

Interspecific variation and impact of clear-cutting on natural ^{15}N abundance and N concentration in the needle-to-soil continuum of a boreal conifer forest

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ABSTRACT

The primary objective of this paper is to study the interspecific variation of ^{15}N natural abundance in two dominant conifer tree species, Scot pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* L. Karst) in a N-limited mixed boreal coniferous forest in southern Finland. Both a mature tree stand (a natural forest stand) and a stand of seedlings in a clear-cut area were considered. We analyzed %N and $\delta^{15}\text{N}$ natural abundance in needles, branches, litter and soil of the both above-mentioned stands. Pine needles had higher N concentrations than spruce needles, both in mature forest (pine = 1.09%, SE \pm 0.02 and spruce = 0.79%, SE \pm 0.02) and in the clear-cut area (pine = 1.01%, SE \pm 0.07 and spruce = 0.74%, SE \pm 0.04). Furthermore, pine needles were significantly more depleted in $\delta^{15}\text{N}$ natural abundance than the spruce needles, both in the mature forest (pine = -5.6‰ , SE \pm 0.1‰ and spruce = -4.0‰ , SE \pm 0.2‰) and in the clear-cut sites (pine = -2.8‰ , SE \pm 0.2‰ and spruce = -2.1‰ , SE \pm 0.3‰). The more pronounced depletion of ^{15}N in the pine foliage might be connected to its different fungal associates in the roots compared to spruce roots. We assume that the mycorrhizal N-uptake is very prominent at the N-limited site. After clear-cutting, needles of the seedlings and the uppermost part of soil organic layer were found to be more ^{15}N -enriched than at the natural forest site. This was attributed to an increased level of nitrification in the clear-cut site soil.

Keywords: ^{15}N natural abundance; soil; nitrogen; Scot pine; Norway spruce; clear-cut

Under nitrogen-limited conditions, coexisting species may tap different sources for nutrient supply and this may lead to significant differences in plant nutrition even in the same habitat (Schulze et al. 1994). Boreal forests play a substantial role in the global carbon (C) cycle. A better understanding of N dynamics is needed because of the intimate connection between cycling of N and C in the biosphere (Ågren and Bosatta 1996). Nitrogen occurs in organic and inorganic forms and circulates via complex processes among many different compartments in forest ecosystems. Because many of these processes exhibit an isotope effect (i.e. discrimination against ^{14}N or ^{15}N), N isotopes ratio may be used to study ecosystem N cycling (Nadelhoffer and Fry 1994). The ecosystems vary with the plant natural ^{15}N abundance. In addition to the observed trends of plant $\delta^{15}\text{N}$ across different ecosystems, strong variations in $\delta^{15}\text{N}$

may occur among species within an ecosystem (Stewart and Schmidt 1999, Hobbie et al. 2000). This variation in $\delta^{15}\text{N}$ values among different species indicates their different sources of N uptake, since the N-sources vary in their $\delta^{15}\text{N}$ values (DeLucia et al. 1988, Gower and Richards 1990, Marshall and Zhang 1994).

In order to analyze how different species coexist in a nutrient-limited environment, we investigated ^{15}N natural abundance in two dominant conifer tree species in a mixed boreal coniferous forest in southern Finland. The two dominant tree species studied are Scot pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* L. Karst). We anticipated that both tree species will vary in their N-dynamics and one of them would be more efficient in N-acquisition.

Clear cutting is one of the most common silvicultural practices in Finland. Annually some

100 000–200 000 hectares 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 are not known. The other goal of this paper is to document the impacts of clear-cutting on N concentrations and the natural abundance of ^{15}N in forest soils. Our hypothesis on the possible impacts of clear-cutting on the forest soil is that at the clear-cut site the difference between the $\delta^{15}\text{N}$ of the upper soil horizon and lower soil horizon should be narrower as compared to the undisturbed forest soil profile. After clear cutting, the nitrification increases and ^{15}N -enriched NH_4^+ is produced in the soil. The leaves (mainly herbaceous layer in clear-cut sites) takes ^{15}N -enriched NH_4^+ from the soil (as NO_3^- leaches down) and the leaves of clear-cut sites, hence, will be more ^{15}N -enriched as compared to the undisturbed mature forest. In the mature forest the nitrification rate is very low and no isotopic enrichment of NH_4^+ due to the nitrification exists, thus the leaves of the natural site should be depleted in ^{15}N compared to the clear-cut sites.

The aim of this paper is to assess:

1. Interspecific variations of N concentrations and ^{15}N natural abundance in needles, branches, and litter;
2. N concentration and ^{15}N gradients along the soil depth;
3. The impact of clear-cutting on the N concentration and $\delta^{15}\text{N}$ distribution in the seedlings and in the forest soil.

MATERIAL AND METHODS

Site description

Two research sites, a natural and mature forest and a nearby recent clear-cut site (5 years old) were selected in southern Finland (61°48'N, 24°19'E). The studied natural boreal coniferous forest site is about 130 years old and it comprises of two dominant conifer tree species, Scot pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). The clear-cut site is adjacent to the natural site and the clear-cutting was done in 1998. The average

annual precipitation in the area is 709 mm and the annual mean temperature during the growing season (May–September) is 12.6°C. The research site is located at the altitude of about 150 m a.s.l. The soil is haplic podzol, which has emerged from under the glacial ice about 10 000 years ago. The soil of the study area consists of homogenous glaci-fluvial sand. The bedrock is mainly acidic granite. The atmospheric N-deposition is very low (less than 5 kg/ha/year) (Kumala et al. 1998).

Sampling

The stand in the area is a mixed forest of pines and spruces. In February–March 1998 a small (size around 1 ha) clear-cut was made within the stand, and the rest of the stand was left untouched to be used as a control forest for clear-cut area. The plant samples (foliage, litter and branches) of mature trees were collected from the trees of the original closed forest. All the pines in the stand were in the dominant canopy class, so only one pine was sampled. Typically for spruces, trees were present in dominant, intermediate and suppressed canopy positions. One sample tree from each canopy layer was randomly selected. Samples of current year and one-, two- and three-year old foliage and branches were taken during spring before the growth period started. The samples were taken from three different proportional heights (bottom, middle and top) of the tree canopy.

The seedlings growing below mature trees and on the clear-cut area were sampled five years after clear-cutting, also before the beginning of the growth period. The current year needles and branches from the top whorls of the seedlings were taken. Litterfall of the clear-cut trees was sampled with 12 circular collectors of 0.5 m² surface area at the height of 1.5 m. The collection was carried out between years 1993–1998 and separated for needles and other litter material. After the clear-cut the litter collection was ceased.

The soil core samples from the time preceding the clear-cut were not available, so we took the soil samples ($n = 8$) representing closed canopy conditions from the mature stand and the clear-cut area soil samples ($n = 8$) from the middle of the clear-cut. The samples were taken at random with a steel soil core sampler (49.5 deep × 5 cm diameters). The soil cores were cut into 0.5–2 cm slices for the laboratory analysis.

For all plots, the soil cores were separated according to their soil horizon and $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$

concentrations were measured by FIA (flow injection analyzer) from the soil solution separated by centrifugation drainage technique described by Giesler and Lundström (1993).

Analytical methods

All the plant and soil samples were dried at 70°C and samples were ground into a fine powder in a planetary mill. Nitrogen and carbon of plant and soil samples were analyzed by CNS analyzer (LECO Corporation, St. Joseph, MI, USA). The isotope of N was measured on the Finnigan MAT Delta Plus stable isotopic ratio mass spectrometer (IRMS) equipped with an elemental analyzer for conversion of N into N₂ (at the Institute of Soil Science and Forest Nutrition, University of Goettingen, Germany). Results of the IRMS measurement were given in δ notation. The δ values of isotope N are expressed as ‰ and calculated as follows (Shearer and Kohl 1993):

$$\delta X = (R_{\text{sample}}/R_{\text{atmos}} - 1) \times 1000 \quad (\text{‰})$$

where: X = ¹⁵N/¹⁴N ratio, R_{sample} = X present in samples, R_{atmos} = X present in atmosphere as standard

RESULTS

Natural δ¹⁵N abundances in the needles and branches by height and age classes of the closed forest site

The δ¹⁵N values did not change continuously from current year to 3-year old needles in either of the tree species (Figure 1). For both species, ¹⁵N abundance depleted significantly (*P* ≤ 0.05) from current year to 2-year old needles and remained almost constant in older needles, except for spruce needles in the bottom part of the canopy. The ¹⁵N natural abundance in the needles was almost constant along the height of the tree. Nitrogen concentrations in the needles decreased significantly (*P* ≤ 0.05) with age in both tree species. Similar to δ¹⁵N values, there were no significant variations of N concentrations in the needles by height, although for spruce a slight but insignificant increase in N concentrations with increasing height was observed (Figure 1). This figure further shows that both species differed significantly (*P* ≤ 0.05) in their N concentrations and ¹⁵N natural abundance. The pine needles had significantly higher N concentrations than spruce needles and the pine needles were significantly more ¹⁵N-depleted than the spruce needles.

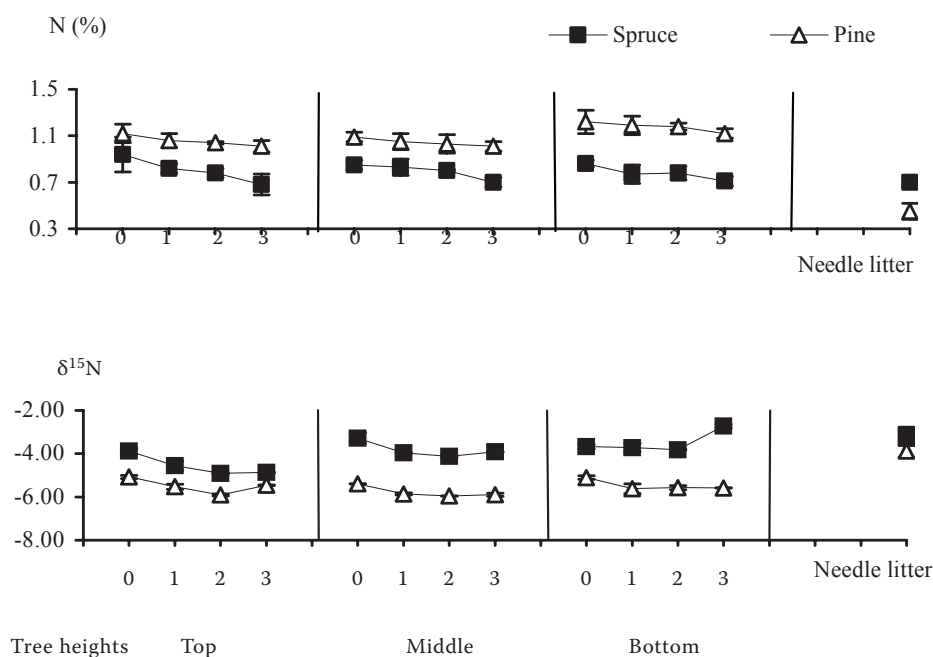


Figure 1. %N and δ¹⁵N (‰) in the needles taken from different heights of spruce and pine trees by the age of needles (years) including needle litter (*n* = 1–3, error bars represent standard error of means)

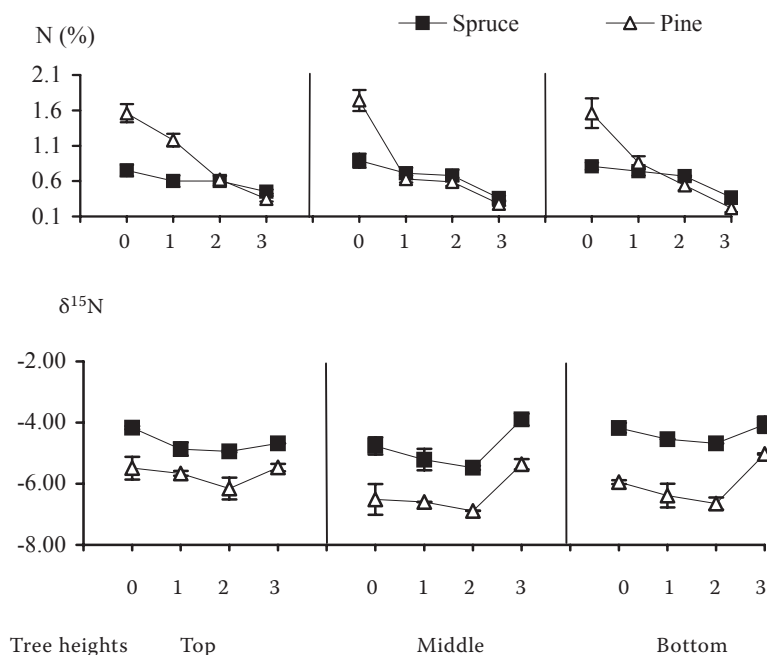


Figure 2. %N and $\delta^{15}\text{N}$ (‰) in the branches of trees taken from different heights of spruce and pine trees by the age of branches (years) ($n = 1-3$, error bars represent standard error of means)

The age dependency in the $\delta^{15}\text{N}$ values of both tree species was more pronounced in branches than in needles (Figure 2). $\delta^{15}\text{N}$ values decreased significantly ($P \leq 0.05$) from current year to 2-year old branches and increased again in the 3rd year branches of both tree species. Similar to needles, there was no significant height variation in $\delta^{15}\text{N}$ of the branches of either species. N concentration in the pine branches was significantly higher ($P \leq 0.05$) than that in the spruce branches (Figures 1 and 2), but branch N concentrations did not significantly differ between the examined heights of trees.

Natural $\delta^{15}\text{N}$ abundance and N concentrations in needle-to-soil continuum

For both stands, we observed a typical ^{15}N enrichment from the different tree components (needles, needle-litter and branches) to different soil depths; ^{15}N increased in the order vegetation < humus < mineral soil (Figure 3). For the needles of the closed forest site, the total mean value (across all needle height and age classes) of $\delta^{15}\text{N}$ in the spruce needles (-4.0‰ , $\text{SE} \pm 0.2\text{‰}$) was significantly ($P \leq 0.05$) higher than the value of pine needles (-5.6‰ , $\text{SE} \pm 0.1\text{‰}$) (Figure 3). Similar results were observed with the seedling needle $\delta^{15}\text{N}$ values, i.e. spruce seedling needles in closed forest were significantly more ^{15}N -enriched

(-5.0‰) than pine needles (-6.0‰). Same as in the closed forest, spruce needles at the clear-cut site were significantly ($P \leq 0.05$) more ^{15}N -enriched than pine needles. The mean $\delta^{15}\text{N}$ values of both spruce (-2.1‰ , $\text{SE} \pm 0.3$) and pine seedling needles (-2.8‰ , $\text{SE} \pm 0.2$) at the clear-cut site were significantly more enriched than those found in mature tree needles as well as needles of seedlings grown in the closed forest (Figure 3). For the closed forest, pine needle N concentrations were significantly ($P \leq 0.05$) higher (1.09% , $\text{SE} \pm 0.02$) compared to spruce (0.79% , $\text{SE} \pm 0.02$). For the clear-cut site, seedlings needles N concentrations in pine (1.01% , $\text{SE} \pm 0.07$) were significantly ($P \leq 0.05$) greater than those found in spruce (0.74% , $\text{SE} \pm 0.04$) (Figure 4). At the clear-cut site, N concentrations of needles of both tree species were generally slightly lower compared to those in the closed forest (Figure 4).

Spruce needle litter of the closed forest site, (-3.2‰ , $\text{SE} \pm 0.6$) was slightly more ^{15}N -enriched (but insignificantly) than the pine needle litter (-3.9‰ , $\text{SE} \pm 0.6$). In both tree species, the needle litter was more ^{15}N -enriched in comparison to the green needle in both species. ^{15}N -enrichment of litter by 1.7‰ (green needle – needle litter) in pine was significantly higher compared to spruce (^{15}N -enrichment by 0.8‰). The litter of both species contained lower N concentrations than the green needles due to the translocation of mobile N

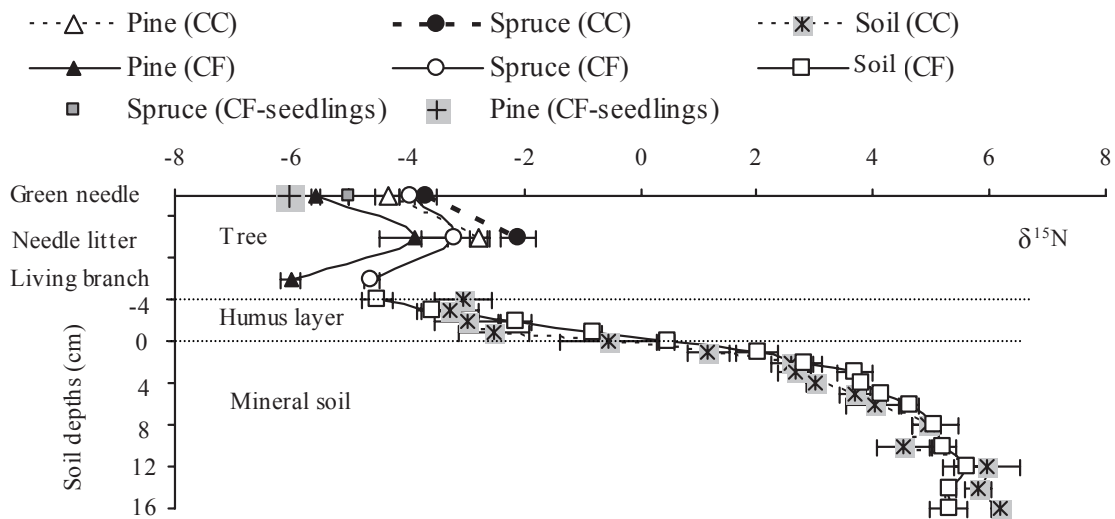


Figure 3. Mean $\delta^{15}\text{N}$ values (‰) in the needle-to-soil continuum of both closed forest and clear-cut sites (CC = clear-cut, CF = closed forest, $n = 3-8$, error bars represent standard error of means)

to twigs and branches before their fall. The re-translocation of N calculated as the percentage difference of N between oldest age class of green needle and the litter (i.e. oldest age class green needle – litter/oldest age class green needle \times 100) by pine needle litter was significantly higher (57%) compared to spruce needle litter (1.41%).

For the closed forest, the branches of spruce (-4.6% , $\text{SE} \pm 0.1$) were significantly ($P \leq 0.05$) more enriched in ^{15}N compared to the branches of pine (-6.0% , $\text{SE} \pm 0.2$). Similar order in comparison between species, but with more enriched values were obtained for the clear-cut site. The living

branches of spruce seedlings (-3.7% , $\text{SE} \pm 0.2$) in a clear-cut site were also significantly ($P \leq 0.05$) more enriched in ^{15}N in comparison to the branches of pine seedlings (-4.3% , $\text{SE} \pm 0.2$). The branches of both tree species were significantly ($P \leq 0.05$) more depleted in ^{15}N than their needles. N concentrations in the branches of both tree species at the clear-cut site were slightly lower than those observed in the closed forest (Figure 4). Furthermore, pine branches had significantly ($P \leq 0.05$) higher N concentration (0.78% , $\text{SE} \pm 0.06$) than spruce branches (0.60% , $\text{SE} \pm 0.03$) and this difference was also similar for the needles (Figure 4).

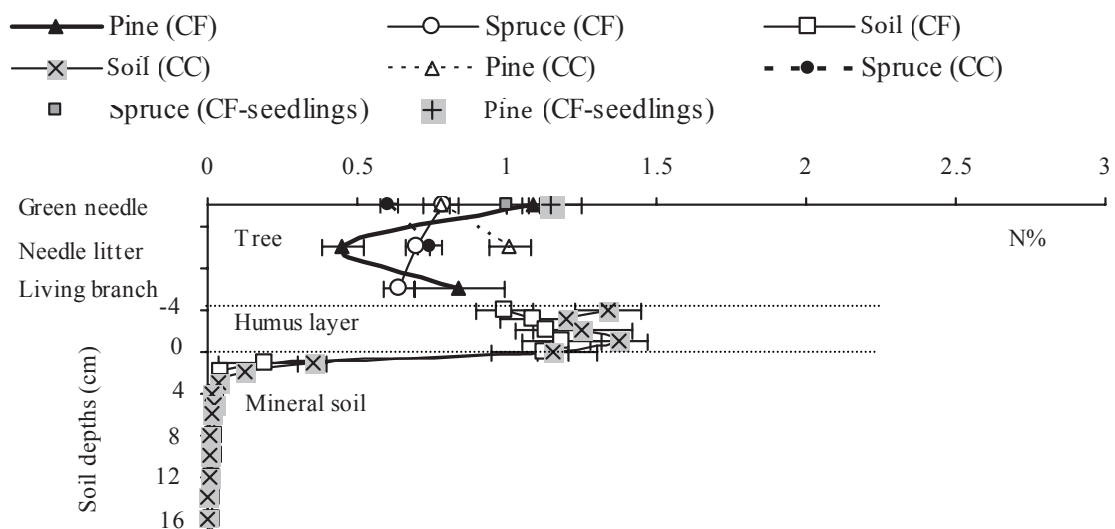


Figure 4. Mean N% values in the needle-to-soil continuum of both closed forest and clear-cut site (CC = clear-cut, CF = closed forest, $n = 3-8$, error bars represent standard error of means)

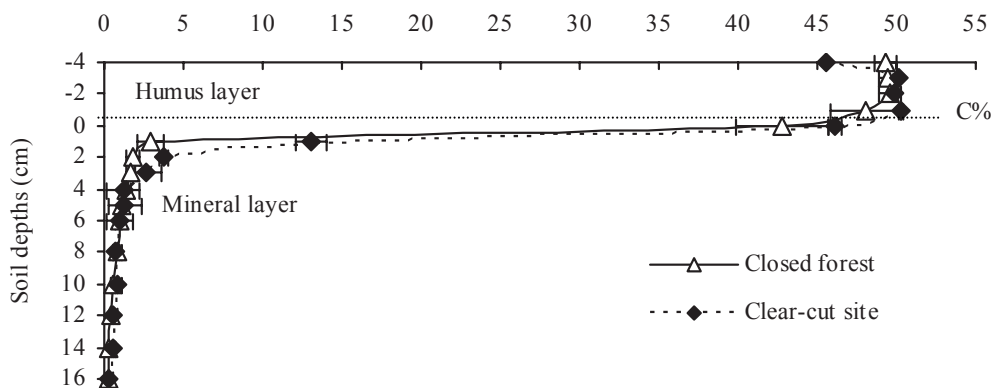


Figure 5. Mean C% values in the different layers of soils of both closed forest and clear-cut site ($n = 8$, error bars represent standard error of means)

In general, we observed typical ^{15}N enrichment with the increasing soil depths (Figure 3) for the soil of both closed and clear-cut forest sites. In the natural forest site the variations of $\delta^{15}\text{N}$ from the uppermost organic soil layer to the lowermost mineral soil depths ranged from -4.5‰ (± 0.27) to $+5.6\text{‰}$ (± 0.41), whereas in the clear-cut stand it was from -3.3‰ (± 0.49) to $+6.2\text{‰}$ (± 0.13). From the Figure 3 it is evident that both plots differed significantly only in their humus $\delta^{15}\text{N}$ values, but they did not differ significantly in their mineral soil $\delta^{15}\text{N}$ values. The uppermost soil organic layer (0 cm depth) of the clear-cut site was significantly ($P \leq 0.05$) more enriched in $\delta^{15}\text{N}$ (-3.0‰ , $\text{SE} \pm 0.50$) compared to that of closed forest (-4.5‰ , $\text{SE} \pm 0.27$). Opposite to the $\delta^{15}\text{N}$ trend, there is a decreasing trend of N and C concentrations with the increasing soil depths in both plots (Figures 4 and 5).

Figure 6 illustrates the $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ concentrations of the centrifuged soil water in different horizons of the forest and clear-cut site soils. From this figure, we can observe that $\text{NO}_3\text{-N}$ concentration in soil water is significantly higher after clear-cut.

DISCUSSION

Trends in the N concentrations and $\delta^{15}\text{N}$ values in the needles and branches of closed forest sites according to the age and the height

The ^{15}N abundance levels of the vegetation of our research sites are consistent with the results reported for other conifer forests (Gebauer and Schulze 1991, Gebauer and Dietrich 1993, Garten

and Miegroet 1994, Koopmann et al. 1997, Sah and Brumme 2003). However, higher positive values of $\delta^{15}\text{N}$ in the needles of conifer species (from -2.14 to -1.70‰) were reported in N-saturated forests of Europe; they were attributed to higher anthropogenic N-deposition (containing enriched ^{15}N) at these sites (Gebauer et al. 1994, Koopmann et al. 1997, Sah and Brumme 2003).

Our findings that the needle ^{15}N abundance (in both conifer tree species) decreased from current to 2-year old needles and remained constant in older needles, corresponds to other studies (Gebauer and Schulze 1991, Gebauer et al. 1994, Koopmann et al. 1997, Emmet et al. 1998). The non-continuous shift of $\delta^{15}\text{N}$ values from current year to 3-year old needles indicates major transformations of N between plant compartments. A decrease in $\delta^{15}\text{N}$ values for current year to 2–3-year old needles reflects the fact that the younger needles are anabolically more active than older needles, and thus represent a greater sink for assimilated nitrogen. Conversely, an increase in $\delta^{15}\text{N}$ values in older needles may reflect ^{15}N -discrimination with catabolic breakdown and a subsequent export of nitrogenous compounds from the older leaves. Kolb and Evans (2002) from their greenhouse ^{15}N -labelling studies of deciduous plant species also supported this view experimentally, suggesting ^{15}N -discrimination occurs with reallocation of recycled N (from stem) to younger needles. They further concluded that the contribution of recycled nitrogen to leaf production varied with timing of leaf development; as more leaves were produced, the contribution of recycled N decreased until all leaf N was derived from absorbed sources (other than recycled). This pattern of reliance

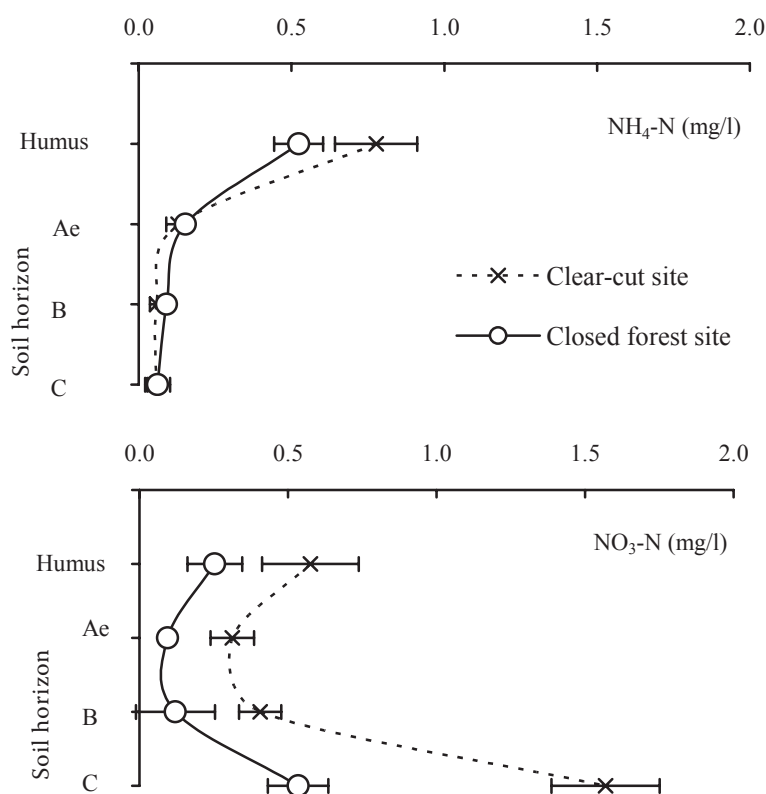


Figure 6. $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ concentrations in the different soil horizons of both closed and clear-cut forests

on recycled N for early leaf production was also found in herbaceous perennials (Bausenwein et al. 2001a, b), shrubs (Grelet et al. 2001), deciduous (Nielsen et al. 1997, Malaguti et al. 2001) and evergreen trees (Proe and Millard 1995, Stephens et al. 2001). Thus the reliance of perennial plants on recycled N for spring leaf production appears to be a widespread phenomenon, which suggests that many plants have enhanced seasonal uptake of N by sequestering a substantial portion of N from ephemeral tissues.

The ^{15}N -discrimination with recycling of N is likely to be due to the incomplete breakdown of N storage proteins into different amino acids that are transported through the xylem and incorporated into new leaf tissue. Few studies suggest that a few amino acids (such as, asparagine, glutamine, aspartic acid and arginine) may be involved in N remobilization (Malaguti et al. 2001). All of these (with the exception of aspartic acid) contain more than two N atoms, and it was found that at least with arginine the $\delta^{15}\text{N}$ value of the amino acid varied greatly depending on the extent of N enrichment at various positions (Medina and Schmidt 1982). Molecular heterogeneity in ^{15}N -enrichment could be the result of different enzymatic reactions in-

involved in forming the molecules and/or different catabolic pathways leading to slight differences in N source pools (Yoneyama et al. 1998). Another process that may cause differences in isotopic composition of internal N pools is discrimination during loss of volatile amines or ammonia during the protein hydrolysis that accompanies leaf senescence (Shearer and Kohl 1986).

The $\delta^{15}\text{N}$ values of branches found in our study correspond to other studies and are lower than in the needles studied by other researchers (Gebauer and Schulze 1991, Emmet et al. 1998). The age dependency was more pronounced in branches than in needles. The trend of decreasing $\delta^{15}\text{N}$ values from current year to 2-year old branches and increasing again from 2nd year to 3rd year branches corresponds to other studies (Emmet et al. 1998). Similar to needles, this indicates a greater sink for assimilated N in younger branches.

Interspecific variations of foliar and litter $\delta^{15}\text{N}$ and N concentrations in closed forests

N concentrations in all studied vegetation components (except for the litter) are significantly

higher in pines compared to spruces. The litter fall of both tree species in our study were more ^{15}N -enriched compared to green needles and can be attributed to ^{15}N discrimination during retranslocation of N from needles to twigs before needle litterfall (Gebauer and Schulze 1991, Gebauer et al. 1994, Nasholm 1994).

Needles of pine were much more ^{15}N -depleted than those of spruce, which means that pine takes more ^{15}N -depleted N during plant N-uptake compared to spruce at the same site. This might be due to several reasons such as rooting depth variations between tree species and mycorrhizal infections variations. The interspecific foliar N and $\delta^{15}\text{N}$ variations due to different rooting depth are based on the fact that soil tends to become $\delta^{15}\text{N}$ enriched with the increasing depth. In our studies, the ^{15}N -enrichment of needles in pine cannot be related to the rooting depth, as both species are rooted primarily in the upper organic soil horizon (Helmisaari et al. 1999). Another reason might be the variation in the fungal associates of roots in both tree species. In our studies no mycorrhizal studies of roots have been done, but some other studies reported differences in fungal associates in pine and spruce roots on the same stand (Bothwell et al. 2001). The mycorrhizal fungi associated with a tree species influence its nutrition as they differ in their ability to capture, store and transfer N to the host (Abuzinadah et al. 1986, Hobbie et al. 2000). Hence, we assume that ^{15}N -depletion of pine needles might be attributed to the different types of mycorrhizal associations in pine roots in comparison to spruce roots; this may lead the differences in the proportion of mycorrhizal N-uptake. We assume that pine takes more depleted N due to the higher proportion of its mycorrhizal N uptake as soil N source compared to spruce, since the isotopic fractionation during N-transfer from mycorrhizas to plants leads to depletion of $\delta^{15}\text{N}$ values compared to the source soil N.

In our case, the amount of N atmospheric deposition was negligible and the site was N-limited; thus the role of mycorrhizas appears to be important during plant N-uptake. These observations support our assumptions that in our N-limited sites, higher N concentrations in pine are due to higher proportion of N uptake from mycorrhizal fungi as soil N source. Similar results were reported in other studies, and they were attributed to the higher proportion of mycorrhizal infections in pine roots and not to the rooting depths (Bothwell et al. 2001, Kitayama and Iwamoto 2001). Such characteristics of pine species may thus allow

pines to outperform spruce on N-limited sites (Bothwell et al. 2001).

The trend of $\delta^{15}\text{N}$ from needle-to-soil continuum in closed forest

Our results have shown that generally the natural abundances of ^{15}N in the vegetation and soil occurred in the following order: branches < green needles < needle litter < uppermost soil organic layer < mineral soil. This typical ^{15}N -enrichment from the vegetation to soil observed in our study is consistent with other studies; this pattern reflects an isotopic discrimination of $\delta^{15}\text{N}$ during mineralisation of soil N as indicated by the decrease of total soil N (C does not increase along with depth) with depth (Shearer et al. 1974, Nadelhoffer and Fry 1988, 1994, Gebauer and Schulze 1991, Garten and Miegroet 1994, Högberg et al. 1996, Koopmann 1996, Koopmann et al. 1997, Emmet et al. 1998). The mechanistic level is still controversial. ^{15}N discrimination during microbial decomposition and leaching of depleted nitrate may be the most important process, resulting in the gradual ^{15}N -enrichment of the residual organic matter (Nadelhoffer and Fry 1988, 1994, Mellilo et al. 1989).

Impacts of clear-cutting on the needle and soil ^{15}N -fractionation

Our hypothesis on the possible impacts of clear-cutting on the forest soil ^{15}N fractionation is presented in Figure 7. After clear-felling, the nitrification increases and ^{15}N -enriched NH_4^+ is produced in the soil (Högbohm et al. 2002). The foliage of trees and herbaceous layer in clear-cut sites should take ^{15}N -enriched NH_4^+ from soil and leaves of clear-cut sites; hence, it will be more ^{15}N -enriched compared to the undisturbed natural forest. This assumption is supported by our results, i.e. seedling needles of both tree species and the upper soil organic layer are more ^{15}N -enriched at the clear-cut site than those of closed forest site. Such changes in N cycle and patterns will ultimately feed back on soil profile development as shown in Figure 5. Therefore, we assumed that the difference between $\delta^{15}\text{N}$ of the upper soil horizon and lower soil horizon, at the clear-cut site, should be very narrow compared to the undisturbed forest soil profile; this assumption is supported by our study as well (Figure 7).

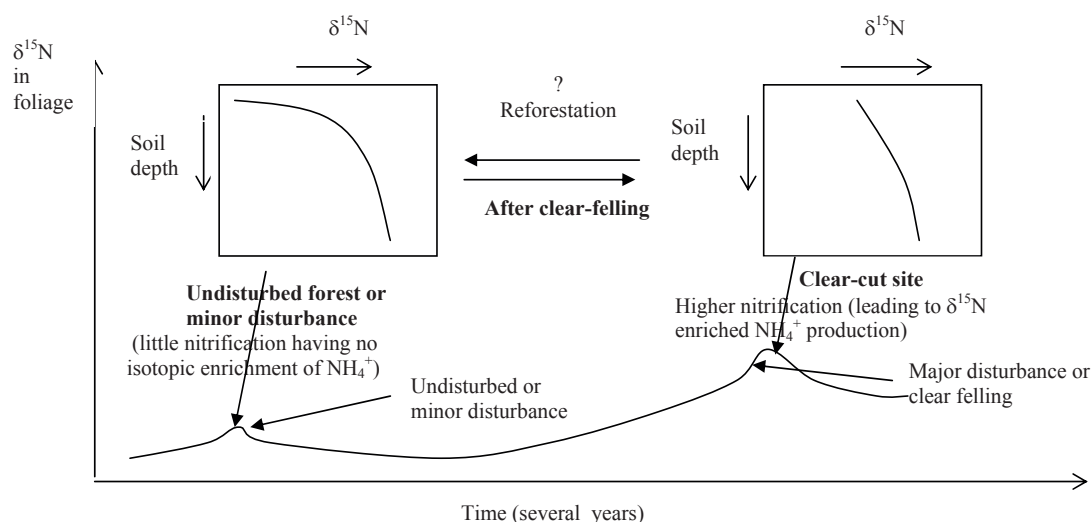


Figure 7. Hypothetical development of $\delta^{15}\text{N}$ of foliage of forest trees during a phase from undisturbed to clear-cutting over time. The $\delta^{15}\text{N}$ of soil profiles at two points in time are shown in inserts (modified after Högborg 1996)

In the natural forest, little nitrification occurs and has no isotopic enrichment of NH_4^+ and the leaves of the natural site are depleted in ^{15}N compared to the clear-cut sites. Such changes in N cycle patterns will ultimately feed back on soil profile development as shown in Figure 7. In our studied sites we observed significantly higher NO_3^- -N concentrations in soil water (25 cm depth) from the clear-cut sites than at the closed forest site (Figure 6).

The interspecific variations in natural ^{15}N abundance in the vegetation of the same habitat observed in our study reflect their different N sources. Furthermore, we also recorded that ^{15}N natural abundance in needles and soil also functions as an indicator of the N dynamics after clear-cutting. However, at present we have no data on the long-term effect of reforestation as shown in Figure 7, but we assume that the reforestation after clear-cutting would result in a declination of NO_3^- -leaching, which would subsequently lead to ^{15}N -depletion of needles and humus compared to clear cutting condition; in other words, this process should be reversible. Further measurements of the fluxes of C and N through mycorrhizal fungi are needed to assess properly their role in the ecosystem and to test the suggested hypotheses accounting for the observed patterns in plant $\delta^{15}\text{N}$ values.

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