net mineralization rates to elucidate direct effects of abiotic factors on ammonification rates, thereby excluding microbial N immobilization that might be affected by the nutrient status of the soil microbes. Gross N mineralization rates were determined by using a <sup>15</sup>N pool dilution method (Myrold and Tiedje 1986; Schimel et al. 1986). Aliquots of 500 μl of a 0.25 mM solution of (<sup>15</sup>NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub> (10 at% <sup>15</sup>N) were applied to each of two sub-samples of 1 g of sieved soil (125 nmol in total). The samples were then mixed thoroughly and incubated at ambient soil temperature for 4 and 24 h. A 4-h delay before starting the experiment was necessary to ensure that the ammonium pool was uniformly labelled. The incubation was stopped by extracting the samples with 12 ml of 1 M KCl for 1 h and subsequent filtration. Prior to analysis, 100 mg of MgO were added to each of the extracts and they were incubated for 5 days together with acid traps to recover the liberated NH<sub>3</sub>. The acid traps consisted of 2 circles of ash-free filter papers, each containing 4 μl of 2.5 M KHSO<sub>4</sub>, wrapped in Teflon<sup>®</sup> tapes. After drying, <sup>15</sup>N enrichment of

NH<sub>4</sub><sup>+</sup> was measured by continuous-flow isotope ratio mass spectrometry using an elemental analyser (EA 1110, CE Instruments, Milan, Italy) coupled to a gas IRMS system (DeltaPLUS, Finnegan MAT, Bremen, Germany). Rates of gross N mineralization were calculated using the equation described by Barrett and Burke (2000).

### Statistical analysis

Data were analyzed using one-way analysis of variance (ANOVA, multiple range test, Tukey HSD). Differences between mean values of the two soil horizons were tested at the *P* < 0.05 level. A principal component analysis (PCA) was carried out separately for organic and mineral horizons. The analysis included climate variables (MAT and MAP), soil characteristics (water content, bulk density and, additionally for mineral horizons, clay content and pH), nutrient pools and ratios (total C and N, C/N ratio, SOM, DIN, DON, microbial N) as well as soil processes (C and N mineralization and C-to-N mineralization ratio). Before running the PCA, variables were standardized by subtracting the average from each variable and then dividing it by the standard deviation. No replications for MAT and MAP at each of the experimental sites were available; we therefore used only one value for these parameters in the PCA analysis. The results were summarized using biplot and scatter diagrams. A cluster analysis (group average method, squared Euclidean) was performed to show distances between the vegetation cover of the different sites. All statistical analyses were performed using Statgraphics 5.0 (Stats Incorporated).

## Results

### Soil characteristics

Several trends in the physical and chemical characteristics of the soils along the transect could be observed, such as a clear decrease of pH values in mineral horizons and, with the exception of the tundra site, a decrease in clay content (Table 2). We also found a significant differences soil water content in the organic horizons along the

**Table 2** Description of soil profiles along a latitudinal transect through Western Siberia

Site	Soil type <sup>a</sup>	Horizon	Depth (cm)	Bulk density (g cm <sup>-3</sup> )	Clay content (% < 0.001µm)	pH <sub>water</sub>	Water content (% fresh matter)	SOM (kg m <sup>-2</sup> )
Steppe	Glossic Chernozem <sup>b</sup>	Ah	18	1.34	45.6	7.1	17.1 (0.38)a	22.78 (0.85)b
Forest Steppe Meadow	Glossic Chernozem <sup>b</sup>	O	2	0.31			20.3 (1.23)a	2.24 (0.17)a
		Ah	37	1.17	31.1	6.7	15.3 (0.19)a	50.88 (1.97)c
Forest	Planysol <sup>b</sup>	O	5	0.30			38.6 (4.20)b	7.64 (0.56)b
		A	10	1.03	19.3	5.6	16.4 (2.25)a	20.17 (9.46)b
Southern Taiga	Orthieutric Albeluvisol <sup>c</sup>	O	1–5	0.24			47.6 (4.21)b	5.60 (0.94)b
		A	6	1.31	12.4	4.2	18.6 (0.70)a	5.83 (0.82)ab
Northern Taiga	Eutric Leptosol <sup>c</sup>	O	2–3	0.24			37.2 (1.67)b	3.16 (0.34)a
		El	4–7	1.44	3.2	3.9	14.0 (1.26)a	1.86 (0.54)a
Southern Tundra	Cryosol <sup>c</sup>	O	2	0.22			66.4 (1.86)c	7.11 (0.11)b
		A	4–11	0.65	23.6	3.6	32.5 (7.17)b	14.20 3.40)ab

Within one horizon, values followed by different letters are significantly different at  $P < 0.05$  (ANOVA, Tukey HSD)

<sup>a</sup> Soil classification according to WRB (World Reference Base for Soil Resources, FAO 1998)

<sup>b</sup> Parent materials were loess-like Aeolian sediment

<sup>c</sup> Parent materials were sandy depositions of river Ob

transect (Table 2). The soil organic matter content was significantly higher in the organic horizons (but not in the mineral horizons) of the tundra sites, and the C/N ratios were higher in the northern taiga and the tundra compared to the southern ecosystems along the transect (Table 3). In order to gain further insights into the soil nitrogen status in the different sites, total N and concentrations of ammonium, nitrate and dissolved organic nitrogen (DON) were measured. Total N was highest at the forest steppe forest and at the tundra site within the organic soil horizons, while in the mineral horizons highest levels were found in the southern ecosystems (Table 3). No clear pattern along the transect could be elucidated with respect to ammonium, nitrate and DON (Table 3).

#### Microbial biomass and activity

Microbial nitrogen was 4–11-times higher than the soluble N (DON and inorganic nitrogen) in the organic horizons and equal to 3 times higher in the mineral horizons (Table 3). The nitrogen in the microbial biomass therefore made up for a significant proportion (up to 7%) of the total soil nitrogen. Surprisingly, however, no significant

differences in microbial N were found along the transect, although this might have been the case, if the extraction efficiency would differ along the transect.

As expected, higher heterotrophic respiration rates were measured in the organic horizons compared to the mineral soil layers at all sites on a dry matter basis (Fig. 1A) as well as on a SOM basis (data not shown). In the upper soil horizon the highest respiration was observed in the forest steppe forest and in the southern tundra, while this pattern was lesser pronounced in the mineral horizons. Gross N mineralization rates were not significantly different in the mineral horizons. Among the organic horizons the two sites in the forest steppe biome had highest values, whereas the mineralization rates at the tundra were very low (Fig. 1B). In the northern taiga and tundra, the gross N mineralization rates were even higher in the mineral horizons than in the organic horizons. When we calculated the process data on a per gram SOM rather than on a per gram soil basis, the same tendencies between organic and mineral horizons were found, except for the gross N mineralization rates in forest steppe and southern taiga soils, which were higher in mineral compared to organic horizons (data not shown).

**Table 3** Soil organic matter and nutrient status of sampled soil horizons along the latitudinal transect through Western Siberia

Site	Horizon	Soil organic matter (% dm)	Total C (% dm)	Total N (% dm)	C/N ratio	Ammonium ( $\mu\text{g NH}_4^+$ -N $\text{g}^{-1}$ dm)	Nitrate ( $\mu\text{g NO}_3^-$ -N $\text{g}^{-1}$ dm)	Dissolved organic N ( $\mu\text{g DON g}^{-1}$ dm)	CFE N flush <sup>a</sup> ( $\mu\text{g N g}^{-1}$ dm)
Steppe	Ah	9.5 (0.3)ab	3.1 (0.1)a	0.3 (0.0)abc	12.3 (0.4)a	0.9 (0.1)a	0.8 (0.59)c	26.1 (4.5)ab	60.1 (3.6)a
	O	28.3 (2.2)a	12.4 (1.5)a	0.9 (0.1)a	13.4 (0.2)a	8.8 (1.6)a	3.6 (1.1)b	27.6 (7.9)a	243.8 (43.05)a
Forest Meadow	Ah	12.7 (0.5)ab	5.5 (0.3)a	0.5 (0.0)c	12.2 (0.1)a	0.8 (0.4)a	nd	20.4 (8.6)ab	67.4 (25.1)a
	O	62.4 (6.1)b	27.7 (2.1)b	1.5 (0.1)b	18.4 (0.4)ab	62.5 (9.3)c	0.5 (0.3)a	101.8 (30.9)b	316.2 (107.7)a
Southern Taiga	A	21.9 (10.2)b	5.1 (1.3)a	0.4 (0.1)bc	14.4 (0.3)a	4.1 (2.6)a	0.4 (0.0)a	27.4 (9.5)ab	51.8 (36.7)a
	O	38.9 (6.6)ab	19.8 (3.2)ab	0.9 (0.1)a	21.61 (1.1)b	33.1 (7.1)b	1.2 (0.2)a	54.2 (11.0)ab	255.0 (30.3)a
Northern Taiga	A	3.4 (0.5)ab	1.6 (0.2)a	0.1 (0.0)a	11.5 (0.5)a	2.1 (0.3)a	0.7 (0.1)bc	10.7 (1.1)ab	13.1 (3.42)a
	O	43.9 (4.7)ab	24.1 (2.3)b	0.8 (0.1)a	31.1 (1.3)c	5.0 (0.8)a	0.3 (0.1)a	29.8 (3.4)a	211.1 (26.9)a
Southern Tundra	El	2.4 (0.7)a	1.6 (0.4)a	0.1 (0.0)a	21.5 (1.1)b	0.9 (0.2)a	0.2 (0.0)ab	9.2 (1.3)a	13.6 (7.0)a
	O	80.8 (1.2)c	38.9 (0.9)c	1.2 (0.1)ab	33.7 (3.0)c	11.6 (3.9)ab	1.1 (0.3)a	81.9 (21.0)b	457.3 (99.6)a
	A	17.4 (3.6)ab	5.5 (2.3)a	0.2 (0.1)ab	20.5 (2.6)b	1.3 (0.2)a	0.4 (0.1)abc	58.1 (12.4)b	32.9 (213.0)a

<sup>a</sup> Chloroform fumigated extraction nitrogen flush

Values are means of 5 replicates  $\pm$  SE. Within each column and for each horizon, values followed by different letters are significantly different at  $P < 0.05$  (ANOVA, Tukey HSD); nd = not detectable

The ratio of N mineralization of organic to mineral horizons decreased significantly from 4.1 to 0.2 along the transect (Fig. 1B). Interestingly, the ratio of carbon mineralization (microbial respiration) to gross N mineralization—calculated as carbon mineralized per unit N mineralized—was constant in mineral horizons, but increased significantly with latitude from 4.7 to 340.5 within the organic horizons (Fig. 2).

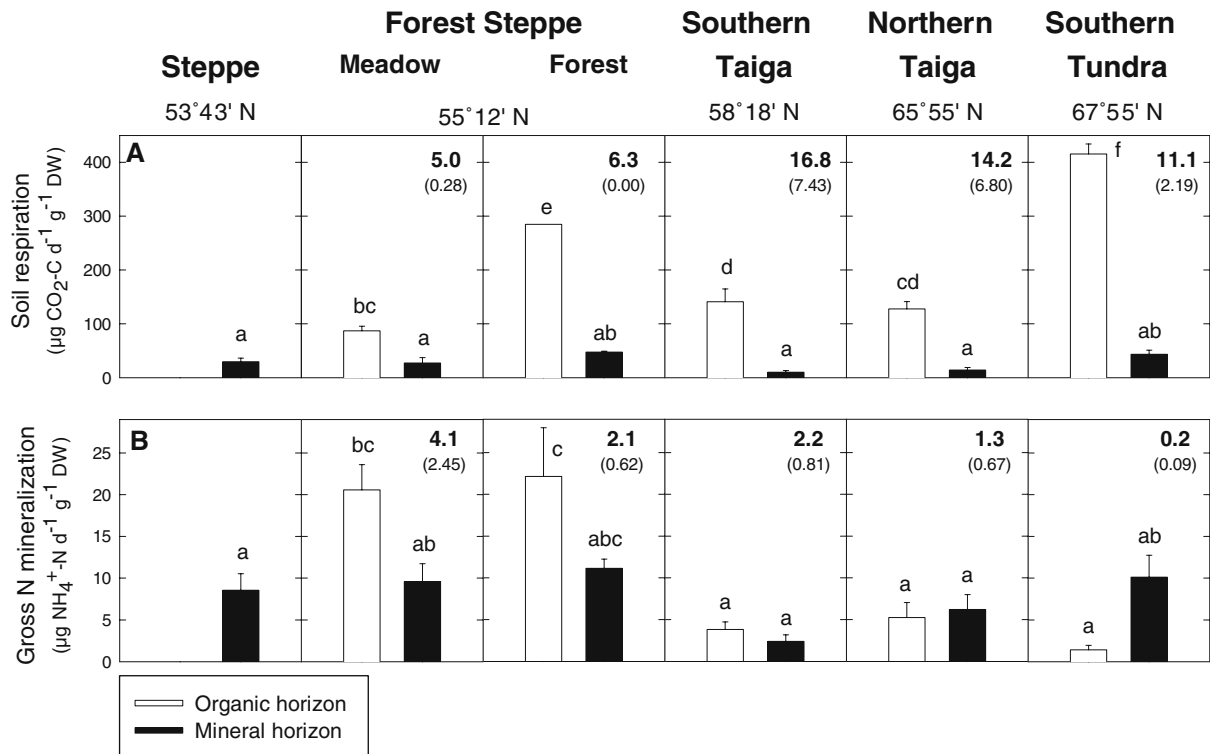
### Microbial community structure and vegetation cover

The analysis of the bacterial community structure, based on the presence of particular DGGE bands, in the organic and mineral soil layers revealed that the communities in the same soil layers were more similar throughout the transect than the communities in different soil layers at the same sites (Fig. 3). Within each of the horizons, neighbouring sites were relatively similar, indicating only a gradual change of microbial communities with large distances of hundreds of kilometres.

Obviously, the vegetation pattern changed dramatically along a 1800-km transect (Table 1). In order to quantify the similarity of vegetation between sites and to compare it to the pattern of the microbial community we conducted a cluster analysis for the plant species abundance (Fig. 4). In this analysis the northern sites (taiga and tundra) and the two most southern sites (steppe and meadow of the forests steppe biome) exhibited the smallest distances indicating that the vegetation at the forested sites and the tundra are more similar to each other than to the vegetation at the southern biomes. Therefore, the plant community structure showed a similar pattern along the transect as the microbial community structure of organic horizons, although the similarity within the microbial community was generally much higher.

### Principal component analysis

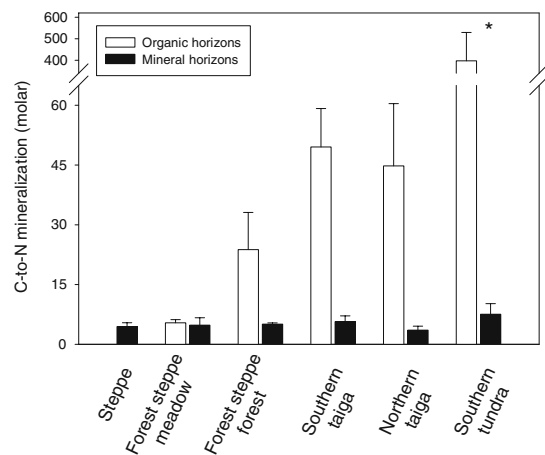
We conducted a principal component analysis to elucidate physical, chemical and climatic constraints on soil processes along the transect. The analysis yielded a clear separation of the biomes



**Fig. 1** Soil respiration rates ( $\mu\text{g CO}_2\text{-C d}^{-1} \text{g}^{-1}$  dry matter, 1A) and gross N mineralization rates ( $\mu\text{g NH}_4^+\text{-N d}^{-1} \text{g}^{-1}$  dry matter, 1B) in organic (open bars) and mineral horizons (closed bars) of different biomes along a south-north transect in Western Siberia. Bars represent mean values of 5 replicates  $\pm$  SE. There was no organic

horizon in the steppe. Within each figure, bars with different letters are significantly different (ANOVA, Tukey HSD,  $P < 0.05$ ). Values in bold (SE in parentheses) represent ratios of organic to mineral horizons of soil respiration (A) or gross N mineralization rates (B), respectively

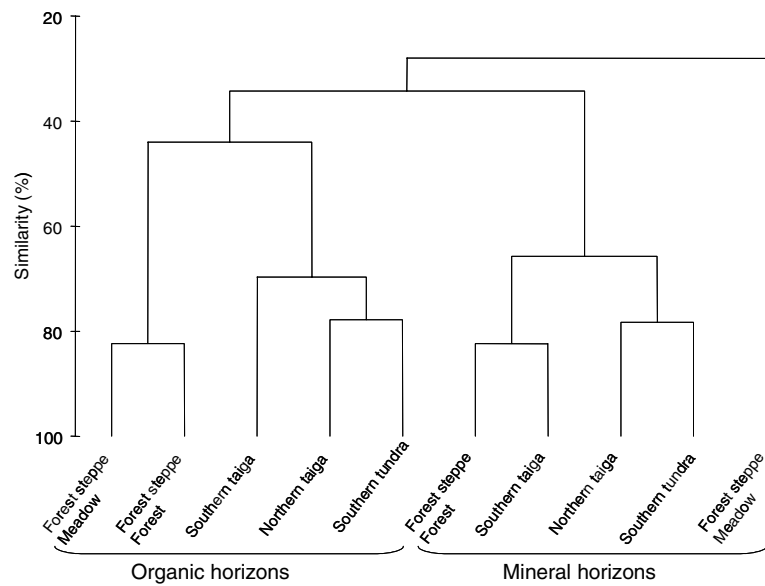
with respect to the several principal components (PC; Fig. 5). In the case of organic horizons, three components were extracted (Figs. 5A and 5B), which accounted for a total of 82.6% of the variability in the original data. PC 1 was composed of carbon-related parameters (soil total C, SOM, heterotrophic respiration) and soil water content and separated forested sites from steppe and tundra. The forest vegetation sites were separated by PC 2, which was mainly controlled by N related parameters (DIN, gross N mineralization, total N and soil C/N ratio). In the case of the mineral horizons the first three components account for 69.6% of the variability in the data (Figs. 5C and 5D). Within the mineral horizons, the tundra site was separated from the other sites by PC 2, which was composed of soil water content, C/N ratio and MAT. The underlying parameters for the separation of the other sites consisted of MAP, clay



**Fig. 2** Molar ratios of C-to-N mineralization in organic (open bars) and mineral (closed bars) horizons along a latitudinal transect in Western Siberia. Bars represent means of 5 replicates  $\pm$  SE. An asterisk (\*) indicates a significant difference at  $P < 0.05$  (ANOVA, Tukey HSD)



**Fig. 3** Similarity dendrogram (group average linking method) of the bacterial communities in the soils along the Western Siberian transect, based on the similarities (Bray–Curtis similarity) among DGGE band patterns

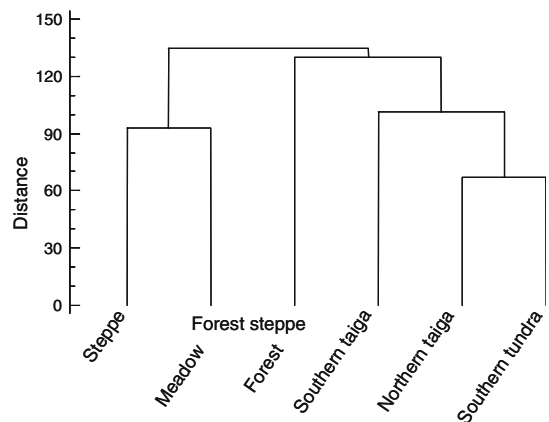


content and pH (PC 1). The PCA analysis, which is based on a multiple correlation analysis, also revealed that MAT was strongly but negatively correlated with the soils C/N ratio, both in mineral and organic horizons. We therefore conducted a univariate correlation analysis that showed that MAT was highly significantly correlated with soil C/N ratios ( $r^2 = 0.80$ ,  $P < 0.001$ , and  $0.72$ ,  $P < 0.001$  for organic and mineral horizons, respectively; data not shown).

## Discussion

Transect studies allow to elucidate and compare constraints on ecological processes at the investigated ecosystems (Steffen et al. 1999). In this study we focussed on heterotrophic respiration and gross N mineralization rates as microbial processes that are essential to ecosystem functioning. Along the 1800-km transect through Western Siberia significant differences were found in both heterotrophic respiration rates and gross nitrogen mineralization (Figs. 1, 2 and 5). Beside the ecosystem-specific constraints of microbial processes (see below for detailed discussion) several general trends along the transect became evident. In the organic soil horizons heterotrophic respiration was negatively correlated with soil water and total C content

( $r^2 = -0.58$ ,  $P < 0.001$  and  $r^2 = +0.76$ ,  $P < 0.001$ ), while gross nitrogen mineralization rates were positively correlated with temperature ( $r^2 = +0.40$ ,  $P < 0.001$ ) and negatively correlated with C/N ratios ( $r^2 = -0.42$ ,  $P < 0.001$ ; Fig. 5A). The latter indicates that vegetation cover, i.e. litter quality and input, and soil nutrient status are of utmost importance for these processes, as has also been suggested by others (Sjörgersten et al. 2003, Nadelhoffer et al. 1991, Santruckova et al. 2003). It is likely that the soil

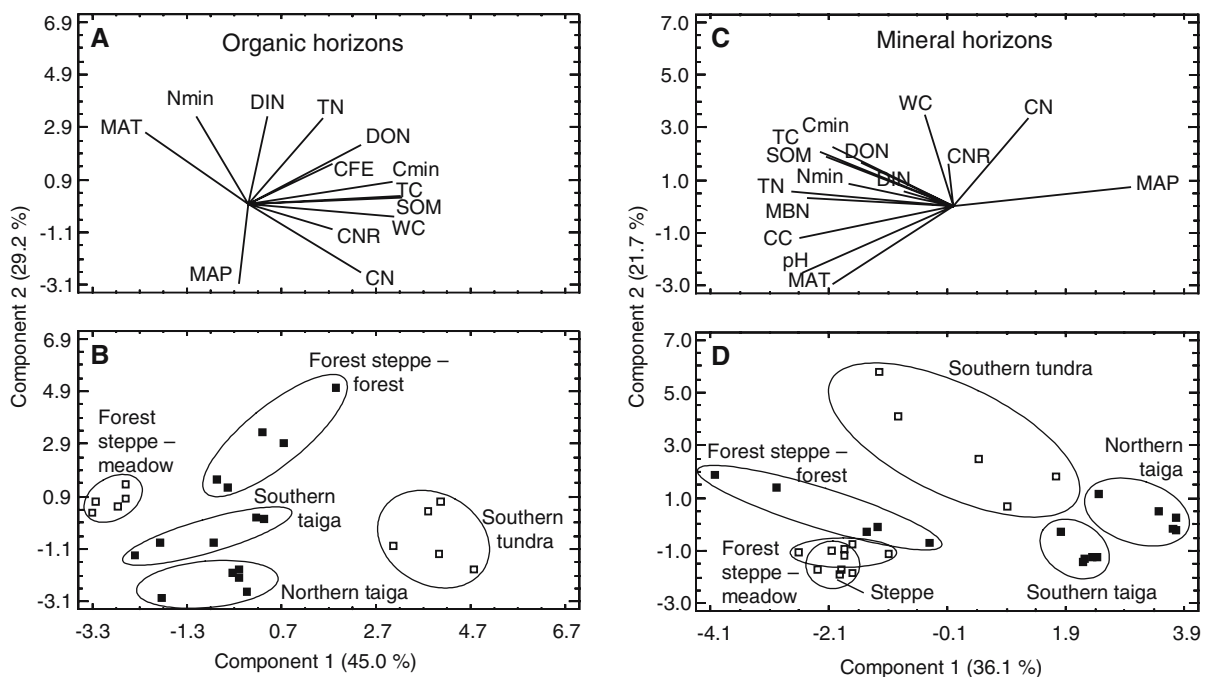


**Fig. 4** Cluster analysis (mean average, squared Euclidean) showing the similarities of the vegetation cover within the Western Siberian transect. The most abundant 61 plant species of all ecosystems were chosen for this analysis

C, N and C/N ratio is a function of the changing vegetation and the aboveground litter, as we found for example a constant increase in soil C/N ratios with litter C/N ratios (Table 3 and unpublished results).

This is consistent with our finding that the pattern of microbial composition, which is responsible for nutrient turnover, was similar to the pattern of vegetation composition along the transect in organic soils. Together, these results suggest that the patterns of soil C and N cycling were regulated by the interaction of plant community composition and their associated substrate inputs with the direct climate effects on decomposition and C accumulation. Similarly, it has been shown in a transect study along the Yenisei river in Central Siberia, that carbon transformation rates were more strongly correlated to SOC quality and soil texture (Santruckova et al. 2003).

In our study, rates of carbon and nitrogen cycling in mineral horizons were significantly correlated with MAP ( $r^2 = -0.48$ ,  $P < 0.001$  and  $r^2 = -0.35$ ,  $P < 0.001$ , respectively) but not with MAT (Fig. 5C). Although it is unchallenged that microbial processes are temperature and moisture sensitive (Schmidt et al. 2002, Lükewille and Wright, 1997, Niklinska et al. 1999), our results indicate that such processes may be constrained by other factors at least in the short-term. However, in the long-term, environmental conditions caused the soil conditions, such as organic matter composition or stoichiometry, that have been found to more directly regulate microbial activities in the short-term. Thus, several constraints may obscure the intrinsic sensitivity of decomposition to environmental conditions, but these constraints themselves may be sensitive to climate in the longer-term (Davidson and Janssens, 2006)



**Fig. 5** Principal component analysis showing the grouping of soil samples of organic (A and B) and mineral (C and D) horizons in response to vectors describing climate, soil pool and soil activity variables. The analysis was separated into two plots: a vector plot of the soil variables (A, C) and the separation of samples in response to these vectors (B, D). Open symbols represent treeless vegetation sites and closed symbols represent forested vegetation sites. MAT

(mean annual temperature), MAP (mean annual precipitation), CC (clay content), pH (pH value), WC (water content), TC (total carbon), TN (total nitrogen), CN (soil C/N ratio), DIN (dissolved inorganic nitrogen), SOM (soil organic matter), DON (dissolved organic nitrogen), MBN (microbial nitrogen),  $C_{min}$  (soil respiration),  $N_{min}$  (gross N mineralization), CNR (C-to-N mineralization ratio)

In our study physical factors such as pH values and clay content mainly controlled process rates in mineral horizons, while vegetation and climatic conditions played a more pronounced role in the determining processes in organic horizons. The differences in the constraints on microbial processes with soil depth were reflected by considerable differences in microbial community structure between the two horizons studied (Fig. 3). When looking at individual ecosystems along the transect, however, a more distinct picture of the controls on microbial processes could be developed. Heterotrophic respiration rates exhibited highest rates at the forest of the forest steppe and at the tundra, but for different reasons. In the forest of the forest steppe biome, where *Betula pendula* and *Populus tremula* dominated the vegetation, the litter quality is favourable for microbial activity compared to the taiga (Berg 2000). Tundra soils, on the other hand, are known to contain a large proportion of labile carbon (Sjörgersten et al 2003). Labile carbon as energy source may have stimulated soil respiration at warmer temperatures in early summer, when our samples were taken, as has been also reported for tundra soils in Alaska (Hobbie et al. 2002). At the remaining sites, where heterotrophic respiration was significantly lower, heterotrophic respiration might have been limited by the poor litter quality of coniferous vegetation, e.g., a high C/N ratio and high lignin content (Vance and Chapin 2001; Berg et al. 2000). Mineral horizons exhibited remarkably constant heterotrophic respiration rates along the transect and thus across a wide mean annual temperature range. This would suggest that heterotrophic respiration is not primarily controlled by temperature. However, as pointed out recently, the temperature-sensitivity of current carbon stocks strongly reflect the relative abundances of carbon substrates of different decomposability (Davidson and Janssens 2006), which may have varied strongly along the different biomes in our study.

In contrast to heterotrophic respiration, N turnover rates were significantly correlated with temperature at least in organic horizons ( $r^2 = +0.40$ ,  $P < 0.001$ ). Again, this may be due to substrate effects rather than to temperature. The lower N mineralization rates in the northern

taiga and tundra are likely to be the result of lower litter quality, higher C/N ratios and hence lower nutrient availabilities of the northern ecosystems (Table 3; Vance and Chapin 2001; Priha and Smolander 1999). Unexpectedly, gross N mineralization rates in the mineral horizons were similar to or even exceeded those in the organic horizons in the taiga and tundra. Thus, at the northern-most sites, gross N mineralization rates increased with soil depth in contrast to decreasing C mineralization rates. It has been shown that net N mineralization increased with soil depth in arctic ecosystems, which was interpreted as a decrease of microbial immobilization with depth (Nadelhoffer et al. 1991). Our results, however, suggest that an increased gross mineralization could also be the reason for such a feature.

The mineralization of organic matter was therefore spatially decoupled for nitrogen and carbon in the northern taiga and southern tundra (Fig. 2), since most of the C mineralization took place in the organic horizons, while most of the N mineralization took place in the mineral horizons. This was not only true on a soil dry matter basis, but could also be observed on an area basis (data not shown). Such observations have been reported recently for other arctic ecosystems (Kaiser et al. 2005). Our study, however, revealed that this is a special feature of tundra ecosystems, since it was only weakly pronounced in the taiga and could not be observed in the deciduous forest or meadows (Fig. 2). The low N mineralization but high C mineralization rates in the organic horizon at the northern sites of the transect may be explained by high C/N ratios at these sites. Along the transect, there was a significant inverse relationship between the soil C/N ratio and the gross N mineralization rate. Together with the high ratio of carbon-to-nitrogen mineralization this suggests that the microbial community was strongly N limited in tundra soils (Clein and Schimel 1995). If nitrogen is limiting, microorganisms may still take up organic nitrogen, but will not release ammonium to the surrounding soil (Kielland 1994, Schimel and Bennet 2004), explaining why microbial N is not lower in tundra soils compared to all other soils. Our results are compatible with the concept of a so-called “overflow mechanism”, in which microbes

exhaust a C-rich organic pool until they start to mineralize N under insufficient N supply and high C/N ratios of decomposition substrates (Weintraub and Schimel 2003; Schimel and Weintraub 2003). Our findings that N might be the main limiting factor for decomposition in northern ecosystems are consistent with several studies reporting on N limitation in boreal and tundra ecosystems (Van Cleve and Yarie 1986; Shaver and Chapin 1995; Kaiser et al. 2005).

Climate models predict that MAT and MAP in Western Siberia will increase more than the global average, especially in the north (IPCC 2001; Maxwell 1996). This may have different implications for decomposition of organic material at different latitudes. First, our results indicate that increasing temperatures along the transect may exhibit stronger effects on microbial processes of the upper soil horizons than of the mineral soils in the short-term, because the predicted atmospheric warming will affect the upper soil layers earlier and will exhibit a less pronounced effect on lower horizons, and in the longer term, since increased temperatures may change the litter quality and quantity and thus the nutrient availability for microbial decomposition processes. Second, expected changes certainly depend on the initial state of the different ecosystems: in the dry south (steppe and meadow of the forest steppe), a better water availability through increasing MAP might benefit decomposition and therefore nutrient turn over. In the N-limited ecosystems in the north (taiga and tundra), increasing temperatures may change N mineralization rates leading to enhanced N availability and plant productivity (Oechel et al. 2000). This may also lead to a change in litter quality due to changes in plant species composition, for example if the latitudinal tree-line would change. On the other hand, the organic C pools in the northern soils may be more vulnerable to decomposition than those in the south, at least in the organic soil horizons, because of their high C/N ratios, which may cause nitrogen limitation of the microbial decomposer community. A recent study in a tundra ecosystem indicated that in the longer term, increasing nitrogen availability may also lead to a loss of carbon in the mineral horizons (Mack et al. 2004). It remains unclear, however,

how changing climatic conditions may affect vegetation and microbial communities and thus, may affect ecosystem functioning. In our analysis, fewer changes in microbial community structure were detected along the 1800-km transect than within a few centimetres in the soil profile, indicating that climate change may not exhibit pronounced direct effects on microbial community structures.

**Acknowledgements** We thank Andreas Blöchl, Angelika Haslinger, Olga Pisarenko and Lena Widemann for help in the field, and Dror Minz, for help with establishment of the DGGE. We further would like to thank Wolfgang Wanek, Andreas Schindlbacher and Joshua Schimel for valuable comments on the manuscript. Special thanks to Franz Starlinger for help with the statistics. This work was supported by the Austrian Academy of Science (IGPB-25 to AR), the Austrian Federal Ministry of Education, Science and Culture and Yamburg Gaz Dobycha, Russia.

## References

- Amato M, Ladd JN (1988) Assay for microbial biomass based on ninhydrin-reactive nitrogen in extracts of fumigated soils. *Soil Biol Biochem* 20:107–114
- Arft AM, Walker MD, Gurevitch J, Alatalo JM, Bret-Harte MS, Dale M, Diemer M, Gugerli F, Henry GHR, Jones MH, Hollister RD, Jonsdottir IS, Laine K, Levesque E, Marion GM, Molau U, Molgaard P, Nordenhall U, Raszhivin V, Robinson CH, Starr G, Stenstrom A, Stenstrom M, Totland O, Turner PL, Walker LJ, Webber PJ, Welker JM, Wookey PA, Walker MD (1999) Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. *Ecol Monogr* 69(4):491–511
- Barrett JE, Burke IC (2000) Mineral nutrition, substratum ecology and pollution. *Soil Biol Biochem* 32:1707–1716
- Bazilevich NI (1993) Biological productivity of ecosystems of Northern Europe. Nauka Publisher, Moscow
- Berg B (2000) Litter decomposition and organic matter turnover in northern forest soils. *Forest Ecol Manage* 133:13–22
- Berg B, Johansson MB, Meentemeyer V (2000) Litter decomposition in a transect of Norway spruce forests: substrate quality and climate control. *Can J Forest Res-Revue Canadienne De Recherche Forestiere* 30(7):1136–1147
- Clein JS, Schimel JP (1995) Nitrogen turnover and availability during succession from alder to poplar in Alaskan taiga forests. *Soil Biol Biochem* 27(6):743–752
- Davidson EA, Janssens IA (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440(9):165–173

- Hobbie SE, Miley TA, Weiss MS (2002) Carbon and nitrogen cycling in soils from acidic and nonacidic tundra with different glacial histories in Northern Alaska. *Ecosystems* 5(8):761–774
- IPCC (2001) Climate change 2001: Working Group I: The Scientific Basis. University Press, Cambridge
- Janse I, Bok J, Zwart G (2004) A simple remedy against artifactual double bands in denaturing gradient gel electrophoresis. *J Microbiol Methods* (57):279–281
- Jonasson S, Michelsen A, Schmidt IK (1999) Coupling of nutrient cycling and carbon dynamics in the arctic, integration of soil microbial and plant processes. *Appl Soil Ecol* 11:135–146
- Jonasson S, Chapin FS, Shaver G (2001) Biogeochemistry in the Arctic: patterns, processes, and controls. In: Schulze E, Heimann M, Harrison S, Holland E, Lloyd J, Prentice IC, Schimel J (eds) Global biogeochemical cycles in the climate system. Academic Press/Max-Planck-Institute for Biogeochemistry, Jena, Germany, pp 139–150
- Kaiser C, Meyer H, Biasi C, Rusalimova O, Barsukov P, Richter A (2005) Storage and mineralization of carbon and nitrogen in soils of a frost-boil tundra ecosystem in Siberia. *Appl Soil Ecol* 29(2):173–183
- Kandeler E, Gerber H (1988) Short-term assay of soil urease activity using colorimetric determination of ammonium. *Biol Fertil Soils* 6:68–72
- Kielland K (1994) Amino acid absorption by arctic plants: implications for plant nutrition and nitrogen cycling. *Ecology* 75:2373–2383
- Lükewille A, Wright RF (1997) Experimentally increased soil temperature causes release of nitrogen at a boreal forest catchment in southern Norway. *Global Change Biol* 3(1):13–21
- Mack MC, Schuur EAG, Bret-Harte MS, Shaver GR, Chapin III FS (2004) Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. *Nature* 431:440–443
- Maxwell B (1996) Recent climate patterns in the Arctic. In: Oechel WC, Callahan T, Gilmanov T, Holten JJ, Maxwell B, Molau U, Sveinbjörnsson B (eds) Global change and arctic terrestrial ecosystems. Springer, New York, pp 21–46
- Muyzer G, de Waal EC, Uitterlinden AG (1993) Profiling of complex microbial populations by denaturing gradient gel electrophoresis analysis of polymerase chain reaction-amplified genes coding for 16S rRNA. *Appl Environ Microbiol* 59:695–700
- Muyzer G, Hottenträger S, Teske A, Waver C (1995) Denaturing gradient gel electrophoresis of PCR-amplified 16S rDNA – a new molecular approach to analyse the genetic diversity of mixed microbial communities. In: Akkermans ADL, van Elsas JD, de Bruijn FJ (eds) Molecular microbial ecology manual 3.4.4. Kluwer Academic Publishers, Dordrecht, pp 1–23
- Myrold DD, Tiedje JM (1986) Simultaneous estimation of several nitrogen cycle rates using  $^{15}\text{N}$ : theory and application. *Soil Biol Biochem* 18:661–665
- Nadelhoffer KJ, Giblin AE, Shaver GR, Laundre JA (1991) Effects of temperature and substrate quality on element mineralization in six arctic soils. *Ecology* 72(1):242–253
- Niklinska M, Maryanski M, Laskowski R (1999) Effect of temperature on humus respiration rate and nitrogen mineralization: implications for global climate change. *Biogeochemistry* 44:239–257
- Oechel WC, Hastings SJ, Vourlitis GL, Jenkins M, Riechers G, Grulke N (1993) Recent change of arctic tundra ecosystems from a net carbon dioxide sink to a source. *Nature* 361:520–523
- Oechel WC, Vourlitis GL, Hastings SJ, Zulueta RC, Hinzman L, Kane D (2000) Acclimation of ecosystem  $\text{CO}_2$  exchange in the Alaskan Arctic in response to decadal climate warming. *Nature* 406:978–981
- Öhlinger R (1995) Soil respiration by titration. In: Schinner F, Öhlinger R, Kandeler E, Margesin R (eds) Methods in soil biology. Springer, Berlin, Heidelberg, New York, pp 95–98
- Peterjohn WT, Melillo J, Steudler P, Newkirk KM, Bowles FP, Aber JD (1994) Responses of trace gas fluxes and N availability to experimentally elevated soil temperatures. *Ecol Appl* 4:617–625
- Priha O, Smolander A (1999) Nitrogen transformations in soil under *Pinus sylvestris*, *Picea abies* and *Betula pendula* at two forest sites. *Soil Biol Biochem* 31:965–977
- Santruckova H, Bird MI, Kalaschnikov YN, Grund M, Elhottova D, Simek M, Grigoryev S, Gleixner G, Arneth A, Schulze ED, Lloyd J (2003) Microbial characteristics of soils on a latitudinal transect in Siberia. *Global Change Biol* 9:1106–1117
- Schimel JP, Jackson LE, Firestone MK (1986) Spatial and temporal effects on plant-microbial competition for inorganic nitrogen in a California annual grassland. *Soil Biol Biochem* 21:1059–1066
- Schimel JP, Weintraub MN (2003) The implications of exoenzyme activity on microbial carbon and nitrogen limitation in soil: a theoretical model. *Soil Biol Biochem* 35:549–563
- Schimel JP, Bennet J (2004) Nitrogen mineralization: challenges of a changing paradigm. *Ecology* 85(3):591–602
- Schmidt IK, Jonasson S, Shaver GR, Michelsen A, Nordin A (2002) Mineralization and distribution of nutrients in plants and microbes in four arctic ecosystems: responses to warming. *Plant Soil* 242:93–106
- Shaver GR, Chapin III FS (1995) Long-term responses to factorial NPK fertilizer treatment by Alaskan wet and moist tundra sedge species. *Ecography* 18:259–275
- Shaver GR, Canadell J, Chapin FS, Gurevitch J, Harte J, Henry G, Ineson P, Jonasson S, Melillo J, Pitelka L, Rustad L (2000) Global warming and terrestrial ecosystems: a conceptual framework for analysis. *Bioscience* 50(10):871–882
- Shaw RM, Harte J (2001) Response of nitrogen cycling to simulated climate change: differential responses along a subalpine ecotone. *Global Change Biol* 7:193–210

- Sjögersten S, Turner BL, Mahieu N, Condron LM, Wooley PA (2003) Soil organic matter biochemistry and potential susceptibility to climatic change across the forest-tundra ecotone in the Fennoscandian mountains. *Global Change Biol* 9(5):759–772
- Sollins P, Glassman C, Paul EA, Swantson C, Lajtha K, Heil JW, Elliott ET (1999) Soil carbon and nitrogen. Pools and fractions. In: Robertson GP, Coleman DC, Bledsoe CS, Sollins P (eds) *Standard soil methods for long-term ecological research*. Oxford University Press, Oxford, pp 89–105
- Steffen WL, Scholes MC, Valentin C, Zhang X, Menaut J-C, Schulze ED (1999) The IGBP terrestrial transects. In: Walker B, Steffen WL, Canadell J, Ingram J (eds) *The terrestrial biosphere and global change. Implications for natural and managed ecosystems*. Cambridge University Press, Cambridge, pp 66–87
- Stolbovoi V, McCallum I (2002) *Land resources of Russia* (CD). International Institute for Applied Systems Analysis and the Russian Academy of Science, Laxenburg, Austria
- Swift MJ, Heal O-W, Anderson JM (1979). *Decomposition in terrestrial ecosystems*. Blackwell, Oxford
- Van Cleve K, Yarie J (1986). Interaction of temperature, moisture and soil chemistry in controlling nutrient cycling and ecosystem development in the Taiga of Alaska. In: Van Cleve K, Chapin III FS, Flanagan PW, Viereck LA, Dyrness CT (eds) *Forest ecosystems in the Alaskan Taiga, ecological studies*. Springer, New York, pp 160–189
- Vance ED, Chapin FS (2001) Substrate limitations to microbial activity in taiga forest floors. *Soil Biol Biochem* 33:173–188
- Weintraub MN, Schimel JP (2003) Interactions between carbon and nitrogen mineralization and soil organic matter chemistry in arctic tundra soils. *Ecosystems* 6(2):129–143