Fine root growth and element concentrations of Norway spruce as affected by wood ash and liquid fertilisation

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Abstract

A field experiment to test various management practices of sustainable forestry was conducted in a Swiss spruce forest for two growing seasons. Treatments were a control (C), yearly application of 4000 kg ha^{-1} wood ash (A), daily irrigation with a steady state fertilisation as 'optimal nutrition' (F) and irrigation with a water control (W). Samples were taken on a 5 × 5 m grid once a year with a soil corer to determine fine root biomass (≤ 2 mm) and soil pH of the topsoil. A subset of the fine root samples was further analysed for its nutrient composition by CN and ICP-AES analyses. The dynamics of root growth were observed with the aid of ingrowth-cores after 1, 1.5, and 2 years of treatment and the growth pattern was analysed in terms of biomass, tips, forks, length and root diameter of the samples. The A, F and also the W treatment resulted in a significant increase of soil pH in the topsoil. The fine root density increased over the two growing seasons, irrespective of the treatment. The root growth was only slightly different between the treatments with a initially faster growth under the A treatment. The W treatment reduced the number of root tips and forks, and the root length, while the A treatment increased the number of root tips, forks and the root length, but reduced the diameter. The differences between the three harvesting times (March 1999, October 1999, March 2000) of the ingrowth-cores stressed seasonal differences in root growth and the development of quasi 'steady state' root dynamics. The root turnover was not changed by the treatments. The elements in the fine roots were strongly affected by the treatments A and F and sometimes by W. Fine root N increased with the F treatment, while C concentrations decreased under the A, F and W treatments. The Ca and Mg concentrations were strongly enhanced by A but also by the F treatment. The K and P concentrations in the fine roots were improved by all three applications. Due to the pH increase Al, Fe and Mn concentrations in the fine roots were decreased by the A and F treatments. S and Zn concentrations showed inconsistent changes over the growing seasons. The results of this study were comparable with those of other studies in Europe and confirm the abilities of the fine roots as indicators of forest nutrition, to some extent more sensitive than the commonly used foliar analysis.

Introduction

The consequences of high N depositions and soil acidification are reported as nutritional imbalances, often deficiencies in Mg, P or K (Hüttl, 1990; Linder, 1995; Matzner and Murach, 1995; Salih and Andersson, 1999; Schulze and Freer-Smith, 1990) in relation to

N. In Switzerland mainly imbalances of N and P have been reported in spruce forests (Flückiger and Braun, 1998; Landolt, 1997). To compensate nutritional imbalances of trees and acidification of forest soils, several ameliorating methods have been applied (e.g., Eriksson et al., 1998; Hahn and Marschner, 1998a; Meiwes, 1995; Nilsson et al., 2001; Persson and Ahlström, 1994; Rapp, 1992; Vance, 1996). The effects of wood ash applications on forest soils have

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been studied extensively (e.g., Bramryd and Frans-man, 1995; Eriksson, 1998; Kahl et al., 1996; Meiwes, 1995; Vance, 1996), but only few studies have dealt with the effects on the fine roots (e.g., Clarholm, 1998; Persson and Ahlström, 1992, 1994). Another amelioration technique, which has been applied mainly in Scandinavia, is a steady state or compensatory fertilisation, which supplies the nutrients that are needed. The success of this practice is usually monitored by foliage analyses (Linder, 1995). Such a steady state fertilisation can result in a long term amelioration of the nutritional status of the trees, improving the resistance of the forest ecosystem against stress factors (Hüttl, 1990). The hypothesis that fine root-based parameters are suitable as a complement to soil and foliar indicators (Bakker, 1999; Persson et al., 1995) is investigated in the present study.

The 'HARWA' field experiment was established to monitor effects of both wood ash recycling and steady state fertilisation on a forest ecosystem dominated by Norway spruce. In Switzerland at present more than 25 000 000 kg wood ash deriving from energy production have to be discarded every year and wood as a renewable energy source is underpinned for the future by forest policy (SAEFL, 1999). Thus, there is a need to evaluate the possibilities of wood ash recycling and to assess the effects of wood ash application in Swiss forests. The objectives of the present study were to investigate within a field experiment the element changes in the fine roots deriving from the ameliorating treatments. Furthermore, possible effects on root growth and root growth dynamics were studied. Together with the soil pH and element changes in the needles an evaluation of the fine root-based parameters as indicators of plant availability of elements in the forest soil were conducted.

Materials and methods

Field experiment

The experiment was conducted in a spruce forest on the Swiss Plateau. The 'Schladwald' (N 47°30′34″/E 08°20′50″, 464 m a.s.l.) forest is located about 25 km northwest of Zürich, Switzerland. The 70-year-old stand is classified as a *Galio odorati–Fagetum luzu-letosum* (Ellenberg and Klötzli, 1972), dominated by Norway spruce (*Picea abies* (L.) Karst.). The herb-layer vegetation is composed by *Anemona nemorosa* L., *Galium odoratum* (L.) Scop., *Lamium galeobdolon*

(L.) Nath., *Oxalis acetosella* L., and *Rubus fruticosus* L. The stand has a density of approximately 440 trees ha^{-1}, with the stems evenly distributed. The soil is an acidic brown earth ('Dystric cambisol', FAO, 1988; compare also Bundt et al., 2001). According to Zimmermann and Frey (2002), the top soil is characterised by: low pH value (3.5), low C (44.0 mg g^{-1}) and low N-content (2.7 mg g^{-1}), low cation exchange capacity (96 μmol$_c$ g^{-1}) and base saturation (BS, 32%), low exchangeable base cations Ca (24.7 μmol$_c$ g^{-1}) and Mg (4.0 μmol$_c$ g^{-1}), and high exchangeable Al (46.3 μmol$_c$ g^{-1}). The 15-year average of annual precipitation is 1076 mm and of air temperature is 9.6 °C (SMA, 1998).

The experiment was set up as a random block design with four treatments and four replicated plots resulting in a 0.8 ha investigation area. The plots of each treatment ranged between 200 and 600 m^2 in size. The experimental treatments were: a control without any treatment (C), irrigation of stream water (W), irrigation of liquid fertiliser (F), and the application of wood ash (A). The wood ash, deriving from wood chip combustion, was applied by hand on 25 May 1998 and 23 July 1999. The F treatment was based on a nutrient combination according to Ingestad and Lund (1986) related to 70 (1998) or 100 (1999) kg N ha^{-1} (Table 1). The pH of stream water used for dilution of the fertiliser and for the W treatment was about 8.5. The wood ash and stream water were analysed, and inputs of elements estimated (F including the contribution of the stream water, Table 1). The F and W treatments were irrigated each night from 25 May 1998 to 28 September 1998 and from 6 May 1999 to 27 September 1999 except for days with intensive rain.

Sampling design

Samples of soil and roots were taken in April in each of the years 1998, 1999 and 2000. The samples were taken independently of the plot design in a 5 × 5-m grid over the investigation area (Figure 1). At each sampling point three soil cores (100 mm depth, diameter 85 mm) were collected. The soil consisted of two horizons: Ah (the uppermost mineral soil layer, characterised by an accumulation of humified organic matter) and B (mineral soil layer formed below the Ah horizon), and each horizon from all three cores was pooled separately. The samples were sieved, the fine roots (≤ 2 mm) of Norway spruce were isolated from each bulk sample and washed. The roots were dried
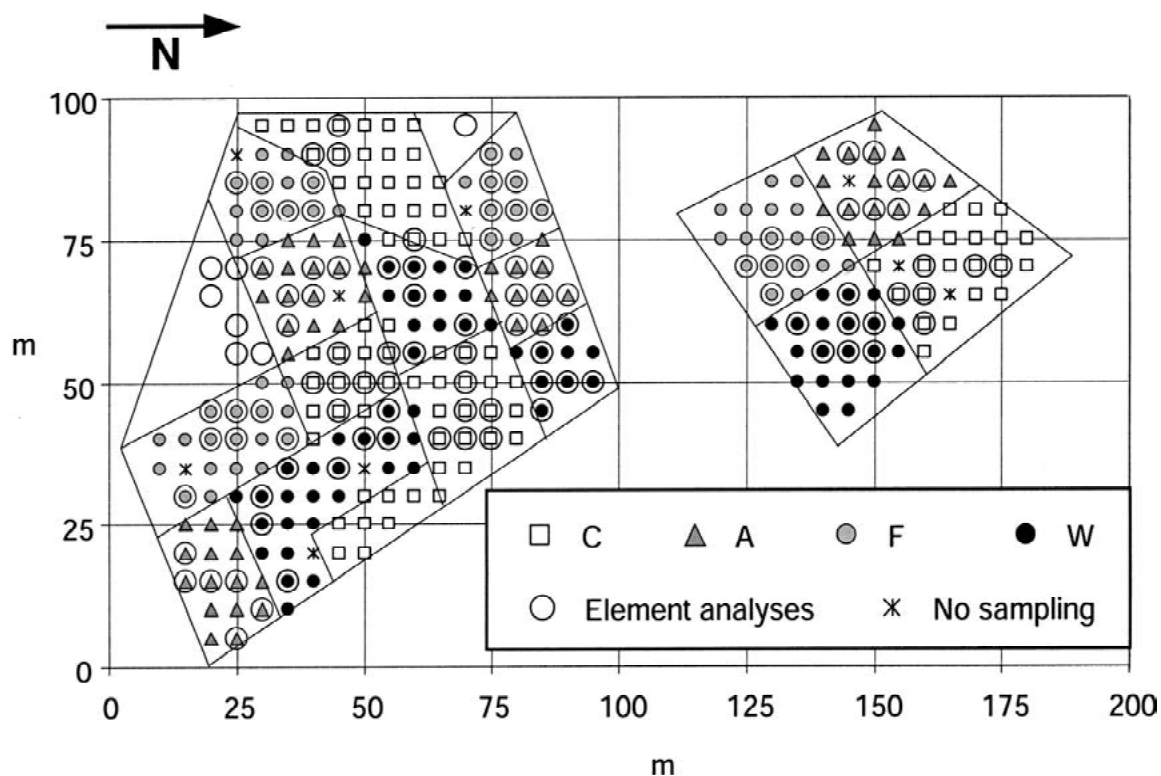
Figure 1. Sampling design on a 5 × 5-m grid and assigned treatments: C – control; W – water; F – liquid fertiliser; A – ash plots; encircled – sampling positions with element analyses of fine roots.

Table 1. Element input (kg ha^{-1} year^{-1}) by the treatments: A – wood ash; F – fertiliser; W – water; C – control; n.d. – not determined

Elements	C	A	F		W[a]
			1998	1999	
N	0	<0.01	77	100	7
S	0	26	17	18	12
P	0	63	13	17	0.1
Ca	0	1140	183	184	182
K	0	232	64	85	3
Mg	0	76	33	35	25
Fe	0	20	0.2	0.3	0.2
Mn	0	19	0.07	0.08	0.03
Zn	0	0.7	<0.01[b]	<0.01[b]	n.d.
Al	0	23	<0.03	<0.03	<0.03
Cu	0	0.5	<0.01[b]	<0.01[b]	n.d.
Cd	0	0.02	n.d.	n.d.	n.d.

[a]Import of the stream water extrapolated with element concentrations of the water.
[b]Estimated input of stream water negligible.

at 60 °C for at least 3 days and weighed (separated by horizon).

Needles were sampled in winter (December, January) of 1997/98 and 1999/2000 from 136 selected spruce trees within the experimental site. Trees were located at a minimum distance of 4 m to the neighbouring-treatment plot. One hundred medial needles were taken from a shoot from the uppermost whorl of the sample tree. Needle samples were dried at 65°C until constant weight.

Analyses

The analyses of soil pH in a 0.01 *M* CaCl$_2$ extract (Brunner et al., 1999) and fine root biomass (dry weight, DW) was conducted for each of the 257 sample points. The fine root material of 110 selected samples from the Ah horizon (Figure 1) and the needle samples of the 136 trees were ground with a mill (Retsch MM2000) for further analyses. Total C and total N were measured with a CN auto-analyser (N2500, Carlo Erba Instruments). Other elements were measured after digestion of the ground material

in a high pressure microwave (Milestone MLS Ultraclave) by ICP-AES (Optima 3000, Perkin-Elmer).

Ingrowth-cores

To study the root growth dynamics, three trees per plot and three plots per treatment were selected, resulting in a total of 36 sample trees. These trees were mainly located in the centre of the plots. At each sample tree, nine 'ingrowth-cores' were installed in May 1998. First, the soil was taken out with a soil corer (diameter 55 mm) to about 100 mm depth, divided by horizons and sieved. A net-cylinder of glass fibre (110 mm height, 50 mm diameter, 5 mm mashes) was installed into the hole, before the root-free soil was replaced, horizon by horizon in the hole. The minimum distance between two cores was 100 mm, and the distance from the sample tree was 1.0–1.5 m.

Harvest of ingrowth-cores

The ingrowth-cores were harvested in March 1999, October 1999 and March 2000, approximately 1, 1.5, or 2 years after installation. At each sampling event three ingrowth-cores per tree were harvested using a large soil corer (diameter 85 mm). The soil cores were taken to the lab in plastic bags and stored at $4\,°C$ for a maximum of 3 days until analysis. With a sharp knife the roots and soil were cut off the net-cylinder. The soil depth was measured and the cylinder was opened with the aid of scissors. Horizons were not analysed separately, because after the first harvest it was observed that the original horizons had been disturbed by the installation procedure. Roots of Norway spruce were washed out, scanned and the architecture was analysed with the Winrhizo® software (Regent Instruments Inc.). Afterwards the roots were dried ($60\,°C$, 3 days) and the biomass was determined.

Turnover

Root turnover was calculated according to a modified equation in Gill and Jackson (2000):

$$\text{Root turnover} = \frac{\text{Annual belowground production}}{\text{Mean belowground standing crop.}}$$

The turnover was calculated as the quotient from the production of fine roots per year as measured by the ingrowth-core after 2 years, and related to the mean standing biomass of fine roots, estimated from the grid sampling results averaged over the 3 years.

Statistics

Statistical analyses were performed as provided by Statview 5.0 (SAS Inc., Cary). To analyse differences in soil pH and the fine root biomass in grid-samples, a repeated-measurement ANOVA and a Fisher's PLSD post-hoc test were performed within one treatment on the differences between the years. The changes in element concentrations were analysed on differences between the treatments by a one-way ANOVA at a 5% probability level. The ingrowth-core data were analysed with a one-way ANOVA on treatment effects at a 5% probability level, within one harvest. Furthermore, a two-way ANOVA on treatment and time was conducted to reveal differences between the three harvesting events. For the parameters concerning the growth pattern (tips, length, forks, diameter), samples without fine roots were not considered.

Results

Biomass, growth dynamic and soil pH

The fine root biomass as monitored by the soil coring was not affected by the treatments when considering Ah and B horizon separately (Table 2). However, if data were related to both horizons, there was a significant difference in fine root density between the harvesting events in samples of C and A treated plots (Table 2). In the soil of the A plots a significantly higher root density was observed after 2 years. The root density in the soil of C plots was in the year 2000 higher than in the year 1998. A generally increasing root density was observed within the 2 years, irrespective of the treatments (Table 2). The mean annual turnover of fine roots was not affected by the treatments (Table 2, lower part) and ranged from 0.6 to 1.0 year^{-1}.

One year after installation the ingrowth-cores revealed a higher proportion of fine root biomass in the cores of the A plots than in the cores of the W plots (Figure 2). The biomass of fine roots in the cores at the second or third harvest, after 1.5 and 2 years, did not differ between the treatments. The root growth pattern was affected by the treatments. Taking all single differences into account (Figure 2), the W treatment seemed to reduce the number of root tips and forks, and reduced the root length. The A treatment increased the number of root tips, forks and the root length, but reduced the diameter of the fine roots (Figure 2).

Table 2. Biomass (kg m^{-3}) and turnover (year^{-1}) of fine roots as presented in various horizons and affected by the treatments. Different letters indicate a significant difference of biomass between the years within one treatment and soil horizon with $p < 0.01$. Fine root turnover is given in the lower part and letters indicate differences between the treatments with $p < 0.01$

Year	C	A	F	W
Biomass (Ah-horizon, 0–30 mm)				
1998	1.15 a	2.19 a	1.75 a	1.26 a
1999	1.34 a	1.86 a	1.61 a	1.26 a
2000	1.59 a	2.51 a	2.10 a	1.28 a
Biomass (B-horizon, 30–100 mm)				
1998	0.19 a	0.27 a	0.28 a	0.22 a
1999	0.22 a	0.36 a	0.30 a	0.23 a
2000	0.21 a	0.35 a	0.35 a	0.21 a
Biomass (Ah+B horizon, 0–100 mm)				
1998	0.38 b	0.60 b	0.62 a	0.44 a
1999	0.47 ab	0.72 b	0.62 a	0.45 a
2000	0.52 a	0.91 a	0.76 a	0.53 a
Turnover (Ah+B horizon, 0–100 mm)				
1998–2000	1.04 a	0.67 a	0.66 a	0.59 a

Results depended also on the harvest time. A two-way ANOVA revealed a lower fine root biomass in the ingrowth-cores after 1 year than after 1.5 years. After 2 years the biomass was comparable to that after 1.5 years. The diameter of the roots was larger at the last harvest, after 2 years, than at the harvest after 1.5 years. After 1.5 years the roots had a higher density in forks, more tips and a higher length than in both harvests after 1 or after 2 years.

When the pH of the soil (Ah horizon) was considered at the same sample points from which the fine roots of the element analysis derived, an elevated pH in the plots of all three treatments was observed in both years. While the change in pH in the soil of F and W treated plots was in a similar range, the pH of the A-treated plots made a large shift of about 1.5 units after 2 years of treatment (Figure 3). In general (results of all sample locations) the pH in the Ah horizon of the soil was increased by A, F, and W after the first and even more after the second growing season (Table 3). In the mineral soil of the B horizon the pH shift was less pronounced and was significant in the three treatments only after the second year (Table 3).
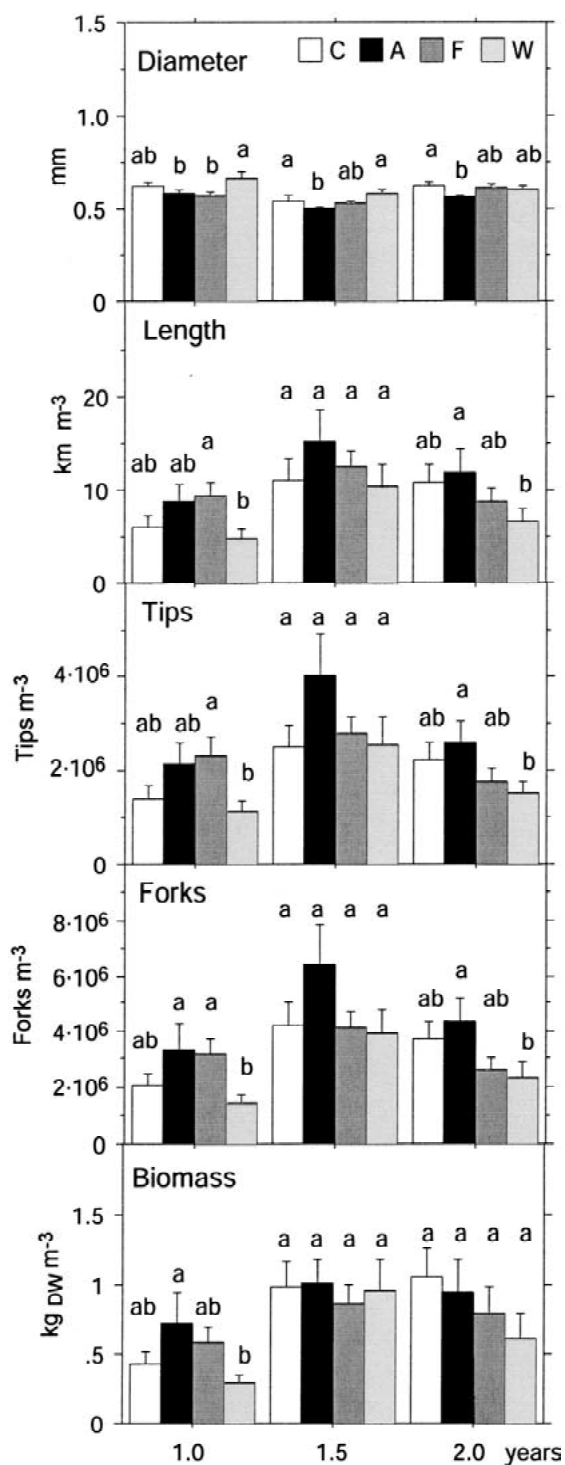

Figure 2. Biomass given as fine root density (kg $_{DW}$ m^{-3}), amount of forks, tips, length (km) per m^3 soil and fine root diameter (mm) of the ingrowth-cores samples, columns represent means $\pm$ SE of the respective parameter ($n = 27$). Different letters indicate a significant difference with $p < 0.05$ according to a one-way ANOVA on the factor treatment within one harvest.
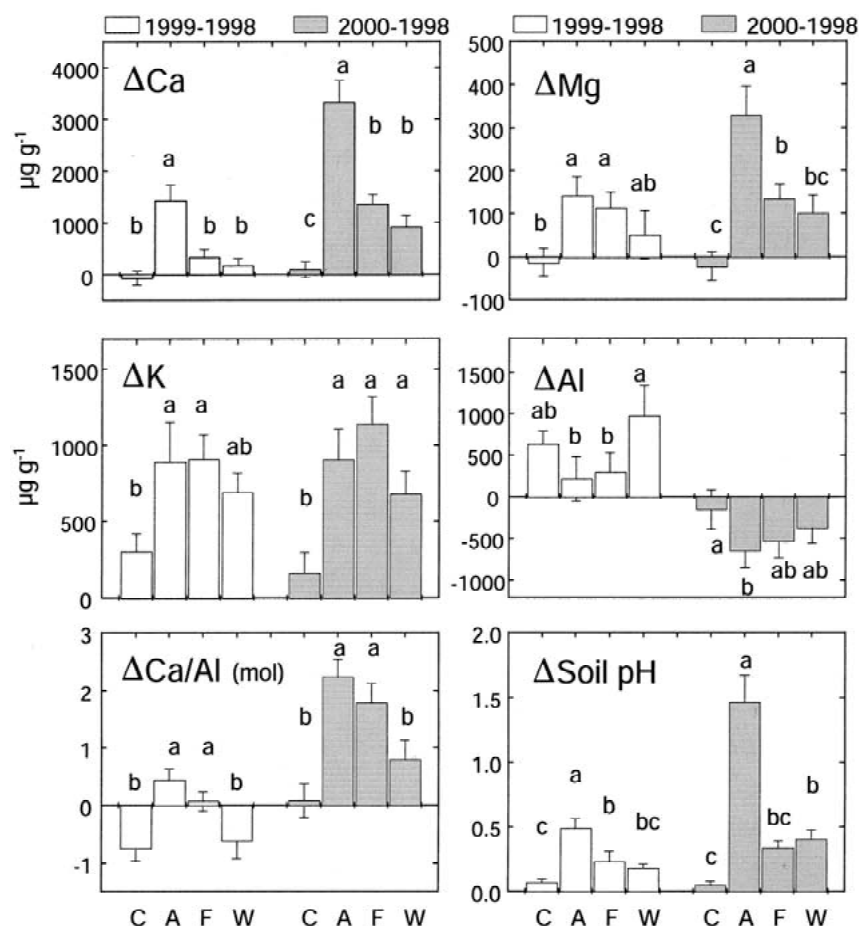
Figure 3. Changes in Ca, Mg, K, Al concentrations, in the molar Ca/Al ratio in the fine roots, and in the soil pH after 1 and after 2 years of treatments, columns represent a mean ± SE ($n = 25 - 31$): C – control; W – water; F – liquid fertiliser; A – ash. Different letters indicate a significant difference with $p < 0.05$ according to a one-way ANOVA on the factor treatment concerning the differences of a harvest from the concentrations measured before treatments started (1998).

Table 3. Soil pH in the soil core samples. Different letters indicate a significant difference between the years within one treatment and soil horizon with $p < 0.01$

Year	C	A	F	W
pH (Ah-horizon, 0–30 mm)				
1998	3.28 a	3.26 c	3.25 c	3.34 b
1999	3.30 a	3.70 b	3.38 b	3.45 b
2000	3.35 a	4.63 a	3.50 a	3.66 a
pH (B-horizon, 30–100 mm)				
1998	3.46 a	3.47 b	3.45 b	3.50 b
1999	3.49 a	3.51 b	3.46 ab	3.51 b
2000	3.50 a	3.67 a	3.51 a	3.55 a

Elements in the fine roots

No differences (one-way ANOVA, $p < 0.01$) in the fine root elements were detected between the designated plots in the samples of 1998, before the treatments started (data not shown). Within the 2 years of treatment Ca, Mg, K, and P concentrations in the fine roots of Norway spruce were improved by the A as well as by the F treatment (Figures 3 and 4) compared to the C. The W treatment also had a significant effect on the changing of the K and Ca concentrations after 2 years of treatment years. The Al, Fe, and Mn concentrations were decreased in the A and F treated roots compared to the C and W treatments (Figures 3 and 4). Thus, the molar Ca/Al ratio was significantly enhanced by the A and F treatments (Figure 3). The S and Zn concentrations were not dependent on the

treatment applied (Figure 4), although these elements showed differences between the years. The N concentration of the roots was only significantly changed by the F treatment after 1 year. After 2 years the increase in the N concentration in the roots of F treatment was significantly different from the change with the A treatment, where the concentration decreased (Figure 4). The changes in the C concentration after the second growing season differed between the A treatment, where C tended to decrease, and the W and C treatments, where the C concentration increased. The C/N ratio in the fine roots was decreased by the F treatment, while the A treatment seemed to have a slight positive effect after 2 years (Figure 4).

Mean Cu concentrations in the fine roots were in the range of 9.0–10.4 $\mu g\ g^{-1}$ (data not shown). The majority of Cd concentrations measured was below the detection limit of 1.5 $\mu g\ g^{-1}$. An accumulation, that means increased concentrations in the fine roots due to the A treatment, of heavy metals such as Cu, Cd (data not shown), and Zn (Figure 4) was not observed in the roots after 2 years with a total wood ash input of 8000 kg ha^{-1}.

Elements in needles

Within 2 years an increase of the N and P concentrations in the current needles was observed under the F treatment. The N concentrations in the needles were in general higher in the 2000 than in the 1998 samples, before treatments (Table 4). Mg, Ca, S, and Al concentrations were not significantly changed in the current foliage. K concentrations were increased by the A and F treatments but also in the control plots. The Mn concentrations decreased in the C and W treatments, while Zn was increased in the foliage of the A and F treated trees. Fe concentrations were increased irrespective of the treatment (Table 4).

Discussion

Root growth

The root biomass in the topsoil was not affected by the treatments during the observation period. However, a significantly higher root density was observed in the C and A plots, and there only after 2 years of treatments. The fine root density was already different among the plots designated to the treatments before the experiment started in spring 1998. In a similar experiment in

Sweden wood ash application led to a decrease in fine root biomass in the topsoil (Clemensson-Lindell and Persson, 1995). In an experiment in Germany the fine root biomass was strongly enhanced by a high input of Mg in a spruce forest within three growing seasons, while a combined K and Mg fertilisation showed no growth effects (Raspe et al., 1994).

Production of fine roots as estimated from ingrowth-core data showed a high variation, which is comparable to the variation in other earlier studies (e.g., Persson et al., 1998). Laboratory experiments have shown that high N supply could lead to reduced root growth (George et al., 1999) and also to increased root growth (George and Marschner, 1996). In the present study, the F treatment contained 70–100 kg N ha^{-1} year^{-1}, yet a change in relative root growth was not observed. In comparison, Magill et al. (2000) did not observe an influence on fine root biomass after several years of N addition in a pine or a hardwood stand, but a change in storage N due to enhanced N concentrations in the fine roots (Magill et al., 2000).

The two growing seasons observed were a short period in the time scale of trees. Stober et al. (2000) reported significant differences in fertilised against unfertilised ingrowth-cores within two growing seasons in various spruce forests, while after only one growing season no effects had been observed. As early as half a year after installation Raich et al. (1994) observed differences between N fertilised ingrowth-cores and the remaining cores. In the present study the higher proportion of roots grown in the cores after 1 year under the F and A treatment was probably attributed to the fine roots foraging for nutrients. Although the initial growth dynamics were influenced by the A and F treatments, the final fine root density was not affected by the treatments.

Persson et al. (1998) observed a stabilisation of growth with exclusion of N and S, the main contributors to soil acidification, by a roof. The roots grew stouter and shorter, which the authors concluded to be a sign of higher root vitality and enhanced mycorrhization. In contrast, in the present study the A treatment resulted in longer and thinner roots and more branches. Another experiment in a Norway spruce forest in Sweden also reported increased length of fine roots with wood ash application (Clemensson-Lindell and Persson, 1995). Thus, the change to a greater branching intensity and length in root growth could have been caused by improved soil pH and nutrient availability. The fine root turnover observed in the present study was within the range of temperate coni-
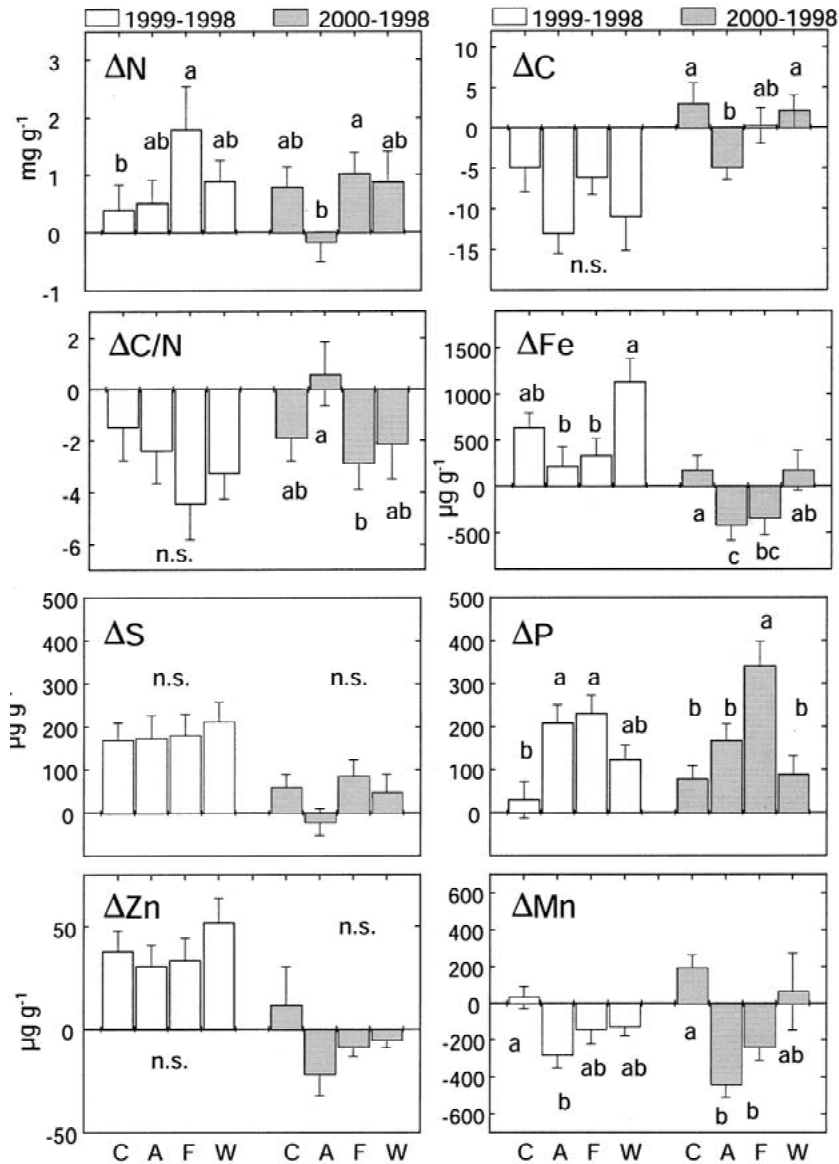
Figure 4. Changes in N, C, Fe, S, P, Zn, Mn concentrations and in the C/N ratio in the fine roots after 1 and after 2 years of treatments, columns represent a mean ± SE ($n = 25 - 31$): C – control; W – water; F – liquid fertiliser; A – ash. Different letters indicate a significant difference with $p < 0.05$ according to a one-way ANOVA on the factor treatment concerning the differences of a harvest from the concentrations measured before treatments started (1998).

ferous forests as described by Gill and Jackson (2000). Strubelt et al. (1998) using a similar method obtained a turnover of 0.4–1.3 year^{-1} with *Pinus* in Germany, which is comparable to our results.

Elements

The elements in the fine roots of the present study were in the range of reported values for other European study sites (Table 5). The N concentration was moderate compared to high values reported from Germany and France and low values in Sweden. The Ca, Mg, and K concentrations in the roots were high compared to results from Germany, France, and Sweden. In the present study N was enhanced in the fine roots only by the F treatment. The fine roots might be a significant sink for added N as has been observed earlier: Magill et al. (1997) calculated that about 15% of the

Table 4. Element concentrations (mg g^{-1} DW) in the current needles before the treatments and after 2 years of treatment (harvest in autumn of the previous year): ns – not significantly different, *, **, *** difference with $p < 0.05$, $p < 0.01$, $p < 0.001$, respectively

Elements	C		A		F		W		Suff. range[a]
	1998	2000	1998	2000	1998	2000	1998	2000	
N	15.1	15.9*	14.9	15.7*	14.4	15.8***	14.8	15.3^{ns}	13.5–17.0
S	0.93	0.88^{ns}	0.92	0.96^{ns}	0.93	0.96^{ns}	0.90	0.88^{ns}	No data
P	1.40	1.32^{ns}	1.38	1.43^{ns}	1.31	1.42*	1.33	1.31^{ns}	1.3–2.5
Ca	4.60	4.14^{ns}	4.54	4.47^{ns}	5.33	5.29^{ns}	4.44	3.89^{ns}	3.5–8.0
K	3.37	4.00**	3.68	5.10***	3.37	4.78***	3.69	3.81^{ns}	5.0–12.0
Mg	0.92	0.94^{ns}	0.94	1.05^{ns}	1.02	1.07^{ns}	0.89	0.89^{ns}	1.0–2.5
Fe	0.038	0.042**	0.039	0.046***	0.038	0.049***	0.035	0.043***	No data
Mn	1.96	1.66***	1.85	1.72^{ns}	2.21	2.08^{ns}	2.16	1.83**	0.05–0.5
Zn	0.016	0.018^{ns}	0.017	0.024**	0.021	0.026***	0.019	0.018^{ns}	0.015–0.06
Al	0.08	0.07^{ns}	0.08	0.08^{ns}	0.08	0.09^{ns}	0.07	0.07^{ns}	No data

[a]Range of concentration described as sufficient for the respective element by Bergmann (1993).

N applied over 6 years was retained through a change in root storage N in red pine. The observation that N addition led to higher N concentrations in spruce fine roots was confirmed, among others, by Stober et al. (2000). Hahn and Marschner (1998b) investigated the element concentrations in fine roots of Norway spruce under acid irrigation and liming. On the acid irrigated plot Ca and Mg in the roots decreased, but 2 years after the end of irrigation no difference was found. Liming increased root concentrations of Ca and Mg, and reduced Mn and Al (Hahn and Marschner, 1998b). The results of liming were similar to the wood ash effects observed in the present study. In a field experiment on the effect of the alkalising compounds wood ash and lime on the fine roots of spruce, Ca, Ca/Al ratio, Mg, P, and K were enhanced in the roots (Persson and Ahlström, 1994), comparable with the results in the present study. In contrast to our results, the concentrations of Mn increased 2 years after ash application, while we observed decreasing concentrations in the roots.

Considering the critical molar Ca/Al ratio for Al stress in the fine roots of 0.2 (Cronan and Grigal, 1995), however, the roots in the present study, which had a molar Ca/Al ratio of about 1.5 (data not shown) before the treatments, were far from being under Al stress. This was also due to the comparably high Ca concentrations in the fine roots and needles, and, therefore, an assumedly good Ca supply in Swiss forests (Tables 4 and 5, Brunner et al., 2002; Landolt, 1997).

Hüttl (1990) described long lasting improvement in Mg and K nutrition through a balanced fertilisation. In contrast, Ohno and Erich (1990) observed a decreasing relative availability of Mg and K through wood ash additions. Their finding that Ca was the most available nutrient after wood ash application (Ohno and Erich, 1990) agreed with the present results obtained with fine roots. Furthermore, the changes observed with the A treatment in the fine roots matched with the results observed in the upper soil after wood ash application in the USA (Kahl et al., 1996), where the availability of Mn and Al was decreased, while the Ca, K and Mg availability in the top soil and the soil pH increased.

Fine root versus *needle elements*

All elements measured in the needles were within the 'typical' range of Norway spruce needle elements in Switzerland (Landolt et al., 1989). In comparison to a European survey (Stefan et al., 1997), N and Mn concentrations were in the upper third, while K, S, Mg, and Zn concentrations were in the lower third of the European range (Stefan et al., 1997). This observation is confirmed by comparison with general knowledge about plant nutrition (Bergmann, 1993): P, Mg, Zn, and K were close to the lower limit, whereas other nutrients were basically in the range of 'sufficient' supply (Bergmann, 1993). Mn was measured in high concentrations compared to the range defined as 'sufficient'. However, the Mn concentrations in the shoot are quite variable, and especially with a low

Table 5. Element concentrations (mg g^{-1}$_{DW}$) in fine roots of Norway spruce of Unterehrendingen compared to results from other Swiss and European Norway spruce forest stands: n.d. – not determined

	Unterehrendingen	Alptal[a]	Beatenberg[a]	Chironico[a]	Waldstein[b]	Aubure[b]	Skogaby[b]
		Switzerland			Germany	France	Sweden
Age (years)	70	200	200	160	80	100	30
Elevation (m asl)	450	1160	1510	1360	700	1050	100
Soil pH (0–100 mm)	3.3	5.4	2.9	3.7	3.5	3.7	4.0
Elements (mg g^{-1}$_{DW}$)							
N	13.9	10.1	11.6	13.9	16.9	16.2	9.7
S	0.98	0.78	n.d.	1.16	1.28	1.17	0.7
P	1.18	0.65	n.d.	0.88	1.05	1.30	0.6
Ca	4.13	7.96	4.31	7.13	3.40	2.94	2.2
K	3.13	3.30	2.21	3.69	0.65	0.75	0.4
Mg	0.76	1.05	0.78	1.33	0.40	0.41	0.5
Fe	1.59	2.33	0.12	4.19	n.d.	n.d.	n.d.
Mn	0.80	0.29	0.19	0.32	n.d.	n.d.	n.d.
Zn	0.08	0.10	0.13	0.38	n.d.	n.d.	n.d.
Al	2.03	2.81	0.20	5.78	n.d.	n.d.	n.d.

[a]Data from LWF for Alptal, Beatenberg and Chironico according to Brunner et al. (2002).
[b]Data from NYPHIS/CANIF for Aubure, Waldstein, Skogaby according to Bauer et al. (2000).

soil pH, high Mn concentrations have been reported (Marschner, 1995).

With a biogeochemical model it was calculated that the fine roots (assuming one turnover a year) contribute one-third of the global annual net primary production (Jackson et al., 1997) and thus play an important role, not only in the tree physiology, but also in the quantitative contribution to the nutrient budget of a tree. Foliage analyses have been used for a long time to estimated the nutritional status of a tree or a whole forest, but in some aspects the element concentration of the foliage might be misleading. For example heavy metals are immobilised very rapidly and mostly enriched in the roots and not transported to the shoots, as known from laboratory evidence (e.g., Stienen and Bauch, 1988). Also nutritional elements of low mobility, such as Ca might be underestimated if analysed only in the foliage. Changes in the soil should logically be reflected earlier in the roots than in the shoots, and this was confirmed by the present study. While a significant influence of the applied wood ash on the Ca concentrations in the fine roots was observed, no such effect was evident in the current needles. In contrast to its low concentration in the cytosol, Ca has elementary functions in the plant metabolism (Reddy, 2001). Low amounts of Ca are sufficient to preclude deficiency and a surplus of Ca can be detoxified in the apoplast or as Ca-oxalate in the needles (Gülpen et al., 1995). Like Ca, most of the Al supplied to a Norway spruce root

is immobilised in the root apoplast (Marschner, 1995; Heim et al., 1999), therefore molar Ca/Al ratios in roots might give a more reliable estimate of a potential Al stress than in the shoots. In addition, the concentrations of Mg were also enhanced in the roots, but not in the needles. Mg has been shown to be more critical than Ca in forest nutrition (Hüttl, 1990), because Mg becomes easily limited on Mg poor soils.

The change in soil pH had a direct influence on the nutrient availability in the soil. For example, the decrease in Mn concentration in the fine roots is a consequence of a decreased availability of Mn to the roots because of an increased pH with the A and F treatments (Marschner, 1995). Thus, our results support the evaluation of Bakker (1999) that fine root nutrients are suitable indicators of forest nutrition, but should be supported by certain soil parameters.

Concluding remarks

The application of wood ash or of a fertilisation, as observed in this study on the fine roots of Norway spruce, was appropriate to mitigate acidification and its consequences, such as deficiency in, e.g., K, P, and Mg. Thus, the recycling of wood ash to the forest is confirmed as a suitable method in the short-term view, always bearing in mind certain prerequisites for the quality and amount of the wood ash (Kahl et al., 1996).

Although no accumulation of heavy metals in the fine roots was observed in the present study, in the long-term view mobilisation of heavy metals could occur (Zhan et al., 1996). Therefore, heavy metal concentrations in the wood ash should be kept as low as possible by the use of uncontaminated wood and a technically sound combustion. A long-term evaluation of all aspects, from the effects on the soil biology to the effects on the tree growth, is essential with respect to the sustainability of the fertilisations.

In analogue to their physiological position, the fine roots as indicators of the nutritional status of a forest soil can be assumed to be, from a temporal point of view, mediators between the soil, which reflects the current status on the one hand and the foliage, which integrates over a long period of time on the other hand. The results confirm that fine root data can complement soil and foliar indicators in evaluating site conditions. Thus, it would be worthwhile to include parameters based on fine roots in monitoring programs such as the UN/ECE-ICP forest (ICP, 1998).

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