IMPACTS OF $(NH_4)_2SO_4$ DEPOSITION ON NORWAY SPRUCE (*PICEA ABIES* [L.] KARST) ROOTS

M. CARNOL[1*,2], P. CUDLÍN[3] AND P. INESON[2]

[1*]*University of Liège, Dept. Botany B22, Microbial Ecology and Radioecology, 4000 Liège, Belgium;* [2]*Institute of Terrestrial Ecology, Soil Ecology Section, Merlewood Research Station, Grange-over-Sands, Cumbria LA11 6JU, United Kingdom;* [3]*Institute of Landscape Ecology, Academy of Sciences of the Czech Republic, Na Sadkach 7, Ceské Budejovice, Czech Republic. * Address for correspondence*

(Received 25 September 1998; accepted 25 February 1999)

Abstract. The effects of enhanced $(NH_4)_2SO_4$ (NS) deposition on Norway spruce (*Picea abies* [L.] Karst) fine root biomass, vitality and chemistry were investigated using root-free in-growth cores reproducing native organic and mineral soil horizons. The cores were covered and watered every 2 weeks with native throughfall or throughfall supplemented with NS to increase deposition by 75 kg ha^{-1} a^{-1} NH_4^+-N (86 kg ha^{-1} a^{-1} SO_4^{2-}-S). The in-growth cores were sampled after 19 months and assessed for root biomass, necromass, length, tip number, tip vitality and fine root chemistry. Root biomass and fine root aluminium (Al) concentration were negatively correlated, but NS deposition had no effect on root growth or root tip vitality. NS deposition caused increased fine root nitrogen (N) concentrations in the organic horizon and increased Calcium (Ca) concentrations in the mineral horizon. Fine root biomass was higher in the organic horizon, where fine root Al and potassium (K) concentrations were lower and Ca concentrations higher than in the mineral horizon. Results highlighted the importance of soil stratification on fine root growth and chemical composition.

Keywords: ammonium sulphate, roots, in-growth cores, *Picea abies*

1. Introduction

Increased inorganic nitrogen (N) deposition over the last few decades has become a major concern for the health of European forests. Some forest ecosystems, where N no longer limits primary production, become N saturated and the excess N is thought to contribute to forest decline (Nihlgård, 1985; see review by Ortloff and Schlaepfer, 1996). In particular, N in the form of NH_4 in excess of plant and microbial demands can acidify soils if nitrified and leached from the soil, causing loss of base cations or mobilisation of phytotoxic aluminium (Al) (Reuss and Johnson, 1986). Al has long been known to be toxic to plant roots, particularly for cultivated plants (Wheeler *et al.*, 1992). However, in forest soil solution, Al may be organically complexed and, hence, less toxic (Dahlgren *et al.*, 1991).

Decreases in root biomass, mycorrhizal infection and shifts in the mycorrhizal populations have frequently been reported in forests heavily subjected to acid rain (Cudlin and Kropacek, 1990; Jansen and Dighton, 1990). Such observations are often associated with extreme localized pollution. In contrast, the effects of increased N deposition over large areas in Europe are more variable. Decreased (Alexander and Fairley, 1983; van Dijk *et al.*, 1990; Clemensson-Lindell and Persson, 1995), unchanged (Majdi and Rosengren-Brinck, 1994; Seith *et al.*, 1996), and increased (Ahlström *et al.*, 1988) root production have been reported for conifers under high N deposition. This indicates that root responses to increased N deposition may depend strongly on the chemical and physical properties of the soil. Furthermore, root tips might be damaged, and their nutrient uptake capacities impaired, even with unchanged root biomass. Magnesium (Mg) deficiency symptoms in conifers may reflect impaired

Water, Air, and Soil Pollution **116:** 111-120, 1999.

nutrient uptake through antagonism between NH_4 with Ca and Mg (Jorns and Hecht-Buchholz, 1985; Hecht-Buchholz *et al.*, 1987). Increased N uptake may also lead to relative nutrient deficiencies through increased growth and subsequent limitation of other nutrients, referred to as the 'dilution effect' (Nihlgård 1985; Ortloff and Schlaepfer, 1996). Ca/Al molar ratios < 1 are thought to represent a toxicity threshold for Al in solution culture experiments (Rost-Siebert, 1983; Ulrich *et al.*, 1984). Yet, for forest soils total Al and inorganic monomeric Al might represent better indicators (Joslin and Wolfe, 1988). However, an extensive literature review including laboratory and field studies with a range of species, led Cronan and Grigal (1995) to conclude that the soil solution Ca/Al molar ratio is a satisfactory index by which to assess the ecological risk associated with forest health.

The main objective of this study was to determine the influence of high N deposition on the health of Norway spruce roots, by measuring root parameters in the field subjected to $(NH_4)_2SO_4$, applied to mimic polluted throughfall. As sulphate (SO_4^{2-}) behaved as a conservative ion and as major changes in soil solution ionic concentrations at this site were related to nitrate (NO_3^-) (Carnol *et al.*, 1997a), the large sulphur (S) input did not seem to interfere with chemical processes and the conclusions of this study.

2. Material and Methods

2.1. Study Site

The experiment was undertaken in a 42 year old Norway spruce (*Picea abies* [L.] Karst) stand, 3500 stems ha^{-1}, located in Grizedale forest, NW United Kingdom (National Grid Ref. SD326915). The stand was located on an acid brown soil with clay texture and slight seasonal water-logging. No ground storey vegetation was present. The site was at 170 m a.s.l. with a mean annual soil temperature (0-5 cm depth) of 7.8 °C and rainfall of 1900 mm (June 1992-1993). The soil chemistry has been described in Carnol *et al.* (1997b) and Raubuch (1992); relevant characteristics are given in Table I.

TABLE I

Total soil element content (µg g^{-1} dw), exchangeable cations (µeq g^{-1} dw) with the percentage (%) of the total exchangeable cations and pH in the organic and mineral horizons (means of seven replicates).

Carnol *et al.* (1997b) Raubuch (1992)

	Total element content (µg g^{-1})					Exchangeable cations (µeq g^{-1})							
	Al	Ca	Mg	K	P	Al	Ca	Mg	K	C (%)	N (%)	CEC	pH_{H2O}
Ol	3199	1462	573	1008	874	-	-	-	-	43.9	1.5	-	4.1
Of	2372	1107	560	616	884	-	-	-	-	45.3	1.6	-	3.9
Oh	5394	298	588	793	903	-	-	-	-	34.1	1.9	-	3.6
mineral (0-5cm)	19243	2963	3284	1983	783	113	4.3	3.6	1.2	30.7	1.9	123	3.7
(%)	-	-	-	-	-	(91)	(3.6)	(2.9)	(1.0)	-	-	-	-
mineral (5-8 cm)	-	-	-	-	-	112	3.7	3.2	0.9	34	2.1	121	3.8
(%)	-	-	-	-	-	(93)	(3.2)	(2.6)	(0.7)	-	-	-	-

TABLE II

Fine live root tip development stages and vitality classes

(Kocourek and Bystrican, 1989; Chemlikova *et al.*, 1992; Ruess *et al.*, 1996)

	Stage/Class	Description
Root tip development	1	root initiation
	2	elongated root tip with root hairs
	3	club-shaped short roots without hairs, tip slightly swollen, fine roots appear hyaline
	4	tip considerably swollen or clubbed, with first mycorrhizal structures, the Hartig net, but no fungal mantle
	5	fully developed mycorrhiza (Hartig net and fungal mantle)
Root tip vitality	Turgid	young turgid tip, assumed to be have absorptive function
	Shrivelled	older tip, live and functioning vascular tissues, but believed to be not absorptively functioning
	Dead	brittle root, dead vascular cylinder

2.2. SAMPLE COLLECTION AND ANALYSES

Root-free in-growth cores (Persson, 1990) reproduced organic (8 cm) and mineral soil horizons (7 cm) to 15 cm depth. They consisted of a cylindrical nylon mesh bag (Netlon®, mesh size 5 mm), containing the reconstructed Ol, Of, Oh and top mineral horizons, which were inserted into the holes left previously by the removal of the soil cores. The 10 replicates were individually covered with a Perspex® sheet (30*30 cm), 10 cm above the ground. In-growth cores were watered every 2 weeks with throughfall collected in the field, representing the mean throughfall volume over this time. The treatment started 6 months after installation and consisted of $(NH_4)_2SO_4$ added to increase deposition by 75 kg ha^{-1} a^{-1} NH_4^+-N (86 kg ha^{-1} a^{-1} SO_4^{2-}-S). Native throughfall deposition at this site was 9 kg ha^{-1} a^{-1} NH_4^+-N and 34 kg ha^{-1} a^{-1} SO_4^{2-}-S (1992-1993). The $(NH_4)_2SO_4$ additions were incorporated into the throughfall at each watering event, to simulate increased deposition by polluted throughfall.

Nineteen months after installation, the in-growth cores were removed from the field and divided into organic and mineral soil horizons. The soil was washed off the roots by aid of a root washing machine, consisting of a 1 mm sieve placed beneath a gently sprinkling water jet. Live and dead roots were then picked manually from amongst the needles and debris from the sieve. Soil remaining on live fine roots was removed by gently cleaning with fine brushes under deionised water. Roots were analysed for biomass, necromass, root length, root tip number (RTN), root tip vitality (defined below) and fine root chemistry. They were divided into coarse (>1 mm) and fine (<1 mm) roots. Distinction between the live and dead root fractions was made on visual criteria; living roots are firm, light coloured and present a good adhesion between the cortex and the periderm (Persson, 1990); dead roots are dark and brittle, and the absence of a live vascular cylinder is verified by teasing the root strand between tweezers. The fine root fraction was sub-sampled for chemical analysis and estimation of vitality, made after fixation in gluteraldehyde. Root lengths were determined with the gridline intersect method (Giovannetti and Mosse, 1980).

Fine root tips were counted under the dissection microscope, and divided into 5 classes of root tip development and 3 vitality classes (Kocourek and Bystrican, 1989;

Chemlikova *et al.*, 1992; Ruess *et al.*, 1996) (Table II). Visual distinction between stages 4 and 5 was possible after 'calibration' of the observer, by examination of thin longitudinal and cross sections under the epifluorescent microscope after staining in a solution of cotton blue in lactoglycerin (Cudlin, 1991). Root dry weights were recorded after drying to constant weight at 85°C.

2.3. Chemical Analyses

Sub-samples of fine live roots for chemical analyses were dried at 85°C and wet-digested in a H_2O_2/H_2SO_4 digestion mixture containing Se and $LiSO_4$ (Allen, 1989). Al recovery was improved by re-boiling the digestion mixture, which had been diluted with 10 ml distilled water. Al, Ca, Mg and potassium (K) contents were determined using an ICP, and N was determined colorimetrically (indophenol blue) using a Skalar autoanalyser.

2.4. Statistical Analyses

Statistical analyses were carried out using the SAS GLM procedure, an ANOVA technique with correction for missing values (Student's T-test). Two-way ANOVA was used to test individually for NS deposition/block and soil layer/block effects. When block was not significant, effects were tested with one-way ANOVA. Percentage data were transformed (arcsine square root; Sokal and Rohlf, 1981) before statistical analyses (SAS Institute Inc., 1989). Relationships between variables were investigated using Pearson's correlation coefficient. Due to the labour intensive nature of the determinations, 8 replicates were analysed for fine root biomass and vitality whereas all 10 replicates were analysed for fine root chemistry and coarse root biomass. Results are expressed per litre of soil volume.

3. Results and Discussion

3.1. Root Biomass

Increased NS deposition did not significantly ($p<0.05$) affect coarse, fine live, fine dead or total fine root biomass (Figure 1), neither did it have any significant effect on the total root tip number (RTN) or root tip density (RTD), defined as the ratio of live root tips (turgid+shrivelled) to live root length (Table III). Similarly, the biomass ratios of dead/live root (31-36%) and total fine root/coarse root (3-9%) were not influenced by the NS deposition treatment. Proportions of coarse, fine live and dead roots relative to total root dry weight varied between 16-32%, 53-63% and 15-20% respectively, with no significant effects of NS deposition or soil horizon. Hence, the addition of 75 kg ha^{-1} a^{-1} NH_4^+-N did not alter root biomass production in our experiment. Although, in a previous experiment, increased NS deposition had led to higher soil solution Al concentrations (Carnol *et al.*, 1997a,b), in the range reported to cause a decrease in fine root biomass (Joslin and Wolfe, 1988). Still, the difference in soil solution Al concentrations between controls and NS treatments was relatively small (Carnol *et al.*, 1997b). Furthermore, carbohydrate supply from the tree canopy also controls root

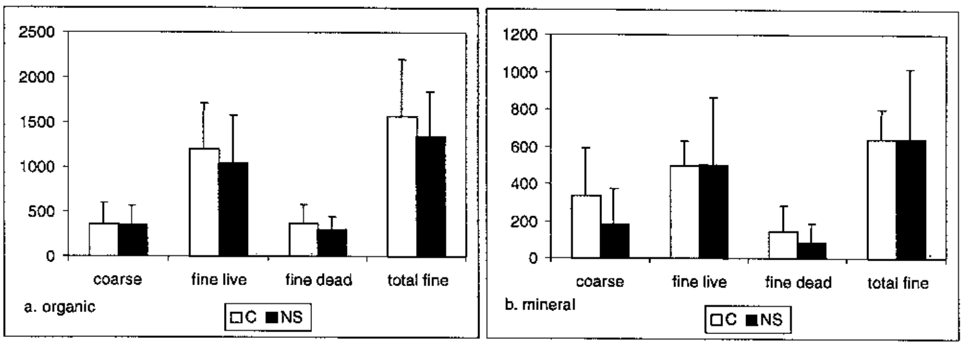

Fig. 1. Coarse, fine live, fine dead, total fine root biomass (mg l^{-1} soil) grown into the organic (a) and mineral (b) soil horizon of in-growth cores (mean and sd) under control (C) and increased $(NH_4)_2SO_4$ deposition (NS). There were no significant NS deposition effects; for significant differences between soil horizons, see text.

TABLE III

Total number of root tips (RTN) and root tip density (RTD, tips m^{-1}) of roots grown into in-growth cores (mean and sd); C: control, NS: increased $(NH_4)_2SO_4$ deposition. Different letters denote significant ($p<0.01$) differences between organic and mineral horizon; there were no significant NS deposition effects.

	Organic		Mineral	
	C	NS	C	NS
RTN	8533 (4108)a	7576 (3785)a	3521 (1471)b	3262 (2008)b
RTD	325 (38)a	331 (61)a	284 (77)a	287 (51)a

biomass production (Marshall and Waring, 1985). In our study, as treated areas were only a small fraction of the whole rooting system, translocation between roots might have moderated treatment effects on root biomass. Whatever the cause, this study has revealed no toxic effects of NS additions (75 kg ha^{-1} a^{-1} NH_4^+-N) on root biomass.

Soil horizon however did exert a significant influence on root growth. The dry weight of coarse roots was significantly higher in the organic layers with a mean across both treatments of 350 mg l^{-1} compared to 260 mg l^{-1} in the mineral layer. Dry weights of fine live, fine dead, total fine roots and RTN were also significantly higher in the organic horizon (Figure 1, Table III). The ratio dead/live roots was unaffected. Decreasing root density downward from organic surface horizons to mineral soil horizons is in agreement with general findings from the literature (Schneider *et al.*, 1989; Majdi and Persson, 1993, 1995). This experiment has demonstrated that when the local soil strata is reproduced in in-growth cores, roots re-establish normally by comparison with the use of uniform substrate where the vertical distribution of fine roots tends to be lost (Matzner *et al.*, 1986).

3.2. Root tip vitality

No roots were observed in development stage 2 (for description of stages, see Table II). The development stages 1 and 3 showed a similar distribution in both soil horizons irrespective of NS treatment (Table IV), with a mean value across horizons and treatments of 0.4% for stage 1 and 1.1% for stage 3. Development stages 4 and 5 were

TABLE IV

Proportions of turgid, shrivelled and dead root tips and root tips in the development stages 1-5 (%; mean and sd) for roots grown into the organic and mineral horizon of in-growth cores. C: control, NS: increased $(NH_4)_2SO_4$ deposition.

	Variable	Organic		Mineral	
		C	NS	C	NS
Vitality	Turgid	46.6 (22.6)	49.8 (13.7)	61.8 (20.7)	60.4 (16.6)
	Shrivelled	39.6 (20.4)	34.4 (8.8)	29.6 (15.9)	26.7 (17.2)
	Dead	13.8 (10.5)	15.8 (8.9)	8.6 (6)	12.9 (8.3)
Development	Stage 5	51.5 (21.3)	54.3 (24.6)	59.4 (28.9)	64 (33)
	Stage 4	46.5 (21.2)	44.3 (24.8)	39.4 (28.4)	34.6 (32.8)
	Stage 3	1.6 (1.6)	1.1 (1)	0.8 (0.9)	0.9 (0.7)
	Stage 1	0.4 (0.2)	0.2 (0.3)	0.4 (0.3)	0.4 (0.2)

TABLE V

Proportions of root tip development and vitality classes (%) on the total number of root tips (mean and sd) for roots grown into the organic and mineral horizon of in-growth cores. C: control, NS: increased $(NH_4)_2SO_4$ deposition.

Development	Vitality	Organic		Mineral	
		C	NS	C	NS
5	turgid	30.1 (13.7)	33.7 (17.1)	42.5 (29.9)	41.7 (27.8)
	shrivelled	16.1 (21.7)	13.5 (13.1)	12.5 (13.7)	16 (20.7)
	dead	5.3 (4.7)	7.1 (5.0)	4.4 (3.7)	6.3 (5.6)
4	turgid	15.5 (10.4)	15.6 (8.2)	18.7 (12.6)	18.2 (19.9)
	shrivelled	22.7 (14.9)	20.2 (10.7)	16.6 (16.3)	9.9 (8.5)
	dead	8.3 (8.3)	8.5 (8.1)	4.1 (3.5)	6.6 (7.8)
3	turgid	0.9 (1.2)	0.4 (0.4)	0.4 (0.7)	0.4 (0.2)
	shrivelled	0.6 (0.4)	0.5 (0.6)	0.4 (0.4)	0.4 (0.4)
	dead	0.1 (0.2)	0.2 (0.1)	0 (0)	0.1 (0.1)
1	turgid	0.1 (0.2)	0.1 (0.1)	0.1 (0.1)	0.1 (0.1)
	shrivelled	0.2 (0.1)	0.1 (0.1)	0.2 (0.2)	0.3 (0.2)
	dead	0.1 (0.1)	0 (0.1)	0.1 (0.1)	0 (0.1)

dominant and shared the remaining proportion. There were no significant differences between treatments, and mean values were 42.0% for stage 4 and 56.5% for stage 5, showing that most root tips were mycorrhizal.

Proportions of turgid, shrivelled and dead root tips were 53, 33 and 13% respectively, and there were no significant treatment effects (Table IV). However, a lower proportion of turgid root tips and a higher proportion of shrivelled root tips were apparent in the organic compared to the mineral horizon. This could indicate recent unfavourable conditions, such as summer drought, for root growth in the upper horizon, or a slower ageing processes in the mineral soil (Hendrick and Pregitzer, 1992). In the mineral layer, the proportion of dead root tips was slightly (but not significantly) higher in the NS treatment compared to control.

Individual root tip classes were dominated by dead, shrivelled or turgid root tips in vitality classes 4 and 5 (Table V) and were unaffected by horizon and deposition treatments. However the proportion of 'turgid 5' roots was higher (not significant) in the mineral layers (42%), compared to the organic layers (32%) and was compensated by lower proportions of shrivelled and dead roots of stages 4 and 5.

These results showed that root vitality, as defined by visual criteria was not influenced by the high NS deposition treatment. Wallander and Nylund (1992) likewise observed little change in the fungal biomass viability in *Pinus sylvestris* seedlings treated with high NH_4-N concentrations, although the extramatrical mycelium decreased. Arnebrant (1994) found that species composition of the mycorrhiza fungi changed in response to high N supply.

3.3. Fine root chemical composition

In the organic horizon, fine root N content was significantly increased from 21.7 to 24.0 mg g^{-1} dw (Figure 2) in NS treated in-growth cores, indicating enhanced N uptake in response to the additional N. Increased root N content following NS application was also observed in spruce roots growing in the organic and top mineral layer, which was associated with a decreased Mg content (Majdi and Rosengren-Brinck, 1994). Boxman *et al.* (1988) reported cation efflux from roots at high NH_4 supply. However, in our study, there was no evidence of decreased Mg or Ca root contents due to increased N uptake. Instead, NS deposition led to an increase in fine root Ca contents, increasing the molar Ca/Al ratio in roots of the mineral soil horizon (Figure 2). NS deposition can increase Ca mobilisation in the upper soil horizons by exchange reactions with NH_4^+ or due to Ca leaching associated with the mobile NO_3^- anion (Carnol *et al.*, 1997a). This may explain the increased root uptake of Ca in the mineral horizon under NS.

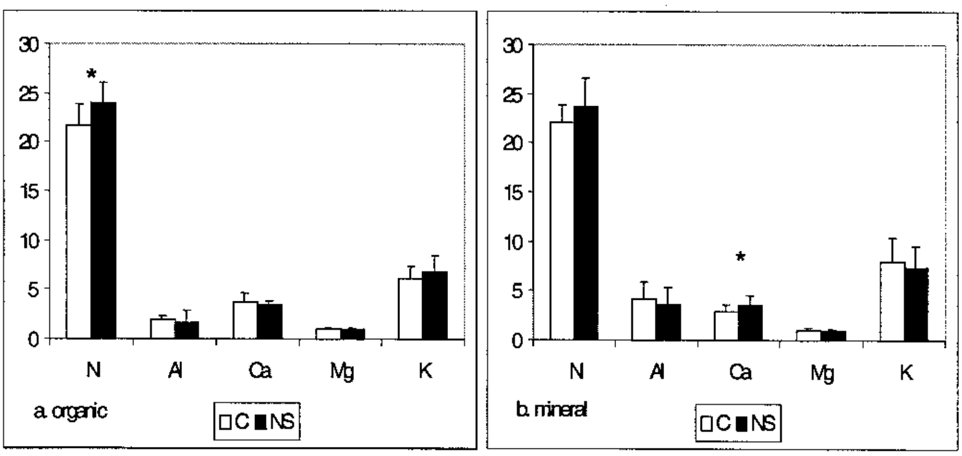

Fig. 2. Chemical content of fine live roots (mg g^{-1} dw) grown into the organic (a) and mineral (b) soil horizon of in-growth cores (mean and sd) under control (C) and increased $(NH_4)_2SO_4$ deposition (NS). * Significant NS deposition effects ($p<0.05$); for significant soil horizon effects, see text.

Root concentrations of Al, Mg and K were not influenced by NS deposition in either soil horizon. Although soil solution Al concentrations were increased by NS (Carnol *et al.*, 1997b), fine root Al concentrations did not increase. However, soil solution (Carnol *et al.*, 1997b) and root data were not collected simultaneously, and

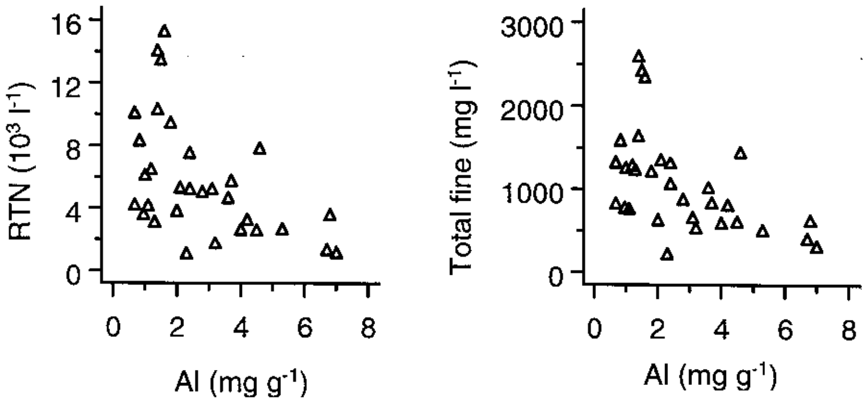

Fig. 3. Relationship between fine root Al content (mg g^{-1} dw) and growth characteristics of Norway spruce roots grown into in-growth cores. RTN: total number of root tips (n=31), total fine: total biomass of fine roots (n=32). Log-linear regression: $p<0.001$; adj r^2: 0.31 (total fine), adj r^2: 0.31 (RTN).

year-to-year variation could explain this difference. Furthermore, rhizosphere nutrient availability plays an important role in root uptake (Majdi and Rosengren-Brinck, 1994; Rosengren-Brinck *et al.*, 1995). These authors reported decreased rhizosphere Al concentrations and increased Ca concentrations and Ca/Al ratios following NS treatment. Rhizosphere soil chemistry may thus differ from bulk soil solution chemistry, and this could explain the lack of marked treatment effects.

Fine root Al concentrations were significantly ($p<0.05$) higher and fine root Ca concentrations significantly lower in the mineral soil horizon, leading to lower Ca/Al, Mg/Al molar ratios compared to the organic horizon, irrespective of treatment. Fine root K concentrations were significantly ($p<0.05$) higher in the mineral soil horizon (control treatment only). This vertical stratification in fine root chemistry is probably related to a gradient of availability of these elements in the soil profile. Similar increases in root Al concentration and decreases in root Ca concentration with soil horizon have been reported (Dahlgren *et al.*, 1991; Majdi and Rosengren-Brinck, 1994). The lower Ca root concentration in the mineral horizon could be due to competition with Al for adsorption sites (Truman *et al.*, 1986; Hecht-Buchholz *et al.*, 1987), or a lower availability of Ca in this layer. Lower Al uptake in the organic layer has been related to a higher proportion of organically chelated Al in the soil solution (Cronan *et al.*, 1986; Joslin and Wolfe, 1988). Higher fine root K contents in the mineral horizon may be related to a synergism in Al and K adsorption (Truman *et al.*, 1986), or higher K availability in this horizon.

Fine root Al concentration was negatively correlated to the logarithm of fine root biomass (r^2: 0.34, adj r^2: 0.31; $p<0.001$) and to the logarithm of RTN (r^2: 0.33, adj r^2:

0.31; p<0.001) (Figure 3). This significant negative relationship indicated that the reduction in root biomass and RTN in the mineral layer might be due to high concentrations of plant available Al. Root biomass reductions due to Al have been reported in several controlled experiments (Joslin and Wolfe, 1988; Boxman *et al.*, 1991; Oleksyn *et al.*, 1996). Total Al concentrations in soil solution seem to be a good predictor of fine root biomass (Joslin and Wolfe, 1988) and, in this study, total dissolved Al concentrations rose to ca. 0.8 meq l^{-1} (Carnol *et al.*, 1997b), with Ca/Al molar ratios of as low as 0.25. Values of this magnitude have been reported to adversely affect fine root biomass and nutrient uptake (Van Praag *et al.*, 1985; Majdi and Persson, 1993; Cronan and Grigal, 1995).

4. Conclusions

After one year, bi-weekly additions of $(NH_4)_2SO_4$ (at 75 kg ha^{-1} a^{-1} NH_4^+-N) to local throughfall did not lead to impaired root growth or root tip vitality, as defined by visual criteria. A clear vertical stratification of fine root growth and chemical composition was demonstrated (independent of NS treatment). Lower fine root biomass in the mineral soil horizon was correlated with higher fine root Al concentrations. When reproducing local soil horizons, the in-growth core technique provides a useful method for studying treatment effects on roots of mature trees in the field. The major advantage compared to a sequential coring technique is that measured effects are not confounded by pre-treatment conditions, as all roots sampled have been equally subjected to experimental treatments.

Acknowledgements

This study was part of the CORE project, funded by the Commission of the European Communities (DGXII). M. Carnol acknowledges funding by a Sectoral grant under the STEP programme (CEC, DGXII) and financial support from the SSTC (Services du Premier Ministre, Services fédéraux des affaires scientifiques, techniques et culturelles) during the preparation of the manuscript. The authors thank staff of the Chemistry Section, ITE Merlewood, Grange-over-Sands, UK, for training in the digestion procedure and performing soil solution and root chemical analyses. We thank the two referees and Dr L.J. Sheppard for their constructive comments on the manuscript.

References

Ahlström, K., Persson, H. and Börjesson, I.: 1988, *Plant Soil* **106**, 179.

Alexander, I.J. and Fairley, R.I.: 1983, *Plant Soil* **71**, 49.

Allen, S.E. (ed.): 1989, *Chemical Analysis of Ecological Materials*, Blackwell, London p. 368.

Arnebrant, K.: 1994, *Mycorrhiza* **5**, 7.

Boxman, A.W., Krabbendam, H., Bellemakers, M.J.S. and Roelofs, J.G.M.: 1991, *Environ. Pollut.* **73**, 119.

Boxman, A.W., Van Dijk, H.F.G. and Roelofs, J.G.M.: 1988, *Plant Soil* 680.

Carnol, M., Ineson, P., Anderson, J.M., Beese, F., Berg, M.P., Bolger, T., Coûteaux, M.-M., Cudlin, P., Dolan, S., Raubuch, M. and Verhoef, H.A.: 1997a, *Biogeochem.* **38**, 255.

Carnol, M., Ineson, P. and Dickinson, A.L.: 1997b, *Environ. Pollut.* **97**, 1.

Chemlikova, E., Cudlin, P. and Radosta, P.: 1992, in L. Kutschera, E. Hübl, E. Lichtenegger, H. Persson and M. Sobotik (eds.) *Root Ecology and its Practical Application*, Verlag Gumpenstein, Irding.
Clemensson-Lindell, A. and Persson, H.: 1995, *Plant Soil* **168-169**, 167.
Cronan, C.S. and Grigal, D.F.: 1995, *J. Environ. Qual.* **24**, 209.
Cronan, C.S., Walker, W.J. and Bloom, P.R.: 1986, *Nature* **324**, 14.
Cudlin, P.: in 1991, *Methods in Microbiology* Vol. 23, 365, Academic Press.
Cudlin, P. and Kropacek, K.: 1990, in H. Persson (ed.) *Above and Below-Ground Interactions in Forest Trees in Acidified Soils*, p.44, Commission of the European Communities.
Dahlgren, R.A., Vogt, K.A. and Ugolini, F.C.: 1991, *Plant Soil* **133**, 117.
Giovannetti, M. and Mosse, B.: 1980, *New Phytol.* **84**, 489.
Hecht-Buchholz, C., Jorns, C.A. and Keil, P.: 1987, *Journal of Plant Nutrition* **10**, 1103.
Hendrick, R.L. and Pregitzer, K.S.: 1992, *Ecology* **73**, 1094.
Jansen, A.E. and Dighton, J.: 1990, *Effects of Air Pollutants on Ectomycorrhizas*, p.58, Commission of the European Communities.
Jorns, A. and Hecht-Buchholz, C.: 1985, *AFZ* **46**, 1248.
Joslin, J.D. and Wolfe, M.H.: 1988, *Can. J. For. Res.* **18**, 1614.
Kocourek, R. and Bystrican, A.: 1989, *Agr. Ecosyst. Environ.* **28**, 235.
Majdi, H. and Persson, H.: 1993, *Scand. J. For. Res.* **8**, 147.
Majdi, H. and Persson, H.: 1995, *Plant Soil* **168-169**, 151.
Majdi, H. and Rosengren-Brinck, U.: 1994, *Plant Soil* **162**, 7.
Marshall, J.P. and Waring, R.H.: 1985, *Can. J. For. Res.* **15**, 791.
Matzner, E., Murach, D. and Fortmann, H.: 1986, *Water Air Soil Pollut.* **31**, 273.
Nihlgard, B., 1985, *Ambio* **14**, 2.
Oleksyn, J., Karolewski, P., Giertych, M.J., Werner, A., Tjoelker, M.G. and Reich, P.B.: 1996, *Trees* **10**, 135.
Ortloff, W. and Schlaepfer, R.: 1996, *Allg. Forst. Jagdztg.* **167**, 184.
Persson, H.: 1990, in A.F. Harrison, P. Ineson and O.W. Heal (eds.) *Nutrient Cycling in Terrestrial Ecosystems: Field Methods, Application and Interpretation*, 198, Elsevier, Essex.
Raubuch, M.: 1992, *Wechselwirkungen zwischen mikrobiologischen und chemischen Parametern in Waldböden unter Berücksichtigung des atmosphärischen Eintrags*, Göttingen, Berichte des Forschungszentrums Waldökosysteme, Reihe A, Bd. 89.
Reuss, J.O. and Johnson, D.W.: 1986, *Acid Deposition and the Acidification of Soils and Waters*, Springer-Verlag, New York, p. 119.
Rosengren-Brinck, U., Majdi, H., Asp, H. and Widell, S.: 1995, *New Phytol.* **129**, 537.
Rost-Siebert, K.: 1983, *Allg. Forst. Jagdztg.* **38**, 686.
Ruess, L., Sandbach, P., Cudlin, P., Dighton, J. and Crossley, A.: 1996, *Pedobiologia* **40**, 51.
SAS Institute Inc.: 1989, *SAS/STAT User's Guide, Version 6*, SAS Institute Inc., Cary, NC, p. 943.
Schneider, B.U., Meyer, J., Schulze, E.-D. and Zech, W.: 1989, in E.-D. Schulze, O.L. Lange and R. Oren (eds.), *Forest Decline and Air Pollution*. Springer Verlag, p. 370.
Seith, B., George, E., Marschner, H., Wallenda, T., Schaeffer, C., Einig, W., Wingler, A. and Hamp, R.: 1996, *Plant Soil* **184**, 291.
Sokal, R.R. and Rohlf, F.J.: 1981, *Biometry*, Freeman, New York.
Truman, R.A., Humphreys, F.R. and Ryan, P.J.: 1986, *Plant Soil* **96**, 109.
Ulrich, B., Pirouzpanah, D. and Murach, D.: 1984, *Forstarchiv* **55**, 127.
Van Dijk, H.F.G., De Louw, M.H.J., Roelofs, J.G.M. and Verburgh, J.J.: 1990, *Environ. Pollut.* **63**, 41.
Van Praag, H.J., Weissen, F., Sougnez-Remy, S. and Carletti, G.: 1985, *Plant Soil* **83**, 339.
Wallander, H. and Nylund, J.E.: 1992, *New Phytol.* **120**, 495.
Wheeler, D.M., Edmeades, D.C., Christie, R.A. and Gardner, R.: 1992, *Plant Soil* **146**, 61.