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Effects of long-term fertilisation and growth on micronutrient status in Norway spruce trees

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Abstract

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Effects of fertilisation treatments (amounts and composition) on needle concentrations of micronutrients (boron, copper, iron, manganese and zinc), were studied in a long-term fertilisation experiment with young Norway spruce (*Picea abies* (L.) Karst.) in Central Sweden. Stored current-year's needles (1967–1989), and material from a biomass sampling in 1989, were used to determine changes in micronutrient status with stand development, and to estimate total amounts of micronutrients, in all aboveground organs for a wide range of nutrient regimes and stand productivities. Different combinations of nitrogen, phosphorus, potassium, calcium, magnesium and micronutrients were applied. Fertilisation resulted in a wide range of growth rates: the most optimal treatments grew more than three times as fast as the control stands. When micronutrients were included among the elements supplied, internal concentrations of boron, manganese and zinc increased. Needle concentrations of copper and iron were, however, not affected by fertiliser treatment or by differences in growth rate. While copper concentrations in all aboveground organs were similar between treatments, large amounts of iron were stored in the branches. With increasing growth rates the increased amount of iron incorporated into needle biomass was balanced by a decrease in concentration and amount of iron in the branches. Boron concentrations in needles from fertilised trees were occasionally close to deficiency levels when trees were not supplied with boron. Boron appeared to be retranslocated from older needles to current developing shoots, thereby reducing the 'dilution effect' caused by increased biomass production.

Keywords: N, B, Fe, Cu, Zn, allocation, conifer, deficiency, mineral nutrition, trace elements.

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Introduction

The nutrient requirements for growth of higher plants have been studied for more than a century, and a vast literature has been published on the subject (*cf.* Marschner, 1986; Mengel & Kirkby, 1987). A number of elements has proved to be essential for the functioning of plants. Based on the amounts needed in plant tissue, these elements are often divided into macro- and micronutrients, (macronutrients $>500\ \mu g\ g^{-1}$ and micronutrients $<50\ \mu g\ g^{-1}$ dry mass). In Swedish forest stands growing on mineral soils, nitrogen is nearly always the main limiting factor and micronutrients are usually available in excess of physiological requirements (*cf.* Tamm, 1991; Linder, 1995). The risk of reaching deficient (when visible symptoms appear) or growth-limiting levels of micronutrients, increases in forest plantations (*e.g.* Hill & Lambert, 1981; Nambiar, 1984), especially when they are fertilised with macronutrients (*e.g.* Van Lear & Smith, 1972; Aronsson, 1983).

Even though small-scale forest fertilisation experiments were performed at the turn of the 19th century, it was not until the 1950s that the study of the relationship between nutrients and ecosystem functioning was recognised as a science in its own right (*cf.* Tamm, 1991). At about this time, a series of small-scale forest fertilisation experiments was established in Sweden, mainly focussing on macronutrients, nitrogen and phosphorus in particular. These experiments indicated a need for long-term nutritional experiments, in which the nutrient status of the trees was better controlled. Therefore, a series of experiments was started to determine the primary production of forest ecosystems at optimum nutrient levels, and to study disturbances in ecosystem functions under supra-optimal nutrient regimes (Tamm, 1968; Tamm, Aronsson & Burgtorf, 1974).

Since Swedish soils are young, micronutrients are normally present in sufficient amounts and deficiencies are rarely observed in forests (*cf.* Aronsson, 1984). However, as early as the 1950s and 1960s, growth disturbances in stands on peatland and in fertilised stands on mineral soils were identified as being caused by micronutrient deficiencies (Romell, 1950; Ingestad, 1958, Albrektsson, Aronsson & Tamm, 1977). Growth disturbances occurred when large amounts of nitrogen were applied, and boron in particular became deficient. The initial reports were followed by similar observations in Finland (Huikari, 1977), Norway (Braekke, 1977; 1979), and Sweden (Aronsson, 1980; 1983).

Nutrient concentrations in living tissues need not reach deficiency levels, *i.e.* visible symptoms or damage, to have a strong effect on biomass allocation and growth in trees (*cf.* Ericsson, 1991; McDonald, Ericsson & Ingestad, 1991). Effects on growth caused by limiting addition rates and internal concentrations of macronutrients in seedlings (*e.g.* Rook, 1991) and field-grown trees (*e.g.* Linder, 1987; Oren, Schulze, Werk & Meyer, 1988); are relatively well described. By contrast, our understanding of the effects of micronutrient limitations in seedlings (*cf.* Göransson, 1993; 1994; Göransson & McDonald, 1993) or forest stands (*cf.* Ahrens, 1964; Aronsson, 1983; Linder, 1995) is very limited. Except when damage has occurred, the micronutrient status of trees has rarely been analysed in natural forests or long-term fertilisation experiments (*e.g.* Bergmann, 1986).

The aim of the present study was to determine the effects of stand age, growth rate and long-term fertiliser application on between-year variation in needle concentrations of micronutrients, and their amount and distribution in the above-ground biomass of Norway spruce. The experimental site Stråsan, which is part of the 'Forest nutrient optimisation experiments' established in the late 1960s, was used for the study (*cf.* Tamm, 1968; 1991). Stored current-year needles and material from a biomass sampling in 1989 were used to determine changes in micronutrient status with stand development. Results concerning macronutrient distribution in the above-ground tree components and soil in some of these stands, were recently reported by Eriksson, Berdén, Rosén & Nilsson (1996).

Materials and methods

The study was performed in the 'optimum nutrition experiment' Stråsan, situated in central Sweden (60°55′N, 16°01′E, 350 m a.s.l.). The

annual mean temperature is 3.2 °C, with the highest monthly mean temperature in June (15 °C) and the lowest in January (−8 °C). Annual precipitation is about 750 mm, the highest precipitation being in August and September. The soil is mainly a haplic podsol (FAO), and except in extreme years, soil water is not a limiting factor for growth (*cf.* Högberg, Johannisson & Hällgren, 1993). A detailed description of the site, experimental design and treatments can be found in Tamm *et al.* (1974) and Tamm (1991). A complete list of previous publications from the Stråsan experiment was compiled by Gay, Tamm, Aronsson, Flower-Ellis & Linder (1994).

The experimental area was clearfelled during the winter of 1956-57, burned the following summer, and planted in 1958 with seedlings of Norway spruce (*Picea abies* (L.) Karst.). The fertilisation treatment commenced in 1967 and was continued with annual applications during more than 20 years. Nitrogen (N) was supplied every year and other elements at varying intervals. The years, rate, and composition of fertiliser additions for the period 1967 1988 are given in Tables 1 and 2.

Time series of needle micronutrients (1966–1989)

Initial needle samples were taken in 1966 and thereafter current needles were sampled in late autumn each year. The samples were initially taken from the third whorl (from the top) and later from the upper third of the crown. Each sample consisted of needles taken from 10 trees per stand. The needles were dried for 48 hours at 85 °C, before being ground in a ball-mill and analysed for nutrients. The residue of each sample was stored in a sample archive. Needles from seven sampling occasions, from the start of the treatments in 1967 until 1989, were analysed to determine changes in micronutrient status with stand development. The following treatments were chosen for the analysis of micronutrients: control (C), N_1, N_2, N_3, N_1P_2, N_1P_2+, N_2P_2+ and N_2P_2Ca+, where N and P are nitrogen and phosphorus, and N_2, N_3, P_2 are multiples of N_1 and P_1. Only plots with the high addition rate of phosphorus (P_2) were used (Table 1). Treatments denoted by (+) indicate that these stands received potassium (K), magnesium (Mg), and a mix of micronutrients (*cf.* Tables 1, 2) at short intervals. One of the treatments (N_2P_2Ca+) also received 4000 kg ha^{-1} of calcium (Ca) at the start of the experiment.

Table 1. *Amounts (kg ha^{-1}) of nitrogen (N), phosphorus (P), potassium (K), and magnesium (Mg), supplied during the experimental period, 1967–1989. The individual treatments were a combination of these supply rates, i.e. in 1967 a treatment denoted N_2P_2 was supplied with 120 kg N and 40 kg P ha^{-1}, and during the whole period the supply was 1760 kg N and 300 kg P ha^{-1}. (After Tamm, 1991)*

	Treatment							
Year	N_1	N_2	N_3	P_1	P_2	K	Mg	Ca
1967	60	120	180	20	40	80	22	4000
1968	60	120	180					
1969	60	120	180	20	40	80	22	
1970	40	80	120	10	20			
1971	40	80	120					
1972	40	80	120					
1973	40	80	120					
1974	40	80	120	20	40	80	22	
1975	40	80	120					
1976	40	80	120					
1977	30	60	90	20	40	80	22	
1978	30	60	90					
1979	30	60	90					
1980	30	60	90	20	40	80	22	
1981	30	60	90					
1982	30	60	90					
1983	30	60	90					
1984	30	60	90	20	40	80	22	
1985	30	60	90					
1986	30	60	90					
1987	30	60	90					
1988	30	60	90	20	40	65	18	
1989	30	60	90					
Total	880	1760	2640	150	300	545	150	4000

Biomass sampling (1989)

In 1989, a detailed sampling and nutrient analysis was made on the aboveground biomass in a number of the stands. Treatments chosen for biomass sampling were control (C), N_1P_1, N_2P_2, N_3P_2, N_1P_1+, N_2P_2+, N_2P_2Ca+, which were partly different from those used for the time series of needle nutrients. The treatments N_1P_1 and N_1P_1+ were discontinued in 1986 (*cf.* Tamm, 1991), but this was considered to be of minor importance for the purpose of the present study. Biomass samples were taken on two plots per treatment. Trees were chosen as the tree of mean basal area for the plot plus and minus one

Table 2. *Amounts (kg ha^{-1}) of boron (B), zinc (Zn), copper (Cu), and manganese (Mn) supplied in treatments receiving micronutrients. The micronutrient mix also contained cobalt and molybdenum, of which the total addition during the experimental period 1967 to 1988 was 0.33 kg ha^{-1} each. (After Tamm, 1991)*

	Element			
Year	B	Zn	Cu	Mn
1967	0.2	0.2	0.3	0.8
1969	0.8	0.7	1.2	2.7
1974	0.6	0.5	0.9	1.9
1977	1.2	1.0	1.7	3.9
1980	1.2	1.0	1.7	3.9
1984	2.5	–	–	–
1988	1.1	1.5	0.4	5.4
Total	7.6	4.9	6.2	18.6

standard deviation. The trees were divided into current year's needles, older needles, branches, stem wood and stem bark. For further details regarding the biomass sampling, see Eriksson *et al.* (1996).

Micronutrients were analysed in the following categories: (i) current needles, (ii) 'needles', where current and older needles were mixed (iii) branches, and (iv) 'stem', where stem wood and stem bark were merged. To scale up from nutrient content of sample trees to nutrient content per hectare, a modified version of the method described by Madgwick (1982) was used, whereby stem volume instead of basal area was used as scaling factor.

Nutrient analysis

Nitrogen concentrations were determined by a modified version of the method described by Kirsten & Hesselius (1983), using an elemental combustion analyser (Carlo Erba ANA 1500, Carlo Erba Strumentazione, Milan, Italy). All nutrients except nitrogen were analysed with a plasma emission photospectrometer Jobin Yvon JY 70 plus (Jobin Yvon, Longjumeau, France). The plant material was dissolved in a mixture of 10 ml nitric acid (HNO_3) and 1 ml perchloric acid ($HClO_4$). The samples were heated in Teflon tubes on aluminium blocks to 110–130 °C for about 8 hours. The acid was evaporated until 0.25 ml perchloric acid remained, diluted in warm distilled water, then adjusted to 35 ml at room temperature. All nutrient concentrations are expressed in relation to tissue dry mass.

Results

Growth and dry-matter allocation

Fertilisation with N and P resulted in a dramatic increase in aboveground production (Fig. 1, 2). In 1983, before the first thinning, stem volume on the (N_1P_1) plots was three times as high as on control plots. A double (N_2P_2) or triple (N_3P_2) supply of N, combined with a double rate of P, had not increased production more than the supply of K, Mg, and micronutrients (N_1P_1+). When the higher rate of N and P supply was combined with K, Mg, and micronutrients (N_2P_2+), the accumulated stem volume was increased by a further 35%. In 1983,

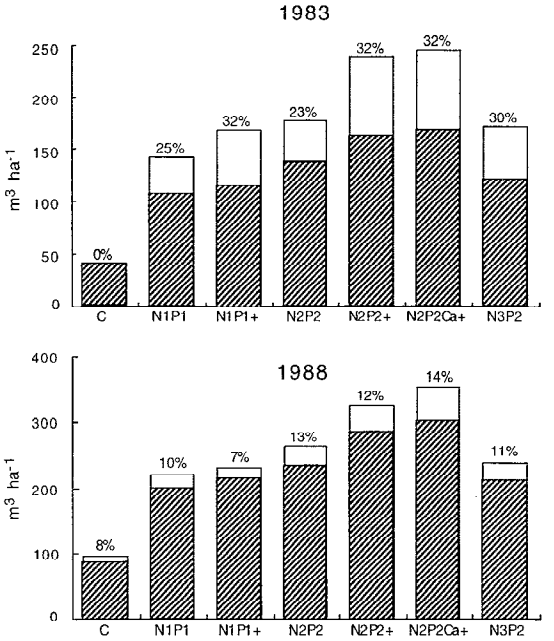

Fig. 1. The amount of stem volume (total column) in young fertilised stands of Norway spruce after 15 (1983) and 21 (1988) years' treatment. Different amounts of nitrogen, alone and in combination with other nutrients, were annually applied. The individual treatments were a combination of supply rates, *i.e.* a stand denoted N_2P_2 had received twice as much N and P as the treatment N_1P_1 (*cf.* Tables 1, 2). Stands receiving K, Mg, and micronutrients are indicated by +. The open part of each column gives the absolute volumes removed by thinning, in 1983 and 1988. The relative amounts removed in each stand are given in per cent of the volume before thinning. For further explanations, see text.

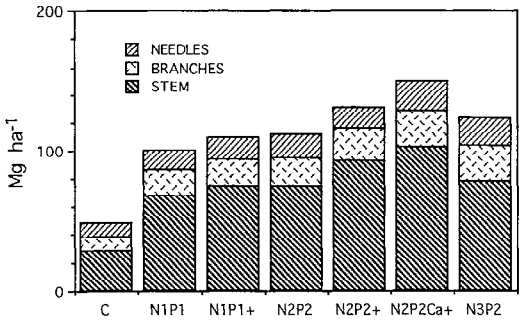

Fig. 2. The amount of standing biomass (Mg dry mass ha^{-1}) in young fertilised stands of Norway spruce after 21 years' treatment. The amount of bark is included in the values given for branches and stems, but in Table 3 these components are given separately. For further explanations, see Fig. 1.

there was no extra effect on stemwood volume of the initial supply of Ca to some of the plots (N_2P_2Ca+). At the time of the sampling in 1989, however, these plots contained 10% more stemwood, by both volume and mass, than did plots (N_2P_2+) which, except for Ca, had received the same nutrient supply (Table 3).

After more than 20 years' treatment, the partitioning of aboveground biomass (Fig. 2, Table 3) was similar in all treatments, except in control plots and plots supplied with triple rates of N (N_3P_2). Approximately 60% of the biomass was found in stemwood, 12–15% in needles, and 11–14% in branches. Trees on control plots, and those receiving the high N supply (N_3P_2), contained a smaller fraction of stemwood (Control $p=0.0026$, N_3P_2 $p=0.014$) than trees in other treatments. Stems in these stands accounted for little more than 50% of the aboveground biomass, and a significantly larger proportion of the standing biomass was found in needles (Control $p=0.0004$, N_3P_2 $p=0.084$). The ratio between stem and needle dry mass was 2.94 for control trees, and 3.85 for trees from N_3P_2 plots. The stem:needle ratios in other treatments varied between 4.34 and 5.88. The highest ratio (5.88) was found in trees on the N_2P_2+ plots.

Time series of needle micronutrients (1966–1988)

There were pronounced between-year variations in the concentration of most of the analysed micronutrients (*cf.* Fig. 3, 4). Most of this variation, however, occurred during the first third of the treatment period (1967–1974), and seemed to coincide with the time required to obtain 'stable' nitrogen concentrations (*cf.* Fig. 3a,b). The pattern of change during this period differed between elements and was affected by treatment.

The concentration of boron [B] in needles from control plots was rather constant (*ca.* 15 μg g^{-1}) throughout the experimental period (Fig. 3c), but decreased to less than 10 μg g^{-1} when stands were supplied with fertiliser without micronutrient addition. When B was included in the fertiliser, needle [B] was maintained equal to or above the concentration in control needles (Fig. 3d). Pronounced peaks in [B] were found when needles sampled in the years of B addition were analysed (1974 & 1984).

The needle concentrations of copper (Fig. 3e,f) were rather stable throughout the treatment period (3–5 μg g^{-1}), except for a peak

Table 3. *Amount (Mg dry mass ha^{-1}) of needles, branches (including bark), stemwood, stembark, and attached necromass in some stands at Stråsan, after 21 years' treatment. The amounts of macronutrients and micronutrients supplied are given in Tables 1 and 2, respectively. Stands which were supplied with micronutrients are shown in the Table by +*

	Treatment						
Fraction	Control	N_1P_1	N_1P_1+	N_2P_2	N_2P_2+	N_2P_2Ca+	N_3P_2
Needles	9.7	14.1	15.3	16.9	16.0	20.8	20.0
Branches	7.1	13.7	14.0	14.4	15.2	19.4	17.7
Stemwood	25.3	60.9	67.0	66.5	84.4	93.4	70.3
Stembark	3.3	6.6	7.2	7.5	8.3	8.9	7.1
Dead	2.4	5.0	6.1	6.4	7.5	7.0	8.5
Total	47.8	100.3	109.6	111.7	131.4	149.5	123.6

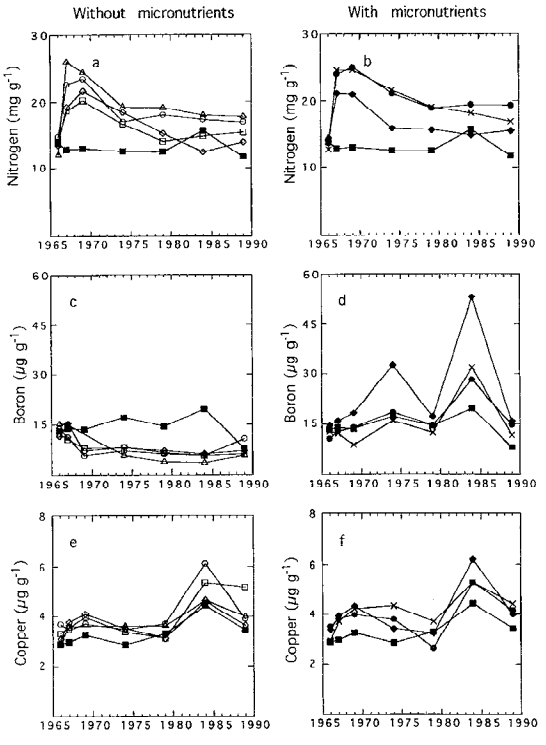

Fig. 3. Nitrogen (a, b), boron (c, d), and copper (e, f) concentrations in current year's needles in Norway spruce trees sampled in late autumn, 1966 to 1989. Fertiliser treatments were started in 1967. Micronutrients were always added as a mix (boron, copper, manganese and zinc) and together with potassium and magnesium. Stands supplied with micronutrients are indicated by +. The treatments were: control (■), N_1 (□), N_1P_2 (◇), N_2 (○); N_3 (△), N_1P_2 + (◆), N_2P_2 + (●), and N_2P_2Ca + (×). For further explanations, see Fig. 1.

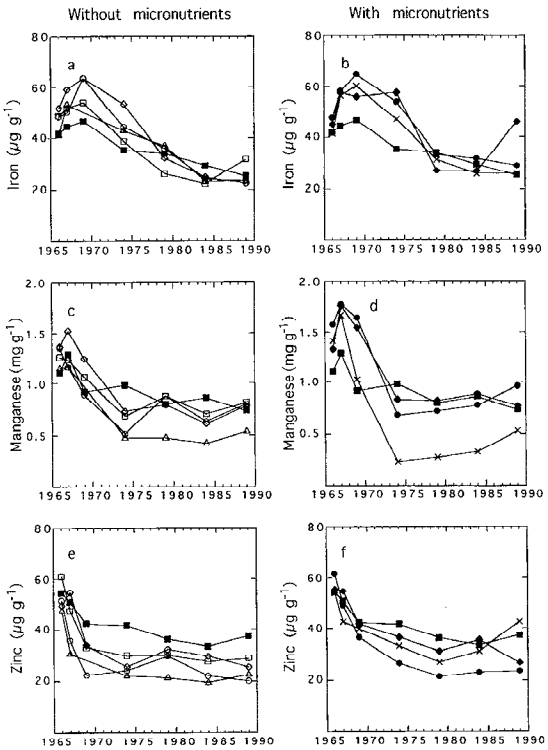

Fig. 4. Iron (a, b), manganese (c, d), and zinc (e, f) concentrations in current year's needles in Norway spruce trees sampled in late autumn, 1966 to 1989. Fertiliser treatments were started in 1967. The treatments were: control (■), N_1 ( ), N_1P_2 (◇), N_2 (○); N_3 (△), N_1P_2 + (◆), N_2P_2 + (●), and N_2P_2Ca + (×). For further explanations, see Fig. 3.

found in all 1984 samples. there was no significant effect of the micronutrient additions on [Cu] in any of the treated stands.

During the first few years' treatment, [Fe] in current-year's needles increased from about 40–50 µg g^{-1} (1966) to 50–60 µg g^{-1} (1969; Fig. 4a,b). A small increase was noted even in needles from control plots. After 1969 there was a steady decrease in needle [Fe], and in 1989 the concentration in all treatments, except one (N_1P_2 +), was below 20 25 µg g^{-1}, *i.e.* no long-term effect was found as a consequence of the added micronutrient fertiliser.

There was a rapid decrease in needle [Mn] in all treatments during the first third of the treatment period (Fig. 4c,d). The smallest decrease was in needles from control plots, from 1.3 mg g^{-1} (1967) to about 1 mg g^{-1} (1974). The largest change was found in needles from plots to which ca had been added (n_2P_2Ca +), where needle [Mn] decreased from 1.6 to below 0.3 mg g^{-1} during the first seven years. After 1974, needle [Mn] remained rather stable. The addition of micronutrients had a small effect on [Mn], but did not increase the concentrations above those of the control needles (Fig. 4d).

The change in needle [Zn] over time resembled the pattern found in [Mn], but the initial fall in needle concentrations was more rapid (Fig. 4e,f). In stands which did not receive extra micronutrients (Fig. 4e), the fall occurred within three years (1966–1969), but where micronutrients were applied, the rate of decrease was slower (Fig. 4f). Needle [Zn] in all treated stands fell below the control concentrations, but remained rather stable after the initial decrease.

Biomass sampling (1989)

Boron

The most pronounced effect of long-term fertilisation on concentrations, and total amounts of element in the aboveground biomass components, was found for boron (Fig. 5). [B] in stems and branches was rather constant and independent of treatment, but needle [B] varied considerably. The concentration in current needles was higher than that in the control in all treatments, and [B] was positively affected by the extra supply of micronutrients. When extra boron had not been supplied, [B] in the total needle biomass, was, however, lower than that in control trees, indicating a retranslocation of boron from older to younger foliage.

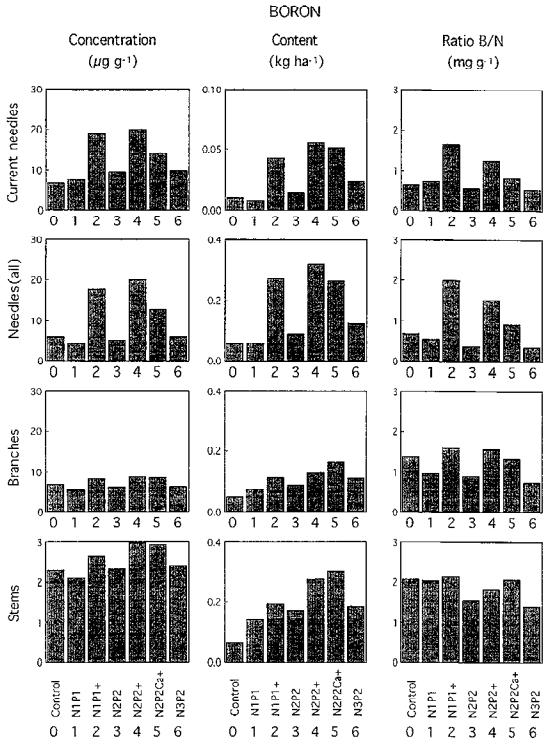

Fig. 5. Boron concentrations (left column), total content (middle column), and the ratio between boron and nitrogen (right column) in the aboveground organs of 30-year-old Norway spruce trees from control plots and five different long-term fertiliser treatments, after 21 years' treatment. Different amounts of nitrogen, alone and in combination with other nutrients, were annually applied. The individual treatments were a combination of supply rates, *i.e.* a stand denoted N_2P_2 had received twice as much N and P as the treatment N_1P_1 (*cf.* Tables 1, 2). Stands receiving K, Mg, and micronutrients are indicated by +. For further explanations, see text.

The total needle content of B (kg ha^{-1}) was four to five times higher in plots which had received additions of micronutrients, than in control plots or plots fertilised with N and P only. The effect was seen also in the total B content of branches and stems, but the amounts were determined to a larger degree by biomass accumulation than by the extra supply of boron. Fertilisation did not decrease the B : N ratio in current needles, but without addition of B, the B : N ratio in the total needle biomass, and branches, fell below the ratios found in control trees. The B : N ratio in stems was unaffected by fertilisation as well as by growth rate.

Copper

[Cu] in all aboveground biomass components was very constant and did not reflect treatment or growth rate (Fig. 6). The same [Cu] was found in all components (5–6 μg g^{-1}), with the exception of stems, in which the concentration was considerably lower (*ca.* 1.5 μg g^{-1}). The

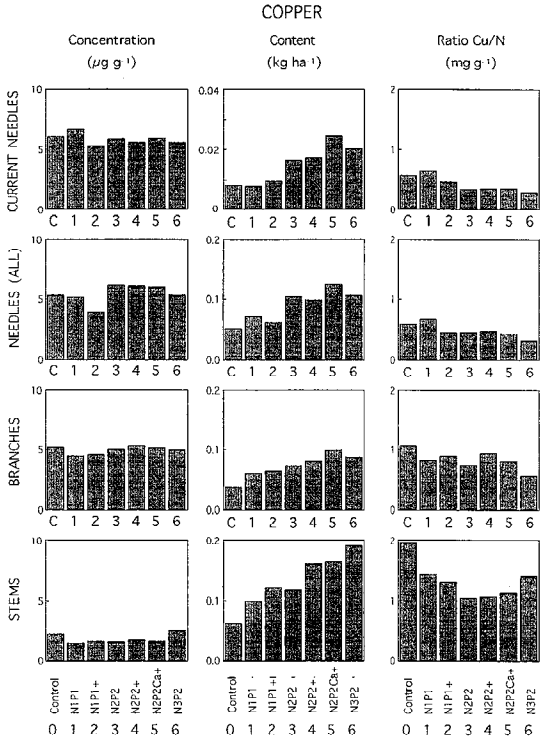

Fig. 6. Copper concentrations (left column), total content (middle column), and the ratio between copper and nitrogen (right column) in the aboveground organs of 30-year-old Norway spruce trees from control plots and five different long-term fertiliser treatments, after 21 years' treatment. For further explanations, see Fig. 5.

somewhat higher stem [Cu] in trees from control plots (2.2 μg g^{-1}) and N_3P_2 (2.4 μg g^{-1}), resulted from a few sample trees' having much higher stemwood [Cu].

The total amount of Cu (kg ha^{-1}) was directly proportional to the differences in standing biomass, the main pool of Cu being found in the stemwood. As an effect of stable tissue [Cu], variations in the Cu:N ratios were caused by variations in N rather than in Cu.

Iron

Needle concentrations of Fe were stable (*ca.* 30 μg g^{-1}) across treatments (Fig. 7), except for a higher concentration found in foliage from the N_2P_2 + treatment, which had a mean [Fe] of 39 μg g^{-1}. This higher [Fe] was the effect of a considerably higher [Fe] in trees on one of the two N_2P_2 + plots. [Fe] in branches varied by a factor of two, branches on control plots having the highest concentration (110 μg g^{-1}), and a decreasing trend in [Fe] was observed with increasing rate of fertilisation. A similar pattern was found in stem [Fe], but here the [Fe] were much lower (4–8 μg g^{-1}).

Independent of treatment, most of the Fe was found in branches (0.8–1.1 kg ha^{-1}), with a relatively small variation with treatment. There was, however, considerable variation between treatments in the relative proportion of Fe in different organs.

Fertilisation decreased the Fe:N ratio in foliage, but the most pronounced effect was in woody biomass components, where Fe:N ratios decreased as an effect of a decrease in [Fe] with increasing [N].

Manganese

Needle [Mn] decreased as an effect of fertilisation, especially at higher rates of supply (Fig. 8). The high N treatment (N_3P_2) resulted in needle [Mn] decreasing to less than one-third

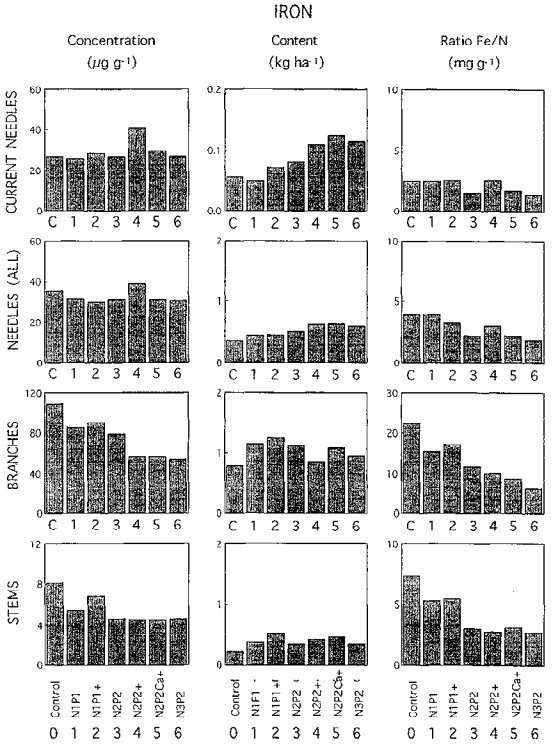

Fig. 7. Iron concentrations (left column), total content (middle column), and the ratio between iron and nitrogen (right column) in the aboveground organs of 30-year-old Norway spruce trees from control plots and five different long-term fertiliser treatments, after 21 years' treatment. For further explanations, see Fig. 5.

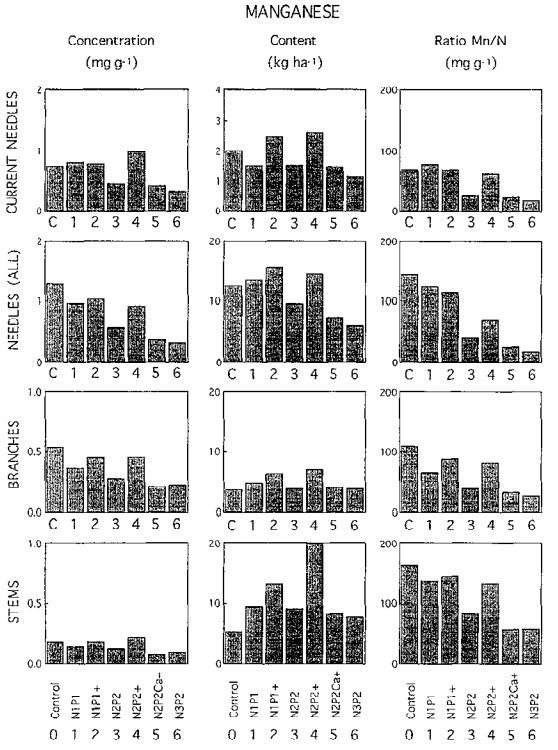

Fig. 8. Manganese concentrations (left column), total content (middle column), and the ratio between manganese and nitrogen (right column) in the aboveground organs of 30-year-old Norway spruce trees from control plots and five different long-term fertiliser treatments, after 21 years' treatment. For further explanations, see Fig. 5.

of the concentrations found in control trees. When micronutrients were included, a positive effect on [Mn] was observed, except in trees on plots which initially had received Ca (N_2P_2Ca+). The highest [Mn] was found in needles and the lowest in stemwood. With fertilisation, there was a decrease in the Mn : N ratio, the most marked decrease occurring in the N_3P_2 treatment, where the ratio fell to 20 mg g^{-1}, as compared to 150 mg g^{-1} on control plots.

Zinc

There was a pronounced decrease in [Zn] in current needles as an effect of fertilisation (Fig. 9). The decrease was, however, fully counterbalanced by the addition of micronutrients. At higher supply rates of N (N_2, N_3), the mean [Zn] of all needles was lower (10–20 µg g^{-1}) than in control needles (60 µg g^{-1}), indicating a transport of Zn from older to younger foliage. With increasing rates of fertilisation, the Zn : N ratios decreased in all organs, but most of all in the foliage.

Accumulated amounts of nitrogen and micronutrients

After 21 years' treatment, there was considerable variation in the amounts and patterns of accumulation of nitrogen and micronutrients in the aboveground biomass (Fig. 10). The total amount of nitrogen in the biomass (kg ha^{-1}) followed the increase in supply rate, and was closely related to the total standing biomass (*cf.* Fig. 1). Copper followed the same pattern, and showed no increased accumulation as an effect of the supply of micronutrients. The total aboveground amount of Fe was approximately the same in all fertilised stands, and no effect was seen of differences in fertiliser regimes. The amount of Zn was similar to that for Fe (2 kg ha^{-1}), but here a positive effect of the additions of micronutrients was evident. This was also the case for the accumulated amount of Mn which, in spite of the fact that it was ten times higher as compared with Fe and Zn, still showed a clear response to the added micronutrient mix. The most positive response to the addition of micronutrients was, however, seen in the accumulated amount of B. All treatments resulted in an increased boron accumulation, but where extra B had been given, the total amount was approximately twice as high as in the equivalent treatment without micronutrients.

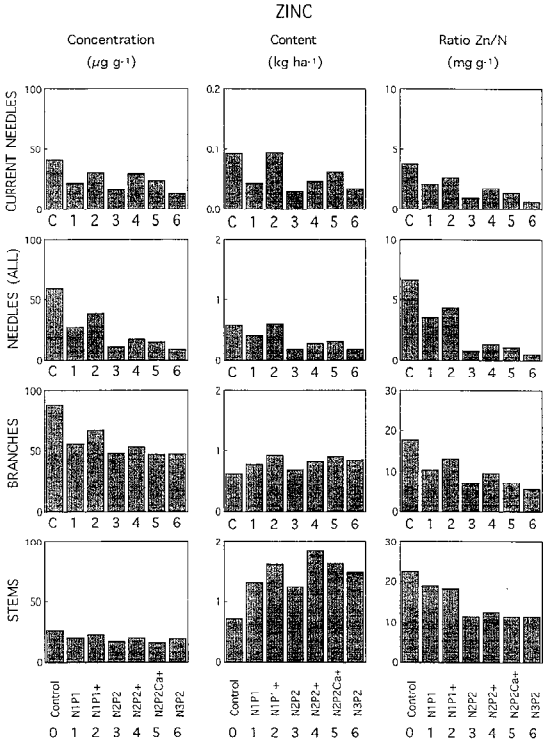

Fig. 9. Zinc concentrations (left column), total content (middle column), and the ratio between zinc and nitrogen (right column) in the aboveground organs of 30-year-old Norway spruce trees from control plots and five different long-term fertiliser treatments, after 21 years' treatment. For further explanations, see Fig. 5.

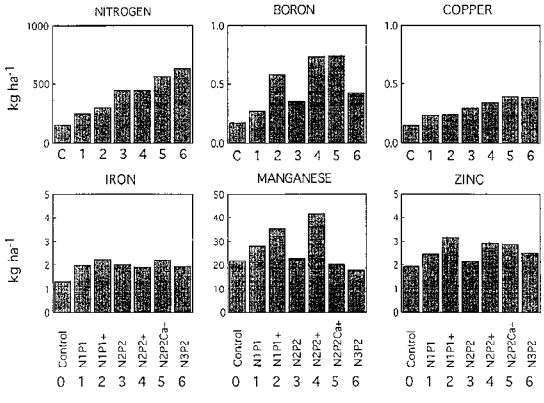

Fig. 10. The total content of nitrogen, boron, copper, iron, manganese and zinc in the aboveground organs of 30-year-old Norway spruce trees from control plots and five different long-term fertiliser treatments, after 21 years' treatment. Stands receiving K, Mg, and micronutrients are indicated by +. For further explanations, see Fig. 5.

Discussion

Growth and allocation of biomass

Fertilisation with nitrogen in temperate forests normally gives a strong positive effect on tree growth (*e.g.* Linder, 1987; Tamm, 1991), even in areas with rather high rates of anthropogenic nitrogen deposition (*e.g.* Nilsson & Wiklund, 1994). The Stråsan site was initially nutrient-poor, and the prescribed burning, which preceeded planting, decreased the amount of available N even further (*cf.* Tamm *et al.*, 1974). The annual N deposition at Stråsan is low, 4–8 kg $ha^{-1}a^{-1}$ (*cf.* Lövblad, Kindbom, Grennfelt, Hultberg & Westling, 1995), hence a pronounced response to N fertilisation could be expected (*cf.* Linder, 1987; Tamm, 1991). The accumulated aboveground biomass and stem volumes (1958–1989), after 21 years' annual N fertilisation and frequent addition of P, were two to three times higher than those in control stands (Fig. 1, Table 3). The most productive stands (N_2P_2+, N_2P_2Ca+), reached, towards the end of the treatment period, annual rates of stem volume production exceeding 25 m^3 ha^{-1} a^{-1}, which is exceptional for conifer stands at such high latitude (*cf.* Linder, 1990; Tamm, 1991).

The partitioning of biomass in seedlings (*e.g.* Rook, 1991; McDonald *et al.*, 1991) and forest trees (*e.g.* Linder & Rook, 1984; Ingestad & Ågren, 1991) is strongly affected by the availability of nutrients. In 1989, the control trees at Stråsan had more biomass in branches and needles in relation to stemwood, than was found in the fertilised trees (Fig. 2, Table 3). These results agree with an earlier sampling (1982), in which some of the same stands were included (Axelsson & Axelsson, 1986). Axelsson and Axelsson (1986) also included stumps and coarse roots in their sampling and found, in agreement with earlier forest experiments (*cf.* Linder, 1990), that relatively less biomass is allocated belowground, when nutrient availability is improved by fertilisation. This is also supported by the fact that, on control plots, only 26% of the soil carbon (down to 80 cm) was found in the mor layer, whereas the mor layer on fertilised plots (N_1P_1, N_2P_2, N_3P_1) contained more than 32% (Eriksson *et al.*, 1996). A further factor which could affect the pattern of biomass allocation, is the degree of canopy closure. At the time of the 1989 biomass sampling, control stands had not closed canopy, which in most of the treated stands had occurred seven years earlier (*cf.* Axelsson & Axelsson, 1986). Before canopy closure, a larger number of living branch whorls can be maintained, which will affect the relative proportion of different components in the tree (*cf.* Madgwick & Tamm, 1987).

Between-year variations in needle concentrations

One of the aims of the nutrient 'optimisation experiments' was to establish different needle concentrations of macronutrients, and thereafter to maintain them at separate levels (*cf.* Tamm, 1968; Tamm *et al.*, 1974). Rather stable [N] were obtained after approximately five years (see Tamm, 1991 for annual [N]), but the levels were not in proportion to the supplied amounts (Fig. 3a,b). It took approximately the same length of time before the concentration of micronutrients (B, Cu, Mn, Zn) had reached 'stable' levels (Fig. 3, 4). In stands which did not receive K, Mg and a mix of micronutrients, the concentration of all micronutrients, except Cu, decreased during the initial period of the experiment. In plots fertilised with micronutrients, the only effect observed was increased [B], which throughout the experimental period stayed above [B] in control trees (Fig. 3d). The initial decrease in needle micronutrient concentrations is interpreted as mainly being a 'dilution effect', caused by growth increasing without a corresponding increase in nutrient availability in the soil. However, there may also have been some interactions between nutrient elements, resulting in changes in both availability and uptake of different nutrient elements. It should be noted that the initial supply rates of macronutrients (*cf.* Table 1), were high in relation to the demand of the young spruce stands.

In an earlier study, Aronsson (1983) found that damage, caused by boron deficiency, increased when [B] in current needles fell below 5 μg g^{-1}. This level corresponds well with critical levels given by Stone (1968) and Möller (1984), but is lower than levels suggested by other authors (*e.g.* Jones, 1972; Nihlgård, 1990). In a current long-term nutrient experiment in young Norway spruce at Flakaliden in northern Sweden, however, no damage was seen during the first seven years of treatment, in spite of

autumn [B] consistently being 3–4 μg g^{-1} (*cf.* Linder, 1995).

The years selected for micronutrient analysis coincided on four occasions with years when micronutrients were applied (1967, 1969, 1974, 1984), but on one of these occasions (1984), only B was added. In the time series, it is only in [B] that an effect of the addition can be seen, especially after the large supply in 1984 (Fig. 3d). The peak in [Cu] seen during the same year, cannot have been the effect of nutrient supply, since it occurred both in plots with, and plots without, addition of micronutrients (*cf.* Fig. 3e,f).

The between-year variation in concentrations of Cu (Fig. 3e,f) and Fe (Fig. 4a,b) was not affected by the supplying of the micronutrient mix. One reason could be that the elements were supplied in the form of sulphates, which is not as efficient as when the elements are chelated (*cf.* Lindsay, 1974). Cu is readily immobilised in the humus layer, while Fe to a large extent can be oxidised into insoluble forms (Mengel & Kirkby, 1987).

After the initial period of change in most elements (1967–1974), [Cu] varied between 3–4 μg g^{-1} (Fig. 3e,f), and [Fe] between 20–30 μg g^{-1} (Fig. 4a,b). [Cu] was low in relation to most 'critical' values found in the literature (*e.g.* Turvey, 1984; Hunter, Hunter & Nicholson, 1990; Nihlgård, 1990), but consistent with [Cu] found at Flakaliden (Linder, 1995) and [Cu] considered to be satisfactory by Ahrens (1964) and Will (1985). [Fe] was lower than the concentration recommended as 'optimal for plant growth' by Göransson (1993), but similar to [Fe] found in current needles at Flakaliden. The fact that needle concentrations were stable, in spite of increased demand (growth), at the same time as the Fe pool in the branches decreased, is a strong indication that Fe is not limiting.

[Mn] in needles decreased by more than 50% during the seven years (Fig. 4c,d), but was still more than one order of magnitude above the concentration considered optimal for plant growth (*cf.* Göransson, 1994).

Needle [Zn] decreased rapidly during the first few years (Fig. 4e,f), but the rate of decrease was somewhat lower on plots receiving micronutrients. After the initial decrease, [Zn] stabilised at 20–40 μg g^{-1}, the control trees having the higher concentrations. The lower part of the range is close to the [Zn], reported by some authors to be the point at which deficiency symptoms appear (*e.g.* Ballard & Carter, 1985; Nihlgård, 1990). [Zn] at Stråsan are considerably lower than those observed at Flakaliden, but well above the target value (9 μg g^{-1}) used as optimal for Zn in that experiment (*cf.* Linder, 1995).

Micronutrient allocation in aboveground biomass

The total content of B increased with fertilisation (Fig. 10), and was considerably higher in stands which had received additions of micronutrients. The increased amount of B was found in all aboveground biomass components, but was most pronounced in foliage (Fig. 5). Current needles had higher [B] than the mean concentration in all needles, indicating an increase in structural mass with age or transport of B from older to younger foliage. The decrease in concentration was, however, larger than can be expected from the mean increase in structural mass which occurs with age in Norway spruce needles (*cf.* Flower-Ellis, 1993). Another explanation could be that passive transport of B via the transpiration stream cannot counterbalance leakage of B from older needles. The most plausible interpretation, however, seems to be that, despite reports of the immobility of B within plants, there is some reallocation of B from older to younger foliage (*cf.* Raven, 1980; Chamel, 1981; Dugger, 1983). This is supported by observations of retranslocation of most elements out of senescing needles of Scots pine (Helmisaari, 1992).

The total amount of Fe in the aboveground biomass was found to be independent of treatment and growth (Fig. 10), which can be interpreted as an uptake of all available Fe in the soil. The highest [Fe] were found in branches (Fig. 7), in contrast to agricultural plants, where most of the Fe is found in the chloroplasts (Neish, 1939; Dekock, Commisiong, Farmer & Inkson, 1960), where excess Fe is stored as phytoferritin (Barton, 1970; Hyde, Hodge, Kahn & Birnstiel, 1963; Mengel & Kirkby, 1987). Evidence for the role of branches and twigs as storage organs for excess Fe is that there was a corresponding decrease in branch [Fe] when the total Fe content in the needle biomass increased as an effect of treatment. The net result was a constant total aboveground Fe content

(Fig. 10), independent of treatment, indicating reallocation of Fe from branches to needles.

Most of the total Zn was found in stemwood, and the amounts increased in relation to production (Fig. 9). Since total Zn in the aboveground biomass was unaffected by treatment, except for somewhat higher amounts on plots which had received micronutrients (Fig. 10), the amount available for other organs was reduced, which resulted in decreased needle [Zn] (Fig. 9). Zinc is considered to be rather immobile in plants (Mengel & Kirkby, 1987), in older leaves especially (Rinne & Langston, 1960; McGrath & Robson, 1984). However, in treatments in which the pronounced reduction in available Zn reduced needle [Zn] to low levels, the concentrations were higher in current than in older foliage, indicating a reallocation of Zn. This result is contrary to findings by Loneragan (1975) and McGrath & Robson (1984), who reported that Zn transport, from older to younger tissues, is particularly reduced in Zn-deficient plants. This discrepancy may be the effect of differences between species, and in degree of stress.

The only micronutrient present in amounts and concentrations far above the physiological requirement, was Mn (Fig. 8). The high amounts found in various aboveground components can therefore not be interpreted as the 'normal' allocation pattern of Mn. The addition of Ca at the start of the experiment had a strong negative effect on [Mn], and on Mn content in all aboveground organs. This was probably the effect of decreased Mn availability, since higher pH reduces the solubility of Mn (Lindsay, 1972; Kabata-Pendias & Pendias, 1984). Even though the addition of Ca reduced needle [Mn] by more than 60%, the needle concentrations were still more than one order of magnitude above 'critical' levels (*cf.* Hill & Lambert, 1981). That the uptake of Mn was determined by availability in the soil can be seen by the fact that almost all of the supplied Mn (18.5 kg ha^{-1}) was recovered in the aboveground biomass (N_1P_1 +: 12 kg ha^{-1}, N_2P_2 +: 18.5 kg ha^{-1}).

Interaction between nutrients is an important factor to take into account when considering effects of fertilisation on availability, uptake, and allocation in plants. Therefore, the application of some nutrients may have an effect on the availability of others, through soil processes, competition for active root uptake, or even directly on physiological processes. Many such interactions involving micronutrients have been reported, but their effect cannot be evaluated in the present study.

Conclusions

Long-term fertilisation, with annual application of nitrogen and phosphorus, resulted in large increases in biomass production, which decreased the needle concentrations of boron, manganese and zinc, but not of copper and iron. Except in the case of boron, frequent additions of potassium, magnesium, and a mix of micronutrients (B, Cu, Mn, Zn), could not compensate for the 'dilution effect' on needle concentrations caused by increased biomass production.

The accumulated amount of copper in the aboveground biomass was directly related to the amount of biomass, *i.e.* was not controlled by availability in the soil, but by a 'physiological demand'. Total amounts of iron, manganese, and zinc, on the other hand, were not affected by biomass production, *i.e.* amounts in the biomass reflected the accumulated soil availability of these elements.

To meet increasing demands for nutrients for the production of new foliage, boron and zinc were reallocated from older foliage, but iron was stored in the branches, and when needed, was reallocated to new foliage.

References

Adriano, D.C. 1986. *Trace Elements in the Terrestrial Environment.* Springer-Verlag. Berlin. 533 pp.

Ahrens, E. 1964. Untersuchungen über den Gehalt von Blättern und Nadeln verschiedener Baumarten an Kupfer, Zink, Bor, Molybdän und Mangan. *Allgemeine Forst- und Jagdzeitung 135*, 8-16

Albrektson, A., Aronsson, A. & Tamm, C.O. 1977. The effects of forest fertilization on primary production and nutrient cycling in the forest ecosystem. *Silva Fennica 11*, 223-239.

Aronsson, A. 1980. Frost hardiness in Scots pine (*Pinus silvestris* L.). II. Hardiness during winter and spring in young trees of different mineral nutrient status. *Studia Forestalia Suecica 155*. 27 pp.

Aronsson, A. 1983. Growth disturbances caused by boron deficiency in some fertilized pine and spruce stands on mineral soils. *Communicationes Instituti Forestalis Fenniae 116*, 116-122.

Aronsson, A. 1984. The effects on needle nutrient contents after fertilization with some micronutrients in a young stand of Scots pine. *Journal of the Royal Swedish Academy of Agriculture and Forestry. Supplement 16*, 67-70. (In Swedish with English summary.)

Axelsson, E. & Axelsson, B. 1986. Changes in carbon allocation patterns in spruce and pine trees following irrigation and fertilization. *Tree Physiology 2*, 189-204.

Ballard, T.M. & Carter, R.E. 1985. Evaluating forest stand nutrient status. *British Columbia, Mining and Forestry Land Management. Report 29*. 36 pp.

Barton, R. 1970. The production and behaviour of phytoferritin particles during senescence of *Phaseolus* leaves. *Planta 94*, 73-77.

Bergmann, W. 1986. *Ernährungsstörungen bei Kulturpflanzen.* VEB Gustav Fischer Verlag, Jena. 306 pp.

Braekke, F.H. 1977. Fertilization for balanced mineral nutrition of forests on nutrient-poor peatland. *Suo 28*, 53-61.

Braekke, F.H. 1979. Boron deficiency in forest plantations on peatland in Norway. *Norwegian Forest Research Institute. Report 35.3.*

Chamel, A.R. 1981. Distribution of foliar-applied boron measured by spark-source mass spectrometry and laser-probe mass spectrography. *Plant Physiology 67*, 457-459.

Dekock, P.C., Commisiong, K., Farmer, V.C. & Inkson, R.H.E. 1960. Interrelationships of catalase, peroxidase, hematin, and chlorophyll. *Plant Physiology 35*, 599-604.

Dugger, W.M. 1983. Boron in plant metabolism. In: Inorganic plant nutrition (eds. A. Läuchli & R.L. Bieleski). *Encyclopedia of Plant Physiology 15B*, 628-650.

Ericsson, T. 1991. Dry matter partitioning at steady state nutrition. In: Above and below ground interactions in forest trees in acidified soils. *Air Pollution Research. Report 32*, 236-243. Commission of European Communities. Brussels.

Eriksson, H., Berdén, M., Rosén, K. & Nilsson, I.S. 1996. Nutrient distribution in a Norway spruce stand after long-term application of ammonium nitrate and super phosphate. *Water, Air and Soil Pollution 92*, 451-467.

Flower-Ellis, J.G.K. 1993. Dry-matter allocation in Norway spruce branches: a demographic approach. *Studia Forestalia Suecica 191*, 51-73.

Gay, C., Tamm, C.O., Aronsson, A., Flower-Ellis, J.G.K. & Linder, S. 1994. A user's manual for the Ekologen database system. *Swedish University of Agricultural Sciences, Deptartment of Ecology and Environmental Research Report 59*. 118 pp.

Göransson, A. 1993. Growth and nutrition of small *Betula pendula* plants at different relative addition rates of iron. Trees 8, 31-38.

Göransson, A. 1994. Growth and nutrition of small *Betula pendula* plants at different relative addition rates of manganese. *Tree Physiology 14*, 375-388.

Göransson, A. & McDonald, A.J.S. 1993. Growth and nutrition of small *Betula pendula* plants at different relative addition rates of iron, manganese and zinc. *Plant and Soil 155/156*, 469-472.

Helmisaari, H.-S. 1992. Nutrient retranslocation within the foliage of *Pinus sylvestris*. *Tree Physiology 10*, 45-58.

Hill, J. & Lambert, M.J. 1981. Physiology and management of micronutrients in forest trees in Australia. In: *Proceedings, Australian Forest Nutrition Workshop, Productivity in Perpetuity*, pp. 93-103. CSIRO, Melbourne, Australia.

Högberg, P., Johannisson, C. & Hällgren, J.-E. 1993. Studies of ^{13}C in the foliage reveal interactions between nutrients and water in forest fertilisation experiments. *Plant and Soil 152*, 207-214.

Huikari, O. 1977. Micronutrient deficiencies cause growth disturbances in trees. *Silva Fennica 11*, 251-255.

Hunter, I.R., Hunter, J.A.C. & Nicholson, G. 1990. Current problems in the copper nutrition of radiata pine in New Zealand: A review. *Forest Ecology and Management 37*, 143-149.

Hyde, B.B., Hodge, A.J., Kahn, A. & Birnstiel, M.L. 1963. Studies on phytoferritin: I. Identification and localisation. *Journal of Ultra Structure Research 9*, 248-258.

Ingestad, T. & Ågren, G.I. 1991. The influence of plant nutrition on biomass allocation. *Ecological Applications 1*, 168-174.

Ingestad, T. 1958. Studies on manganese deficiency in a forest stand. *Meddelanden från Statens Skogsforskningsinstitut 48,4*, 20 pp.

Jones, J.B. 1972. Plant tissue analysis for micronutrients. In: *Micronutrients in Agriculture*, pp. 319-346 (eds. J.J. Mortvedt, P.M. Giordano & W.L. Lindsay). Soil Science Society of America.

Kabata-Pendias, A. & Pendias, H. 1984. *Trace Elements in Soils and Plants.* CRC Press. 293 pp.

Kirsten, W.J. & Hesselius, G.U. 1983. Rapid, automatic, high capacity Dumas determination of nitrogen. *Microchemical Journal 28*, 529-547.

Linder, S. 1987. Responses to water and nutrition in coniferous ecosystems. In: *Potentials and Limitations of Ecosystem Analysis.* (eds. E.-D. Schulze, & H. Zwölfer). Ecological Studies 61: 180-202. Springer-Verlag Berlin-Heidelberg-New York.

Linder, S. 1990. Nutritional control of forest yield. In: *The Marcus Wallenberg Foundation Symposia Proceedings 6: Nutrition of Trees*, pp. 62-87. ISSN 0382-4647.

Linder, S. 1995. Foliar analysis for detecting and correcting nutrient imbalances in Norway spruce. *Ecological Bulletins (Copenhagen) 44*, 178-190.

Linder, S. & Rook, D.A. 1984. Effects of mineral nutrition on carbon dioxide exchange and partitioning of carbon in trees. In: (eds. G.D. Bowen & E.K.S. Nambiar) *Nutrition of Plantation Forests*, pp. 211-236. Academic Press, London.

Lindsay, W.L. 1972. Inorganic phase equilibria of micronutrients in soils. In: *Micronutrients in*

Agriculture, pp. 41-58 (eds. J.J. Mortvedt, P.M. Giordano & W.L. Lindsay). Soil Science Society of America.

Lindsay, W.L. 1974. Role of chelation in micronutrient availability. In: *The plant root and its environment*, pp. 507-524 (ed. E.W. Carson) University Press of Virginia.

Loneragan, J.F. 1975. The availability and absorption of trace elements in soil-plant systems and their relationship to movement and concentration of trace elements in plants. In: *Trace Elements in Soil-Plant-Animal Systems*, pp. 109-134 (eds. D.J.D. Nicholas & A.R. Egan). Academic Press.

Lövblad, G., Kindbom, K., Grennfelt, P., Hultberg, H. & Westling, O. 1995. Deposition of acidifying substances in Sweden. *Ecological Bulletins (Copenhagen) 44*, 17-34.

Madgwick, H.A.I. 1982. Estimating the above-ground weight of forest plots using the basal area ratio method. *New Zealand Journal of Forest Science 11*, 278-286.

Madgwick, H.A.I. & Tamm, C.O. 1987. Allocation of dry weight increment in crowns of *Picea abies* as affected by stand nutrition. *Oikos 48*, 99-105.

Marschner, H. 1986. *Mineral Nutrition of Higher Plants*. Academic Press. 674 pp.

McDonald, A.J.S., Ericsson, T. & Ingestad, T. 1991. Growth and nutrition of tree seedlings. In: *Physiology of Trees*, pp. 199-220 (Ed. A.S. Raghavendra). John Wiley & Sons Inc.

McGrath, J.F. & Robson, A.D. 1984. The distribution of zinc and the diagnosis of zinc deficiency in seedlings of *Pinus radiata*. *Australian Forest Research 14*, 175-186.

Mengel, K. & Kirkby, E.A. 1987. *Principles of Plant Nutrition*. International Potash Institute. Worblaufen-Bern. 687 pp.

Möller, G. 1984. Aspects of micronutrients in forestry with special regard to the boron situation. *Journal of the Royal Swedish Academy of Agriculture and Forestry. Supplement 16*, 41-58. (In Swedish with English summary.)

Nambiar, E.K.S. 1984. Plantation forests: Their scope and a perspective on plantation nutrition. In: *Nutrition of Plantation Forests*, pp. 1-17 (eds. G.D. Bowen & E.K.S. Nambiar). Academic Press.

Neish, A.C. 1939. Studies on chloroplasts: II. Their chemical composition and the distribution of certain metabolites between the chloroplasts and the remainder of the leaf. *Biochemical Journal 33*, 300-308.

Nihlgård, B. 1990. The vitality of forest trees in Sweden – stress symptoms and causal relations. In: *Vitality Fertilization – Present Knowledge and Research Needs*, pp. 45-70 (eds. L.-E. Liljelund, J.-E. Lundmark, B. Nihlgård, H.-Ö. Nohrstedt & K. Rosén). Swedish Environmental Protection Agency. Report 3813. Solna, Sweden. (In Swedish with English summary.)

Nilsson, L.-O. & Wiklund, K. 1994. Nitrogen uptake in a Norway spruce stand following ammonium sulphate application, fertigation, irrigation, drought and nitrogen-free-fertilisation. *Plant and Soil 164*, 221-229.

Oren, R., Schulze, E.-D., Werk, K.S. & Meyer, J. 1988. Performance of two *Picea abies* (L.) Karst. stands at different stages of decline: VII: Nutrient relations and growth. *Oecologia 77*, 163-173.

Raven, J.A. 1980. Short- and long-distance transport of boric acid in plants. *New Phytologist 84*, 231-249.

Rinne, R.W. & Langston, R. 1960. Effect of growth on redistribution of some mineral elements in peppermint. *Plant Physiology 35*, 210-215.

Rook, D.A. 1991. Seedling development and physiology in relation to mineral nutrition. In: (ed. R. van den Driessche) *Mineral Nutrition of Conifer Seedlings*, pp. 85-111. CRC Press Inc.

Romell, L.G. 1950. Excursion to upper Norrland. In: *Proceedings of the Seventh International Botanical Congress*, pp. 130-131. Almqvist & Wiksell, Stockholm.

Stone, E.L. 1968. Microelement nutrition of forest trees: A review. In: *Symposium on Forest Fertilization Theory and Practice*, pp. 132-175. Knoxville, USA.

Tamm, C.O. 1968. An attempt to assess the optimum nitrogen level in Norway spruce under field conditions. *Studia Forestalia Suecica 61*. 67 pp.

Tamm, C.O. 1991. *Nitrogen in Terrestrial Ecosystems*. Ecological Studies 81. Springer-Verlag. 115 pp.

Tamm, C.O., Aronsson, A. & Burgtorf, H. 1974. The optimum nutrition experiment Stråsan. A brief description of an experiment in a young stand of Norway spruce (Picea abies). *Royal College of Forestry, Department of Forest Ecology and Forest Soils, Research Notes 17*. 29 pp.

Turvey, N.D. 1984. Copper deficiency in *Pinus radiata* planted in a podzol in Victoria, Australia. *Plant and Soil 77*, 73-86.

Turvey, N.D. & Grant, B.R. 1990. Copper deficiency in coniferous trees. *Forest Ecology and Management 37*, 95-122.

Van Lear, D.H. & Smith, W.H. 1972. Relationships between macro- and micronutrient nutrition of Slash pine on three coastal plain soils. *Plant and Soil 36*, 331-347.

Will, G. 1985. Nutrient deficiencies and fertiliser use in New Zealand exotic forests. *Forest Research Institute, Rotorua, New Zealand, Bulletin 97*.

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