Is site productivity permanently changed by repeated fertilisation?

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To be submitted: Canadian Journal of Forest Research

Abstract

Nitrogen (N) fertilisation increases tree production in boreal forests, but it is poorly known how long the fertiliser effect will remain after the end of the fertilisation. We studied a Scots pine stand during 17 years of annual fertilisation with N and other nutrients followed by a period of 19 years of no fertilisation. Fertilisation increased needle N concentrations, but once fertilisation was stopped the concentrations dropped to the level of the unfertilised trees within five years. Leaf area index was 10% higher in fertilised than in unfertilised plots 19 years after the end of fertilisation. Basal area and stem volume in fertilised plots were twice those in unfertilised plots at the end of the fertilisation period. The growth in the fertilised plots remained higher, even when the effects of tree size were accounted for. Fourteen years after the end of fertilisation, fertilised plots had higher soil carbon (C) pools, but similar annual C mineralisation as unfertilised plots. Fertilised plots had higher soil N pools and higher field net N mineralisation. The fertilisation resulted in a long-term increase in the forest production and probably caused a shift in N uptake from organic towards inorganic forms.

Introduction

Forest production and C sequestration in forest ecosystems in northern temperate and boreal regions is generally limited by lack of nutrients, particularly N (e.g. Vitousek and Howarth 1991; Tamm 1991). Many attempts have been made to identify maximal growth rates of coniferous trees by using varying fertiliser and water additions (optimisation experiments) (e.g. Tamm et al. 1999, Aronsson et al. 1999, Linder 1995). A leading idea is that with a continuous addition of nutrients a progressively larger proportion of the nutrients circulating within the ecosystem will be derived from the applied fertiliser, and when the additions are ended, the ecosystem will continue to function at a higher production level (Aronsson and Elowson 1980; Ingestad 1987).

In response to nutrient additions, there are normally rapid initial increases in tree growth and nutrient contents in trees and soil (Tamm et al. 1999). Soil C stocks also increase as a result of increased litter input and decreased CO_2 evolution rates (e.g. Persson et al. 2000, Sjöberg et al. 2003; Högberg et al. 2006, Franklin et al. 2003) but slower than the soil N accumulation such that C-to-N ratios in the soil decrease (Aronsson et al. 1999, Hyvönen et al. 2007, Högberg et al. 2006, Ladanai et al. 2007, Sjöberg et al. 2003). However, not all of the added nutrients contribute to C sequestration, and N-use efficiency (amount of C sequestered per unit N added) varies between experiments. N use efficiency in trees has been found to be strongly dependent on soil N status and increases from close to zero at C/N 25 in the humus layer up to 40-50 kg (C) kg^{-1} (N) at C/N 35 (Hyvönen et al. 2008). Low application rates are also more efficient for C storage than high application rates. N use efficiency is also species and age dependent being higher in young stands of *Picea abies* (L.) Karst. than in *Pinus sylvestris* L. stands while there is practically no difference in old stands. At N-rich sites higher N-use efficiency was observed when N was added together with P and K showing that other elements will become limiting with increasing N availability (Tamm 1991, Hyvönen et al. 2008).

Increased forest production due to fertilisation or N deposition (Kahle et al. 2008, Magnani et al. 2007, Thomas et al. 2010) is an important net sink in the global carbon budget. A still unsolved problem is whether tree production will decline in parallel with the decline in N addition/deposition or if it can be kept at a high level as a consequence of a higher storage and turnover of added/deposited N.

High levels of N deposition are in large areas of the world increasing tree growth rates (Kahle et al. 2008) and can even reach levels where N no longer limits growth (N saturation) (e.g. Aber et al. 1988). It is, therefore, likely that the response to N deposition in many forested ecosystems will go down in the future.

In this paper we examine the duration of fertilisation effects on tree growth and soil C and N stores by using data from a 14-19 year-period without nutrient additions following an experimental period of 17 years with fertilisation and irrigation in a *P. sylvestris* stand in central Sweden. We analyse how the cessation in nutrient and water additions affected (i) nutrient concentrations in needles, (ii) tree growth, (iii) soil C and N pools, and (iv) soil C and (net) N mineralisation.

Materials and Methods

Site description

An experiment (labelled Ih 2) was laid out in 1974 in a young *P. sylvestris* stand at Jädraås, central Sweden (60º50' N, 16º29' E, 185 m a s l) (Axelsson and Bråkenhielm 1980, Aronsson and Elowson 1980). The mean annual temperature is 3.8 ^{o}C and the mean annual precipitation is 600 mm. The experimental area is an opening in a surrounding old pine stand. The soil profile is an iron-podzol and the dominant fraction of the soil texture is medium sand down to the depth of 15 cm and a mixture of coarse and medium sand in the deeper mineral soil layers. Soil pH was 4.3 in the humus layer and 5.0-5.1 down to the depth of 20 cm in the mineral layer. The plant community was in 1974 classified as a *Cladonia-Pinetum* (*boreale*) or lichen-dwarf-shrub type (Bråkenhielm 1974).

The stand was naturally regenerated from seed trees left after cutting the previous forest in 1957. Soil scarification in patches was made, probably around 1958, and the seed trees were cut down in 1962. The mean date of birth of the trees is 1959 (Flower-Ellis et al. 1976). The young stand was cleaned and space regulated in 1973 before onset of the experiment. At the start of the experiment in 1974 there were 1050-1500 trees per ha with an average height of 2.1 m. The stand was thinned in autumn 2007.

Experimental design

The irrigation-fertilisation experiment was laid out as a randomised block design with four treatments in five blocks. In this study we only use three or four of the five blocks because three plots (0, I, F) in one block were clear-cut in 1980 and two more plots (0, I) were clear-cut in 2007. The plots were 20x20 m with a margin of 5 m on each side. Neighbouring plots with different treatments were isolated from each other by sheets of aluminium inserted to a depth of about 30 cm. The four treatments in the experiment were: control plots (0), irrigation (I), fertilisation (F)

and irrigation + fertilisation (IF). Irrigation was supplied from sprinklers placed at a height of about 50 cm above ground level. Irrigation normally took place every day, except after heavy rains when the irrigation programme was modified to account for the rain. Fertilisation in the F plots was done manually with solid fertiliser once a year at the start of the growing season. N was applied annually between 1974 and 1990 but K and P only once every third year (Table 1). In the IF treatment, a complete fertiliser mixture consisting of both macro- and micronutrients was applied in fixed proportion to N (see Table 2). The fertiliser was applied as a very dilute solution, using the same equipment as for irrigation. The irrigation and nutrients were applied five days a week from mid-May to mid-August each year apart from the first year.

Ground vegetation

The ground vegetation developed differently in the fertilised and unfertilised plots. At the time of the soil sampling in 2004 (see below), the ground vegetation in the control and irrigation plots consisted of mosses (e.g. *Pleurozium schreberi* (Brid.) Mitt., *Dicranum* spp. and *Hylocomium splendens* (Hedw.) B.S.G. and dwarf-shrubs (*Vaccinium myrtillus* L., *V. vitis-idaea* L. and *Calluna vulgaris* L.). The ground vegetation in the N-fertilised plots became rapidly dominated by *Chamaenerion angustifolium* (L.) Scop. and *Rubus idaeus* L. (Persson 1981) but a return towards similar ground vegetation as in the unfertilised plots is underway.

Tree volume

All trees were marked with numbers at the start of the experiment. Measurements of diameter at breast height (mm) and tree height (dm) were made every year between 1974 and 1992. Measurements were also made in 1996, 2000, 2007, and 2009. Measurements were mostly done at the end of the growing season but sometimes in the spring before the start of the growing season. In the latter cases, measurements were dated as being done at the end of the previous growing season. Growth estimates were calculated by the Unit for Field-based Forest Research, SLU and obtained from the "Ekologen database" (Gay et al. 1994). Since information on individual tree diameters and heights for the period 1974-1986 is not available we have for consistency in estimates calculated average tree volumes, V m^3, from average tree diameters, d cm (from basal area and stand density), and average heights, h m, using the following equations

$$V = 0.22 + 0.1066d^2 + 0.02085d^2h + 0.008427dh^2 \quad (1)$$

for 1974 (trees with d < 5 cm) (Näslund 1947) and

$$V = 10^{-1.38903+1.84493\log(d)+0.06563\log(d+20.0)+2.02122\log(h)-1.01095\log(h-1.3)} \quad (2)$$

for 1979-2007 (trees with $d > 5$ cm) (Brandel 1990). When compared to volumes calculated from individual tree data for the period 1990-2007 we found that equation (2) underestimates the stand volume by approximately 6%. We have therefore increased all volumes calculated from equations (1) and (2) by 6% in our estimates.

Nutrients in needles

Nutrient concentrations at the end of the growing season in needles have been measured continuously (Gay et al. 1994). The total N content was determined by Kjeldahl digestion between 1974 and 1987. Total C and total N in samples after 1988 were determined with a Carlo-Erba NA 1500 Analyzer. For the analysis of the other elements the needle samples were weighed after drying at 105 ^{o}C and wet-combusted in a mixture of nitric acid/perchloric acid (ratio 2.5:1.0). The elements K, Ca and Mg were determined using an atomic absorption spectrometer (1974-1984) and later by ICP emission spectrometry (Plasma 200). The elements P and Mn were determined colorimetrically until 1984 and thereafter together with K, Ca, and Mg. Parallel analyses were made at every change in methods.

Basal area specific leaf area index

LAI-2000 measurements (LAI) were carried out in September 2009 with the LAI-2000 Plant Canopy Analyzer (Li-Cor Inc.). The LAI-2000 instrument's optical sensor consists of five detectors arranged in concentric rings measuring radiation between 320 and 490 nm, i.e., in the range where the scattering from leaves is minimal. Canopy gap fraction in the zenith angle band 0º - 38° was calculated as the ratio of below- and above-canopy readings by the corresponding detector ring. The below-canopy radiation was measured 1 m above ground, so that only trees were included in the field of view. Above-canopy measurements were collected by automatic logging every 15 s in an open area close to the study site.
The stand was thinned in 2007 to the same basal area in all plots. The LAI in 2007 in plots before the thinning was calculated from the basal area in 2007 before thinning and assuming the same relation as between LAI 2009 and basal area in 2007.

Soil sampling

Soil samples were collected in November 2004 from the FH layer (O_{e+a} horizon) and the 0-5, 5-10, 10-20, 10-30 and 30-50 cm mineral soil layers at eight spots within each of the 16 plots. There was no litter (L) layer proper, and the litter material was interwoven in the moss layer. Because of the difficulty of separating needle litter from mosses and the small amount of litter materials, the

L layer was not included in the soil sampling. All sub-samples at different depths at the same spot were taken below each other to have the soil samples from an unbroken soil profile. The FH samples were taken with a 25 cm x 25 cm frame, and the mineral soil samples were taken with a 50 mm diameter soil corer. Samples from the same soil layer and plot were pooled to form a composite sample.

Laboratory treatment

The soil samples were air-dried and kept at 5 ºC before sieving and weighing at room temperature. The FH material was sieved through a 5-mm mesh, whereby roots, stones and buried branches were sorted out. The mineral soil layers were sieved through a 2-mm mesh. Subsamples were removed from the sieved materials for determination of dry weight, KCl-extractable inorganic N and pH(H_2O). Dry matter was determined after drying at +105 ^oC for 24 h. Total C and N concentrations were determined in a Carlo-Erba NA 1500 Analyzer. Soil pH was measured in the supernatant after revolving flasks with a mixture of soil/distilled water (1:1 by volume) for 2 h followed by sedimentation and aeration for 22 h. Because soil pH was always below 6, we assumed that there was no carbonate C.

After sample preparation, which was finished after about 4 weeks from sampling, FH and mineral soil subsamples (corresponding to 16 and 100 g dry wt, respectively) were placed in plastic jars (50 cm^2 surface area and 466 cm^3 volume). The jars had a lid with a 5-mm diameter aperture for gas exchange. These soil microcosms were incubated in the laboratory at constant temperature (15 ºC) and moisture (60% WHC, water-holding capacity) to determine C mineralisation (CO_2 evolution) and net N mineralisation and potential nitrification. A whole incubation period lasted for 39 days. CO_2 measurements were performed once a week to obtain mean respiration rates for the first 20 days, whereas net N mineralisation was estimated for the whole 39-day period.

To determine C mineralisation, the containers were periodically closed with airtight lids with a rubber septum. Background gas samples were taken after 15 min from the headspace with a syringe and were injected into a gas chromatograph (Hewlett Packard 5890, H.P Company, Avondale, PA, USA). The measurement was repeated when an appropriate amount of CO_2 had accumulated in the jars, from 120 min to 24 h, depending on the respiration rate. The mass of C evolved per jar was calculated according to Persson et al. (1989) and data on the C pools in each soil layer enabled us to calculate C mineralisation rates per m^2. Because roots and mycorrhizal mycelia were almost entirely removed by sieving, and because there was a delay of 4 weeks

between sampling and start of incubation, we considered the estimated C mineralisation to be of heterotrophic and not autotrophic origin.

Inorganic N (NH_4^+-N + NO_3^--N) was extracted from subsamples of 10 and 20 g fresh wt from the organic and mineral soil, respectively, with 100 ml 1 M KCl solution in a rotary shaker for 1 h. The filtrate was photometrically analysed on a FIA STAR 5010 analyser. Because no leaching could occur in the jars, inorganic N accumulated in the samples, and the accumulation rate was considered as net N mineralisation rate. A destructive sampling was made after 39 days after the start of the incubation to calculate the accumulation rates of inorganic N. Net N mineralisation and nitrification were calculated using the following equations (Robertson et al. 1999): net N mineralisation = $[(NH_4^+–N + NO_3^–N)_f - (NH_4^+–N + NO_3^–N)_i]/T_d$; net nitrification = $[(NO_3^–N)_f - (NO_3^–N)_i]/T_d$ where the subscripts i and f indicate concentrations measured before and after aerobic incubation, respectively, and T_d indicates incubation time in days. A negative value indicates microbial net immobilisation. Potential net N mineralisation and nitrification rates were expressed as μg N $(g\ C)^{-1}\ d^{-1}$.

Extrapolation to the field was made by multiplying the C mineralisation, the net N mineralisation and the net nitrification rates obtained in the laboratory at 15 °C (expressed per g of C) by (1) the amount of C per soil layer, (2) the number of days per year (365), (3) a temperature-dependent factor (F_{ST}) and (4) a moisture-dependent factor (F_{SM}). F_{ST} (Eq. 3) was calculated for each soil layer and month (Persson et al. 2000) with input data from soil temperatures (ST) measured at 5 cm depth at Jädraås. F_{SM} (Eq. 4) was calculated for each soil layer and month with input data from measurements of soil moisture (SM) at 10 cm depth. The response function for soil moisture (F_{SM}) was based on Seyferth (1998), who found a linear relation between relative water content (x) and C mineralisation rate.

$$F_{ST} = (ST - ST_{min})^2 / (T_{ref} - ST_{min})^2 \quad (3)$$

$$F_{SM} = 0.8x + 0.2 \quad (4)$$

where ST is the soil temperature in the field (°C), ST_{min} is -6.2 (°C), T_{ref} is the lab incubation temperature (15 °C), and x =fraction of optimum soil moisture (our lab condition of 60% WHC was considered as 1 as well as the winter moisture of 70% water content in the humus layer and 40% water content in the upper mineral soil). After integration for the whole year, the correction factor for converting the rates obtained in the laboratory at 15 °C to those in the field soil at Jädraås was estimated to be 0.32.

Statistics

The experiment had four treatments (control, irrigation, fertilisation and irrigation + fertilisation) and four blocks (three blocks for the LAI study). The statistical analysis was made by an ANOVA with blocks and treatments. Mean values for the soil chemical data were compared for each of the soil layers. In case of significant differences ($P<0.05$) between treatments, pair-wise comparisons were made by t-tests. SAS for Windows, version 9.2 (2008), was used for the statistical tests. The LAI study was similarly analysed as an ANOVA with blocks and treatments, and the mean values were compared for each of the band of angles.

Results

Needle concentrations

Nitrogen concentrations in current needles in the control and irrigated plots varied between 10 and 13 mg g^{-1} during the entire observation period between 1974 and 2004 (Fig. 1). Fertilisation, both with and without irrigation, increased the concentration of N in current needles to between 15 and 20 mg $(g\ dw)^{-1}$ until 1990 when the fertilisation was ended (Fig. 1). During the following years, N concentrations in fertilised plots decreased to the same levels as in the unfertilised plots (Fig. 1). Both kinds of fertilisation drove down the concentrations of other elements relative to N to levels during the period 1974 to 1990. When the fertilisation was stopped, the concentrations of these elements, relative to N, went up to levels making N clearly limiting again (Figs 1 and 2).

Tree growth (including dead and thinned trees)

The fertilised trees increased more rapidly in basal area than the unfertilised trees during the 17 years with nutrient addition, but from then on the basal area growth rates became more similar in the different treatments (Fig. 3 A). Height growth increased more in fertilised than in unfertilised plots, though the response was not as evident as for basal area development (Fig. 3 B). As a result, the stem volume increased markedly more in the fertilised plots than in the unfertilised plots (Fig. 3 C). At the end of the fertilisation period in 1990, the stem volumes in the fertilised F and IF plots were approximately twice as large as in the unfertilised 0 and I plots. In 1990, 16 years after the start of the experiment, the 0 and I plots had almost the same stem volume as the F and IF plots after 10 years of fertilisation (Fig. 3 C).

The difference in basal area and stem volume between fertilised and unfertilised trees was maintained also after the fertilisation was stopped (Fig. 3). The dynamics of the basal area growth showed a bell-shape form with a maximum at a basal area of 15-20 $m^2\ ha^{-1}$ for both fertilised and unfertilised treatments (Fig. 4). The total basal area growth in the fertilised plots was higher than

in the unfertilised plots during the period of fertilisation, even when growth is compared at equal basal areas. During the first years after the termination of fertilisation, the trees in the fertilised plots grew faster than those in the unfertilised stands. The growth in the fertilised trees successively declined to the same level as in the unfertilised trees, although the trees were considerably larger. At the last thinning, which brought all plots to an equal basal area, there was no clear difference in the basal area growth of fertilised and unfertilised trees.

The LAI-2000 measurements (LAI)

The LAI-2000 estimates in 2009 showed a tendency of being somewhat higher in the fertilised plots than in the unfertilised plots (*P* varying between 0.07 and 0.10 for most bands, Table 3). Leaf area per basal area in 2009 was insensitive to both treatment and choice of measurement band. To convert basal area in 2007 to LAI representing LAI before thinning we took the average over all treatments for the band 0º - 38º (with average variability) resulting in an LAI of 0.092 m^2 per cm^2 basal area. In 2007, before the thinning, significantly higher LAI ($P<0.05$) was found in F and IF plots than in 0 and I plots, and there was also a significant difference between the combined unfertilised and fertilised treatments (Table 3).

C and N stocks

Soil C and N pools in 2004 were also affected by the fertilisation treatment (Table 4). The effect was most marked in the FH layer, where the C pools in the F and IF plots were 44 and 60% higher than in the 0 and I plots, respectively, as compared to 15 and 28% higher for the whole soil profile. Irrigation had a tendency to decrease the soil C store.

The effect of fertilisation was more pronounced on soil N than on soil C pools as higher soil N pools were observed in almost all examined soil layers in fertilised plots (Table 4). The increase in N pools after fertilisation was most marked in the FH layer, where the N pools in the F and IF plots were 56 and 101% higher than in the 0 and I plots, respectively, as compared to 22 and 45% higher for the whole soil profile. The effect of fertilisation on soil N could also be seen in lower C/N ratios (Table 4) that were most marked in the FH and 0-10 cm layers.

C and N mineralisation

Carbon mineralisation rates at a constant temperature of 15°C and 60% WHC differed between treatments only in the FH layer. In this soil layer, C mineralisation rates were estimated to be 65% lower in F than in 0 plots and 63% lower in IF than in I plots (Fig. 5, Table 4). There were no significant differences between treatments in the other soil layers or seen as a whole for the entire soil profile.

Net N mineralisation rates at 15°C and 60% WHC were significantly ($p<0.05$) higher (3-8 times) in the fertilised plots (F and IF) than in the unfertilised plots (0 and I) in the FH and mineral soil layers to a depth of 20 cm (Fig. 5, Table 4). The fertilisation effect became less pronounced at greater depths, and there was almost no net N mineralisation detectable at 30-50 cm depth in any of the treatments. All net N mineralisation occurred as NH_4^+ accumulation, and no accumulation of NO_3^- could be detected.

Carbon mineralisation (heterotrophic respiration, Rh) in the field was estimated by using C mineralisation rates at 15°C and 60% WHC, estimates of C pools and data on field soil temperature and moisture. Rh was estimated to vary between 2100 and 2400 kg C $ha^{-1}yr^{-1}$ for all treatments (Table 4). The lower C mineralisation rates in the F and IF plots in the FH layer were compensated for by higher C pools resulting in similar Rh for all treatments.

In contrast to C mineralisation, net N mineralisation was estimated to be higher in the F and IF plots (approximately 70 kg $ha^{-1}yr^{-1}$) than in the 0 and I plots (11-16 kg $ha^{-1}yr^{-1}$) (Fig. 6, Table 4). The difference was particularly evident in the top soil layers. Consequently the ratio of mineralised C to mineralised N differed largely between unfertilised and fertilised plots (Table 4). In the FH layer, the 0 and I plots had C_{min}-to-N_{min} ratios of about 400-700, whereas F and IF plots had C_{min}-to-N_{min} ratios of 30-65, i.e. ten times lower. In the whole soil profile investigated, the C_{min}-to-N_{min} ratios were 130-220 for the 0 and I plots and 33 for both F and IF plots.

Discussion

Tree responses

Fertilisation with N (as well as P, K and other nutrients) increased both growth rates of trees and N concentrations in the needle biomass during the treatment period of 17 years. At the end of fertilisation period in 1990 also LAI-2000 estimates were higher in fertilised plots (Stenberg 1994). Five years after the cessation of fertilisation, N concentrations had dropped to the level in the unfertilised plots. In spite of declining N levels in the needle biomass, the basal area growth remained for several years higher than in the unfertilised plots at equal tree basal area (Fig. 4). This indicates that needle nutrient concentration is not the only factor determining potential growth in this type of forest ecosystems. The estimates of LAI in 2009 indicate that there was a 10% larger needle mass in the fertilised as compared to the unfertilised trees (Table 3). Our LAI estimation in September 2009 might be lower than expected due to ongoing litterfall. On the other hand LAI-2000 reflects shoot silhouette area rather than leaf area and a decrease in LAI due to litterfall is only partly detected by LAI-2000 measurements (Stenberg et al. 1994). We related

LAI to basal area over bark (0.092 m^2 per cm^2 basal area) which also is lower than LAI per cm sapwood reported by Stenberg et al. (1994) for the same experiment in 1990. Thus, higher basal area growth several years after cessation of fertilisation might have been due to higher leaf mass.

The low concentrations of N in the current and one-year old needles in the unfertilised plots indicated N deficiency for most of the time between 1974 and 2004 (Braekke et al. 1998, Linder 1999). However, even in the fertilised plots, N concentrations did not reach the 18 mg g^{-1} that has been judged as required for maximum growth for Norway spruce; this level should be applicable to Scots pine as well. This is a result of a rapidly expanding canopy in response to fertilisation but also an indication that this type of soil lacks the potential to support high rates of N delivery. The low concentrations of other essential nutrients, low even in proportion to fertiliser composition, may be another explanation of the failure to reach maximum production.

The main growth response to fertilisation was found in basal area growth, whereas height growth did not respond equally much. This is a surprising result considering that height growth curves are normally used to predict productivity levels. However, similar results with little response in height growth but large response in basal area growth have been obtained in other annually fertilised pine trials (Weetman et al. 1988, Aronsson et al. 1999, Tamm et al. 1999, Kishchuck et al. 2002). Amponsah et al. (2004) concluded that higher water flow capacity of lower branches may reduce water support to upper branches of trees fertilised annually.

The interpretation of the significance of fertilisation after the cessation of fertiliser addition is complicated by the natural dynamics in forest growth during stand development. It is a well known phenomenon that tree growth rates decline with age or tree size (Waring and Schlesinger 1985, Ryan et al. 1997, 2004). The fertilised trees in this experiment grew more when compared to unfertilised trees of equal sizes, and the unfertilised trees did not seem to catch up. Basal area increment in both unfertilised and fertilised plots had culminated before the fertilisation was terminated and therefore it is difficult to know if the decline in basal increment is due to the size/age of trees or cessation of fertilisation. There is also a problem that the range in overlap of basal areas after the fertilisation has been terminated is small. The growth after the thinning in 2007 indicates that at equal basal areas (Fig. 4), the previously fertilised trees are doing no better than the unfertilised trees and for all treatments the growth is lower than expected from earlier performance. This low growth is likely a result of that the remaining trees had not adapted to the extra resources released by the thinning.

Soil responses

The soil response to fertilisation is important for the interpretation of the fertilisation effect. The increase in soil C stock in the FH layer after fertilisation accompanied with a decline in C mineralisation rate resulted in an almost equal heterotrophic respiration as in the unfertilised plots. C mineralisation in other parts of the soil profile seemed to be unaffected by fertilisation.

Net N mineralisation, on the other hand, increased 5-6 times in relation to the unfertilised plots. This is in agreement with Chen and Högberg (2006), who found that gross N mineralisation was still three times higher than in control plots after suspension of N fertiliser for 14 years. Another way of looking at the changes in the soil C and N turnover is that although the C/N in the soil profile (down to 50 cm) declined from 33 in the unfertilised plots (0 and I plots) to 31 and 28 in the F and IF plots, respectively, the ratio of C_{min}-to-N_{min} dropped from 130 and 220 in the 0 and I plots to 33 in both F and IF plots (Table 4). Thus, the fertilised plots mineralised C and N in proportion to the organic C and N present in the soil, whereas the unfertilised plots mineralised more C and less N than indicated from the substrate composition. Because C mineralisation (per hectare and year) did not differ between treatments, the main explanation of the high C_{min}-to-N_{min} in the 0 and I plots is low net N mineralisation.

In principle, this relative difference in C and N mineralisation should lead to decreasing C/N ratios in the soil unless other mechanisms utilising soil C and N in different proportions act as a counterbalance. An increasing number of studies have shown that organic N forms, primarily in the form of amino acids, are taken up by plants in boreal forests (Näsholm et al. 1998, Nordin et al. 2001, Persson and Näsholm 2001, Kielland et al. 2007), and amino acids contribute substantially to the N economy of boreal and arctic plants (Lipson and Näsholm 2001, Schimel and Bennett 2004). Numerous studies have shown that ectomycorrhizal fungi can utilise a wide range of amino acids as sources of both N and C (Plassard et al. 2000) and that a proportion of the assimilated N is transferred to the host plant (Abuzinadah et al. 1986, Taylor et al. 2004). Recent studies have also shown that the ability of ectomycorrhizal fungi to degrade proteins by extracellular proteases is widespread (Nygren et al. 2007). It is, therefore, very likely that not only inorganic N but also organic N were taken up by the pine trees in the 0 and I plots, where the net N mineralisation was low.

Another way of realising the importance of organic N uptake is to consider how much of the N uptake might be supplied by N mineralisation. The production of stem biomass was almost 10 m^3 ha^{-1} yr^{-1} in both fertilised and unfertilised plots after the end of fertilisation (not directly seen but

can be derived from Fig. 3 C). With a wood density of 420 kg m^{-3} and an N concentration of 1 g kg^{-1}, the necessary N uptake is 4.2 kg ha^{-1} yr^{-1}, respectively. The needle biomasses in 2007 can be estimated with standard allometric functions (Marklund 1988) to around 6000 kg dry wt ha^{-1} with a turnover rate of 25% yr^{-1} (Ågren et al. 2007). With an N concentration of 4 mg g^{-1} in needle litter (Berg et al. 1991), 6 kg N ha^{-1} yr^{-1} is required to replace what is lost in needle litterfall. Turnover of fine roots contributes more, and Ågren et al. (2007) estimated that the fine root production is 1.5 times needle production. With an N concentration of 7 mg g^{-1} (Pluth et al. 1995), the fine root turnover requires an N uptake of 16 kg ha^{-1} yr^{-1}. The total N uptake by just the trees is thus at least 26 kg ha^{-1} yr^{-1}. In addition, the ground vegetation has also an N uptake which probably adds another 5-10 kg N ha^{-1} yr^{-1} to the uptake. This is much more than the estimated mineralisation in the unfertilised plots but less than that in the fertilised plots. The long-term effect of fertilisation has, therefore, also resulted in a shift from an N economy dominated by organic N uptake to one where inorganic N plays a more prominent role.

In conclusion, the long period of fertilisation with cumulative doses of 1000 and 1760 kg N ha^{-1} induced a change in ecosystem functioning. A higher production level was attained. However, this change does not seem to persist for long once the fertilisation has ceased. There was also a persistent shift towards an N economy with uptake of inorganic N.

Acknowledgements

This work was supported by the Swedish University of Agricultural Sciences through the programme Carbon Sweden. We thank Bertil Andersson and Christer Karlsson for organising the field work and Birgitta Vegerfors-Persson for statistical consultation.

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Table 1. Fertilisation (kg N ha^{-1}) and irrigation (mm) regimes in the Ih 2 experiment at Jädraås. Solid fertiliser (F) was applied in early June with some variation. Irrigation (I) and irrigation + fertilisation (IF) was applied from late May to late August.

Year	IF	F	I	IF
	kg N ha^{-1}	kg N ha^{-1}	mm	mm
1974	70	80	100	100
1975	100	80	300	300
1976	150	80	300	300
1977	150	80	250	250
1978	200	80	220	250
1979	200	80	230	230
1980	200	80	160	160
1981	100	50	165	165
1982	100	50	215	215
1983	100	50	272	272
1984	100	50	245	245
1985	100	50	190	190
1986	50	50	140	190
1987	50	50	170	175
1988	30	30	180	180
1989	30	30	160	160
1990	30	30	260	260
1991	0	0	0	0
1992	0	0	0	0
1996	0	0	0	0
1998	0	0	0	0
2004	0	0	0	0
Total	1760	1000		

Table 2. Composition of liquid (IF) and solid (F) fertilisers in relation to N. The N concentration is set to 100, and the amounts of other elements are expressed in proportion (by weight) to N according to Ingestad (1967) and Aronsson and Elowson (1980). Extra doses of B (2.5 kg ha^{-1}) were given in the F treatment in 1978 and 1980 (Linder 1987).

Element	N	K	P	Ca	Mg	S	Fe	Mn	B	Cu	Zn	Mo	Na	Cl
IF	100	65	13	7	8.5	9	0.7	0.4	0.2	0.03	0.03	0.007	0.0034	0.03
F	100	75	37.5											

Table 3. Mean LAI (m^2 m^{-2}, SE within parentheses, n=3) in the four treatments 0, I, F and IF (see Table 1) in 2009 and mean LAI before thinning as calculated for 2007 in different band of angles. Mean LAI in the combined unfertilised (mean of 0 and I) and fertilised (mean of F and IF) plots are also given. Values with different letters for a band are significantly different at $P<0.05$.

			2009			
Band	0	I	F	IF	Unfertilised	Fertilised
0º - 38º	1.98 (0.17)	1.97 (0.05)	2.22 (0.06)	2.11 (0.04)	1.97 (0.09)	2.16 (0.01)
			2007			
0º - 38º	2.33[a] (0.17)	2.66[a] (0.08)	3.57[b] (0.15)	3.47[b] (0.08)	2.49[a] (0.10)	3.57[b] (0.12)

Table 4. Soil C and N pools, C and (net) N mineralisation rates, potential field C and net N mineralisation and the ratio of mineralised C to mineralised N in different treatments (see Fig. 1) and soil layers in 2004. Values with different letters (for the same variable) are significantly different at $p<0.05$. * denotes weighed means of C and net N mineralisation rates in composite soil layers. nd=not detectable.

	Treat	FH	0-5 cm	5-10 cm	10-20 cm	20-30 cm	30-50 cm
C pool	0	6.9 ^{b}	14	12	12	4.0	2.4
(Mg ha^{-1})	I	5.4 ^{b}	11	10	11	4.2	2.7
	F	9.9 ^{a}	13	13	15	5.6	2.7
	IF	8.6 ^{a}	15	12	14	5.0	3.4
N pool	0	190 ^{b}	390	328	415	157	85
(kg ha^{-1})	I	149 ^{b}	311	283	386	176	104
	F	297 ^{a}	377	393	517	215	116
	IF	300 ^{a}	504	410	488	193	150
C mineralisation rate	0	606 ^{ab}	429 ^{b}	315	220	228	187
(mg CO_2-C kg^{-1} C d^{-1})	I	775 ^{a}	628 ^{a}	375	272	257	268
	F	395 ^{c}	445 ^{b}	365	289	239	250
	IF	491 ^{bc}	417 ^{b}	387	274	258	201
Net N mineralisation rate	0	1.0 ^{c}	2.8 ^{b}	3.3 ^{b}	2.5 ^{b}	2.3 ^{ab}	nd
(mg N kg^{-1} C d^{-1})	I	2.0 ^{c}	2.0 ^{b}	3.4 ^{b}	2.3 ^{b}	1.5 ^{b}	nd
	F	6.2 ^{b}	13 ^{a}	13 ^{a}	14 ^{a}	4.6 ^{a}	nd
	IF	17 ^{a}	13 ^{a}	11 ^{a}	9.4 ^{a}	2.7 ^{ab}	nd
C mineralisation	0	478	711	430	317	105	50
(kg CO_2-C ha^{-1} yr^{-1})	I	487	778	453	362	126	88
	F	451	646	554	502	155	77
	IF	492	715	537	431	153	71
Net N mineralisation	0	0.7 ^{b}	4.9 ^{b}	4.6 ^{b}	3.7 ^{b}	1.7	nd
(kg N ha^{-1} yr^{-1})	I	1.2 ^{b}	2.5 ^{b}	3.6 ^{b}	2.8 ^{b}	0.6	nd
	F	6.9 ^{a}	19 ^{a}	19 ^{a}	24 ^{a}	2.9	nd
	IF	16 ^{a}	24 ^{a}	16 ^{a}	15 ^{a}	1.3	nd
C-to-N ratio (substrate)	0	36 ^{a}	36 ^{a}	36 ^{a}	30 ^{ab}	25 ^{ab}	27
	I	36 ^{a}	35 ^{a}	37 ^{a}	29 ^{ab}	24 ^{b}	26
	F	33 ^{b}	33 ^{a}	34 ^{a}	29 ^{a}	26 ^{a}	23
	IF	29 ^{c}	29 ^{b}	29 ^{b}	28 ^{b}	26 ^{ab}	22
C_{min}-to-N_{min} ratio	0	719	144	94	86	62	nd
(processes)	I	413	314	126	130	146	nd
	F	65	34	29	21	53	nd
	IF	30	29	34	28	76	nd

Figure legends

Fig. 1. Concentration of N in current needles in the Ih 2 experiment. Control (0) is denoted with O, irrigation (I) with Δ, fertilisation (F) with ●, and irrigation + fertilisation (IF) with ▲. Solid lines show N concentrations before 1991 and broken lines show N concentrations after the fertilisation was stopped in 1991. Dotted line shows the N concentration required for maximal growth.

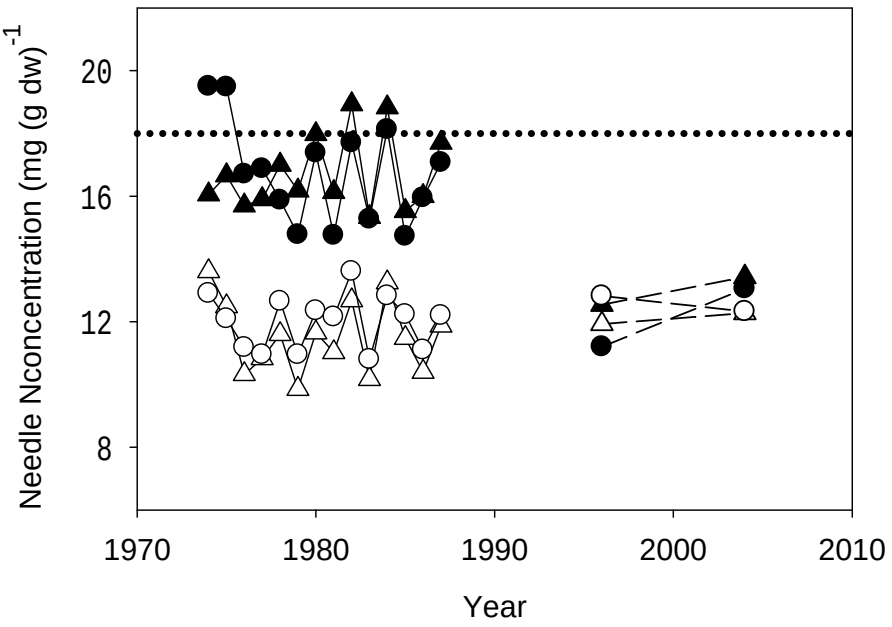
Fig. 2. Element-to-N (N=100) ratios in current needles. Control (0) is denoted with O, irrigation (I) with Δ, fertilisation (F) with ●, and irrigation + fertilisation (IF) with ▲. Solid lines show ratios before 1991 and broken lines ratios after the fertilisation was stopped in 1991.

Fig. 3. Development of basal area, mean height and stand volume in the Ih 2 experiment. Control (0) is denoted with O, irrigation (I) with Δ, fertilisation (F) with ●, and irrigation + fertilisation (IF) with ▲.

Fig. 4. Basal area growth versus standing basal area in the Ih 2 experiment. Control (0) is denoted with O, irrigation (I) with Δ, fertilisation (F) with ●, and irrigation + fertilisation (IF) with ▲. Solid lines indicate period with fertilisation. Broken lines indicate period without fertilisation. Symbols not connected by lines are values after the thinning in 2007.

Fig. 5. C mineralisation rates (top) and net N mineralisation rates (bottom) ± one SE in different treatments and soil layers in laboratory incubations at 15°C and 60% WHC.

Fig. 6. Annual net N mineralisation in different treatments and soil layers as calculated from laboratory incubation, soil pools in the field and corrected for soil temperature and moisture. Intervals indicate SE for the whole soil profile.



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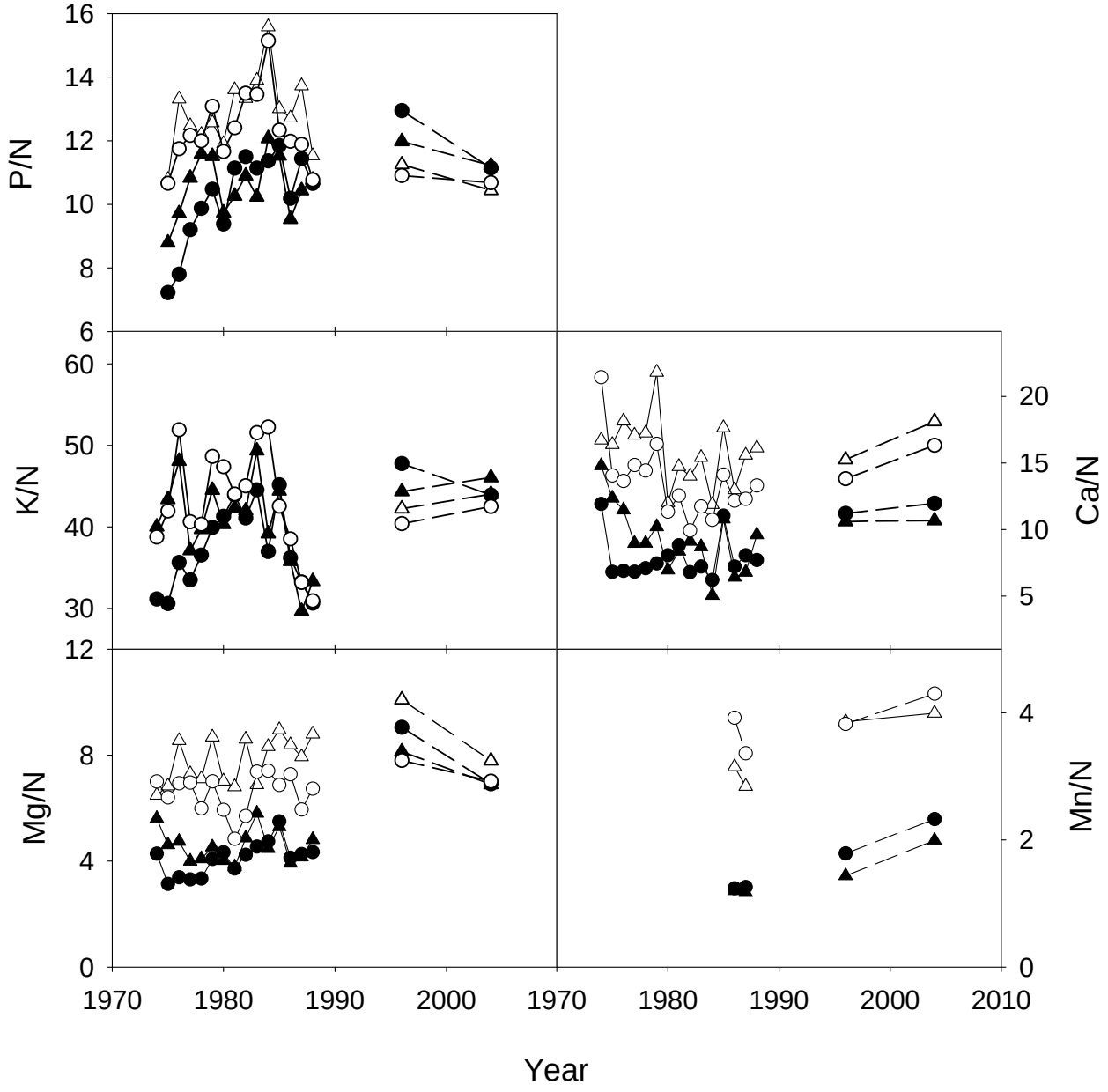

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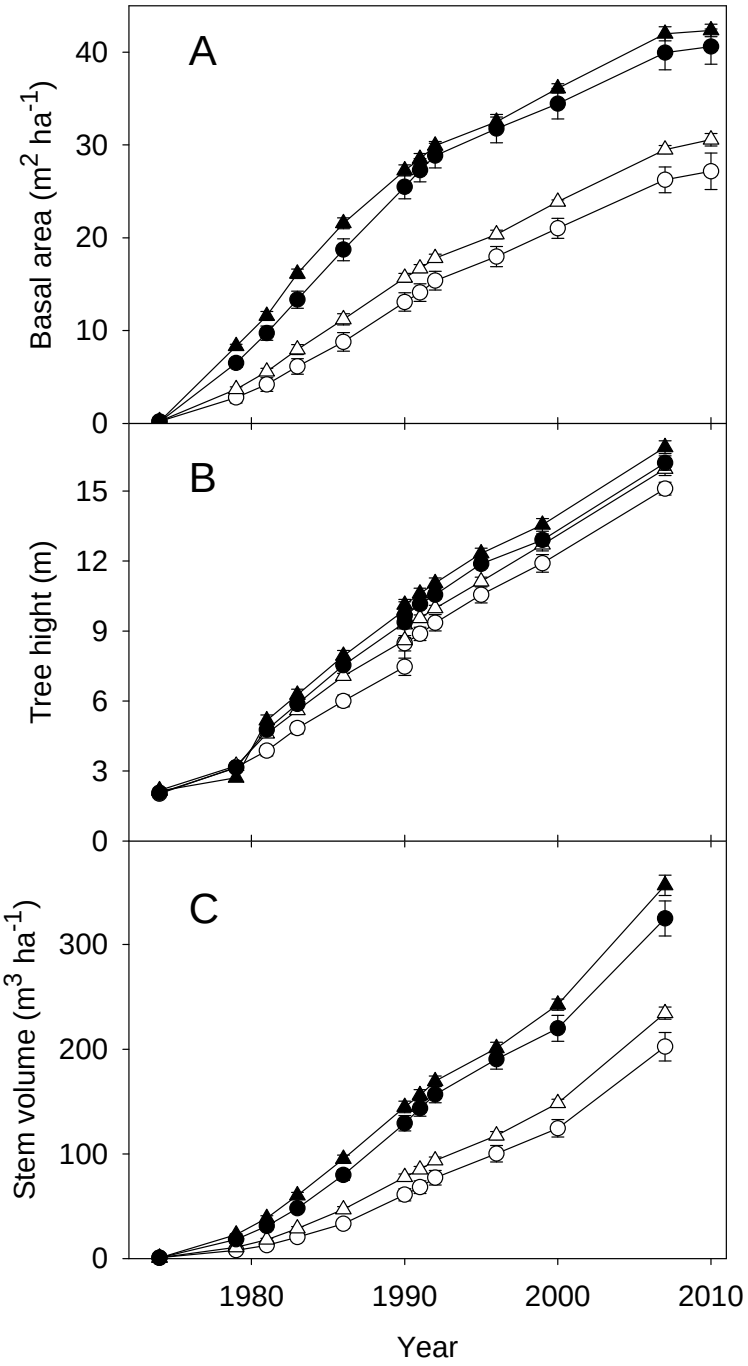

Fig. 3. Development of basal area, mean height and stand volume in the Ih 2 experiment. Control (0) is denoted with O, irrigation (I) with Δ, fertilisation (F) with ●, and irrigation + fertilisation (IF) with ▲.

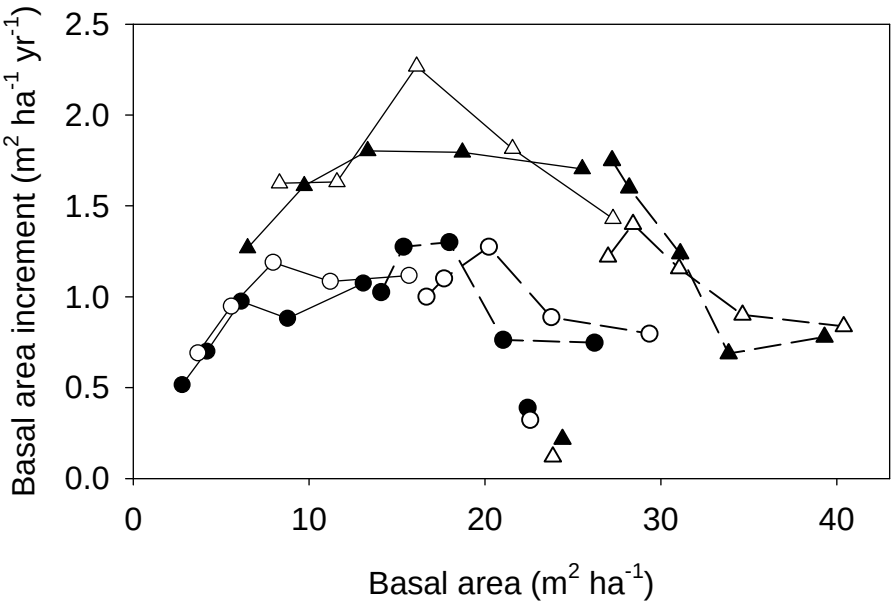

Fig. 4. Basal area growth versus standing basal area in the Ih 2 experiment. Control (0) is denoted with O, irrigation (I) with Δ, fertilisation (F) with ●, and irrigation + fertilisation (IF) with ▲. Solid lines indicate period with fertilisation. Broken lines indicate period without fertilisation. Symbols not connected by lines are values after the thinning in 2007.

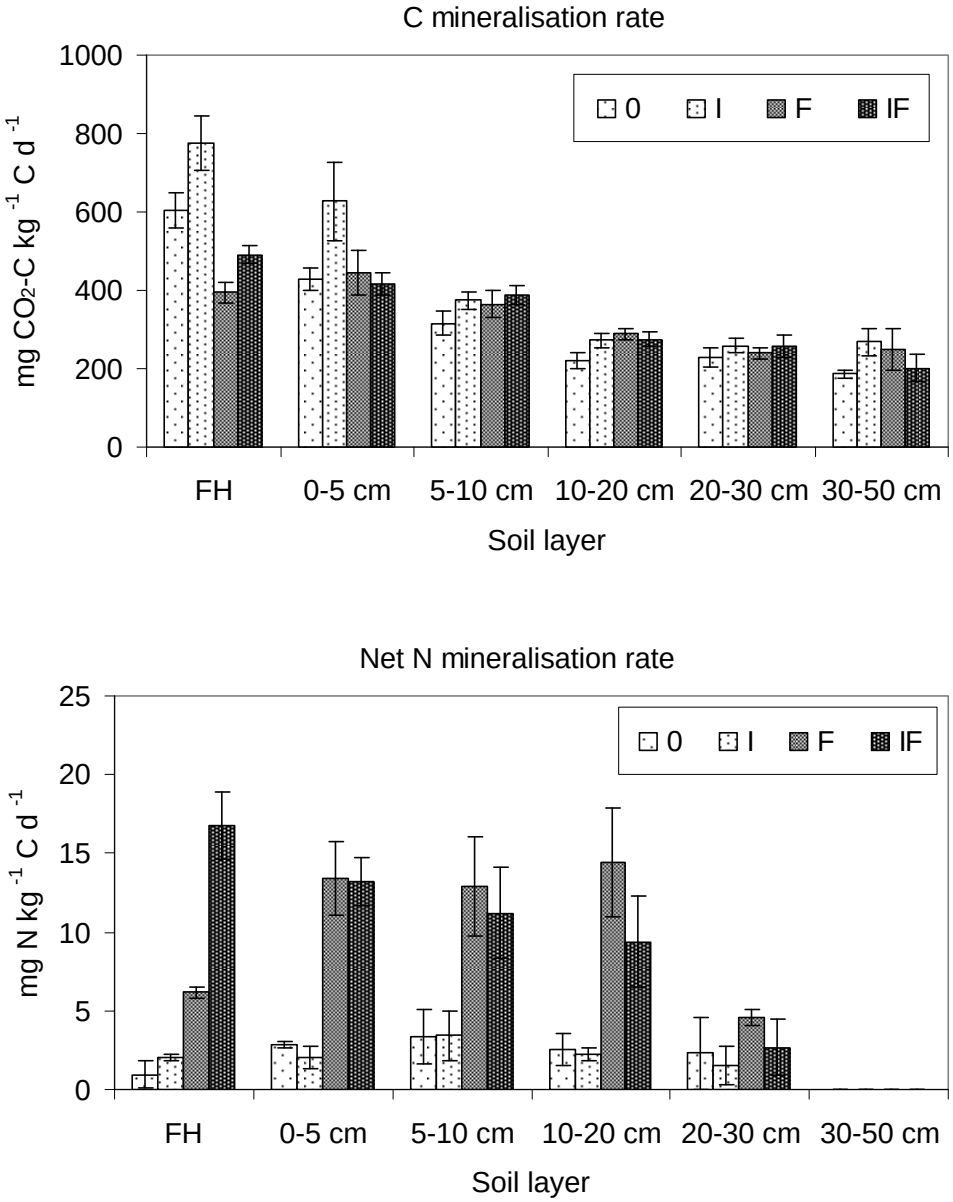

Fig. 5. C mineralisation rates (top) and net N mineralisation rates (bottom) ± one SE in different treatments and soil layers in laboratory incubations at 15°C and 60% WHC. Samples collected in November 2004.

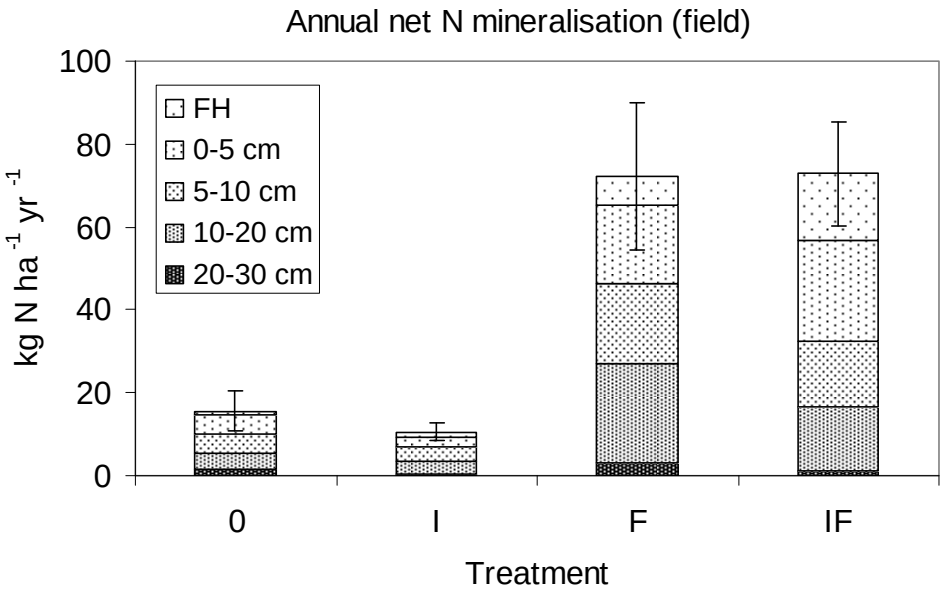

Fig. 6. Annual net N mineralisation in different treatments and soil layers as calculated from laboratory incubation, soil pools in the field and corrected for soil temperature and moisture. Intervals indicate SE for the whole soil profile. Values are representative for 2004.