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Mona N. Högberg · David D. Myrold · Reiner Giesler
Peter Högberg

Contrasting patterns of soil N-cycling in model ecosystems of Fennoscandian boreal forests

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Abstract The low plant productivity of boreal forests in general has been attributed to low soil N supply and low temperatures. Exceptionally high productivity occurs in toe-slope positions, and has been ascribed to influx of N from surrounding areas and higher rates of soil N turnover in situ. Despite large apparent natural variations in forest productivity, rates of gross soil N mineralization and gross nitrification have never been compared in Fennoscandian boreal forests of contrasting productivity. We report contrasting patterns of soil N turnover in three model ecosystems, representing the range in soil C-to-N ratios (19–41) in Fennoscandian boreal forests and differences in forest productivity by a factor close to 3. Gross N mineralization was seven times higher when soil, microbial, and plant C-to-N ratios were the lowest compared to the highest. This process, nitrification and potential denitrification correlated with inorganic, total and microbial biomass N, but not microbial C. There was a constant ratio between soil and microbial C-to-N ratio of 3.7 ± 0.2, across wide ratios of soil C-to-N and fungi-to-bacteria. Soil N-cycling should be controlled by the supplies of C and N to the microbes. In accordance with plant allocation theory, we discuss the possibility that the high fungal biomass at high soil C-to-N ratio reflects a particularly high supply of plant photosynthates, substrates of high-quality C, to mycorrhizal fungi. Methods to study soil N turnover and N retention should be developed to take into account the impact of mycorrhizal fungi on soil N-cycling.

Keywords C-to-N stoichiometry · Forest productivity · Gross N turnover · Mycorrhizal fungi

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M. N. Högberg (✉) · R. Giesler · P. Högberg
Department of Forest Ecology,
Swedish University of Agricultural Sciences,
SLU, 901 83 Umeå, Sweden
E-mail: mona.n.hogberg@sek.slu.se

D. D. Myrold
Department of Crop and Soil Science, Oregon State University,
Corvallis, OR 97331, USA

Present address: R. Giesler
Climate Impact Research Centre,
Department of Ecology and Environmental Science,
Umeå University, 901 87 Umeå, Sweden

Introduction

In Fennoscandian boreal landscapes, there are regular variations in vegetation composition and forest productivity (e.g., Cajander 1926; Hägglund and Lundmark 1977). Regional surveys have shown that these correlate with N concentration and base saturation of the forest floor (Dahl et al. 1967; Lahti and Väisänen 1987). The former agrees with observations of increased forest growth in boreal forests after N additions (Tamm 1991). At the landscape scale, the variations in soil properties, plant species composition, and productivity are strongly related to hill-slope hydrochemistry; large variations can be found within short (< 100 m) distances (Högberg et al. 1990; Giesler et al. 1998; Högberg 2001).

Traditionally, nitrogen supply has been assessed by studies of soil net N mineralization under standardized laboratory conditions (e.g., Jansson and Persson 1982) or in the field (Eno 1960; Binkley and Hart 1989). However, many studies of high-latitude forest soils have seen no net N mineralization or net nitrification during the first months of incubation (e.g., Nadelhoffer et al. 1984; Davidson et al. 1992; Stark and Hart 1997). Some studies, e.g., Chapin et al. (1988) found net N mineralization rates below estimates of plant uptake. This prompted measurements of gross N mineralization and nitrification rates (e.g., Davidson et al. 1991, 1992; Hart et al. 1994a; Stark and Hart 1997; Fisk and Fahey 2001; Carmosini et al. 2002; Merilä et al. 2002). The finding of discrepancies between net N mineralization and plant N uptake also stimulated research on uptake of organic N sources (Chapin et al. 1993; Kielland 1994; Näsholm et al. 1998).

The N availability in soils and above-ground production have for a long time been known to be negatively related to the C-to-N ratio of forest litter (e.g., Vitousek et al. 1982; Pastor et al. 1984). Commonly, a C-to-N ratio of 20 of decomposing materials is regarded as the threshold, below which net N mineralization occurs (e.g., Swift et al. 1979; Myrold 1999). However, Tate (1995) suggests a C-to-N ratio of 30 as the threshold, and Prescott et al. (2000) found net N mineralization in a laboratory study in soils with C-to-N ratios of 34–36. Thus, there may be more complex interrelations between the soil N availability and the availabilities of C and N to soil microorganisms. A recent analysis of controls on gross N-cycling rates in a wide range of terrestrial systems found gross N mineralization to be positively correlated with microbial biomass and soil C and N concentrations, whereas the soil C-to-N ratio exerted a negative effect on mineralization only after adjusting for differences in soil C concentration (Booth et al. 2005).

In a recent conceptual model, Schimel and Bennett (2004) highlight depolymerization of N-containing polymers by microbial (including mycorrhizal) extracellular enzymes, as the critical point in the N-cycle. They described a gradient from low to high N availability. At the poor end, both plants and microbes are supposed to be N-limited and N mineralization does not occur as plants and microbes take up organic N. Towards the rich end, N supply increasingly satisfy the N demands of both plants and microbes; the latter are then C-limited. Hence, more and more N is mineralized and ultimately NH_4^+ is produced in excess, supporting the process of autotrophic nitrification. In another model, Read (1986, 1991) described regular variations among soil conditions, plant community composition, and mycorrhizal associations across latitudinal and altitudinal transects from Arctic or alpine conditions through boreal, and nemoral forests to dry steppe. According to Read this sequence starts with ericoid and ectomycorrhizal associations in ecosystems, where organic N sources predominate, and ends in arbuscular mycorrhizal grasslands, where NO_3^- is the dominant plant N source. Read's model parallels Schimel and Bennett's, which does not acknowledge differences between types of mycorrhiza. We have pointed out that the sequence of mycorrhizal associations identified by Read (1986, 1991) occurs also within short distances along soil N supply gradients in boreal forest landscapes (Högberg et al. 1990, 2003; Giesler et al. 1998). In Fennoscandian coniferous forest soils there is a large contribution by fungi (Söderström 1979; Finlay and Söderström 1989; Frostegård 1996; Pennanen et al. 1999; Högberg et al. 2003), notably ectomycorrhizal fungi (Romell 1935, 1938). The ectomycorrhizal mycelium receives a high-quality C substrate, photosynthates, directly from the plant host (Rygiewicz and Andersen 1994; Smith and Read 1997; Högberg and Högberg 2002), which gives it a unique position within the microbial community in nutrient-poor ecosystems, where other microorganisms are mainly dependent on litter of low quality (high C-to-N ratio). However, trees decrease their C allocation to roots and mycorrhizal fungi when the N supply is high (e.g., Nylund 1988; Wallander and Nylund 1992; Wallenda et al. 1996; Wallenda and Kottke 1998), in accordance with plant allocation theory (Cannell and Dewar 1994; Waring and Running 1998). We thus hypothesized (Högberg et al. 2003) that low soil N supply, and hence low plant productivity and litter C supply to saprotrophs, is associated with a high plant photosynthate supply to mycorrhizal fungi, whereas the reverse occurs under high N supply.

In view of the many observations of the regulatory role of C supply to microbes on soil N turnover (e.g., Swift et al. 1979; Hart et al. 1994a; Kaye and Hart 1997; Schimel and Bennett 2004; Booth et al. 2005), a close re-examination of the interaction between C and N turnover in forest soils is warranted. We have previously studied in great detail soil N supply, microbial community structure, plant community structure and forest productivity across a gradient through three contiguous coniferous forest types (Högberg et al. 1990; Giesler et al. 1998; Nordin et al. 2001; Högberg et al. 2003; Nilsson et al. 2005). Because these encompass the variations in important factors such as soil pH, base saturation, and soil N concentration (and thus C-to-N ratios) found across coniferous Fennoscandian boreal forests (e.g, Dahl et al. 1967; Lahti and Väisänen 1987), we use them as models for similar boreal forests in Fennoscandia. They range from a poor forest with very high C-to-N ratio, where organic N forms dominate among N forms in the soil solution, through a forest with intermediate soil C-to-N ratio, where organic and inorganic N contribute equally, to a highly productive forest with low C-to-N ratio and a dominance of inorganic N species, especially NO_3^- (Nordin et al. 2001). These model ecosystems have very strong bearings on the conceptual models of N-cycling proposed by Schimel and Bennett (2004), and the parallel sequence of mycorrhizal associations described by Read (1986, 1991).

Here, we provide a first description of the relations between soil N transformations and soil properties, notably the C-to-N ratio in soil and in microorganisms, in Fennoscandian coniferous boreal forests of contrasting forest productivity. Using studies of gross and net N transformations and potential denitrification capacity, we demonstrate remarkably contrasting patterns of soil N turnover, which tally with previous reports on differences in plant N source use in these systems (Högberg et al. 1990; Giesler et al. 1998; Nordin et al. 2001).

Materials and methods

Study area

The study area is situated at Betsele in the Umeå River Valley, northern Sweden (64°39′N, 18°30′E, 235 m

above sea level). The slope in this area is only 2 m per 100 m. Mean annual temperature and precipitation are 1.0°C and 570 mm, respectively. On average, the site is covered by snow from late October until early May. Plant growth starts in mid-May. Three contiguous forest types have been identified (Table 1), a dwarf shrub (DS), a short herb (SH), and a tall herb (TH) type (Giesler et al. 1998). A 90-m-long transect through these forest types encompasses the range in soil pH and N concentration, and plant production and community composition in Fennoscandian boreal forests (Giesler et al. 1998). Relations between plants and soils (Högberg et al. 1990; Giesler et al. 1998, 2002; Nordin et al. 2001; Högberg 2001) and among plants, microbes, and soils have been described in detail previously (Högberg et al. 2003; Nilsson et al. 2005). Some important forest floor (mor-layer) characteristics of the different forest types are summarized in Table 2. The soil in the entire area is a sandy till with many boulders. It is classified as a Haplic Podzol (FAO 1988).

The low productive DS forest is an open c. 130-year-old *Pinus sylvestris* forest with a site height index H_{100} of 17 m, and is located in a groundwater recharge area (Table 1). The intermediate SH forest is a dense *Picea abies* forest of similar age with H_{100} of 28 m; here, several short herbs are abundant (Table 1). The highly productive TH type is in a discharge area, dominated by *P. abies*. Here, there is a glade developing after tree falls. The tallest *Picea* tree adjacent to the glade is 36 m. Groundwater discharge in the TH forest type occurs not only for a few weeks during snowmelt, but also under unusually wet conditions in summer and autumn. The groundwater level may rise and fall several decimeters in a day. Through most of the summer the water table is >0.7 m below the surface. Sampling was not conducted during or shortly after discharge events. Across the gradient, forest stem wood productivity increases from 2.9 to 8.0 m^3 ha^{-1} $year^{-1}$ (Högberg et al. 2003).

Gross and net rates of N-cycling

Thrice during the growing season of 1997, 17 June, 4 August, and 27 September, gross rates of N mineralization and nitrification were determined. Three square 225-m^2 plots were laid out to represent the DS, SH, and TH forest types, respectively. Within each of these plots, five square 0.25-m^2 sub-plots were randomly distributed. Between 6 and 14 samples of the organic mor-layer the F + H horizons, (approximately corresponding to Oe + Oa) were taken (core diameter 0.1 m) at each sub-plot and bulked into five composite samples per plot. Roots were carefully sorted out. The remaining soil was gently mixed and soil equivalent to ~25 g dry matter (d.m.) was put into plastic bags. A total of 3.5 ml of 98 atom% $^{15}NH_4Cl$ or $Na^{15}NO_3$ (Cambridge Isotope Laboratories Inc. Andover, 01810 MA, USA) was dispersed slowly into each soil sample by three separate injections using a syringe. This addition of water increased the water content of all sub-samples by ~7% above field-moist condition. The ^{15}N-enriched solution contained 15 mg N l^{-1}; the amount injected corresponded to 2.1 ± 0.3 μg N g^{-1} dry organic matter (o.m). Within 30 s after injection (time zero = t_0), 125 ml 2 M KCl was added to

Table 1 Plant species composition and mycorrhizal associations in three model forest ecosystems along the forest productivity gradient at Betsele

Forest type		
Dwarf shrub	Short herb	Tall herb
Plants		
Pinus sylvestris	**Picea abies**	**P. abies**
Picea abies	*Betula pubescens*	*Aconitum septentrionale*
Betula pubescens	*Maianthemum bifolium Solidágo virgaurea*	*Rubus idaeus*
Empetrum hermaphroditum Vaccinium myrtillus	*Galium trifolium Gymnocarpium dryopteris*	*Actaea spicata*
V. vitis-idaea	*Oxalis acetosella*	*Galium trifolium*
Linnea borealis	*Rubus idaeus*	*Gymnocarpium dryopteris*
	Aconitum septentrionale	*Oxalis acetosella*
	Actaea spicata	
	Linnea borealis	
	V. vitis-idaea	
Dominant mycorrhiza type		
ECM (EM understorey)	ECM (AM understorey)	ECM (AM understorey)
Relative abundance ECM + EM[a]		
100	23	25

Dominant tree species are in bold type. Forest type classification follows Hägglund and Lundmark (1977). Nomenclature of plants follows Tutin et al. (1964). *ECM* Ectomycorrhiza, *EM* ericoid, and *AM* arbuscular mycorrhiza

[a]Abundance of ECM + EM is based on figures on loss of the general fungal biomarker phospholipid fatty acid (PLFA) 18:2ω6,9 originating from ECM + EM extramatrical mycelia during incubation (6 month, 20°C) of soil in the laboratory (Nilsson et al. 2005) Calculated relative abundance of ECM + EM extramatrical mycelia is presented. The abundance of ECM + EM fungal biomarker in the dwarf-shrub forest type was set to 100%. Figures are recalculated from per g dry soil in the original article (Nilsson et al. 2005) to per m^2 by using data in Table 2

Table 2 Summary of selected plant foliar and soil (mor-layer) properties in three forest ecosystems along the forest productivity gradient at Betsele. Foliar C-to-N represents the mean values among species listed in Table 1. Values are means ± 1 SE. Values within a row followed by a different symbols are significantly different (Kruskal-Wallis one-way ANOVA on ranks, $P < 0.05$)

Properties	Forest type		
	Dwarf shrub	Short herb	Tall herb
Plant			
Foliar C-to-N ratio	$46.5^{\dagger} \pm 8.0$	$27.2^{\dagger} \pm 2.6$	$16.6^{\ddagger} \pm 0.2$
Soil			
Chemical			
Organic matter (kg m^{-2})	$2.6^{\dagger} \pm 0.3$	$2.3^{\dagger} \pm 0.2$	$4.6^{\ddagger} \pm 1.0$
Organic matter (g kg^{-1} d.m.)	$910.0^{\dagger} \pm 0.7$	$710.0^{\ddagger} \pm 2.1$	$495.6^{\S} \pm 2.0$
C (g kg^{-1} d.m.)	$446.1^{\dagger} \pm 15.2$	$395.0^{\ddagger} \pm 15.9$	$293.4^{\ddagger} \pm 18.8$
N (g kg^{-1} d.m.)	$11.1^{\dagger} \pm 0.4$	$16.1^{\ddagger} \pm 0.5$	$15.9^{\ddagger} \pm 0.1$
C-to-N ratio	$40.8^{\dagger} \pm 1.2$	$24.5^{\ddagger} \pm 0.5$	$18.8^{\S} \pm 0.9$
NH_4^+ -N (mg kg^{-1} o.m.)	$11.5^{\dagger} \pm 2.3$	$26.3^{\ddagger} \pm 6.1$	$42.3^{\ddagger} \pm 12.5$
NO_3^- -N (mg kg^{-1} o.m.)	$3.2^{\dagger} \pm 0.5$	$11.6^{\dagger,\ddagger} \pm 4.2$	$24.2^{\ddagger} \pm 5.0$
Total C (kg m^{-2})	$1.3^{\dagger} \pm 0.0$	$1.3^{\dagger} \pm 0.1$	$2.7^{\ddagger} \pm 0.2$
Total N (g m^{-2})	$31.2^{\dagger} \pm 1.0$	$52.9^{\ddagger} \pm 1.9$	$147.2^{\S} \pm 9.4$
Water (%)	$225.6^{\dagger} \pm 24.8$	$196.2^{\dagger} \pm 10.9$	$226.3^{\dagger} \pm 20.1$
$pH_{soil\ solution}$	$3.8^{\dagger} \pm 0.0$	$4.9^{\ddagger} \pm 0.2$	$6.4^{\S} \pm 0.1$
Microbiological			
Microbial C (mg g^{-1} o.m.)	$10.9^{\dagger} \pm 2.2$	$10.2^{\dagger} \pm 3.5$	$11.0^{\dagger} \pm 3.5$
Microbial N (mg g^{-1} o.m.)	$0.9^{\dagger} \pm 0.1$	$1.4^{\dagger} \pm 0.3$	$2.3^{\ddagger} \pm 0.1$
Microbial C-to-N ratio	$11.7^{\dagger} \pm 2.0$	$6.9^{\ddagger} \pm 1.6$	$4.8^{\ddagger} \pm 1.3$
Fungal biomarker (mol %)[a]	$14.8^{\dagger} \pm 1.5$	$8.8^{\ddagger} \pm 0.3$	$0.9^{\S} \pm 0.1$
Fungi-to-bacteria ratio[b]	$0.44^{\dagger} \pm 0.10$	$0.18^{\ddagger} \pm 0.02$	$0.02^{\S} \pm 0.00$
DEA (ng N g^{-1} o.m. h^{-1})[c]	$15^{\dagger} \pm 2$	$325^{\ddagger} \pm 125$	$7{,}465^{\S} \pm 836$

Numbers of plant species sampled were 7, 12, and 6 in the dwarf shrub, short herb, and tall herb forest, respectively. Organic matter (o.m.) content of mor-layer, defined as % loss of dry matter (d.m.) after ignition of dried soil (105°C, 24 h; 600°C, 4 h) ($n = 10$). Total soil C and N data ($n = 24$). Seasonal means are shown for NH_4-N, NO_3-N (t_0 extractions) and microbial C and N data. Microbiological data (except DEA) and plant-soil chemistry data are reported in Högberg et al. (2003), and Giesler et al. (1998), respectively. Data on microbial C and N are from the soil samples analyzed in this paper

[a]Amount of fungal biomarker PLFA 18:2ω6,9 in % of mol total microbial PLFAs in F-horizon

[b]The ratio between fungal biomarker PLFA 18:2ω6,9 and defined bacterial PLFA biomarkers in soil

[c]Potential denitrification enzyme activity

one of two sub-samples of each of the five samples per plot. Samples and the extractant were gently mixed by hand at intervals during the 1-h extraction time. The parallel sub-sample, t_{24}, was placed in O_2-permeable polyethylene bags (Eno 1960) and incubated in the field under the mor-layer in the forest type, from which the soil was sampled, for 24 h before extraction. Short-term net N mineralization after 24 h (Stark and Hart 1997), was calculated as the difference in the sum of NH_4^+ and NO_3^- between the t_{24} and the t_0 extracts, (Fisk et al. 1998). Long-term net N mineralization and net nitrification rates were determined in soil equivalent to 25 g d.m. in plastic bags and incubated in the field beneath the mor-layer between 17 June and 4 August (46 days) and between 4 August and 27 September 1997 (54 days). Long-term N net mineralization rate is the change in pool size of NH_4^+ plus NO_3^-. Net nitrification is the change in the pool size of NO_3^- (Sörensen and Jensen 1991; Stark and Hart 1996).

Calculations

It is unclear how fast the disruption of the fungal mycelium during soil sampling affects its N uptake, and hence ^{15}N pool dilution calculations. Söderström and Read (1987) severed mycorrhizal mycelium in laboratory mesocosms and found that the mycorrhizal mycelium, which contributed 30% of the soil respiratory activity, lost more than 50% of its activity within 24 h, i.e., the time of a ^{15}N pool dilution study. However, plant roots in the field, and their fungal symbionts, may contain considerably more non-structural C. In a storage study of a boreal forest soil, Söderström (1979) found no decline in the active fungal mycelium during 48 h. We thus assume that the fungal mycelium behaved as if in the undisturbed soil during the 24 h of incubation.

Gross N mineralization, NH_4^+ immobilization, gross nitrification, and NO_3^- immobilization rates were calculated using equations of Kirkham and Bartholomew (1954) as formulated by Davidson et al. (1991). The term immobilization, as used in the original article, is here replaced by consumption and refers to the sum of all consumptive processes of the labeled pool, i.e., consumption of NH_4^+ includes microbial assimilation, NH_3 volatilization, leaching, and nitrification. Consumption of NO_3^- may include microbial assimilation, leaching, denitrification, and dissimilatory reduction (Davidson et al. 1990, 1991; Hart 1994b). We labeled the product pools (i.e., NH_4^+ for mineralization or NO_3^- for nitrification) and analyzed the soil NH_4^+ and NO_3^- pools

separately. Determination of the fraction of ^{15}N injected that was recovered from the samples extracted at t_0 was made using the following equation, modified from Hart et al. (1994b):

$$\text{Recovery}(\%) = 100 \times [^{15}\text{N excess}(\mu\text{g g}^{-1}\text{o.m.}) \times \text{soil(g o.m.)}/^{15}\text{N injected}(\mu\text{g})].$$

We normalized N transformation data to amount of organic matter, because it is the organic matter, not the mineral soil, that is the source of N mineralized and nitrified (Pastor et al. 1984).

Potential denitrification enzyme activity

On 26 May 1995, mor-layer soil was sampled at every 10 m along the gradient. In the laboratory, 10 g of root-free fresh soil from each position and 80 ml solution consisting of 1 mM glucose, 1 mM KNO_3, and 200 mg chloramphenicol l^{-1} was added to a 125-ml serum bottle, which was sealed, evacuated, flushed with N_2, and filled with 10% acetylene. Samples were shaken continuously. Gas samples were taken at 0, 0.5, 1.0, and 1.5 h and analyzed for N_2O on a gas chromatograph with an electron capture detector. Total N_2O concentration was calculated including N_2O dissolved in the solution, using a Bunsen coefficient of 0.632 (Tiedje 1982).

C-to-N ratios

In each of the three forest types, 24 soil samples were taken within 100-m^2 plots ($n = 24$). The mor-layer soil was sampled (core diameter 44 mm), down to the mineral soil, in the DS, SH, and in the TH forest. Roots (> 1 mm) were sorted out by hand and the soil was dried (70°C, 72 h). Microbial biomass C and N were determined by the fumigation-extraction technique (Högberg et al. 2003) on 17 June, 4 August, and 27 September 1997 on 10 g (ww) of sub-samples of the root-free bulk soil samples used for estimation of gross N mineralization. For comparisons with plant foliar C-to-N ratios we used data from the same plots (Giesler et al. 1998).

C and N analysis

Salt extracts were analyzed for NH_4^+ and NO_3^- colorimetrically using a flow injection analyzer (FIAstar, FOSS TECATOR, Höganäs, Sweden). Dried soil and plant samples and filter discs from the diffusion procedure were analyzed for C% and N%, and ^{15}N, respectively, using a CN analyzer coupled to an isotope ratio mass spectrometer (Ohlsson and Wallmark 1999).

Statistics

We used two-way analysis of variance (ANOVA) to test for differences in N turnover between the three model forest ecosystems and the three sampling occasions. For multiple comparisons Tukey's test was performed using the statistical software SigmaStat 3.0.1 (SPSS Science, Chicago, IL, USA). Within forest types, averages ($n = 5$) from the three forest types and from the three sampling occasions were used for statistical analyses of gross and net N mineralization, NH_4^+ consumption, and recovery of $^{15}NH_4^+$. Temporal variation in gross N turnover in each forest type was tested with Kruskal–Wallis one-way ANOVAs on ranks, with month as a single factor. When a significant ($P < 0.05$) effect of sampling date was found, a Tukey multiple comparisons test followed the ANOVA. Gross and net rates of nitrification, NO_3^- consumption, and recovery of $^{15}NO_3^-$ could be determined in the TH forest type only; comparisons were made between dates of sampling. In the DS and the SH forest type, NO_3^- pool sizes were lower than required to get reliable data on gross rates. Spearman rank order correlation test was used to identify significant correlations. Results are presented as mean ± 1 SE.

Results

Gross N mineralization, N consumption, short- and long-term net N mineralization

Seasonal means of gross NH_4-N mineralization rate were 12.8 ± 3.5, 48.8 ± 14.4, and 93.3 ± 23.7 μg g^{-1} o.m. day^{-1} in the DS, SH, and TH forest types, respectively (Fig. 1a, means per m^2 are found in Table 3). The corresponding NH_4^+ consumption rates were 15.6 ± 3.1, 55.7 ± 15.1, and 76.1 ± 30.3 μg NH_4^+-N g^{-1} o.m. day^{-1}, respectively. Although gross N mineralization and NH_4^+ consumption thus increased along the gradient, only the DS and TH types differed significantly in gross N mineralization per gram o.m. ($P = 0.019$). When calculated per area also SH differed from the TH forest type ($P = 0.015$). Temporal variation in gross N mineralization and NH_4^+ consumption was found in the SH ($P = 0.011$ and $P = 0.017$, respectively) and TH ($P = 0.021$ and $P = 0.004$, respectively) forests only, with highest rates in August (Fig. 1a).

Short-term net N mineralization was negative in the DS and SH forest types, but positive and significant in the TH forest type (Table 3). Seasonal long-term net N mineralization rates were 0.0 ± 0.1, 2.6 ± 0.4, and 13.8 ± 3.1 μg NH_4^+-N g^{-1} o.m. day^{-1} in the DS, SH, and TH forest types, respectively. Long-term net N mineralization rate did not vary with season.

Gross nitrification, nitrate consumption, short- and long-term net nitrification

In the DS and the SH forest types pools of NO_3^- were too small in relation to the tracer added. Hence, the basic assumption of no major change in pool size was violated and, additionally, accurate determination of

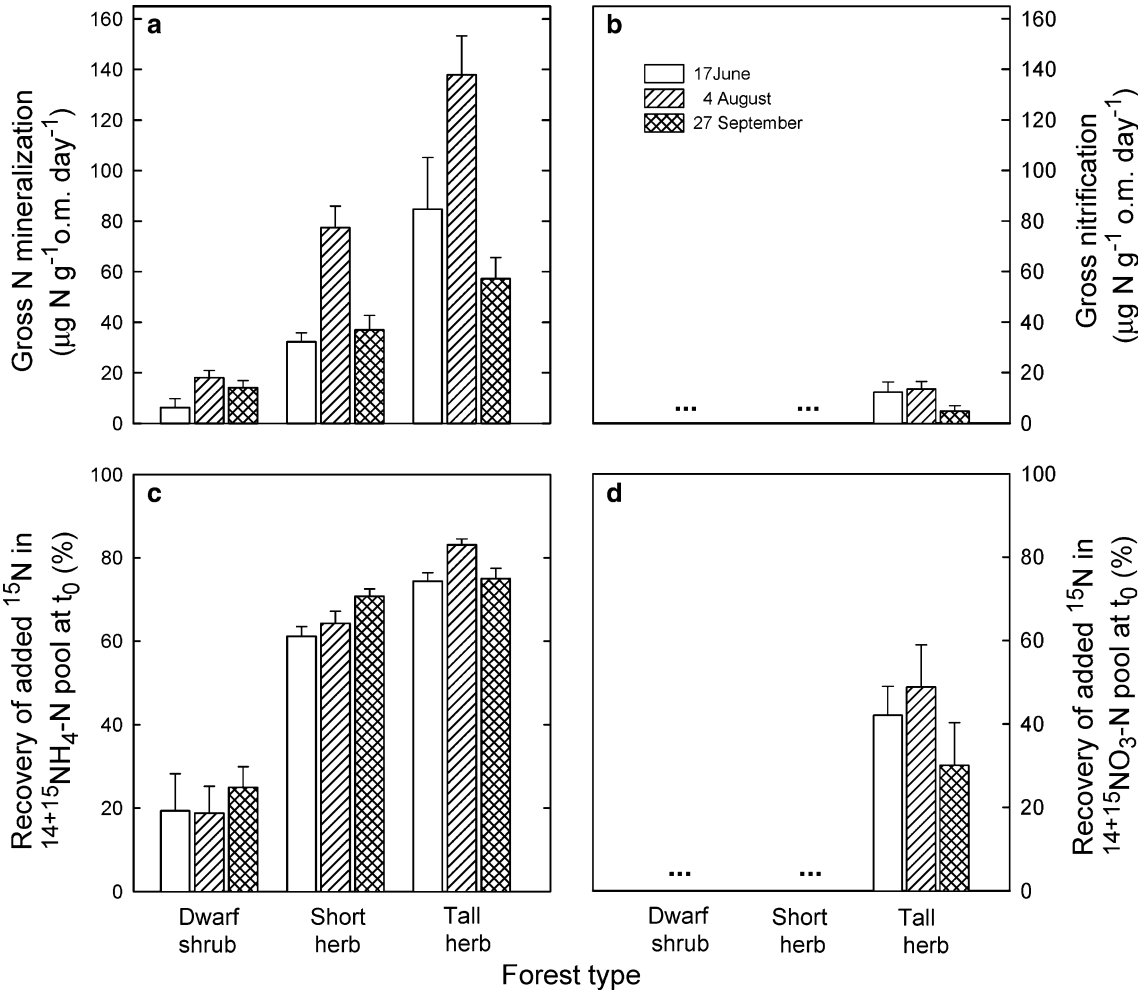

Fig. 1 Gross rates of N-cycling and recovery of added ^{15}N in the dwarf-shrub forest, short-herb forest, and tall-herb model forest ecosystems. These forest types represent common forest types in Fennoscandian boreal forests with high, intermediate, and low soil or plant foliar C-to-N ratios, respectively. **a** Gross N mineralization. **b** Gross nitrification. **c** Recovery of $^{15}NH_4^+$ in the soil $^{14+15}NH_4^+$ pool. **d** Recovery of $^{15}NO_3^-$ in the soil $^{14+15}NO_3^-$ pool. Each *bar* is the means ± 1 SE of three to five replicates. Ellipses (...) indicate not detectable in (**b**), and not applicable in (**d**)

Table 3 Field estimates of gross N mineralization, NH_4^+ consumption, gross nitrification, NO_3^- consumption, net N mineralization, and net nitrification per area (mg N m^{-2} d^{-1}) (rates g^{-1} o.m. are given in Fig. 1) as measured in three model forest ecosystems along the sharp forest productivity gradient at Betsele

Forest type	Date	Gross N mineralization	Gross NH_4^+ consumption	Short-term net N mineralization	Gross nitrification	Gross NO_3^- consumption	Short-term net nitrification
Dwarf shrub	17 June	16.2 ± 9.1	26.2 ± 13.8	−4.9 ± 3.2	...	...	...
	4 August	47.0 ± 7.5	53.5 ± 10.6	−7.0 ± 5.6	...	...	...
	27 September	36.7 ± 84.0	42.3 ± 8.5	−3.0 ± 1.3	...	...	...
	Mean	33.3 ± 9.1	40.7 ± 7.9	−5.0 ± 1.2	...	...	...
Short herb	17 June	73.5 ± 8.1	84.3 ± 6.9	−10.9 ± 1.9	...	...	...
	4 August	176.5 ± 19.3	195.3 ± 19.5	−16.0 ± 1.6	...	...	...
	27 September	84.0 ± 13.4	101.2 ± 19.0	−15.0 ± 6.2	...	...	...
	Mean	111.3 ± 32.7	126.9 ± 34.5	−14.0 ± 1.6	...	...	...
Tall herb	17 June	392.7 ± 95.0	266.1 ± 32.1	181.0 ± 65.0	56.9 ± 20.7	70.9 ± 5.0	−14.0 ± 17.8
	4 August	639.2 ± 71.3	627.7 ± 59.6	50.7 ± 34.3	62.2 ± 18.2	90.3 ± 29.5	−28.0 ± 14.4
	27 September	265.0 ± 39.3	165.1 ± 34.4	123.1 ± 29.0	21.9 ± 10.0	35.7 ± 14.3	−13.7 ± 14.3
	Mean	432.3 ± 109.8	353.0 ± 140.4	118.3 ± 37.7	47.0 ± 12.6	65.6 ± 16.0	−17.4 ± 4.0

The forests range from a poor dwarf-shrub forest type, through an intermediate short-herb forest type to a high productive tall-herb forest type. Short-term rates were estimated after 24 h. For short-term net N mineralization and gross rates of N mineralization and consumption, $n = 5$. For short-term net nitrification, gross rates of nitrification, and consumption, $n = 4$ on 17 June; and $n = 3$ on 4 August; and $n = 5$ on 27 September 1997. Values are means ± 1 SE. Ellipses (...) indicate not detectable

^{15}N atom% was not possible. Gross nitrification and NO_3^- consumption rates showed no significant seasonal variation in the TH forest type (Table 3; Fig. 1b). Seasonal means of gross nitrification and NO_3^- consumption in the TH forest type were 10.2 ± 2.7 and 14.2 ± 3.4 μg g^{-1} o.m. day^{-1}, respectively. Short-term net nitrification rates were below zero at all three dates (Table 3). Long-term net nitrification was very close to zero both early and late in the season in the DS and SH forest types. Seasonal mean in the TH forest type was 14.4 ± 2.9 μg g^{-1} o.m. day^{-1} and the rate was significantly higher than in the other forest types ($P < 0.05$).

Extractability of added $^{15}NH_4^+$ and $^{15}NO_3^-$

Recovery of added $^{15}NH_4$-N in the soil $^{14+15}NH_4$-N pool immediately after addition was significantly lower in the DS compared to in the SH and TH forest types ($P < 0.001$), but did not differ between dates ($P = 0.391$) (Fig. 1c). Seasonal mean recoveries were 21, 65, and 77% in the DS, SH, and TH forest types, respectively. Spearman rank analysis performed on seasonal means along the gradient ($n = 9$) showed, in many cases, strong correlations among % recovery of $^{15}NH_4^+$ in the soil $^{14+15}NH_4^+$ pool, the size of the NH_4^+ pool, gross N mineralization rate, and gross NH_4^+ consumption rate along the gradient. More specifically, in the poor DS forest type, recovery of added $^{15}NH_4$-N in the soil $^{14+15}NH_4^+$ pool immediately after addition was not correlated to NH_4^+ pool size ($P = 0.064$), but correlated to gross NH_4^+ consumption rate ($r = 0.786$, $P = 0.000$, $n = 15$) and gross N mineralization rate ($r = 0.771$, $P = 0.000$, $n = 15$). In the TH forest type, representing high productive forests, there were significant correlations among % recovery and size of the soil NH_4^+ pool ($r = 0.636$, $P = 0.010$, $n = 15$), gross N consumption rate ($r = 0.657$, $P = 0.007$, $n = 15$) and gross N mineralization rate ($r = 0.568$, $P = 0.026$, $n = 15$). However, in the intermediate SH forest type, % recovery of added $^{15}NH_4$-N in the soil $^{14+15}NH_4^+$ pool immediately after addition was not correlated to size of the NH_4^+ pool, nor to gross N mineralization, or gross N consumption ($P = 0.367$, $P = 0.954$, and $P = 0.753$, respectively). Also, the corresponding parameters representing the fate of $^{15}NO_3^-$ in the TH forest type correlated strongly with each other. Mean percent recovery of added $^{15}NO_3$-N at t_0 in the soil $^{14+15}NO_3^-$ pool was 38% in the rich TH forest type, with no seasonal differences ($P = 0.485$) (Fig. 1d), but was positively correlated to pool size of NO_3^- ($r = 0.762$, $P = 0.003$, $n = 12$), gross nitrification rate ($r = 0.895$, $P = 0.000$, $n = 15$), and gross NO_3^- consumption rate ($r = 0.762$, $P = 0.003$, $n = 12$).

Mean residence time of N in different soil N pools

The mean residence time for N, here defined as pool size divided by gross N mineralization (or gross nitrification) rate, was 10 h to 1 day for NH_4-N along the gradient, but varied between 2 and 6 days for NO_3-N in the tall herb forest type (Table 4). No significant differences were found in turnover times in the pools of inorganic N (NH_4^+) and chloroform-labile N between forest types (Table 4).

C-to-N ratios

Plant foliar, mor-layer soil, and microbial C-to-N ratios decreased from the DS, through the intermediate SH, to the TH forest type (Table 2). This decrease was significant throughout the forest types for the soil and microbial C-to-N ratios, whereas plant foliar C-to-N ratio was only significantly different between the DS and TH forest types.

Table 4 Mean residence time of N (days) in three different soil N pools, NH_4^+-N and NO_3^--N and chloroform-labile N, in forest ecosystems denoted dwarf shrub, short herb, and tall herb, representing high C-to-N, intermediate and low C-to-N ratio soils, respectively

Forest type	Date	NH_4-N[a]	NO_3-N[b]	Chloroform-labile N[c]
Mean residence time for N (days)				
Dwarf shrub	17 June	10.0 ± 6.1	...	79.9 ± 43.1
	4 August	1.0 ± 0.1	...	29.1 ± 5.9
	27 September	0.7 ± 0.1	...	27.6 ± 5.4
	Mean	3.9 ± 3.1	...	45.4 ± 17.2
Short herb	17 June	0.6 ± 0.1	...	14.1 ± 1.5
	4 August	0.5 ± 0.0	...	12.1 ± 2.3
	27 September	0.6 ± 0.1	...	14.2 ± 1.7
	Mean	0.6 ± 0.0	...	13.5 ± 0.7
Tall herb	17 June	0.5 ± 0.1	2.8 ± 0.6	11.9 ± 1.8
	4 August	0.5 ± 0.1	2.2 ± 0.4	7.4 ± 0.9
	27 September	0.4 ± 0.0	5.8 ± 1.3	17.2 ± 3.8
	Mean	0.5 ± 0.0	3.6 ± 1.1	12.2 ± 2.8

Mean residence time is the average number of days an N atom resides in each pool. Values are means ± 1 SE. Ellipses (...) indicate not applicable

[a] NH_4-N pool size divided by gross N mineralization rate ($n = 5$)

[b] NO_3-N pool size divided by gross nitrification rate ($n = 4$ on 17 June; $n = 3$ on 4 August; $n = 5$ on 27 September)

[c] N flush after fumigation-extraction divided by gross N mineralization rate ($n = 5$, except in DS soil on 17 June 1997 $n = 3$)

Discussion

Many studies on gross N turnover in high-latitude forest and tundra ecosystems have shown that NH_4^+ production seldom exceeds gross N consumption (all processes consuming NH_4^+) (e.g., Davidson et al. 1992; Fisk et al. 1998; Fisk and Fahey 2001; Perakis and Hedin 2001; Carmosini et al. 2002; Booth et al. 2005). This was also found here in the DS and SH, but not in the TH forest type. The rates of gross N mineralization found in the three forest types (Table 3, Fig. 1) encompassed the variations within Arctic (Fisk et al. 1998), temperate, and boreal soils worldwide (Merilä et al. 2002; Fisk and Fahey 2001; Carmosini et al. 2002; Perakis and Hedin 2001; Davidson et al. 1992; Booth et al. 2005). Rates of gross nitrification in the TH forest type were among the higher reported (Booth et al. 2005).

The fact that gross N mineralization rates were positively correlated to the recovery of added $^{15}NH_4^+$ (t_0) and that recovery increased along with increases in pool sizes and N turnover across the gradient (Fig. 1c), adds support to the idea of decreasing N limitation across the gradient. Abiotic immobilization of NH_3 into humus complexes is possible at high pH micro-sites (Nömmik and Vahtras 1982), but this is unlikely to explain the gross disappearance of added NH_4^+ from the extractable pool in the acid DS forest type soil, as the recovery was higher in the other, less acid, soils.

The mean residence time for NH_4-N was generally <1 day along the gradient, but 2–6 days for NO_3-N in the TH forest type. Booth et al. (2005) found similar residence times in forests worldwide. The turnover rate for chloroform-labile N, representing the actively cycling, cytoplasmic portion of microbial biomass, spanned between 7 and 17 days in the SH and TH forest types (Table 4). Consequently, microbial N turned over within 18–43 days (correction factor = 0.4, Martikainen and Palojärvi 1990), i.e., close to the 23–55 days found by Davidson et al. (1992) in a forest in California. Mean residence times for both inorganic N and microbial N were seemingly higher in the DS forest type, but not significantly so, than in the SH and TH forest types (Table 4).

Thus, we found profound differences among these forest types in in-situ N-cycling. These changes in N-cycling occur along with variations in base saturation and other soil chemical properties. However, soil N is turned over by microorganisms, and their cycling of N should proximally be controlled by their supplies of C and N. In the following, we will discuss these interactions in the three different model forest types studied, which differ in forest productivity by a factor close to 3.

The dwarf-shrub forest type—a system with a tight N cycle

Here, soils, microbes, and plants had the highest C-to-N ratios (Table 2). There was no net N mineralization, and gross NH_4^+ consumption rates exceeded gross N mineralization rates, which were very low (Fig. 1). This should not be taken as evidence of low biological activity, because microbial biomass C (Table 2) and soil respiratory activity were as high in this forest type as in the other forest types (Högberg et al. 2003). The recovery of added $^{15}NH_4^+$ in the soil $^{14+15}NH_4$-N pool was the lowest along the gradient, only 21% within 30 s from addition (Fig. 1c). This agrees with our observation in another DS forest with a similar soil C-to-N ratio, that 78% of the variation in ^{15}N recovered hours after additions of NH_4^+, or glycine, was explained by ^{15}N in the chloroform-labile fraction (Näsholm et al. 1998). We thus attribute this to immobilization by microorganisms, which have a very high C-to-N ratio in this forest type (Table 2). Extremely low recovery of ^{15}N in the soil NH_4^+ pool and rapid microbial immobilization was found 0.5 h after addition by Perakis and Hedin (2001) in forests in Chile, where c. 50% of added ^{15}N was found in the microbial biomass. In the low productive DS forest type studied by us, microbes (saprotrophs and mycorrhizal) are apparently strong N sinks; the DS forest type is a good example of a system without any apparent net N mineralization, but in which the plants undoubtedly take up some soil N (Nadelhoffer et al. 1991; Beier and Eckersten 1998). It is also the forest type in which organic N appears to be relatively more important as plant N source than in the other forest types (Nordin et al. 2001).

The short-herb forest type—a system with a less tight N cycle

In the SH forest type, there was no net N mineralization in the shorter-term (24 h) (Table 3), but significant net N mineralization was observed in the longer field incubations. Although gross NH_4^+ consumption rates exceeded gross N mineralization rates, as in the DS forest type, they were both roughly three times higher than in the DS forest type. This corresponded to a three times higher recovery, 67%, of added ^{15}N in the soil $^{14+15}NH_4^+$ pool than was found in the DS forest type. This suggests that the microbial demand for N is less than in the DS type. We found no evidence of nitrification in our pool dilution or incubation experiments. That nitrification may still occur is indicated by the significantly higher potential denitrification enzyme activity (Table 2). Hence, altogether this seems to be a system similar to the DS forest in view of the relation between NH_4^+ production and consumption, but with tendencies of higher N gross mineralization and lower microbial demand for N than in the DS forest type (Fig. 1a, c).

The tall-herb forest type—a system not limited by N

Gross N mineralization rates exceeded gross NH_4^+ consumption rates in the TH forest; gross N

mineralization rates were substantially higher than in the SH forest type (Fig. 1a), especially when expressed per m^2 (Table 3). The high recovery of ^{15}N in the soil $^{14+15}NH_4$-N pool, 77%, indicated that the microbial demand for NH_4^+ was relatively small. Even the short-term (24 h) incubation showed high net N mineralization (Table 3). Gross NO_3^- consumption rates exceeded gross nitrification rates, indicating strong sinks for NO_3^-, as also suggested by low recovery of $^{15}NO_3^-$ (40%) in the soil $^{14+15}NO_3$-N pool (Fig. 1d). Mean short-term nitrification rates were negative, which was also frequently observed by Stark and Hart (1997) in mineral soils from a wide range of ecosystems. Obviously, denitrification can be a large intermittent sink for NO_3^- (Table 2), but abiotic immobilization may also occur in micro-sites according to the "ferrous wheel hypothesis" (Davidson et al. 2003: according to this hypothesis, NO_3^- is reduced while Fe^{2+} is oxidized; subsequently NO_2^- is fixed into organic matter). The discharge area in the TH forest type is a hot spot for conversion of Fe^{2+} to Fe^{3+} (Giesler et al. 2002), which means that this abiotic sink may be strong. Under the same conditions, P is strongly fixed into unavailable forms when bound to sesquioxides (Giesler et al. 1998, 2002). Hence, N is not limiting because of a limitation by P and/or C. The low microbial C-to-N ratio of 4.8 (Table 2) indicates C limitation, and a dominance of bacteria, as shown by analysis of microbial community structure using phospholipid fatty acids (PLFAs) (Högberg et al. 2003). A fungal PLFA indicator, 18:2ω6,9 (Federle 1986), which includes ericoid mycorrhizal, ectomycorrhizal, and saprotrophic fungi, is extremely low in this forest type (Table 1). Nilsson et al. (2005) demonstrated that the biomass of ectomycorrhizal and ericoid mycorrhizal mycelium in particular, decreased steeply along the gradient in the direction of the highly productive TH forest type. This forest is the only in which the PLFA 16:1ω5 thought to indicate arbuscular mycorrhizal fungi (Olsson 1999) is clearly the dominant fungal PLFA (Högberg et al. 2003). It is also the only forest type in which there is clear evidence of plant N uptake of NO_3^- (Högberg 1990; Giesler et al. 1998; Nordin et al. 2001).

C-to-N stoichiometries along the gradient

Only the TH forest type has a soil with a C-to-N ratio below 20, and is the only forest in which short-term net N mineralization was found (Table 3). However, the critical C-to-N ratio is thought to depend on the relative contribution from fungi and bacteria to soil microbial biomass (Myrold 1999). It is of particular interest that bacteria are relatively homeostatic and maintain C-to-N ratios narrowly around 5, whereas fungi display higher ratios and greater variations in their C-to-N ratios depending on the quality of their substrates (Sterner and Elser 2002). There is a drastic decrease in the fungi-to-bacteria ratio from the DS to the TH forest type (Table 2), and a corresponding decrease was found in the microbial C-to-N ratio (Table 2). The latter apparently parallels the overall decline in plant and soil C-to-N ratio (Fig. 2). Interestingly, the ratio between soil and microbial C-to-N ratios was remarkably constant around 3.7 ± 0.1 (Fig. 2), despite the profound changes in microbial community structure.

Variations in C allocation to mycorrhizal fungi can explain why microbial biomass C and activity vary little along the gradient (Högberg et al. 2003), despite huge variations in soil N turnover, microbial biomass N, and forest productivity. Importantly, low N mineralization cannot be attributed to low microbial activity in general. In another DS forest with high soil C-to-N ratio, girdling of the trees, which stops the flux of photosynthates to roots and mycorrhizal fungi, caused a 50% decrease in soil respiration (Högberg et al. 2001), a loss of >30% of microbial biomass C, and a decrease in microbial C-to-N ratio from 8.9 to 6.6, i.e., 25% (Högberg and Högberg 2002). The effect of girdling on soil respiration was clearly smaller in fertilized plots than in non-fertilized plots (Olsson et al. 2005). The low N mineralization

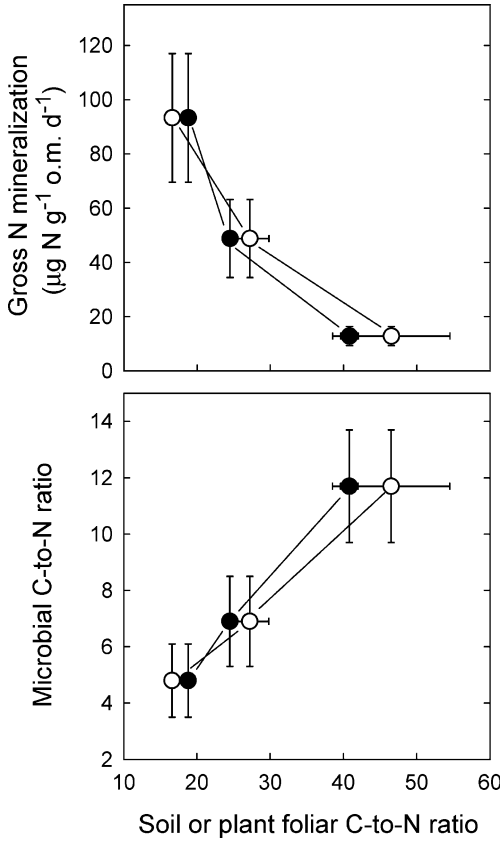

Fig. 2 Stoichiometries among soil and seasonal means of microbial C-to-N ratios and gross N mineralization along with decreasing soil (*filled symbols*) and plant foliar C-to-N ratio (*open symbols*) in the dwarf-shrub, short-herb and tall-herb model forest ecosystems representing common forest types in Fennoscandian boreal forests. **a** Relationships between gross N mineralization rate and soil or plant foliar C-to-N ratio, and **b** between microbial C-to-N ratio and soil or plant foliar C-to-N ratio. Each point is the seasonal mean ± 1 SE

rate in the DS forest type may thus reflect strong biological sinks, notably mycorrhizal fungi. As pointed out by Schimel and Bennett (2004), classical theory viewed plants as inferior competitors and microbes as superior competitors for soil N. This ignores that mycorrhizal fungi are microbial extensions of plant root systems and directly supported by an abundant supply of photosynthate (Smith and Read 1997), in fact a superior C source. This questions the use of the term ''immobilization'' in this context, as a share of the N withdrawn from the soil by mycorrhizal hyphae is actually on its way into plants.

Conclusions and suggestions

Our studies of gross and net turnover of NH_4^+ and NO_3^- pools confirmed profound differences in in-situ N-cycling across this forest productivity gradient. These occur along with variations in base saturation and other soil chemical properties. However, soil N is turned over by microorganisms, which should proximally be controlled by the supplies of C and N to the organisms. This was corroborated by strong correlations among soil and microbial C-to-N ratios, and gross N mineralization rate (Fig. 2). This seemingly supports the classical view of strong links among saprotrophs, their substrates, and soil N turnover. However, the supply of photosynthates to mycorrhizal fungi is expected to increase in the opposite direction in the sense that it is high when high plant foliar and soil C-to-N ratios implies a poor quality substrate for saprotrophs and vice versa (Högberg et al. 2003). This is the only logical explanation of the lack of differences in microbial C (Table 2), despite large variations in plant productivity, plant community composition, mycorrhizal associations, and microbial N. Current methods and models are unable to handle this complexity, i.e., why gross N consumption exceeds gross N mineralization in poor vegetation types, and the impact the shifts in mycorrhizal communities (Table 1, Read 1986, 1991) may have on patterns of soil N-cycling. The way forward must be to quantitatively account for the role played by mycorrhizal fungi.

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