Biogeochemistry (2006) 80:277–288
DOI 10.1007/s10533-006-9023-9

RESEARCH ARTICLE

^{15}N natural abundance of foliage and soil across boreal forests of Finland

S. P. Sah · H. Rita · H. Ilvesniemi

Received: 4 June 2005 / Accepted: 22 March 2006 / Published online: 5 June 2006

Abstract This study presents the latitudinal variation (from 60° 30′ N to 68° 2′ N latitude) of natural abundances of ^{15}N in the foliage, humus and soils of boreal forests of Finland. Our results clearly showed that N concentration of the foliage did not change significantly with latitudes but their ^{15}N values were significantly higher in higher latitude sites relative to that of the mid and lower latitude sites, indicating the different forms of N uptake at the higher latitudes compared to the lower latitudes. We assume that the higher foliage $\delta^{15}N$ values of the higher latitudes trees might be due to either more openness of N cycle (greater proportional N losses) in these latitudes compared to the sites of southern latitudes (lower N losses) or the differences in their mycorrhizal associations. Regression analysis showed that the temperature was the main factor influencing the ^{15}N natural abundance of humus and soil of all forest ecosystems, both before and after clear-cut, whereas rainfall was the main controlling factor to the foliage ^{15}N. Possible reasons behind the increasing $\delta^{15}N$ natural abundances of plants and soils with increasing latitudes are discussed in this paper. The clear-cut did not show any specific trend on the ^{15}N fractionation in humus and soil, i.e. both ^{15}N-enrichment and -depletion occurred after clear-cut.

Keywords ^{15}N natural abundance · Foliage · Clear-cut · Boreal forests · Latitudes · Temperatures · Soil

S. P. Sah (✉)
Department of Forest Ecology, University of Helsinki, PL 27 (Latokartanonkaari 7), FIN 00014 Helsinki, Finland
e-mail: Shambhu.sah@helsinki.fi

H. Rita
Department of Forest Resource Management, University of Helsinki, PL 27 (Latokartanonkaari 7), FIN 00014 Helsinki, Finland

H. Ilvesniemi
The Finnish Forest Research Institute, PL 18, Vantaa Research Centre, Vantaa Unit, 01301 Vantaa, Finland

Introduction

Boreal forest soils are among the largest terrestrial carbon pools, estimated to contain approximately 15% of the soil C storage worldwide (Schlesinger 1977; Post et al. 1982). The boreal forest, which is the second most extensive terrestrial biome on earth, represents a wood resource of global significance that is an important part of the cultural and economic wealth of northern countries. The boreal ecosystems are potentially important in driving changes in atmospheric CO_2 because of their large carbon pools. In confronting a pressing need to improve the management and protection of boreal trees, little is known about N dynamics. A better understanding of N dynamics is needed because of the intimate connection between cycling of N and C in the biosphere (Ägren and Bosatta 1996). In forest ecosystems nitrogen is present both in organic and inorganic forms and it circulates via complex processes among different ecosystem compartments. Because many of these processes cause discrimination of ^{15}N, N isotope ratio can be used to study ecosystem N cycling (Nadelhoffer and Fry 1994; Handley and Scrimgeour 1997; Högberg 1997; Sah and Brumme 2003).

On a global scale the nitrogen storage of soil organic matter has shown to be a function of annual precipitation and mean annual temperature (Jenny 1928; Post et al. 1985). Also the natural abundance of N isotopes in soils and plants has been observed to correlate with environmental variables, most importantly with climate, at both local and global scales (Austin and Vitousek 1998; Handley et al. 1999; Martinelli et al. 1999; Schuur and Matson 2001; Amundson et al. 2003).

The presence of multiple N sources with distinct isotopic values, mycorrhizal associations, temporal and spatial variation in N availability, and changes in plant demand can all have influence on plant $\delta^{15}N$ (Chapin et al. 1993; Nadelhoffer et al. 1996; Handley and Scrimgeour 1997; Michelsen et al. 1996, 1998; Hobbie et al. 2000; Robinson 2001).

This study concerns with the N and ^{15}N natural abundances of foliage, humus and soil of boreal forest across Finland. The mean annual temperature varies from +5°C in southern Finland to −1°C in the north. Therefore, the decomposition rate is higher in southern Finland and hence the source and form of the N uptake of trees can be assumed to differ from each other in different parts of the country and this could be reflected in their foliage $\delta^{15}N$ values. According to the isotope discrimination theory, soil inorganic N would be expected to be more N-depleted than organic N compounds (Nadelhoffer and Fry 1994). In boreal forests, slowly decomposing organic matter tends to become more enriched as decomposition proceeds and ^{15}N depleted NH_4^+ is formed. Furthermore, the oxidation of NH_4^+ to NO_3^- also discriminates against ^{15}N. Hence, at each step in the formation of organic matter to inorganic N, the substrate is left enriched in ^{15}N compared to the products (Nadelhoffer and Fry 1994; Schulze et al. 1994; Handley and Raven 1992). Furthermore, Taylor et al. (2000) indicate that the number fungal species, which are able to utilize organic N, decrease in number as availability of mineral N increases towards the south. Hence we assume that the proportion of organic N uptake (^{15}N-enriched due to decomposition) relative to the inorganic N should be higher in the North.

Most of the forested land area of Finland is subject to forestry operations. Annually some 100,000–200,000 ha of forests are clear-cut. In clear-cut sites, the stems are transported out of the ecosystem, but branches, needles, stumps and roots are left at the site causing an abrupt and massive input of decomposing biomass. At the same time the soil temperature and moisture increases. The effects of the rapid increase in slash and the removal of living trees on the ^{15}N fractionation mediated by changes in the amount of decomposition, plant uptake and leaching of mineralized nitrogen, especially across latitudinal gradients of the boreal forests are less explored. In addition, we have also studied rather older clear-cut sites (15–27 since clear-cut) compared to the sites available in the literature. Most of the literature of clear-cut sites is from 1 to 15 years old sites (Pardo et al. 2002; Matson and Vitousek 1981; Fisk and Fahey 1990).

In a clear-cut forest, nitrification typically returns to pre-cut levels about 3 years after the operation (Fisk and Fahey 1990), and nitrate losses decrease after 3–5 years (Matson and Vitousek 1981; Fisk and Fahey 1990). Kubin (personal communication) shows much longer effects of clear-cut on the increase in groundwater nitrate concentration.

When nitrification decreases, ammonium enrichment will cease, and the plant-available ammonium pool will return quickly to pre-cut $\delta^{15}N$ levels. Leaf $\delta^{15}N$ should then return to pre-disturbance levels as well. Our unpublished data (Sah and Ilvesniemi unpublished data) from another short-term clear-cut sites of a boreal forest has already supported the above mentioned literature studies. Therefore, our aim is to further understand ^{15}N fractionation in a long-tern clear-cut site.

The objective of this paper is to study the variation in the foliar, humus and soil ^{15}N natural abundance over a climatic gradient in Finland, and analyze the role of temperature, precipitation, soil carbon and soil nitrogen in explaining this variation. We also assess whether the clear-cut has had any impact on the ^{15}N fractionation in humus and mineral soil.

Methodology

Site description

To cover the north to south and east to west variation in Finland, 19 forest sites were selected across 60° 30′ N–68° 2′ N and 23° 0′ E–29° 70′ E (Figure 1). At each site three separate plots (30 × 30 m or 50 × 50 m in size) were selected as site level replicates. The soil samples were taken before clear-cut (clear-cuts between years 1975 and 1990) and again in 2001 after clear-cut. A short description of the stands and their locations are given in Table 1 and Figure 1, respectively. The age of the present stands (after clear-cut) varies from 12 to 27 years. Before the clear-cut, all plots except one were Norway spruce dominated. After the clear-cut, 16 of them were planted with Scots pine seedlings, and three with Norway spruce seedlings. After plantation natural regeneration has changed the species composition so that at present in most sites the stands are mixed forests of pine, spruce and birch.

The average annual rainfall in Finland varies from 750 mm in south to less than 500 mm in north (variation between years ranges from 350 to 950 mm), and the annual actual evapotranspiration varies from 450 to 150 mm, respectively. The annual mean temperature during the growing seasons (May–September) changes from 13.4°C in south to 9.7°C in north and the mean annual temperatures vary from 4.9 to 0.7°C (Atlas of Finland 131, Climate). The altitude of all sites was between 120 and 300 m a.s.l. The soils of the sites are podzols. The soil pH (water) varies from 3.44 to 4.87 in humus and from 4.06 to 6.04 in mineral soil. The atmospheric N deposition is very low ranging from 6 kg ha^{-1} year^{-1} in south to 1 kg ha^{-1} year^{-1} in north (Kumala et al. 1998).

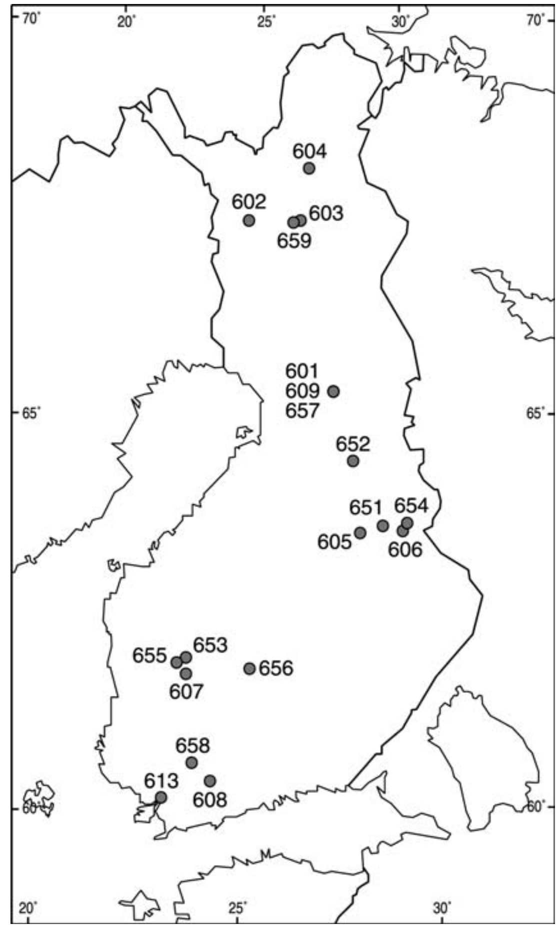

Fig. 1 Map of Finland showing the locations of all 19 forest plots

Foliage and soil sampling

From each site (each site consisted of three plots) 20 humus and 5 mineral soil (0–30 cm) samples were taken. All humus samples and all mineral soil samples of one site were mixed (humus and mineral soil separately) to form one composite sample to represent the site. For each of the 19 sites, the site level result was calculated as an average of three plots. Needle sampling of the planted trees was done on all plots. The samples were taken from the current year needles of the topmost whorls. The needle samples were not taken from trees growing at the site before clear-cut.

Table 1 The study sites and their description

Site No.	Age since Clear-cut	City/village	Trees sp. before clear-cut	Trees Planted	Present dominant tree species	Latitude	Longitude	Present tree species (No. of trees/ha)		
								Pine	Spruce	Broad-leaved
601	27	Pudasjärvi/Pärjä	Spruce	pine	pine	65.3	27	1374	400	14
602	26	Kittilä/Martovuoma	Spruce	Pine	Pine	67.45	24.5	1654	120	106
603	26	Sodankylä/Kuopsusselkä	Spruce	Pine	Pine	67.45	26.5	170	26	0
604	26	Inari/Köysivaara	treeless	Pine	Pine	68.2	27	266	146	14
605	25	Sotkamo/Hiisi	Spruce	Pine	Pine	63.45	28.2	1414	94	294
606	25	Nurmes/Mujejärvi	Spruce	Pine	Pine	63.45	29.5	1654	534	1706
607	22	Kuru/Luode	Spruce	Pine	Pine	61.55	23.5	2120	320	1320
608	22	Karkkila/Rajala	Spruce	Spruce	Spruce	60.3	24.1	0	2306	1586
609	20	Pudasjärvi/Pärjä	Spruce	Spruce	Spruce	65.3	27	14	574	0
613	11	Halikko/Mäyry	Spruce	pine	Broad-leaved	60.3	23	160	574	7440
651	25	Valtimo/Sivakka	Spruce	Pine	Pine	63.45	29	1506	586	894
652	22	Hyrynsalmi/Paljakka	Spruce	Spruce	Spruce	64.4	28.2	0	2294	1680
653	20	Kuru/Iso Mustajärvi	Spruce	Pine	Broad-leaved	62.1	23.5	1320	174	1814
654	20	Nurmes/Korvalampi	Spruce	Pine	Broad-leaved	63.45	29.7	814	40	4600
655	19	Parkanao/Lylyjärvi	Spruce	Pine	Pine	62	23.3	1698	26	1826
656	18	Jämsänkoski/Tärkkilä	Spruce	Pine	Pine	62	25	1894	880	866
657	15	Pudasjärvi/Pärjä	Spruce	Pine	Pine	65.3	27	1400	66	0
658	13	Tammela/Lintumaa	Spruce	Pine	Pine	60.45	24	880	134	414
659	12	Sodankylä/Vuorsosselkä	Spruce	Pine	Pine	67.1	26.3	1466	106	0

Analytical methods

All the needle and soil samples were dried at 70°C and samples were ground into a fine powder in a planetary mill. Nitrogen isotope ratios were measured on a Finnigan MAT Delta plus stable isotopic ratio mass spectrometer (IRMS) equipped with an elemental analyzer for conversion of N into N_2. C- and N-concentrations were analysed by Leco CSN-1000 analyser (Leco Corporation, St. Joseph, MI, USA). Results of the IRMS measurement were given in δ notation. δ-values of isotope of N are expressed as ‰ and calculated as follows:

$$\delta^{15}\mathrm{N} = (R_{\mathrm{sample}}/R_{\mathrm{atmos}} - 1) * 1000, \text{where,}$$
$$R_{\mathrm{sample}} = {}^{15}\mathrm{N}/{}^{14}\mathrm{N} \text{ in samples}$$
$$R_{\mathrm{atmos}} = {}^{15}\mathrm{N}/{}^{14}\mathrm{N}$$
present in atmosphere as standard

Statistical analysis

The ^{15}N in humus and soil (both before and after clear-cut) and in foliage (only after clear-cut) were used as response in regression models, where climate and soil characteristics had the role of explanatory variables. To overcome multicollinearity, we made advantage of the ideas in the EFRA-approach (Rita and Lehtonen 2005 personal communication). There, the basic idea is to study the role and importance of an explanatory variable (e.g. rainfall) by adding other variables (e.g. temperature) into a model that already contains rainfall. Inclusion of other variables gives the effect of e.g. rainfall adjusted for these added variables, for example temperature. If the adjusted and unadjusted effects (=coefficients) of rainfall is similar to each other, we may conclude that rainfall has an independent/autonomous role in the system. If they differ considerably, the effect of e.g. rainfall is mediated through or partly due to the added variable. Supported by this approach, the mechanisms of interplay between the variables are explored.

This approach differs from the standard stepwise multiple regression in that the focus is more in kind of theoretical exploration, abductive reasoning rather than in statistical significances and amount of reduced variation.

The approach is more quantitative in that we look at the coefficients, i.e. effects and their magnitudes and not correlations alone.

Results

Frequency distribution of $\delta^{15}N$ in humus and mineral soils

Figure 2 shows the relative frequency distribution of $\delta^{15}N$ in 52 foliage, 99 humus and 98 mineral soil samples. Most of the foliage samples had negative $\delta^{15}N$ values, nearly 90% of the humus samples were between −2‰ and +2‰ and almost all mineral soil samples were between +2‰ and +8‰. The mean $\delta^{15}N$ values in foliage, humus and mineral soil samples were −1.4‰ (SD = ±0.13‰), +0.9‰, (±0.11) and +5.3‰ (±0.11), respectively, indicating that the living needle biomass in the ecosystem was strongly depleted in ^{15}N and the mineral soil was enriched.

Variation of $\delta^{15}N$ values in foliage, humus and soils along latitudes

In Figure 3, the $\delta^{15}N$ values of the foliage are sorted according to the latitude. The mean values of foliage $\delta^{15}N$ increased significantly ($R^2 = 0.53$) from −4.2‰ in the south to +1.6 in the north. A similar trend could be seen in $\delta^{15}N$ in humus (Fig. 4) and soil (Fig. 5), although their statistical significance was weaker. This trend was more prominent for the humus samples taken before clear-cut ($R^2 = 0.44$) than after clear-cut ($R^2 = 0.32$).

On the contrary to the isotopic differentiation, concentration of N in foliage, humus and soil samples did not change significantly along with the latitudes. The foliar N concentrations for south, middle and north Finland sites are 1.3% (SE = 0.03), 1.2%, (SE = 0.03) and 1.3% (SE = 0.03), respectively. The differences between these three groups were not statistically significant.

The effect of the clear-cut on the $\delta^{15}N$ in humus and mineral soil

When the before clear-cut average values of $\delta^{15}N$ were compared with those measured after clear-cut, $\delta^{15}N$ values differed significantly from each other and both depletion and enrichment of ^{15}N could be seen (Figs. 4, 5). The time elapsed since the clear-cut could not explain the variation found in $\delta^{15}N$ values either. However, the total

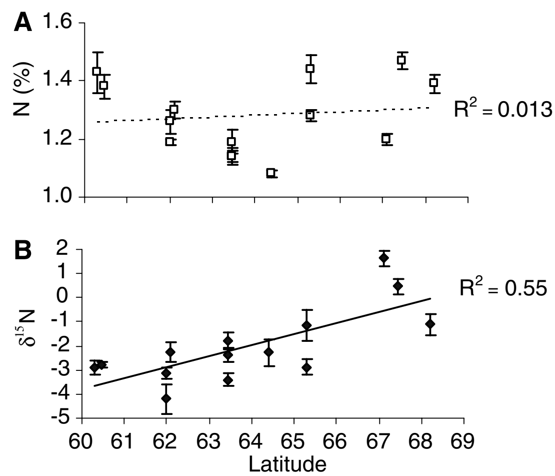

Fig. 3 Foliage nitrogen concentration (**A**) and foliage $\delta^{15}N$ (**B**) along the latitude (n = 3, Error bars represent SE of means)

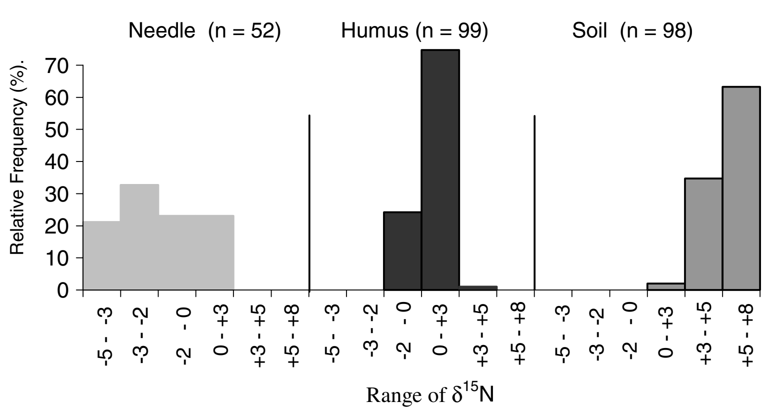

Fig. 2 Relative frequency of $\delta^{15}N$ (‰) natural abundance in the foliage, humus and soil samples. The sample number within each class is presented

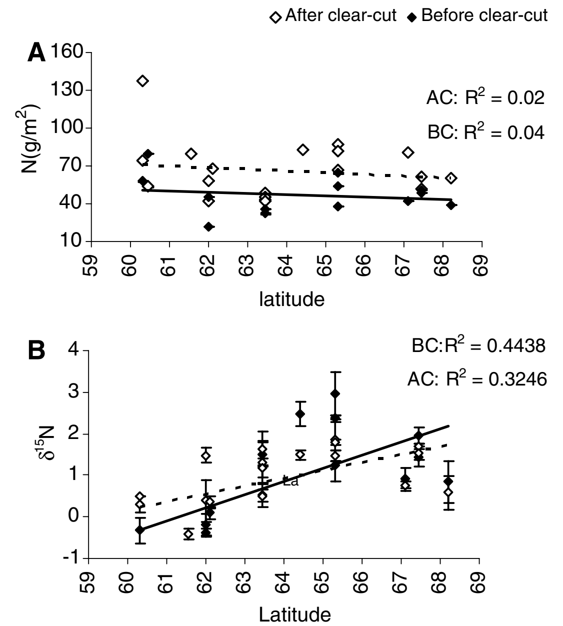

Fig. 4 (**A**) The amount of N (g/m^2) in humus before (BC) and after clear-cut (AC) sorted along latitude (n = 3, error bars represent standard error of mean). (**B**) δ^{15}N values in humus before and after clear-cut. The dotted line shows the linear trend of results along the latitude after clear-cut and the solid line the same trend before clear-cut

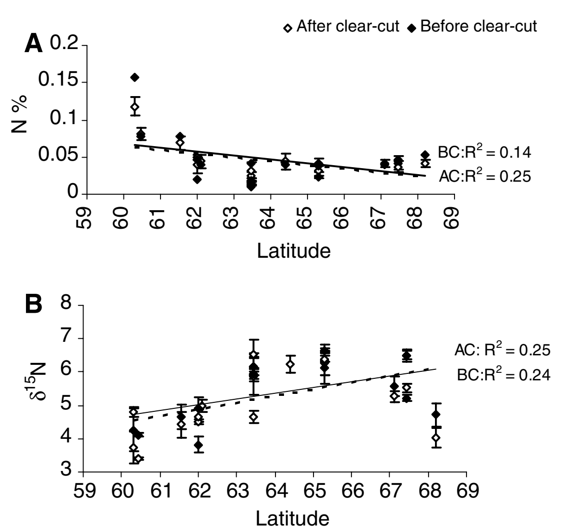

Fig. 5 (**A**) The N (%) in soil before and after clear-cut (n = 3, error bars represent SE of means). The dotted line shows the linear trend of results along the latitudes after clear-cut and the solid line the same trend before clear-cut. (**B**) δ^{15}N values in soil before and after clear-cut sorted along the latitude

amount of elemental nitrogen in humus increased significantly ($P < 0.05$) after clear-cut, but this increase did not depend on the time of clear-cut.

The effect of climate and soil properties on δ^{15}N

Rainfall

When rainfall is the only explanatory variable in the foliage δ^{15}N regression, its estimated coefficient equals −0.026 ($P < 0.05$). This means that an increase of e.g. 10 mm in annual rainfall corresponds to an average decrease of 0.26‰-units in δ^{15}N values in foliage. Inclusion of the other explanatory variables (temperature, nitrogen N and carbon C) into the model, separately or in various combinations, leads to only negligible changes in the estimated value of the coefficient of rainfall; in addition, all these coefficients are statistically significant (Table 2). Rainfall thus seems to be an independent/autonomous determinant of the foliage δ^{15}N content. Its effect can not be reduced to other factors, despite their multicollinear structure.

In the humus (BC) δ^{15}N regressions, inclusion of temperature changes the sign of the estimated coefficient of rainfall. This change takes place both when C and/or N are included into the model or not. Exactly the same pattern can be seen in soil ^{15}N (BC) regressions. The temperature-adjusted effect of rainfall on humus and soil δ^{15}N values (BC) thus seems to give a positive regression coefficient for the model. After clear-cut, both in humus and soil, inclusion of temperature changes the estimated coefficient of rainfall in the same way. The roles of N and C are, however, different than BC. This might reflect the changes caused by clear-cut to the nutrient flows in soil and humus.

Temperature

When temperature is the only explanatory variable in the foliage δ^{15}N regression, its estimated coefficient is always negative. Increased temperature, together with changes in the factors that are connected with it, decreases δ^{15}N. When other

Table 2 Estimates of regression coefficients of rainfall, temperature, N and C in various models with $\delta^{15}N$ values in foliage, humus and soil as response variable, both before and after clear-cut (BC and AC, respectively)

Model variables	Foliage	Humus BC	Humus AC	Soil BC	Soil AC
1. Rainfall (mm)					
Alone	−0.026**	−0.013**	−0.0086**	−0.0067**	−0.0091*
Adjusted for:					
Temperature	−0.027*	+0.0086	+0.0061	+0.024*	+0.013*
Temperature and N%	−0.026*	+0.016	−0.0016	+0.024*	+0.011
N% alone	−0.026*	−0.017**	−0.0067	−0.0052	−0.0050
C (g/m²)	–	−0.012*	−0.0088*	−0.0059*	−0.0092*
Temperature and C	–	+0.015	−0.010	+0.021*	+0.014*
Temperature, C and N	–	+0.019	+0.0023	+0.022*	+0.011
C and N	–	−0.016**	−0.0092**	−0.0061*	−0.0055
2. Temperature (°C)					
Alone	−0.67**	−0.41**	−0.26**	−0.28**	−0.30*
Adjusted for:					
Rainfall	+0.052	−0.63*	−0.41*	−0.87**	−0.61*
Rainfall and N%	−0.0034	−0.91*	−0.19	−0.89**	−0.0051
N% alone	−0.68**	−0.51**	−0.15*	−0.24*	−0.22*
C (g/m) alone	–	−0.41**	−0.21*	−0.25*	−0.30**
Rainfall and C (g/m²)	–	−0.79*	−0.53*	−0.79**	−0.63*
Rainfall, C and N	–	−0.99*	−0.32	−0.83**	−0.52*
C and N	–	−0.51**	−0.26**	−0.25*	−0.22*
3. N (%)					
Alone	+1.56	−0.27	−1.75*	−9.5*	−14.5**
Adjusted for:					
Rainfall	+1.49	−0.93	−1.83*	−7.32*	−11.08*
Rainfall and temperature	+1.50	−0.65	−1.43*	+0.91	−1.32
Temperature	+2.00	−0.84	−1.34*	−3.94	−6.18
C	–	−0.56	−1.89*	−4.55	−11.79
Rainfall and C	–	−1.34	−2.03*	−1.07	−6.51
Rainfall, C and temperature	–	−1.05	−1.44*	+3.34	−0.59
Temperature and C	–	−1.28	−1.55*	+1.55	−2.82
4. C (g/m²)					
Alone		+0.00018	+0.000086	−0.00017*	−0.000015
Adjusted for:					
Rainfall		+0.00018	+0.00014	−0.00016*	−0.000041
Rainfall and temperature		+0.000072	+0.00028*	−0.000042	−0.000022
Rainfall and N%		+0.00017	+0.00022	−0.00014*	−0.00011
Rainfall, temperature and N%		−0.000024	+0.00029*	−0.000069	−0.000025
Temperature		+0.00012	+0.00022	−0.00012*	−0.000016
N%		−0.00024	+0.00016	−0.00012	−0.000069
Temperature and N%		+0.00012	+0.00027*	−0.00013	−0.000080

*Significant at 5% level

**Significant at 1% level

– not measured

explanatory variables are included, this negative effect is prevailed both in soil and humus, BC and AC. Statistical significances are achieved with the exception of inclusion of N alone. But for foliage, inclusion of rainfall changes the coefficient of temperature to a negligible value (which is not significant).

Nitrogen

In foliage, the effect of N concentration on $\delta^{15}N$ values is constantly positive, yet not statistically significant, whereas in humus and soil, both BC and AC, the coefficient is predominantly negative. Statistical significances are concentrated to humus AC. The estimated values of the coefficient are larger than BC. Similar pattern is seen in soil, where even some positive coefficients are observed.

Carbon

In soil, the effect of C on δ^{15}N values is negative, irrespective of the included additional variables. In humus, the effect of C is—with a single exception—positive. However, C seems to have an independent positive effect that cannot be explained by other measured factors.

Discussion

The observed range of natural ^{15}N abundance in the conifer foliage (from −4.9 to +2.8‰) corresponds to other studies on conifer trees (Garten and Miegroet 1994; Emmet et al. 1998; Koopmann et al. 1997; Sah and Brumme 2003). Even a higher foliage δ^{15}N value of +4.6‰ has been reported for European temperate plantation forests, but it has been attributed to the reforestation after the ploughing (Emmet et al. 1998).

The observed ^{15}N-enrichment of foliage with increasing latitude is not consistent with other studies. For example, Handley et al. (1999), using data from a literature survey, reported no relationship between foliar ^{15}N and latitude. Mariotti et al. (1980) examined the plant and soil ^{15}N variation along an elevation gradient (climosequence) in France, and found that both plant and soil ^{15}N declined with increasing elevation (and precipitation and declining temperatures), but they did not propose any mechanism responsible for the isotopic variations.

Plant ^{15}N in general is determined by the source(s) of N, such as (a) nitrogen from internal recycling, (b) nitrogen from symbiotic N_2-fixation, (c) nitrogen obtained directly from the soil via root uptake, and (d) nitrogen obtained from mycorrhizal fungi. Of these four potential pools, nitrogen from internal recycling is generally associated with fairly minor isotopic fractionation (Gebauer and Dietrich 1993; Näsholm 1994; Yoneyama 1995). Nitrogen from symbiotic N_2-fixation is considered to have a relatively constant isotopic signature, as a result of the constant δ^{15}N of the atmospheric pool of N_2, and the very small isotopic fractionation value for the nitrogenase enzyme (Handley and Raven 1992). The last two sources will vary isotopically as a result of local soil conditions. The studies suggest that the foliage δ^{15}N natural abundance might reflect differences in their N sources (Michelsen et al. 1996, 1998; Hobbie et al. 2000). We have not measured the actual root distribution in our sites, but according to Helmisaari et al. (1999), root distribution in podzols is superficial and the phenomenon is more pronounced in northern sites. Therefore, we do not expect any ^{15}N-enrichment in north due to the root depth distribution. In addition to inorganic nitrogen, organic nitrogen might be the dominant source of N in some forested ecosystems, especially in boreal forests (Northup et al. 1995; Persson et al. 2003). Several studies have already indicated that in the boreal forests the mineral N pool is small (Read 1991) and the trees take up organic N via the mycorrhizal associations bypassing mineralization (Näsholm et al. 1998; Northup et al. 1995; Nordin et al. 2001; Persson et al. 2003). Not only the mycorrhizal tree species, but also the non-mycorrhizal (manipulated roots) tree species have been found to be capable of taking organic N from soil in the recent studies (Näsholm et al. 1998, 2000; Lipson and Monson 1998). We presume that a reason for the differences in foliage ^{15}N across Finland might be differences in root mycorrhizal association; in the North it tends to take more organic N.

The observed range of δ^{15}N values from −2.0 to +3.5‰ in the humus layer and +2 to +8‰ in the mineral soil layer from lower latitudes to higher latitudes was similar to those reported from a variety of temperate and boreal forest ecosystems (Shearer et al. 1978; Höberg et al. 1996; Sah and Brumme 2003). Amundson et al. (2003) reported a strong global latitudinal banding with northern ecosystems having the most depleted soil δ^{15}N values and tropical zones having the most enriched δ^{15}N values. Similar to our results, Mizutani et al. (1991), from a study of soils from seabird rookeries along the latitude gradients from 30°N to 80°N, have reported increase in soil δ^{15}N values with increasing latitudes. This was explained by larger kinetic isotope effect during NH_3 volatilization at lower temperature (Wada et al. 1981) and possibly also by more leaching of ^{15}N depleted NO_3^- in colder, wet situations.

In the south to north gradient of our study the evapotranspiration decreases more rapidly than rainfall, and thus the humidity increases to the north even if the amount of rainfall decreases to the same direction. Because in the north more than half of the annual precipitation is snowfall, also the flow peaks are more pronounced in north during the snowmelt period. This can lead to a situation, where the ecosystem is more 'open' in north and a higher proportion of the depleted forms of mineralized nitrogen is lost in the outflow before plants have time to take up the nitrogen, although all the studied ecosystem are nitrogen limited and no significant leaching of NO_3^- from soil of closed forests has been observed (Ukonmaanaho and Starr 2002). However, a long-term increase (1986–2004) in leaching of nitrate nitrogen into ground water has been observed for clear-cut Finnish forests (Kubin personal communication).

Role of atmospheric deposition of NH_4^+ and NO_3^- may also have a role in the ecosystem ^{15}N fractionation, because the proportion of ^{15}N is higher in precipitation which is affected by anthropogenic emissions (Heaton et al. 1997). N in precipitation may be a significant source of tree N uptake in N-limited sites. The amount of N in precipitation is very low in the arctic sites studied close to Swedish heath tundra site (Michelsen et al. 1996) and here few data on rain and snow $\delta^{15}N$ suggests that NH_4^+ in precipitation is greatly ^{15}N enriched, values ranging from +1.9‰ for summer rain to +12.3‰ for winter snow (Michelsen et al. 1996) in contrast to most figures on the precipitation from more polluted temperate regions (Heaton et al. 1997; Sah and Brumme 2003). Hence, this might also cause the foliage ^{15}N-enrichment of boreal trees foliage in the more northern ecosystems. The atmospheric deposition of NH_4^+ and NO_3^- throughout the Finland is very low, less than 2 kg ha^{-1} in North and between 5 and 10 kg ha^{-1} in South (Kumala et al. 1998). But no $\delta^{15}N$ values have been so far analyzed in precipitation of Finland. Precipitation N might be less important source of N for trees but information is needed on precipitation $\delta^{15}N$ in Northern Ecosystems with minute anthropogenic N deposition.

Of the above mentioned potential reasons for the foliar ^{15}N-enrichment of trees in our study, we assume that there might be mainly two type of reasons, namely those connected with the form of N uptake, and those connected with the leaching of depleted ^{15}N-NO_3^-. The simultaneous increase in the ^{15}N ratio in needles, humus and soil cannot be due to a single reason. The proportion of ^{15}N in the whole ecosystem can increase only, if depleted nitrogen forms are either lost out from the system or due to the internal ^{15}N fractionation. In our case, it seems that both factors are affecting the ^{15}N fractionation.

The observed trend of humus layer $\delta^{15}N$ values after different periods of clear-cutting is not consistent with our hypothesis. After clear-cut there is significantly higher amount of easily decomposable organic material in soil and after the clear-cut, soil (and humus) is moister and warmer than that under canopy, creating more favourable conditions for decomposition. It has been shown that nitrate and ammonium concentrations increase in soil solution after clear-cut (Fisk and Fahey 1990; Örlander et al. 1996; Kubin personal communication; Sah and Ilvesniemi unpublished data). Thus, the net effect of nitrification is to enrich the $\delta^{15}N$ of the soil and of the plant available NH4. When nitrification and nitrate loss rates are high, the soil and plants would be expected to have increased $\delta^{15}N$ (Nadelhoffer and Fry 1994) due to the enrichment of ammonium. As mentioned above, some studies from temperate forests, suggest that in the clear-cut forest, nitrate losses decrease after 3–5 years (Matson and Vitousek 1981; Fisk and Fahey 1990). When nitrification decreases, ammonium enrichment will cease, and the plant-available ammonium pool will return quickly to pre-cut $\delta^{15}N$ levels. Leaf $\delta^{15}N$ should then return to pre-disturbance levels as well.

Based on this, it could be assumed that leaching of ^{14}N-rich nitrogen occurs after clear-cut leading to ^{15}N-enrichment in remaining humus. Hence, according to our hypothesis, at least the $\delta^{15}N$ values of humus in older clear-cut sites should have increased or remained at pre-cut level of $\delta^{15}N$ values, but should not have decreased than pre-cut level. However, we observed both increase and decrease in ^{15}N abundances after clear-cut. We assume it to be due to two reasons; (i) Although the amount of litter reaching the soil after clear-cut can be five-fold compared to annual litter fall in the natural stand conditions, it may still be so small that the possible changes caused by increased leaching of ^{14}N are masked by the large storage of nitrogen in soil. (ii) Another most probable reason of this might be due to the methods of sampling of humus. We did not separate the humus samples into the different layers and this might have been more informative, because this is mainly the uppermost forest floor (humus layer), which is primarily affected first after clear-cutting and the deeper humus layer might remain unchanged (Sah and Ilvesniemi unpublished data).

Conclusions

Our results clearly showed that N concentration of the foliage did not change significantly with latitudes but their $\delta^{15}N$ values were significantly higher in higher latitude sites relative to that of the mid and lower latitude sites, indicating the different forms of N uptake at the higher latitudes compared to the lower latitudes. From this study, we hypothesize that the higher foliage $\delta^{15}N$ values of the higher latitudes trees might be due to either more openness of N cycle (greater N losses) in these latitudes compared to the trees of southern latitudes (lower N losses) or the differences in their mycorrhizal associations or both.

While our data indicates that there is a pattern of ecosystem $\delta^{15}N$ values by latitudes, our understanding of the mechanisms behind these processes is still unclear. Our data however indicates a significant influence of temperature and rainfall on the ^{15}N in soil and needle, respectively. Further researches on the temperature effects on the soil are needed.

The impacts of clear-cut on the ^{15}N fractionation in our study do not show any significant trend and this is not consistent with our assumption and we assume that this might be due to the methods of sampling of humus. The separation of humus horizon into different layers might have been more informative.

Acknowledgments The authors thankfully acknowledge the financial support provided by Academy of Finland for completion of this work.

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