

Abstract

Seasonal and spatial variations in foliar nitrogen (N) parameters were investigated in three European forests with different tree species, viz. beech (*Fagus sylvatica* L.), Douglas fir (*Pseudotsuga menziesii*, Mirb., Franco) and Scots pine (*Pinus sylvestris* L.) in Denmark, The Netherlands and Finland, respectively. This was done in order to obtain information about functional acclimation, tree internal N conservation and its relevance for both ecosystem internal N cycling and foliar N exchange with the atmosphere.

Leaf N pools generally showed much higher seasonal variability in beech trees than in the coniferous canopies. The concentrations of N and chlorophyll in the beech leaves were synchronized with the seasonal course of solar radiation implying close physiological acclimation, which was not observed in the coniferous needles. During phases of intensive N metabolism in the beech leaves, the NH_4^+ concentration rose considerably. This was compensated for by a strong pH decrease resulting in relatively low Γ values (ratio between tissue NH_4^+ and H^+). The Γ values in the coniferous were even smaller than in beech, indicating low probability of NH_3 emissions from the foliage to the atmosphere as an N conserving mechanism. The reduction in foliage N content during senescence was interpreted as N re-translocation from the senescing leaves into the rest of the trees. The N re-translocation efficiency (η_r) ranged from 37 to 70 % and decreased with the time necessary for full renewal of the canopy foliage. Comparison with literature data from in total 23 tree species showed a general tendency for η_r to on average be reduced by 8 % per year the canopy stays longer, i.e. with each additional year it takes for canopy renewal. The boreal pine site returned the lowest amount of N via foliage litter to the soil, while the temperate Douglas fir stand which had the largest peak canopy N content and the lowest η_r returned the highest amount of N to the soil. These results support the hypothesis that a high N status, e.g. as a consequence of chronically high atmospheric N inputs, increases ecosystem internal over tree-bulk-tissue internal N cycling in conifer stands. The two evergreen tree species investigated in the present study behaved very differently in all relevant parameters, i.e.

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needle longevity, N_c and η_r , showing that generalisations on tree internal vs. ecosystem internal N cycling cannot be made on the basis of the leaf habit alone.

1 Introduction

Forests cover 44 % of the land area in Europe (FAO, 2006). Nitrogen (N) fluxes and turnover in forests are therefore relevant for biogeochemical cycling of N in Europe (Sutton et al., 2011). Forest ecosystems are generally considered to be adapted to N limitation rather than N excess (Vitousek and Howarth, 1991; Rennenberg et al., 1998; Aerts, 1996; Xia and Wan, 2008). Due to deposition of atmospheric NH_3 , the critical N load for European forest ecosystems may often be exceeded (Cape et al., 2009; Pinho et al., 2012). This may in turn lead to elevated concentrations of NH_4^+ and organic N compounds in the trees and NH_3 emission events (Rennenberg et al., 1998; Fowler et al., 2009). The physiological drivers controlling the direction and magnitude of NH_3 exchange between trees and the atmosphere are not well established. For this reason, more information about seasonal changes in plant N status and turnover is required to improve modelling of NH_3 exchange over forest ecosystems (Massad et al., 2008, 2010).

Even under conditions with high atmospheric N deposition loads to forests, internal N fluxes between the trees and the soil (ecosystem internal cycling) and within trees (tree internal cycling) are generally larger than the external N fluxes associated with leaching and gaseous emissions (Gundersen, 1998; Nadelhoffer et al., 1999). Ecosystem internal N cycling takes place via processes such as litter production, mineralisation and root uptake, while tree internal N cycling occurs via assimilation, re-translocation and storage. By these processes, large amounts of N are kept plant available in the system and are being moderately protected against immobilisation in stable soil organic compounds or losses via leaching and gaseous emission. N in the ecosystem internal cycle is more prone to being lost than N in the tree internal cycle, although foliar N may

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contribute to NH_3 emission in fertile systems under conditions with low atmospheric NH_3 concentrations (Wang et al., 2011).

Internal N re-translocation and cycling patterns in trees are seasonally programmed and closely linked to tree phenology. For instance, in deciduous trees, leaf N tends to be translocated into the woody roots and/or the trunks before leaf fall, to support tree growth in the following spring. In evergreen trees, N stored in previous-years leaves can nourish new leaf growth and, especially in most conifers, the youngest age class of needles are the main sites of N storage (Millard and Grelet, 2010). In N-limited forests, trees face a relatively high selection pressure to balance the N economy with acquisition, retention and remobilization (Pearson et al., 2002). Knowledge about interaction between foliar N status and N re-translocation efficiency in tree species differing in leaf longevity is still limited.

It can be hypothesized that deciduous canopies will distribute N more closely according to the needs for photosynthesis than is the case for longer-lived conifer needles and that the proportion of tree internal N re-translocation in general will be larger in deciduous canopies than in coniferous canopies. Along with this it will be expected that N pollution may lead to an opening of the N cycle, i.e. increase the importance of ecosystem internal over tree internal N cycling with the consequence of higher probability of N losses via leaching and gaseous emissions. To test these hypotheses, the objective of the present work was to investigate the distribution of N pools within the canopies of different forests and relate this distribution to factors and plant strategies controlling leaf development throughout the seasonal course of a vegetation period. The experimental sites included a deciduous and a coniferous forest situated in strong and medium N polluted areas in temperate Europe (The Netherlands and Denmark, respectively) together with a conifer forest in Central Finland with low N pollution. Different N parameters such as chlorophyll, N concentration per unit dry matter, C/N ratio, soluble NH_4^+ , H^+ , and the N content per unit leaf surface area were measured in order to obtain information on the relation to CO_2 assimilation, tree and ecosystem internal N cycling, and potential for NH_3 exchange with the atmosphere.

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2 Materials and methods

2.1 Site description and sampling of plant material

The experimental sites included a Danish beech forest, a Dutch Douglas fir forest and a Finnish Scots pine forest. Details of the three localities are given in Table 1. The mean annual air temperatures in the experimental years were 9.2 and 8.6 °C for the beech forest, 10.2, 10.2 and 8.7 °C for the fir forest and 3.2 and 3.9 °C for the pine forest (Fig. 1). The corresponding precipitation values were 794 and 703 mm, 825, 735 and 780 mm, and 903 and 496 mm (Fig. 1).

It is important to note that the pollution with atmospheric N components differed largely between the sites. The average atmospheric NH₃ concentrations at the Dutch Douglas fir site was much higher (3.9 µg NH₃-N m⁻³) than at the Danish beech forest site (1.3 µg NH₃-N m⁻³) and at the Finish pine site (0.1 µg NH₃-N m⁻³). The NH₃ concentrations were measured with denuders at the sites and are annual averages from monthly integrating samples (Flechard et al., 2011).

Leaves and needles were collected once or twice per month in 2008 and 2009 from the top (representing sun branches) and base (shade branches) of the crowns of 4 sample trees. In addition, monthly samples were taken in the fir forest in 2010. The needle samples were collected to obtain a representative mixture of different age classes. All plant samples were quickly weighed and frozen in liquid nitrogen upon sampling. Representative subsamples were lyophilized or oven dried at 70 °C.

2.2 Leaf analyses

Chlorophyll a (Chl *a*) and chlorophyll b (Chl *b*) concentrations in the leaves and needles were measured because these parameters are useful indicators of the physiological activity and degree of senescence of the tissues. Extraction of chlorophyll was carried out by use of methanol for beech leaves, while dimethyl sulfoxide (DMSO) was used for coniferous needles. For analysis of bulk tissue NH₄⁺ concentrations and pH,

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frozen leaves were ground in 10 mM formic acid or milli-Q water, respectively. NH_4^+ was analyzed using fluorometric detection after derivatization with *o*-phthaldialdehyde by FLUOstar (BMG LABTECH, Germany). For bulk tissue pH measurements, 0.2 g of leaf tissue was homogenized in a mortar on ice using 2 ml of deionized water with a little sand. The homogenate was centrifuged at 14 000 g (4 °C) for 10 min and pH in the supernatant measured with a microelectrode (Metrohm, Herisau, Switzerland).

The NH_3 emission potential of bulk tissue extract was estimated based on the parameter Γ which is defined as:

$$\Gamma = \frac{[\text{NH}_4^+]}{[\text{H}^+]}$$

where $[\text{NH}_4^+]$ and $[\text{H}^+]$ are the NH_4^+ concentration and the proton concentration ($[\text{H}^+] = 10^{-\text{pH}}$) in the extracts, respectively.

Dried samples were analysed for total C and N by mass spectrometry in a system consisting of an ANCA-SL Elemental Analyzer coupled to a 20-20 Tracermass Mass spectrometer (SerCon Ltd., Crewe, UK).

2.3 Calculation of canopy N content and N re-translocation from senescing leaves and needles

The canopy N content (N_c), i.e. the N content of the leaves or needles per unit ground area, was calculated as the product of the measured leaf area index (LAI) and the N content per unit leaf area using measured N concentrations and specific leaf areas (SLA) from beech leaves (30 and 15 m² kg⁻¹ for leaves in canopy top and base, respectively) and Douglas fir needles (79 and 54 m² kg⁻¹ for canopy top and base, respectively). For the boreal pine stand, N_c was calculated as the product of average needle N content, obtained in the present study, and estimated needle masses (466 g DW m⁻²) that were derived from biometric relationships based on measured trunk diameters at 1.3 m and tree heights as input (Repola, 2009).

The N re-translocation in beech was estimated as the product of the measured LAI and the difference in N content per unit leaf area in summer and that of fallen leaves. In the conifer stands the fallen needles were separated from the rest of the litter. The annual dry mass of green and active needles that were later shed in a year was estimated as the product of a published mass loss factor between green and brown needles (1×1.53^{-1} , Helmisaari, 1992) and the measured amount of needle litter production. This needle mass was then multiplied with the differences in N contents between green and brown needles. From mass balance equations and litter production the mass loss factor for the Dutch fir forest was estimated to be 1×1.48^{-1} , i.e. very similar to that of pine.

3 Results

3.1 Chlorophyll in leaves and needles

Both the chlorophyll concentration and the Chl *a*/Chl *b* ratio in beech increased steeply (Fig. 2a1, a2) during the first half of the vegetation period (May to August), i.e. far beyond the leaf expansion phase, which lasted only until June. Senescence started at the end of September and was accompanied by a strong decrease in chlorophyll concentration and subsequent sharp reduction of Chl *a*/Chl *b*. (Fig. 2, a2). Totally different from the deciduous trees, the chlorophyll concentration as well as the Chl *a*/Chl *b* in the evergreen trees remained constant throughout the seasons (Fig. 2b1, b2, c1, c2). In general, the chlorophyll concentration at the canopy base was larger than that at the canopy top in both deciduous and coniferous trees.

3.2 Total nitrogen and carbon concentrations

The seasonal pattern of foliar dry matter N concentration differed among the two leaf habits (Fig. 3a1, b1, c1). The highest N concentrations were observed in beech leaves, peaking at about 3.5 % in very young leaves and thereupon steadily declining to around

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1 % in senescent leaves. In the late summer period of both observed years, senescence started earlier and the reduction in N concentration progressed faster in leaves in the top of the beech canopy, i.e. sun crown leaves, compared to leaves at the base, i.e. shade crown leaves (Fig. 3a1).

5 The N concentration in Douglas fir needles did not show any seasonal trend but varied almost randomly between 1.5 and 2.2 %. In the Scots pine needles, the N concentration increased steadily from around 1 % to 1.3 % over the summer period and thereafter gradually declined over the following winter and spring. The beech and Scots pine canopies had slightly larger N concentrations at the canopy base compared to the
10 top, while the Douglas fir trees had similar N concentrations in both canopy layers. The midsummer N concentration was largest in beech leaves (2.5 %) compared to Douglas fir (2 %) and the boreal pine (1.5 %). The ratio between C and N was relatively low, around 11, in very young beech leaves, but increased dramatically to above 40 during senescence, reflecting N re-translocation from the senescing beech leaves
15 into the tree (Fig. 3a2). Douglas fir needles had a relatively constant C/N around 25 (Fig. 3b2, Table 2), while Scots pine needles during most of the season had values above 40 (Fig. 3c2), i.e. 10 % higher than the beech leaves that were shed from the trees in autumn. Beech leaves had the lowest N content per unit surface area and showed a progressive decline compared to needles of fir and pine, which showed little seasonal variation (Fig. 3a3, b3, c3). The vertical variation in beech leaves was
20 strongest with shade leaves containing only 50 % of the N per unit leaf area compared to the sun crown leaves. Douglas fir shade needles contained approx. 30 % less N, i.e. 2.3 g N m^{-2} , than the sun crown needles with approximately 3.4 g N m^{-2} . In contrast, the N content in pine needles was similar at both heights within the canopy, attaining a value of around 3.3 g N m^{-2} .

3.3 Bulk tissue NH_4^+ and ratio between NH_4^+ and H^+ (Γ value)

Surprisingly high bulk tissue NH_4^+ concentrations, 10 mM in the top canopy leaves, were measured in very young beech leaves sampled in the canopy top just after bud break.

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In fully developed green leaves, bulk tissue NH_4^+ levels were relatively low (around 0.5–1.0 mM), but increased during senescence (Fig. 4a1). Tissue NH_4^+ concentrations in Douglas fir needles were on average around 1.3 mM in base needles and 0.8 mM in top needles, except for the first summer period, where lower values were recorded (Fig. 4b1). Scots pine needles had NH_4^+ concentrations around 0.4 mM, increasing to about 0.6 mM during the summer period, but showed smaller seasonal variation than the other two species (Fig. 4c1).

Bulk tissue Γ (Fig. 4a3, b3, c3), the ratio between tissue concentrations of NH_4^+ (Fig. 4a1, b1, c1) and H^+ (Fig. 4a2, b2, c2), was calculated as a simple indicator for comparison of NH_3 exchange potential among the different tree species. The seasonal variation of Γ values in beech leaves paralleled that of bulk tissue H^+ rather than that of NH_4^+ concentration. Consequently, due to low pH in the young beech leaves, Γ values also turned relatively low (200–400). Beech Γ values peaked at around 400–500 during late summer, but decreased again to around 200 during senescence (Fig. 4a3). This decline occurred in spite of increasing NH_4^+ concentrations due to the substantial decrease in bulk tissue pH (Fig. 4a2).

The coniferous trees exhibited much lower Γ values than the beech (Fig. 4). Douglas fir trees showed clear differences in Γ values between needles in the top and the base of the canopies. The largest Γ values, fluctuating between 20 and 120, were recorded in the base needles due to higher NH_4^+ concentrations and lower H^+ (higher pH). In the top layer, Γ in Douglas fir needles consistently remained very low (< 10 in most cases). Scots pine showed only moderate differences in Γ values between needles between the top and the base of the canopy (Fig. 4a3). In both layers, the Γ values reached a minimum of around 10 during late summer and increased to around 40 during the winter and spring.

3.4 Canopy nitrogen contents, N re-translocation and foliar litter production

The foliage N concentration data obtained in this study were combined with field data from the intensively investigated forest sites in order to obtain information on N cycling

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in the tree stands and in the ecosystems (see Sect. 2.3). Table 2 gives an overview on how the C/N ratio differed between the green and fully active leaves/needles and the brown senescent ones. The change in foliar N content was used to calculate leaf N stocks and fluxes on ecosystem scale. During senescence the C/N ratio increased by 37 % to 50 %. The reduction in N concentration is like in many other studies interpreted as being caused by tree internal N re-translocation, despite possible other mechanisms that might lead to the same phenomenon (see further discussion in 4.3).

The average longevity of the leaves and needles differed not only between the deciduous and the evergreen canopies but as well among the two coniferous tree species (Table 2). The needles were kept longer in the Douglas fir stand compared to the boreal pine stand. Very large differences between the sites were shown in the values for peak summer canopy N content (N_c). The N content of the temperate Douglas fir canopy was 4–5 times larger than those in the two other forests, which had very similar N_c despite their different leaf habits.

The ratios between the fraction of tree internal N cycling (F_i , i.e. N re-translocation) and ecosystem internal N cycling (F_e , i.e. the N flux in total aboveground litter), was calculated as 60 %, 50 % and 89 % for the beech, the fir and the pine forests, respectively (Table 2). In the beech forest intensive fruit production increased the N flux in the litter by 60 % compared to normal years. In such normal years F_i/F_e would most probably be higher. The fraction F_i/F_e depended on the combined effects of the amount and longevity of leaves in relation to the rate of litter production from structural and reproductive plant material. All these factors differed across the investigated forests. The forest with the lowest N status had the highest F_i/F_e .

The absolute amount of N re-translocation was very similar between the two temperate sites (4.4 and 3.4 $\text{gNm}^{-2}\text{yr}^{-1}$), despite their contrasting leaf habit and N_c , while the boreal site re-translocated much less (1.7 $\text{gNm}^{-2}\text{yr}^{-1}$). In relative terms, this picture changed completely. The fraction of N re-translocation relative to the initial N content in the green leaves, or in other words the N re-translocation efficiency (η_r) was lowest in the Douglas fir stand (37 %) and similar among the temperate beech (70 %) and the

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boreal pine stand (62%). The η_r decreased strongly with increasing time it takes on average to renew the foliage completely (Fig. 5). For comparison, we also show similar literature data on this relationship (Staaf, 1982; Son and Gover, 1991; Näsholm et al., 1994; Reich et al., 1995; Escudero and Mediavilla, 2003) in the same graph. When N re-translocation was related to N_c , the contrasts between the sites became even more obvious. Assuming steady state of N_c in the time scale of a few years, we calculated the amount of N that was invested in new leaves during year 2009. The N investment in new foliage is by definition strictly related to the N_c and the averaged longevity of leaves or needles. More interesting is how much of this is covered by formerly re-translocated N and which additional amount needs to be taken from either external N uptake or tree internal reorganisation of N reserves. The resulting additional N-uptake, which is numerically identical with the N flux in foliage litter production, ranged between 19 and 30 % of N_c with beech having the highest and pine the lowest value (Table 2).

4 Discussion

4.1 Differences in seasonal and spatial variation of foliar N concentrations in tree canopies across the investigated forest stands

Foliar N concentrations in beech trees decreased during spring as the leaves expanded and increased in dry matter weight over only a few weeks. During this phase the leaf N was diluted by the build-up of C rich leaf structural material. Thereafter the N concentrations remained constant until the onset of senescence, when N became remobilized from the leaves to perennial woody parts, leading to a rapid decrease in both the N and chlorophyll concentrations (Figs. 3a1 and 2a1; see also Bauer et al., 1997; Millard and Grelet, 2010). The intensive N re-translocation is necessary to conserve N for leaf establishment in spring independently of soil N availability (Santa-Regina and Tarazona, 2001). The N re-translocation efficiency was about 55 % and 76 % for leaves at the canopy base and top of the beech trees, respectively. Similar values have been

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observed for beech trees at different sites in The Netherlands (Staaf, 1982) and in Japan (Yasumura et al., 2005). Beech leaves at the top and the base of the canopy started the growing season with similar dry matter N concentrations, whereupon the base leaves attained higher N concentrations during summer and autumn, reflecting higher chlorophyll concentrations (Fig. 2a1).

Increasing chlorophyll concentrations and Chl *a*/Chl *b* ratio in beech trees during the mature green leaf period in June–August (Fig. 2a1) reflects physiological acclimation to increased irradiation. Chlorophyll *a* participates directly in the light requiring reactions of photosynthesis, while chlorophyll *b* is an accessory antenna pigment acting indirectly in photosynthesis by transferring the absorbed light to chlorophyll *a*.

The evergreen coniferous trees showed much smaller seasonal changes in N pools, including total N, NH₄⁺ and chlorophyll, compared to the deciduous beech trees (Figs. 2, 3 and 4). The analysed needle samples included both current year needles as well as needles from previous years, which may have dampened seasonal changes in N pools. Minor differences in N concentration between different age classes of Douglas fir have previously been observed at the Dutch site, older needles having slightly higher N values than young needles as was also the case for sunlit compared to shade needles (Evers et al., 1991). Slightly higher N concentrations in older needles compared to current year needles was later confirmed by Boxman et al. (1995) and Koopmans et al. (1997). Similar differences in N concentration between young and old needles also occurred in other conifer species (Chapin and Kedrowski, 1983; Hatcher, 1990; Gebauer and Schulze, 1991; Thomas and Mead, 1992). These changes in N concentration reflect that N stored in older needles becomes remobilized to newly emerging and re-growing old needles (Millard and Grelet, 2010).

Evergreen conifers in boreal forests such as the Finnish site studied in the present work have evolved a conservative mechanism of nutrient turnover in order to cope with the relatively infertile soil conditions (Chabot and Hicks, 1982; Givnish, 2002). Their needles are persistent and serve as significant storage organs for carbohydrate and nutrients such as N. This storage reservoir can effectively buffer plant requirements

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when nutrients are not available for uptake from the soil under adverse conditions such as the drought period which occurred in 2009 at the Finnish site (Fig. 1c). Storage forms of N, e.g. vegetative storage proteins, are under these conditions converted to more metabolically active forms, thereby maintaining an overall relatively stable N status (Fig. 3b1, see also Chabot and Hicks, 1982; Millard and Grelet, 2010). The retranslocation of N in Scots pine needles in Finland has been estimated to be around 73 % (Helmisaari, 1992). Across a number of evergreen shrubs and trees, the N retranslocation efficiency was on average reported to be 50 % (Aerts, 1996; SantaRegina and Tarazona, 2001; see Fig. 5).

The higher plasticity of the N contents and chlorophyll concentrations in beech, even after full leaf development, compared to the coniferous trees supported our initial hypothesis that the short lived leaves in deciduous canopies are more flexible to adjust their functioning according to the seasonally changing weather conditions during the vegetation period. The higher degree of shade modification in beech leaves (50 % reduced N content per unit area in shade leaves) as compared to the coniferous canopies shows that beech trees can account for micrometeorological gradients comparably closely. There were also differences between the evergreen canopies – the fir canopy showed still significant shade modification (30 %), the pine forest not. It is obvious that the higher LAI leads to stronger photosynthetically active radiation (PAR) extinction in the fir canopy as compared to the pine forest and, consequently, shade modification is necessary to maintain needles in dark canopy zones. With regard to shade modification the leaf habit is important for the leaf structural development. In deciduous canopies leaves can develop according to the local conditions which might vary little over the course of a year. In conifer canopies leaves live longer and thus their relative position in the crown can change due to growth of new branches in the top. N economy can lead to transient physiological modification to transient shading but needle structures stay more or less the same. This might set limits on shade modification in dense growing conifer canopies compared to deciduous canopies. The findings of this study support this relationship.

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4.2 Seasonal variations in bulk tissue Γ

A useful temperature-normalized parameter for evaluation and modelling of NH_3 exchange between plant leaves and the atmosphere is the apoplastic Γ value (Γ_{apo}) which is equal to the ratio between $[\text{NH}_4^+]$ and $[\text{H}^+]$ in the leaf apoplastic solution (Nemitz et al., 2000; Mattsson and Schjoerring, 2002; Massad et al., 2010; Zhang et al., 2010). In the present work, apoplastic data were not available and we instead looked at the ratio between bulk tissue concentrations of NH_4^+ and H^+ to evaluate its relevance regarding the NH_3 exchange potential at the 3 experimental sites.

The largest bulk tissue Γ values (Γ_{bulk}) were 500 in beech leaves, while in most cases Γ_{bulk} values in Douglas fir and Scots pine needles were below 75 and 40, respectively (Fig. 4). Obviously, the relative differences between the three canopies were not directly related to the atmospheric NH_3 concentrations at the three sites, which were on average 3.9, 1.3 and 0.1 $\mu\text{gNH}_3\text{-Nm}^{-3}$ at the Dutch Douglas fir site, the Danish beech forest site and the Finish Scots pine site, respectively (see Sect. 2.1). Such relationship would not be anticipated because tissue NH_4^+ relations are affected by a range of species-dependent physiological processes involved in N uptake and N turnover in the leaves (Schjoerring et al., 2000). Rather than differences in atmospheric concentrations, the Γ_{bulk} values therefore reflect foliage N status, in agreement with that beech leaves had the highest N concentration, followed by Douglas fir and Scots pine (Fig. 3). The Γ_{bulk} values measured in the 3 tree species were in all cases much lower than those measured previously in grass species (Kruit et al., 2007; David et al., 2009; Mattsson et al., 2009). The question is to what an extent Γ_{bulk} can be used as an estimate of the NH_3 exchange potential of plant leaves. For the coniferous species, the Γ_{bulk} values were considerably lower than previously reported Γ_{apo} values as reviewed by Zhang et al. (2010). Also, a clear seasonal trend in Γ_{bulk} values was not observed for the coniferous species in the present work (Fig. 4). In contrast, Γ_{apo} in Scots pine needles in a mixed coniferous forest subjected to high N deposition were relatively high (3300) during spring and declined to 1375 during the summer/autumn (Neiryinc

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excluded, because the measured bulk tissue Γ values were too small to build up a high enough NH_3 partial pressure in the leaves.

Possible leaching losses from fallen leaves were minimised by fast sampling and analysis. Leaching losses from senescing needles in the canopy were, however, not investigated. If this was a substantial process, it would have been observed as very strong N enrichment in the rain underneath the beech canopy compared to wet deposition. Such enrichment was not observed in canopy throughfall measurements, e.g. at the beech forest, the annual sum of canopy N enrichment in the years 1998 and 1999 was on average 0.66 gNm^{-2} ; the monthly rates during September and October ranged between 0.02 and 0.25 gNm^{-2} (Beier et al., 2001), i.e. only ca. 6% of the estimated N re-translocation measured over one to two months in our study. At least part of this enrichment accounted also for dry N deposition, which makes a major contribution of N leaching to the N loss in senescing leaves even less likely. We cannot entirely exclude any effects of N leaching or NH_3 volatilisation from senescing leaves, but given these considerations the contribution would very likely be small.

4.4 Relationships between nitrogen cycling, leaf habit and N status of the ecosystem

We expected that producing every year an entirely new canopy or not should have large implications for N cycling in forest trees and ecosystems and thus expected that the leaf habit, deciduous vs. evergreen, was a major determinant for the internal N turnover in forest ecosystems. The aboveground litter production is a dominant component of the ecosystem internal N cycle and as long as N is cycling within the trees it is protected against losses via e.g. leaching (NO_3^-), volatilization (NO) and soil immobilisation (NH_4^+ fixation or formation of stable N containing soil organic matter-compounds). Trees can and do control how much N cycles in the ecosystem and how much will be stored within the trees. Our results show that the investigated deciduous forest supplied the ecosystem internal N cycle with only $1.8 \text{ gNm}^{-2} \text{ yr}^{-1}$ leaf litter production compared to $5.8 \text{ gNm}^{-2} \text{ yr}^{-1}$ in the temperate evergreen forest pointing to

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strong differences between trees with different leaf habit. Our data, however, also show that evergreen is not evergreen, meaning that the N flux in needle litter in the boreal pine forest was even lower than in the beech stand, i.e. only 16–17% of that of the temperate Douglas fir stand, despite the fact that the pine forest renews the canopy on average every 2 yr rather than every 2.6 yr as with the Douglas fir stand. The key difference between the two coniferous forest canopies was in N_c which was 5 times larger in the temperate Douglas fir stand than in the boreal pine stand (Table 2). The dominant effect of N_c was alleviated by the differing needle longevity or in other words the fraction of needles renewed every year. Looking at these differences, the role of N re-translocation becomes more obvious. The N re-translocation per unit leaf area of the pine trees reached almost the same efficiency as that of the deciduous forest (62% as compared to 70%) whereas the Douglas fir stand relocated only 53–60% as efficient compared to beech and pine, respectively (Table 2). The high re-translocation in beech matched our expectations, while on the contrary the N re-translocation in the coniferous trees, especially in the pine forest was higher than expected. Comparison with literature data revealed that N re-translocation varies also among deciduous trees. The data show that a simple distinction between deciduous and evergreen mode is not sufficient to generalise our findings. The leaf habit is one factor among others. The two coniferous sites showed that the canopy needle mass and its N content must be taken into account together with differences in the way the evergreen forests renew their canopies and save N via translocation. The results from the three forest sites suggest that some of these processes are not independent to each other; the efficiency with which the N was re-translocated before leaf fall (η_r) and the time needed to renew the canopy, mainly determined by leaf longevity, were related. The longer the needles stayed green, the lower was the η_r . This can be interpreted as a functional adaptation against N losses in trees with short living leaves or needles, i.e. frequent need for canopy renewal. When results from various other studies were included for comparison, the rather strong relationship observed across our three forest sites became weakened (Fig. 5). However, despite large variability especially between temperate

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vs. Mediterranean deciduous trees, the data still show a highly significant decrease in η_r with increasing canopy renewal time (CRT). Because of species specific differences we recommend investigating the relationship between η_r and CRT with a larger data set of forests and possibly other natural and semi-natural systems.

Another explanation for the observed differences in N re-translocation efficiencies could be that the high N availability in the Douglas fir site might have lead to the reduced N re-translocation, because e.g. tree internal buffers for N reserves were already filled. The canopy N content reflects the N status of the system. Higher air concentrations of reactive N compounds (e.g. NH_3) and N deposition loads together with a more productive climate enable the establishment of a larger and more fertile canopy in the Douglas fir stand. The unexpectedly effective N re-translocation in the boreal pine forest supports a possible distinction between N scarce and N rich evergreen ecosystems, leading to a more strict N economy, i.e. reduced ecosystem internal N cycling as our initial hypothesis stated.

Summarising the results from this study, we showed that forests can realise very different mechanisms to keep N losses in foliage litter production low: (i) increased N re-translocation efficiency, (ii) increased leaf longevity, (iii) decreased foliage N content and and (iv) decreased foliage mass. Despite the lowest leaf longevity and highest leaf N contents the beech canopy reduced the N losses via leaf litter production with very efficient N re-translocation and grew only a small amount of leaf mass per unit ground. The N scarce boreal pine forest carried a twice as high foliage mass compared to the beech stand, which was renewed on average every 2yr with a very low N content. Together with still very efficient N re-translocation, the N losses to the soil via foliage litter production were lowest in the boreal pine forest. The temperate, N rich Douglas fir stand had a high leaf N content, built up the by far highest foliage mass and thus canopy N content and had the lowest N re-translocation efficiency. The only mechanism that kept the foliage N in the trees was the longevity of the needles, which was largest among the investigated forests.

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Mechanistic models that aim to represent the dynamics of carbon and N pools and budgets need to include these factors and their relative contribution to conserve the N in forest trees. In general, the N dynamics modules require information about the N supply in the soil, N uptake demand of the tree, N loss and also the N re-translocation before litter fall, e.g. Jansson and Karlberg (2004) and Zhang et al. (2006), where η_c is a necessary input parameter. For realistic modelling the canopy specific differences and possibly interactions between N status and N re-translocation need to be taken into account. The indicated relationship between η_c and CRT might help to describe systematic variation in η_c across forests.

5 Conclusions

Leaf N pools showed clear seasonal changes in beech trees while remained relatively constant in the evergreen canopies, i.e. Douglas fir and Scots pine. The simple to measure Γ in bulk tissue (ratio between bulk tissue concentrations of NH_4^+ and H^+) did not directly relate to the atmospheric NH_3 concentrations at the three sites, while it reflected plant N status in agreement with that beech leaves had the highest N concentration, followed by Douglas fir and Scots pine. Irrespective of the leaf habit, all investigated trees kept the majority of the canopy foliage N in the trees. This was done through effective N re-translocation (beech), higher foliage longevity (fir) or both (boreal pine forest). A simple generalisation of the mechanisms of the tree internal N cycling based on the leaf habit could not be made; the differences between the two investigated evergreen forests were as large as those measured relative to the deciduous canopy. Efficient N re-translocation is not restricted to deciduous canopies but can also be found in the N limited forests, which released the lowest amount of N to the soil via foliage litter and to ecosystem internal cycling in this study. Apart from the efficiency of N re-translocation, the amount of N in the canopy and the fraction of annual leaf renewal are important determinants for the N turnover in trees and the contribution of N uptake from and release to the ecosystem internal N cycle. Our results have indicated that

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there might be a general relationship of decreasing N re-translocation efficiency with the time needed for canopy renewal, i.e. leaves that live longer re-translocate relatively less N during senescence. In the most fertile stand the amount of N in foliage litter was largest, meaning that higher N fertility leads to higher turnover in the ecosystem N cycle with higher risks of losses such as leaching and gas emissions.

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Table 1. The detailed geographic and climatic information of the three forest sites. (http://nitrogen.ceh.ac.uk/nitrogen2011/_oral_presentations/S11_3_lbrom.pdf; Skiba et al., 2009).

Ecosystem	Location	Altitude (m)	Soil	Species	Annual Precipitation (mm)	Annual Temperature / ($T > 10^{\circ}\text{C}$)	Age/ height of trees	Leaf Area Index	More details
Deciduous broad-leaved forest	Soro, DK (55° 29' N, 11° 38' E)	40	Oxyaquic hapludalf	Beech (<i>Fagus sylvatica</i> L.)	730	8.6 (161 d)	90 y/ 25 m	4.6	(Pilegaard et al., 2011)
	Speulderbos, NL (52° 15' N 5° 45' E)	52	Orthic podzol	Douglas fir (<i>Pseudotsuga menziesii</i> (Mirb.) Franco)	900	9.4 (173 d)	46 y/ 32 m	5	(Su et al., 2009)
Evergreen coniferous forests	Hyytiälä, FI (61° 50' N 24° 17' E)	181	Haplic podzol	Scots pine (<i>Pinus sylvestris</i> L)	709	2.9 (116 d)	46 y/ 16 m	4.8	(Launiainen, 2010)

Abbreviation: DK – Denmark, NL – The Netherlands, FI – Finland.

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Table 2. Leaf, needle and canopy properties, N re-translocation and N litter fluxes in three different forests estimated for the year 2009.

	Sorø temperate European beech	Speulderbos temperate Douglas fir	Hyttiälä boreal Scots Pine
C/N in green leaves (Jun–Aug)	19	25	43
C/N in brown leaves (fallen)	38	31	77
Average leaf longevity {average time span of complete canopy re- newal} (yr)	0.5 { 1}	2.6 { 2.6}	2 { 2}
Peak summer canopy N content, N_c (gNm^{-2})	6.2	24	5.4
N flux in total aboveground litter production ($\text{gNm}^{-2}\text{yr}^{-1}$)	7.3 ^a	6.8	1.9
N flux in foliage litter production ($\text{gNm}^{-2}\text{yr}^{-1}$)	1.8	5.8	1.0
N re-translocation by the trees ($\text{gNm}^{-2}\text{yr}^{-1}$)	4.4	3.4	1.7
N re-translocation efficiency ($\%\text{yr}^{-1}$) ^b	70	37	62
N re-translocation by the trees per unit ground area ($\%\text{yr}^{-1}$ relative to N_c)	70	14	32
N flux in the production of new leaves ($\%\text{yr}^{-1}$ relative to N_c)	100	38	51
N uptake for the production of new leaves ($\%\text{yr}^{-1}$ relative to N_c)	30	24	19

^a2009 was a mast year. Fluxes were 36% and 60% higher than in normal years for C and N, respectively.

^b N re-translocation relative to the N content of green fully active leaves in summer.

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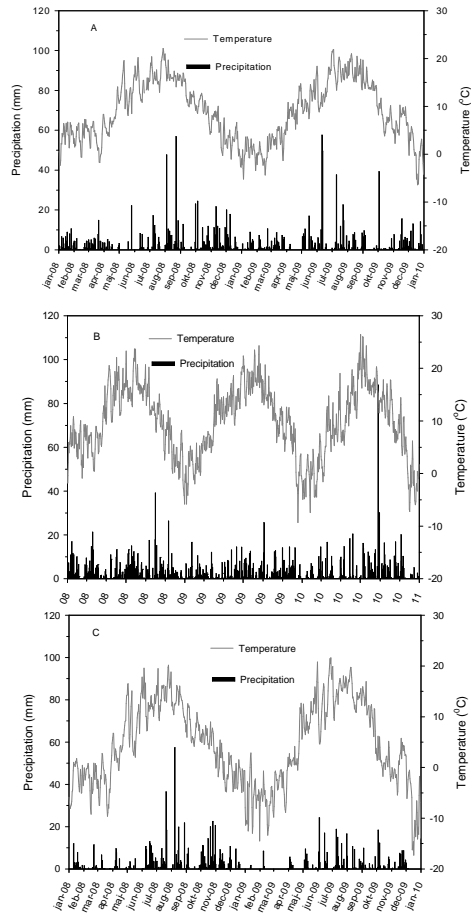


Fig. 1. Seasonal variations of air temperature (grey line) and precipitation (black columns) in the Danish beech forest from 2008 to 2009 **(A)**, the Dutch Douglas fir forest from 2008 to 2010 **(B)** and the boreal Scots pine forest from 2008 to 2009 **(C)**.

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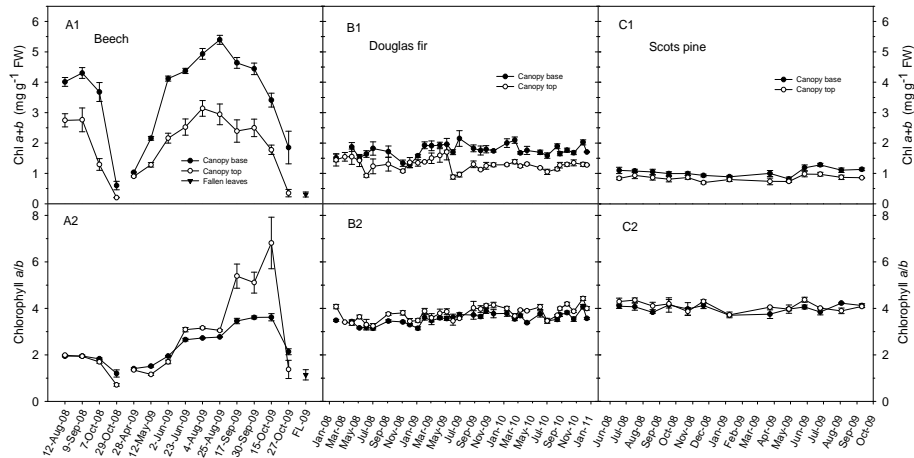


Fig. 2. Seasonal variations in leaf chlorophyll (*a* + *b*) concentrations and chlorophyll *a*/*b* in beech leaves (**A1–2**), Douglas fir needles (**B1–2**), and Scots pine needles (**C1–2**).

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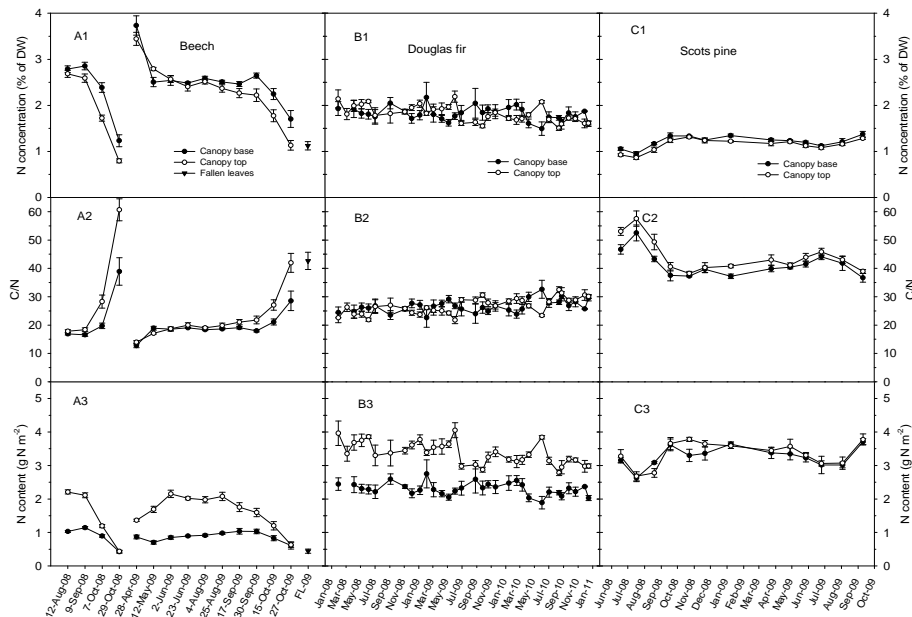


Fig. 3. Seasonal variations in tissue N concentration per dry matter (upper panels), C:N ratio (mid panels) and N content per unit fresh leaf area (lower panels) and in beech leaves (**A1–3**), Douglas fir needles (**B1–3**) and Scots pine needles (**C1–3**).

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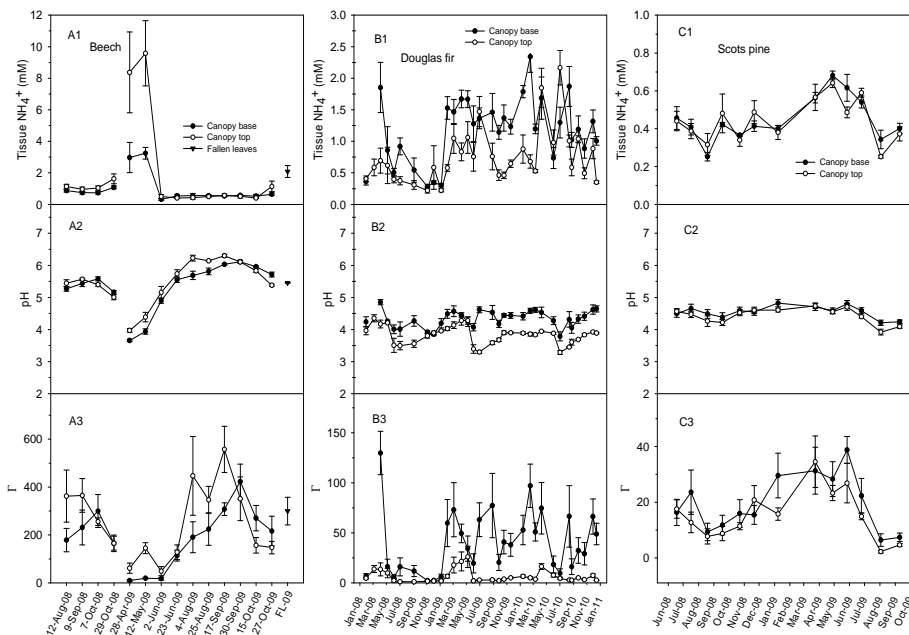


Fig. 4. Seasonal variations in bulk tissue NH_4^+ concentration, pH and tissue Γ in beech leaves (A1–3), Douglas fir needles (B1–3) and Scots pine needles (C1–3).

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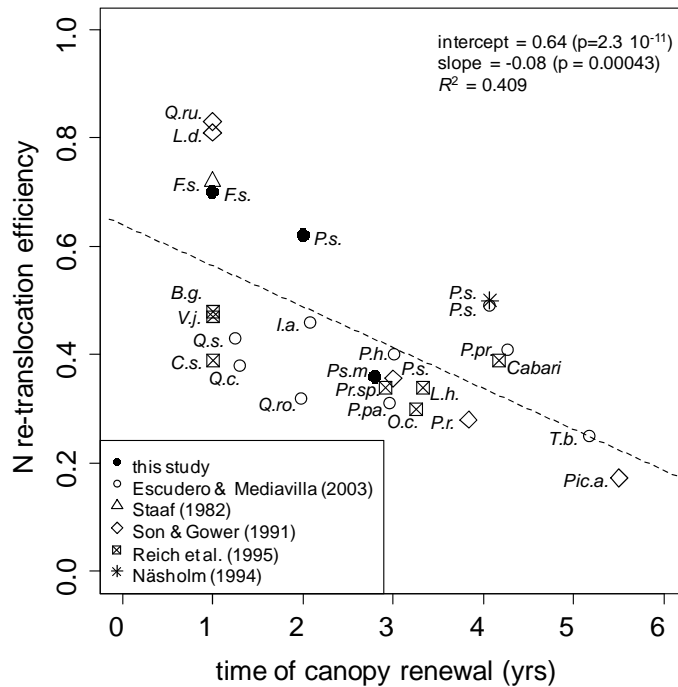


Fig. 5. Relationship between N re-translocation efficiency and time needed for complete foliage canopy renewal in this and other studies. Abbreviated plant taxa: *B.g.*: *Bellucia grossularioides*, *C.s.*: *Clidemia serice*, *Cabari*: *Cabari*, *F.s.*: *Fagus sylvatica*, *I.a.*: *Ilex aquifolium*, *L.d.*: *Larix decidua*, *L.h.*: *Licania heteromorpha*, *O.c.*: *Ocotea costulata*, *P.h.*: *Pinus halepensis*, *P.pa.*: *Pinus pinea*, *P.pr.*: *Pinus pinaster*, *P.r.*: *Pinus resinosa*, *P.s.*: *Pinus sylvestris*, *P.s.*: *Pinus strobus*, *Pic.a.*: *Picea abies*, *Pr.sp.*: *Protium sp.*, *Ps.m.*: *Pseudotsuga menziesii*, *Q.c.*: *Quercus coccifera*, *Q.ro.*: *Quercus rotundifolia*, *Q.ru.*: *Quercus rubra*, *Q.s.*: *Quercus suber*, *T.b.*: *Taxus baccata*, *V.j.*: *Vismia japurensis*. The canopy renewal time for *P.s.* needles in Näsholm et al. (1994) was assumed to be the same as that for *P.s.* in Escudero and Mediavilla (2003).

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