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Abstract:

Nitrogen budgets for Scots pine and Norway spruce ecosystems 12 and 7 years after the end of long-term fertilisation

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Abstract

The magnitude of nitrogen storage and its temporal change in forest ecosystems are important when analysing global change. For example, the accelerated growth of European forests has been linked to increased nitrogen deposition, but the changes in the N inputs that cause long-term changes in ecosystems have not yet been identified.

We used two Swedish forest optimum nutrition experiments with Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.) to study the long-term fate of N applied to these forest ecosystems. In the pine experiment, in addition to fertiliser (NPK) application, soil acidity was manipulated by application of lime and dilute sulphuric acid. From the spruce experiment, we selected treatments with similar fertiliser doses as in the pine experiment and with and without lime addition.

We quantified various terms in the N budget 12 years (pine) and 7 years (spruce) after the last N addition. In the pine ecosystem, large losses of added N occurred, whereas in the spruce ecosystem we recovered more N than could be accounted for by inputs. In the pine ecosystem, increases in N stocks were mainly in the soil, in contrast to the spruce ecosystem where trees accumulated most of the added N. There was no clear pattern in the interaction between acidification/liming and N deposition.

Keywords: Tree growth; Soil nitrogen; Nitrogen budget; *Pinus sylvestris; Picea abies*; Long-term fertilisation; Nitrogen retention; Acidification; Liming.

Introduction

> In a world of global change our society will not survive unless the political decisions taken can be defended in a holistic environmental perspective
>
> Tamm, 1995

The fate of nutrients deposited to terrestrial ecosystems is a key to understanding their impact. Since the early years of forestry, therefore, nutrient relationships in forest ecosystems have been subjected to intensive investigations (e.g. Ebermayer, 1876, 1882; Tamm, 1964; Odén, 1968; Rennie, 1995). More recently, nutrients have been studied in the context of air pollution, particularly the effects of sulphur (S) and nitrogen (N) deposition on nutrient imbalances and leaching (e.g. Nilsson and Wiklund, 1995; Wright et.al., 1995; Mälkönen et al., 1999). Today's urgent issues in forest research are studies of the nutrient impact on tree growth induced by a changing climate. The sequestration of C and N in forests is also a controversial issue in the global change debate (e.g. Tamm et al., 1999; Janzen, 2004) because of the strong coupling between C and N (e.g. Rastetter et al., 1992, 1997). The scope has also been broadened to become a central goal of ecosystem ecology with understanding of how the cycling of nutrients and the growth of organisms are linked (Augustine and McNaughton, 2004). Thus, increased N deposition altering forest nutrient cycling (Ågren and Bosatta, 1988; Aber et al., 1989, Peterjohn et al., 1996) may have a positive or negative impact on forest ecosystems (Mund et al., 2002). Accelerated growth of European forests (Spiecker, 1998) is suggested to be linked to this increased nitrogen deposition (Karjalainen et al., 2006). However, the question is whether this increased growth rate will also be sustained in the future if nitrogen deposition declines.

It seems to be tacitly understood that changes in N inputs will cause long-lasting ecosystem changes (Holland et al., 1997) and that forest ecosystems where nitrogen cycling has been accelerated will be able to maintain an elevated level of biomass production even when the external forcing in terms of N influx is decreased (Ingestad et al., 1981; Ingestad 1987, 1991). However, this aspect has not been tested.

Nutrient budgeting, which indicates trends in resources at the ecosystem level (Ranger and Turpault, 1999), has been widely used to generate quantitative ecological data on ecosystem functions (Ranger et al., 2002) and as an accounting method to elucidate complex nutrient cycles (Duvigneaud and Denaeyer-De Smet, 1970; Bonito et al., 2003). An interest in resource balances in agricultural science dates back to the 1830s (Wild, 1988) and input-output analyses became a major focus of system ecology in the 1950s (Odum, 1968). Many studies of the N budget at forest stand level are available (e.g. Nihlgård, 1972; Helmisaari, 1995; Abrahamsen and Stuanes, 1998; Rolff and Ågren, 1999; Ukonmaanaho and Starr, 2002). However, forests are likely to be heterogeneous in their response to N (Wilson and Emmet, 1999) and the information obtained from budget calculations is site-specific (Ranger and Turpault, 1999) and species-specific (van Breemen, 1995). Furthermore, whereas N availability can vary substantially from year to year, the nitrogen budget changes only on longer time scales (Schimel et al., 1997). This means that the time factor is the greatest obstacle in experimental research in forest ecosystems (Tamm et al., 1984) and short-term studies can give a completely misleading picture of the long-term development (e.g. Ågren and Hyvönen, 2003). Moreover, short-term and long-term results may differ not only in degree but also in direction, but the literature concerning the long-term fate of N applied to forest ecosystems is still rather limited (Aber et al., 1989; Aber and Magill, 2004). Numerous experiments have been designed to address these questions, but it will take years before they yield conclusive evidence.

To date, the focus in studies of element cycling has mainly been on single compounds (Erisman et al., 2003) and despite the well-known role of multiple element interactions in a number of biogeochemical processes, few ecosystem models include them explicitly (Ollinger et al., 2003). Nevertheless, elements interact with each other (e.g. Melillo et al., 2003; Ågren et al., 2003). Thus, interactions between N and S have been documented (Matzner and Murach, 1995; Galloway, 1995, 2003). The N cycle is also affected by liming (Persson et al., 1995; Kreutzer, 1995; Ventera et al., 2004), but we are still lacking information about its long-term effects (Hüttl and Schneider, 1998). Moreover, deposition-induced acidity may in fact have enhanced the N cycle in multiple ways and further studies are also needed to clarify the role of soil acidity in N losses from temperate forest (e.g. Ventera et al., 2004).

The main objective of this study was to explore the long-term nitrogen redistribution in a pine and a spruce boreal forest ecosystem. We used two Swedish long-term optimum nutrition field experiments to quantify various terms in the N budget several years after the last N addition and examined whether retention in different pools varied between the two tree systems. The effects of simultaneous acidification and liming were also investigated.

Materials and methods

Study areas

Two forest stands from the Swedish Forest Optimum Nutrition Experiments (Tamm, 1974a; 1974b), both located in Central Sweden, were studied: E42 with Scots pine (*Pinus sylvestris* L.) at Lisselbo and E26A with Norway spruce (*Picea abies* (L.) Karst.) at Stråsan. In the pine experiment, in addition to fertiliser application (NPK) soil acidity was manipulated by application of lime (Ca) and dilute sulphuric acid in low (Ac1) and high (Ac2) dosages. Only the plots with the intermediate (N2P2K2) level of fertiliser applications were used for the budget calculations here.

From the spruce experiment, we selected treatments with similar fertiliser (N2P2K2) dosage as in the pine experiment and with and without addition of lime. The sites, experimental designs and methods have been described in detail elsewhere (Tamm, 1974a, 1974b; Tamm and Popovic, 1989; Tamm et al., 1999), and only a brief summary of the general characteristics is given in Table 1.

Insert Table 1 here

The pine stand was damaged by heavy snow in late 1988, which caused the loss of an unknown number of trees, and the stand was thinned in 2000. However, at most 2% and 20% of trees on N and no-N plots, respectively, were damaged (Tamm et al., 1999). The spruce stand was thinned in 1982 and 1988. However, the thinnings removed the trees with the smallest diameter and thus only a small amount of nitrogen was removed; in the spruce stand the increase in average tree diameter as a result of the thinning was even large enough to make the allometric functions (see below) predict larger tree biomasses. In our calculations of ecosystem level N budget, we have therefore not included these events.

Nitrogen budgets

The nitrogen storage in the pine stand was estimated for 1971 and 1997, when the first and last soil samplings, respectively, were made. The spruce stand was monitored followed from 1972, when the first basal area measurement was made, until 2003, when the last diameter measurement was made. When the experiments were started in 1969 and 1967 in the pine and spruce stands, respectively, the trees were too small to allow basal area measurements.

We estimated the total content of N in the three most important compartments in the ecosystem [i.e. whole tree biomass, humus layer, and mineral soil 0-20 cm (pine stand) and 0-30 cm (spruce stand)]. The inputs of nitrogen that we included were inorganic fertiliser, wet plus dry deposition, and biological N-fixation. The changes in nitrogen pools were calculated as the differences in nitrogen amounts in trees, humus layer, and mineral soil between the beginning and end of the investigation period.

Data acquisition, estimates and calculations

Most of the data for our calculations were taken from previously published data sets. However, budget components were not always been measured at the same time, so we were obliged to interpolate between observations in several cases.

An annual nitrogen fixation rate of 0.3 kg N ha^{-1} was estimated by Granhall and Lindberg (1980) for a comparable pine stand in central Sweden. This gives inputs of 7.8 and 7.5 kg N ha^{-1} over the investigation periods for the pine and spruce stands, respectively. Atmospheric inputs of oxidised and reduced nitrogen of 191 and 134 kg ha^{-1} for the pine and spruce stand, respectively, were obtained from the MATCH modelling system of SMHI (Swedish Meteorological and Hydrological Institute) (Cecilia Akselsson, pers. comm.).

Biomass of tree components (needles, branches, stems, and coarse roots plus stumps) was estimated from average tree diameter at breast height (dbh) using species-specific regression functions (Marklund, 1988). Tree diameter in the pine stand in 1971 was calculated from basal area (Tamm and Popovic, 1989), while in 1997 it was interpolated from diameter measurements made in 1985 (Tamm and Popovic, 1989) and our own diameter measurements made in 2003. Tree diameter data for the spruce stand for the years 1971 and 1997 were taken from unpublished diameter measurements made in 1972 and 1997 (Linder and Tamm, personal comm.). Additional basal area information was taken from Gay et al. (1994). The N stocks in the tree components were calculated by multiplying the biomass of each component by published nitrogen concentrations (Table 2).

Insert Table 2 here

Initial soil data were missing for the spruce stand and only unpublished soil nitrogen from 1994 were available (T. Persson & M. Sjöberg, pers. comm.). Soil nitrogen data for the pine stands for 1997 were from our own measurements. In each plot, eight sampling points were systematically distributed in a rectangular grid > 5 m from the plot border. The L, F, and H layers (organic layers) were sampled using frames (361 cm^2). The mineral soil was sampled with cores 4.4 cm in diameter in 5-cm increments to a depth of 20 cm. Samples were pooled to one composite sample per plot and soil horizon. After removal of living plant residue, twigs, etc., soil samples were well mixed and sieved fresh: screen mesh 5 mm for organic layers and 2 mm for mineral soil. Bulk density values from the samplings were used for L, F, and H layers, while the bulk density of mineral soil was estimated from the stoniness index (Tamm and Popovic, 1989). Soil N concentrations were determined using dry combustion (NA 1500, Carlo-Erbe Strumentazione, Milan). In 1971, Tamm and Popovic (1989) measured soil nitrogen in the humus layer, which we assumed to correspond to our F+H layer. No mineral soil N data were available from 1971 and were replaced by samplings from 1985 (Tamm and Popovic, 1989; Hallbäcken and Popovic, 1985).

Statistics

For each stand, the effects of treatments were evaluated using analysis of variance (ANOVA). Tukey’s test for post-hoc comparisons of means and least significant difference (LSD) multiple comparison, with sub-plot measurements considered as treatment replicates, were used for cases in which ANOVA revealed significant treatments effects. The results are given as treatment means. The level of significance was set to 5%.

Results

Basal area development

The basal area development for the two stands and different treatments is shown in Figure 1. There was a small but consistent increase in basal area in all the fertilised pine treatments compared to the non-fertilised during the period when fertilisation was taking place (up to 1985). After that, all treatments had similar rates of basal area growth except the NPK treatment, which had a somewhat more rapid development and the untreated, Ca, and Ac1 treatments, which fell behind. In the spruce stand, the growth stimulation was so strong in all fertilised plots that by the end of the fertilisation period (1990), the basal area in the fertilised plots was about three times that in the unfertilised plots. Once fertilisation had ceased, the growth rate on the fertilised plots dropped to that of the unfertilised ones.

Insert Figure 1 here

Nitrogen inputs

The nitrogen budgets for the pine and spruce ecosystems are summarised in Tables 3 and 4, respectively. The total inputs of N (fertilisation, deposition, and biological fixation) to the pine ecosystem over the period 1971-1997 varied from 199 kg N ha^{-1} in unfertilised plots to 999 kg N ha^{-1} in fertilised plots (Table 3). In the spruce ecosystem, the corresponding inputs of N over the period 1972-1997 varied from 142 kg N ha^{-1} to 1382 kg N ha^{-1} (Table 4).

Insert Table 3 and 4 here

N pools in ecosystem compartments

The distribution of N in 1997 between ecosystem compartments in the pine and spruce stands for the various treatments is shown in Figure 2. In both stands the effects of the N additions could still be observed 12 (pine) and 7 (spruce) years after the N additions had ceased. However, there were differences in response. In the pine stand, the NPK-treatment was the only treatment that produced a significant increase in N in the tree biomass (96% above control). The other fertilised plots also had larger amounts of N in the tree biomass, but not significantly so. In the spruce stand, the N additions increased tree biomass N in all treatment combinations (207% above control in both NPK and NPKCa treatments). In addition, the effect of treatments on N stock in spruce biomass was significant already in 1972, four years after the start of fertilisation, when the first biomass estimates were made.

Insert Figure 2 here

As a result of a significant increase in humus N, the N applications caused significant changes in ecosystem N content in three (NPK, NPKAc1 and NPKAc2) of the four treatments in the pine experiment (Fig. 2). The increases in humus N for the NPK, NPKAc1 and NPKAc2 treatments were also large enough to cause a significant increase in total soil N. There was also a significant increase in mineral soil N in the NPK and NPKAc2 treatments. In spite of the changes in amounts of N in individual compartments, the relative distribution of nitrogen between trees and soil did not vary across treatments, with trees containing around 12% of pine ecosystem N (Fig. 3). The relative distribution of N between humus layer and mineral soil (0-20 cm depth) varied between treatments but there seemed to be no systematic variation with treatment; the humus contained around 46% of soil N (down to a depth of 20 cm in the mineral soil).

In the spruce stand, the N fertilisation increased N pools in both the trees and the soil but the increase in the soil was restricted to the humus layer, whereas the mineral soil N pool might rather have decreased (Fig. 3). The uptake of the N fertiliser was proportionally larger in the trees such that in the fertilised spruce stands (Table 4), in contrast to the pine stand (Fig. 3), the distribution of N shifted in favour of the trees. The humus layer also seemed to contain a lower share of the N stock in the spruce stand (around 37% of soil N to a depth of 30 cm in the mineral soil) relative to the pine stand.

Insert Figure 3 here

In 1997, we found more N in the spruce ecosystem than could be explained by the sum of inputs and initial amounts in 1972 (Table 4). The same was true for the unfertilised pine plots, whereas some N was unaccounted for in the fertilised plots (Fig. 4). The budget for soil N in the spruce stand was based on a comparison between control and treated plots in 1997 because initial data were lacking. When we compared the pine stand in the same way, the values in the soil N components changed only slightly and without consequences for the interpretation.

Acidification and liming also affected N accumulation. In both fertilised and unfertilised plots in the pine stand, liming led to a smaller increase in the humus N pool. The amount of N unaccounted for in the pine stand in the NPKCa treatment was also larger than in the NPK treatment. Furthermore, there was a difference in the soil in the pine stand between high and low doses of acidification, with a higher build-up of humus N in the high dosage. There was also an indication that NPK and NPKAc2 led to a larger increase in mineral soil N than NPKAc1 and NPKCa.

Insert Figure 4 here

N unaccounted for

The N budgets did not match. In the pine ecosystem, we found between 16 and 219 kg ha^{-1} more N in the unfertilised plots in 1997 than in 1971 (Table 3). In the fertilised plots, on the contrary, between 254 and 738 kg ha^{-1} was unaccounted for. This unaccounted for N can be represented by the following series:

(NPKAc1, NPKCa) > (NPK, NPKAc2) > (Ca, Ac1, Control, Ac2)

The NPKAc1 and NPKCa treatments were the only treatments with a significant increase in the amount of unaccounted for N compared not only to the control, but also to all other unfertilised plots (Ca, Ac1, Control, Ac2). The other fertilised plots (NPK and NPKAc2) also had higher amount of unaccounted for N than unfertilised plots, but the differences were not significant (5% level).

In the spruce stand at the end of the observation period in 1997, there was between 517 and 591 kg ha^{-1} more N in fertilised plots compared to control plots and the trees in control plots had taken up 250 kg ha^{-1} more N than our estimated input (Table 4).

.1 Discussion

One of the most striking observations from our calculations was the great difference in response between Scots pine at Lisselbo and Norway spruce at Stråsan. Long-term N additions, alone or in combination with sulphuric acid or lime, must therefore be expected to modify N pools in boreal coniferous forest ecosystems in a species-specific and/or site-specific way. The response is also time-dependent. In both stands investigated, the fertilisation increased biomass but this biomass increase was sustained only in the NPK-fertilised plots in the pine forest when the fertilisation had ceased. However, there was a strong tendency for higher biomass in all fertilised spruce plots.

The increased biomass in the spruce stand as a result of fertilisation was accompanied by an increased N concentration in the needles (Table 2). This led to increases of about 1100 kg ha^{-1} in spruce tree N in all plots, with no differences between treatments. Simultaneously, soil N increased by more than 800 kg ha^{-1} but with the extra N concentrated to the humus layer, while the mineral soil N was likely to even have decreased. These increases in spruce ecosystem N pools were larger than the estimated inputs. However, the increase in spruce tree N in the unfertilised plots was 250 kg ha^{-1} more than estimated from deposition and N fixation. Nevertheless, if this extra N is included in the balances for the fertilised plots, there still remains about 300 kg N ha^{-1} to be accounted for.

In the unfertilised plots in the pine stand, the N content in the stand was 120 kg ha $^{-1}$ higher in 1997 than in 1971. If this extra N is included in the N budget for the fertilised stands, the NPKAc1 and NPKCa plots then would have lost as much N as had been added with the fertiliser, whereas the NPK and NPKAc2 plots retained about half the fertiliser added. The allocation of the increases in N differed between stands; the pine stand retained more in the soil than in the trees (about 2/3 in the NPK and NPKAc2 plots) whereas the spruce stand retained somewhat more in the trees than in the soil.

The effects of acidification or liming in addition to the fertilisation had no consistent pattern. There was no growth and N uptake effect of liming in the fertilised pine and spruce stands. With only NPK and NPK in combination with the high acid dosage, there was some increase in N stocks in the pine stand. However, in the low acidification and lime treatments in the pine stand, fertilisation did not increase the N stock. Acidification and liming did not seem to have the same effect without fertiliser as with fertiliser. Without fertiliser, acidification and liming seem to be almost without long-term effects, although it is possible that the high acid dosage increased N stocks somewhat more.

The differences in response between the pine and spruce stands are probably attributable to species differences. The potential of spruce to increase its needle biomass is much larger than that of pine; Ågren (1983) estimated the maximum needle biomasses for pine and spruce to be 20 000 kg DW ha^{-1} and 49 000 kg DW ha^{-1}, respectively. Another aspect is the difference in soil texture, since the pine stand was growing on a coarse sandy soil with lower nutrient retention capacity than the more fine-textured soil in the spruce stand.

We found more nitrogen than could be explained by inputs and initial values in all plots except the fertilised pine plots, where large losses occurred. The losses of N in the fertilised pine plots can be explained as leaching losses. The extra N in the pine stands corresponded only to an extra inflow of 1 to 8 kg ha^{-1} yr^{-1} but was between 10 and 23 kg ha^{-1} yr^{-1} in the spruce stand. There are two potential sources for the extra N in the other stands. First of all, it is likely that some of the nitrogen derived from mineralisation in deeper soil horizons than those included in the budgets. Root activity and nutrient availability in deeper soil layers, which remain poorly explored, may play an important role in ecosystem functioning (e.g. Richter and Markewitz 1995, Jackson, 1999; Jobbagy and Jackson, 2001, 2004). Indications exist that considerable amounts of plant available nitrogen and other nutrients below 20-30 cm depth can be an important resource of nutrients for trees (e.g. Stone and Comerford, 1994; Kowalenko, 1996). Over decade time scales and longer, the release of N from the mineral soil may be a key process for long-term accumulation in both vegetation and the organic horizon (e.g. Ross et al., 2002; Ritter et al., 2003; Finzi and Schlesinger, 2003; Currie et al., 2004). It is also possible that the spruce control plots received N through lateral transport as a result of site topography. In addition, lateral root development and soil mining by roots outside the unfertilised plots is a possible factor of unexplained N accretion in the unfertilised plots (e.g. Högberg, 1991).

Another possible explanation for the N deficit is the uncertainty in the total input. Nitrogen fixation is one uncertain component in the total input because measuring it in natural systems is difficult (Vitousek et al., 2002). There are few studies of nitrogen-fixing root surface bacteria on coniferous trees (Timonen et al., 1998; Chanway et al., 1994). However, non-symbiotic N fixation can be an important input to coniferous forests (Wei and Kimmins, 1998; DeLuca et. al., 2002; Chen and Hicks, 2003; Brunner and Kimmins, 2003) with an observed range for terrestrial cyanobacteria of 1 to 41 kg N ha^{-1} yr^{-1} and with the majority of studies ranging between 1-10 kg ha^{-1} yr^{-1} (West, 1990; Boring et al., 1998; Cleveland et al., 1999). Since liming may affect N fixation negatively by reducing the abundance of bryophytes (mosses) (Motta et al., 1994; Duliere et al., 2000), which are a major nitrogen-fixing component of boreal forests (e.g. Solheim et al., 1996), the underestimation of nitrogen fixation could be higher in the non-limed plots than in the limed plots.

On average, 56% of the N applied, added alone or in combination with acid in high doses, still remained in the soil, which is considerably more than the 30% reported previously (Tamm et al., 1999). On the other hand, when N was added in combination with low acid or lime, only 13% remained in the soil. As a result of the heterogeneity of the soil, one has to be cautious with regard to the reliability of these values. However, it is possible that the N retention capacity of an ecosystem is also determined by interactions with acidity, which complicates the use of the critical load concept (e.g. Pardo and Driscoll, 1996; Emmett and Reynolds, 1996; Augustin and Bolte, 2005).

Artikel II. Conclusions

.1 1. The response of boreal coniferous forest ecosystems to long-term nitrogen addition is time-dependent and modifies N pools in a species-specific and site-specific way.

2. When N additions decline or are terminated, some ecosystems are likely to revert to pre-treatment N stocks.

3. In pine ecosystems, the soil is the major sink for N. In contrast, in spruce ecosystems trees conserve a large proportion of added N.

.2 4. Our results support the statement in the introduction that ‘the accelerated growth of European forests is probably linked to increased nitrogen availability’. However, the differences in growth responses across fertiliser combinations indicate that factors other than nitrogen are of significance.

5. The interaction between N deposition and acidification remains a controversial issue.

6. The risk of nitrogen leaching cannot be assessed only on the basis of nitrogen deposition, since the ability of the ecosystem to retain N also has to be taken into account.

7. Nitrogen budgets for boreal coniferous forest need to include deep mineral soil horizons.

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Table 1. Site characteristics and overview of treatments in the experiments.

Site	Lisselbo	Stråsan
Latitude, Longitude, Altitude [b]	60°28’N; 16°57’E; 80 m	60°55’N; 16°01’E; 350 m
Experiment # [a]	E42	E26A
Tree species [b]	Scots pine (*Pinus sylvestris* L.)	Norway spruce (*Picea abies* (L.) Karst.)
Treatment period [a]	1969-1985	1967-1990
Soil material [b]	Sediment	Till
Soil [b]	Sandy, iron podzol	Glacial till, iron podzol
Mean annual temperature,°C [b]	4.8	3.1
Mean annual precipitation, mm[b]	593	745
Stand age at start of treatment [b]	14	9
Form of N added [b]	Ammonium nitrate (NH_4NO_3)	Ammonium nitrate (NH_4NO_3)
Amount of fertiliser N (kg ha^{-1}) added [a]	240 during 1969-1970 800 during 1971-1985	520 during 1967-1971 1240 during 1972-1990

[a] Tamm and Popovic (1995)

[b] Gay et. al. (1994)

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Table 2. N concentration (mg g^{-1}) in biomass components for Scots pine and Norway spruce and various treatments and years. In the spruce experiment needle N concentrations are given also at the individual plot level.

	Scots pine		***Norway spruce***	
	1971	1997	1972	1997
Stem wood	0.9[a]	0.9[a]	0.94[g]	0.94[g]
Stem bark	3.5[a]	3.5[a]	5.58[g]	5.58[g]
Branches	2.1[a]	2.1[a]	4.94[g]	4.94[g]
Needles	13.4[b]	11.8[c] Control	13.1; 11.5; 9.5[f] Control	15.0; 13; 1[f] Control
		11. 8[d] Ac1		
		11.8[d] Aci2		
		11.9[c] Ca		
		17.8[c] NPK	20.4[f] NPK	17.0; 19.0; 20.0; 21.0[f] NPK
		17.8[e] NPKAc1		
		17.8[e] NPKAc2		
		19.0[c] NPKCa	20.4; 20.5[f] NPKCa	19.8; 18.6[f] NPKCa

[a] measured in 1975 (Tamm et al., 1999)

[b] measured in 1968 (Aronsson, 1982)

[c] measured in 1987 (Nihlgård et.al., 1996) and assumed unchanged (Tamm et al., 1999)

[d] assumed to be the same as for control plots

[e] assumed to be the same as for NPK plots

[f] S. Linder and C.O. Tamm (pers. comm.)

[g] data from the Skogaby Norway spruce stand (G. Ågren, pers. comm.)

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Table 3. Nitrogen stocks in the Scots pine stand in experiment E42 at Lisselbo in 1971 and 1997. Data are averaged over plots. A significant difference (P<0.05) between control and treatments is marked with (*).

Budget items		**Treatments**							
		Control	**Ac1**	**Ac2**	**Ca**	**NPK**	**NPKAc1**	**NPKAc2**	**NPKCa**
Plots		**55, 60**	**63,72**	**69, 57**	**62, 58**	**66, 61**	**70, 64**	**67, 56**	**68, 71**
Line	**N inputs, kg/ha**								
1	*Fertilizer*					800	800	800	800
2	*Fixation*	8	8	8	8	8	8	8	8
3	*Total deposition*	191	191	191	191	191	191	191	191
4	*Σ Input* (1+2+3)	199	199	199	199	999	999	999	999
	N pools in ecosystem compartments, kg/ha								
5	*Trees 1971*	31	23	27	20	35	32	29	34
6	*Trees 1997*	126	129	148	127	247**	173	181	167
7	*Humus 1971* [a]	346	338	373	407	392	564	311	495
8	*Humus 1997*	548	418	557	433	795**	754**	751**	596
9	*Mineral 0-20 cm 1985* [a]	380	511	493	513	702	611	649	540
10	*Mineral 0-20 cm 1997*	409	645	606	595	829**	558	802**	567
11	*Total soil 1971* (7+9)	726	849	866	920	1094	1175	960	1035
12	*Total soil 1997* (8+10)	957	1062	1162	1028	1624**	1312**	1553**	1163
13	*Ecosystem 1971* (5+11)	757	872	893	940	1129	1207	989	1069
14	*Ecosystem 1997* (6+12)	1082	1192	1311	1155	1871**	1485**	1734**	1330
	Pool changes of N, kg/ha								
15	*In trees* (6-5)	95	106	121	107	212**	141	152	133
16	*In humus* (8-7)	202	80	184	26	403	190	440	101
17	*In mineral soil* (10-9)	29	134	113	82	127	-53	153	27
18	*In total soil* (12-11)	231	214	297	108	530	137	593	128

19	*In ecosystem* (14-13)	326	320	418	215	742	278	745	261
	Pool changes of N, **% of Σ input**								
20	*In trees* (15/4*100)	48	53	61	54	21	14	15	13
21	*In humus* (16/4*100)	102	40	92	13	40	19	44	10
22	*In mineral soil* (17/4*100)	15	67	57	41	13	-5	15	3
23	*In total soil* (18/4*100)	116	108	149	54	53	14	59	13
24	*In ecosystem* (17/4*100)	164	161	210	108	74	28	75	26
	Unaccounted N , kg/ha								
25	(4-19)	-127	-121	-219	-16	257	721**	254	738**

[a] Tamm, C.O., Popovic, B. (1989)

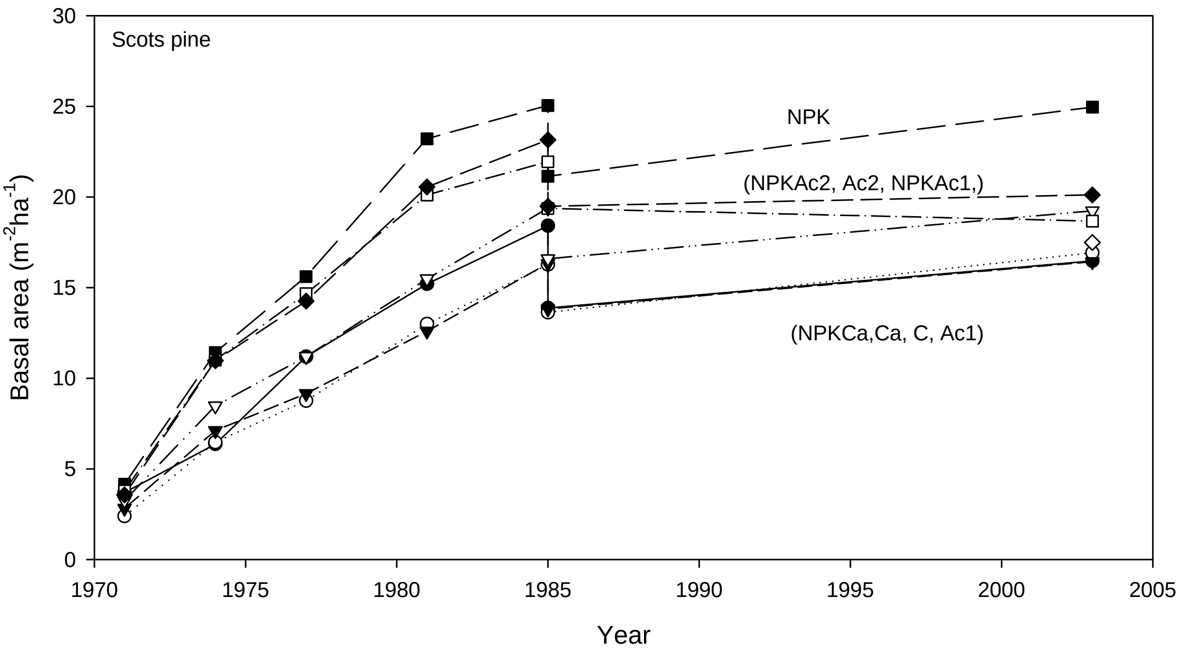
Table 4. Nitrogen stocks in the Norway spruce stand in experiment E26A at Stråsan in 1972 and 1997. Data are averaged over plots. Only plots 13, 46, 19, 39, 4, and 48 are included in soil data. Pool changes and recovery in soil in N treated plots are by difference with control plots. A significant difference (P<0.05) between control and treatments is marked with (*).

Budget items		**Treatments**		
		Control	**NPK**	**NPKCa**
Plots		13, 46, 8	4, 38, 22, 48	19, 39
Line	**N inputs, kg/ha**			
1	*Fertiliser*		1240	1240
2	*Fixation*	8	8	8
3	*Total deposition*	134	134	134
4	∑ *Input* (1+2+3)	142	1382	1382
	N pools in ecosystem compartments, kg/ha			
5	*Trees, 1972*	53	273**	247**
6	*Trees, 1997*	444	1366**	1364**
7	*Humus, 1997*[a]	663	1621	1629
8	*Mineral soil 0-10 cm, 1997*[a]	373	387	386
9	*Mineral soil 10-30 cm, 1997*[a]	920	754	797
10	*Total soil* (7+8+9), 1997	1956	2762	2812
11	*Ecosystem* (6+10), 1997	2400	4128	4176
	Pool changes of N, kg/ha			
12	*Trees* (6-5)	391	1093**	1117**
13	*Humus*		958	966
14	*Mineral soil 0-10 cm*		14	13
15	*Mineral soil 10-30 cm*		-166	-123
16	*Total soil*		806	856
17	*Ecosystem* (12+16)		1899	1973

	Pool changes of N, % of Σ inputs			
18	*Trees* (12/4*100)	276	79**	81**
19	*Soil* (16/4*100)		58	62
20	*Ecosystem* (17/4*100)		137	143
	Unaccounted N, kg/ha			
21	(4-12) Control, (4-17) Treated	- 250	- 517	- 591

[a] data from the Stråsan Norway spruce stand in 1994 (T. Persson, pers. comm.)

Figure 1. Basal area development for pine and spruce stands and different treatments.



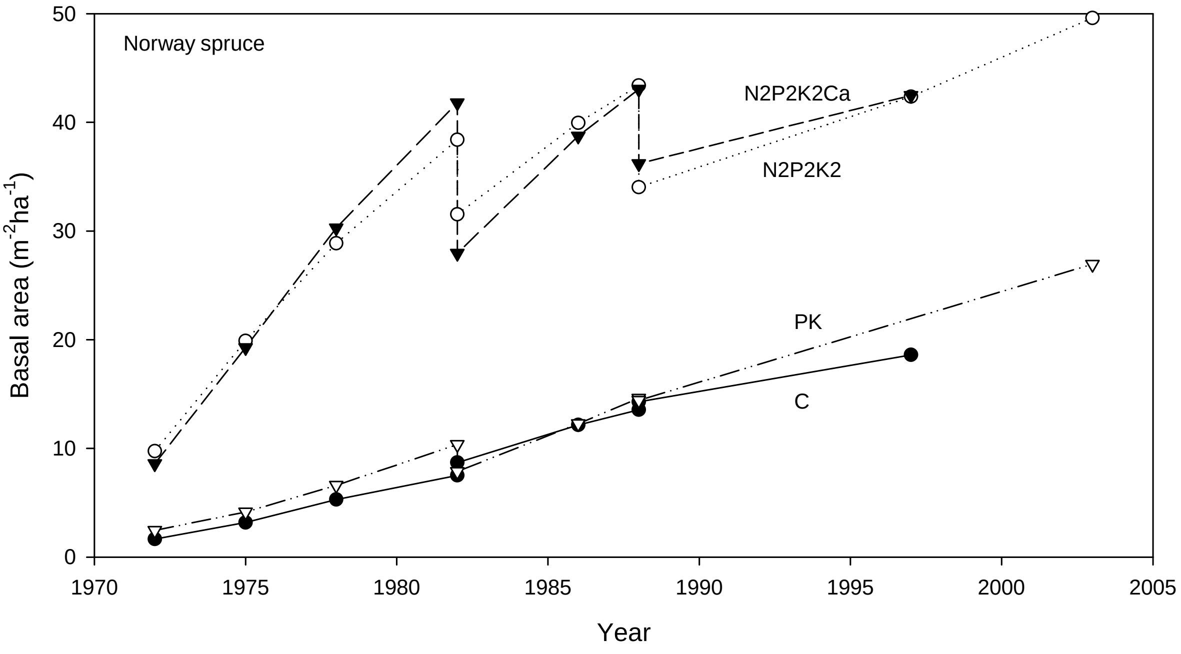


Figure 2. Partitioning of N stores in 1997 between compartments in the pine and spruce ecosystem. Significant differences (P<0.05) between control and treatments are marked with (*).

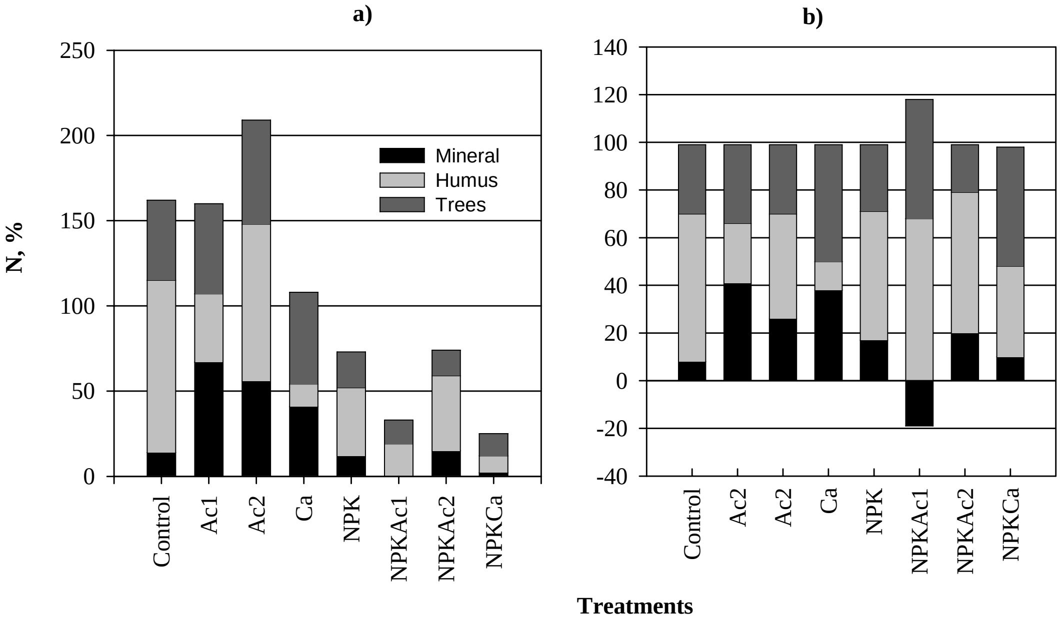


Figure 3. Relative distribution of N in 1997 in the pine and spruce ecosystems.

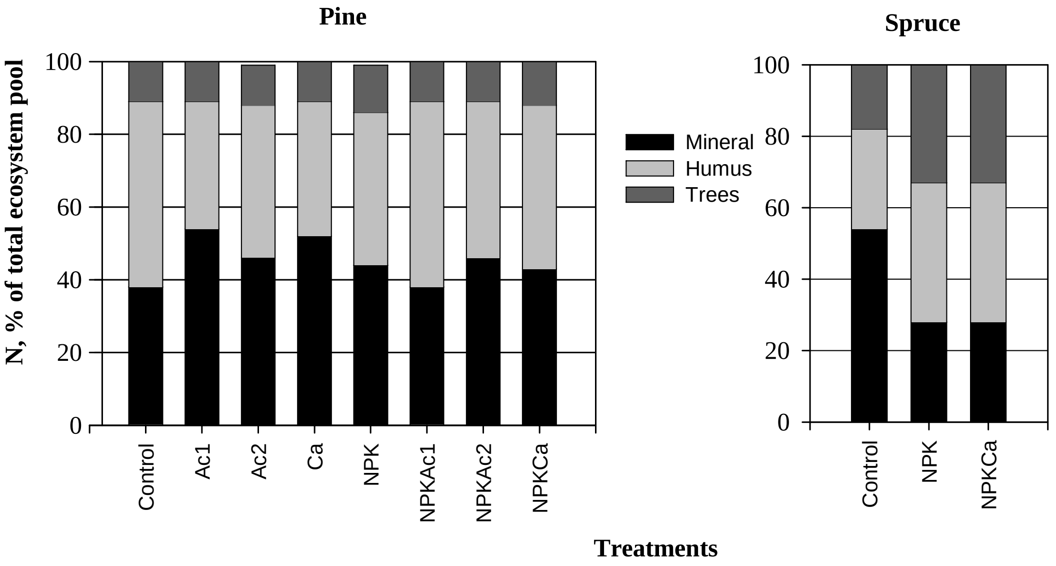


Figure 4. Pool changes of N in pine ecosystem compartments: a) Relative to total inputs; b) Relative to change in ecosystem.