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Morphology, biomass and nutrient status of fine roots of Scots pine (*Pinus sylvestris*) as influenced by seasonal fluctuations in soil moisture and soil solution chemistry

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Abstract

A field monitoring study was carried out to follow the changes of fine root morphology, biomass and nutrient status in relation to seasonal changes in soil solution chemistry and moisture regime in a mature Scots pine stand on acid soil. Seasonal and yearly fluctuations in soil moisture and soil solution chemistry have been observed. Changes in soil moisture accounted for some of the changes in the soil solution chemistry. The results showed that when natural acidification in the soil occurs with low pH (3.5–4.2) and high aluminium concentration in the soil solution ($>$3–10 mg l^{-1}), fine root longevity and distribution could be affected. However, fine root growth of Scots pine may not be negatively influenced by adverse soil chemical conditions if soil moisture is not a limiting factor for root growth. In contrast, dry soil conditions increase Scots pine susceptibility to soil acidification and this could significantly reduce fine root growth and increase root mortality. It is therefore important to study seasonal fluctuations of the environmental variables when investigating and modelling cause-effect relationships.

Introduction

In naturally acidic forest soils, various stresses influence fine root growth and metabolic processes (Marschner, 1989; Gijsman, 1990). Root functioning and mycorrhizal activity may be inhibited by additional stress (Schneider et al., 1989) such as pollutant deposition, when concentrations of toxic substances and leaching losses of nutrients may be enhanced (Schultze, 1989). The most important soil-mediated factors which cause a reduction of fine root growth and mycorrhizal development are: (1) high nitrogen/cation ratios and (2) aluminium toxicity and elevated Al/cations ratios, leading to an increase sensitivity of the root system to environmental stress (drought, nutrient shortage, etc.) (Persson et al., 1995). However, to understand fully the effects caused by additional stress to the forest ecosystem and determine cause-effects relationships between environmental variables, the fine root response to natural ecosystem changes must be taken into account. Many natural processes, including nitrification and cation uptake, result in a natural acidification of poorly buffered soils, even in the absence of acidic deposition. A low NO_3:NH_4 ratio in the soil solution and preferential uptake of NH_4 by roots also lead to a release of protons from the roots which cause acidification at the soil-root interface (Marschner et al., 1985). Ammonium uptake may also induce an efflux of cations from roots, especially Mg (Boxman, 1988). Seasonal changes in the soil water regime (for example rewetting after a dry period) can change soil solution chemistry by decreasing pH, increasing Al and leaching base cations. The result may be lower Ca/Al molar ratio in the soil solution and therefore an increased risk of Al toxicity to fine roots (Cronan and Grigal, 1995). The soil acidification that occurs naturally in the soil is as important as that occurring from anthropogenically polluted acid

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rain. Changes in root development, mineral composition and mycorrhizal association can be sensitive indicators of forest ecosystems (Meyer et al., 1988). Nevertheless, it is necessary to differentiate to what extent such changes could result from effects of air pollutants and to what extent these are induced by the natural processes occurring in the soil environment. The objective of this study was to follow the changes of fine root morphology, biomass and nutrient status in relation to seasonal changes in soil solution chemistry and moisture regime over a two year period in a mature Scots pine (*Pinus sylvestris*) stand on an acid soil.

Table 1. Experimental stand description. Measurements were carried out in May 2000

Species	Scots pine
Age (years)	42
Tree density (tree number per ha)	544
Mean DBH(1.3 m)(cm)	21.5
Mean height (m)	16.7
Average height of dominant trees (m)	18.1
Basal area per hectare (m^2 ha^{-1})	19.7

Material and Methods

Experimental site

The experimental area was located at Headley Park (SU827359), near Alice Holt Forest Research Station, Hampshire, UK. There is a convex slope of 2 degrees and an elevation of 82 m O.D. The experimental stand was a Scots pine (*Pinus sylvestris*) plantation, planted in 1960, with bracken (*Pteridium aquilinum*) as the most abundant understory vegetation. The area of the stand is 0.7 ha, set within a forest block of about 5 ha. The stand summary information is shown in Table 1. The soil at Headley Park belongs to the Shirrell Heath soil series (Jarvis et al., 1984), subgroup: humo-ferric podzol, underlain by Cretaceous Folkestone Beds of sandy lithology. Soil characteristics are presented in Table 2. The mean annual precipitation in the area is approximately 750 mm.

Root sampling and analysis

Root corer sampling was carried out four times over two years (from May 2000). In May 2000, samples were taken very intensively from two plots (each 10 $\times$ 10 m), as 40 and 30 sampling points were chosen respectively to find the statistically acceptable minimum number of samples for subsequent years. In the other three sampling events (October 2000, May and October 2001) only 10 sampling points were chosen per plot (3 plots, each 10 $\times$ 10 m). Roots were sampled in a stratified random sampling design, with each tree as a centre point of each stratum. Each stratum was a circle with radius 2 m and there were five sampling points in it in May 2000 and two sampling points in the other three root sampling events. The sampling points in each stratum were chosen randomly in a polar co-ordinate system. It has been shown that the use of either a stratified random design or a random sampling design do not introduce a systematic error in the fine root density (Olsthoorn et al., 1991). The root corer used in the study was a cylindrical soil coring sampling tube, 6 cm in diameter and 15 cm long with a sharp serrated edge to cut fine roots. It was driven into the soil with a 2 kg hammer. Sampling was carried out to a depth of 60 cm, and four samples were taken at each sampling point at different depths (0–15, 15–30, 30–45 and 45–60 cm). The first sample (0–15 cm) was separated into two subsamples: 0–5 cm and 5–15 cm in order to account for the organic layer. Root samples were processed within 24 h of sampling.

Root samples were washed out from the soil and fine Scots pine roots were separated from the other roots and organic debris. In this study, fine roots were considered the roots with diameter smaller than 2 mm (Persson, 1983; Vogt et al., 1983; Makkonen and Helmisaari, 1998). The root samples were then separated into live and dead root subsamples on the basis of colour, brittleness, structure of the cortex or bark and colour of stale and xylem (Vogt et al., 1981, 1983; Santantonio and Hermann, 1985). The fine root length and determination of root diameter (4 diameter classes: 0–0.5, 0.5–1, 1–1.5 and 1.5–2 mm) were estimated by digital scanning and image analyses using Delta-T Scan image processing software (Kirchhof and Pendar, 1993). The roots were oven-dried at 80 °C for at least 16 h to determine the dry weight of the samples. Root biomass is the live root ($<$ 2 mm) dry weight; root necromass is the dead root ($<$ 2 mm) dry weight. The data presented on fine root dry weight have been corrected for the weight of soil particles that were attached to the roots, by determining the ash content of the samples. Root elemental concentrations (Al, Ca, Mg, K, P, Mn, Fe and S) were analysed after HNO_3 digestion using Inductively Coupled Plasma - Optical Emission Spectroscopy (ICP/OES).

Table 2. Headley Park soil profile analytical data. Ten soil samples were bulked and values are means (Carbon $n = 10$ and others $n = 5$) ± se of the mean

Horizon (depth cm)[a]	F (0-5)	H (5-8)	Ah (8-28)	Ea (28-45)	Bh (45-51)
Exchangeable cations[b]			($cmol_c\ kg^{-1}$)		
Ca^{2+}	4.86±0.11	0.44±0.01	0.22±0.00	0.53±0.01	1.38±0.08
Mg^{2+}	1.28±0.02	0.07±0.00	0.01±0.00	0.02±0.00	0.14±0.01
K^{+}	1.30±0.01	1.30±0.01	nd	nd	nd
Exchangeable acidity[c]	2.57±0.10	2.76±0.07	2.78±0.04	1.72±0.02	1.52±0.03
Al^{3+}[c]	0.42±0.02	1.76±0.07	2.18±0.03	1.33±0.03	1.20±0.04
H^{+}	2.15±0.12	0.99±0.02	0.60±0.01	0.39±0.01	0.33±0.01
CEC[d]	10.01±0.22	4.57±0.08	3.01±0.04	2.27±0.03	3.04±0.14
Base saturation[e] (%)	70.85±0.56	15.61±0.23	7.66±0.16	24.23±0.18	49.73±1.99
Al saturation[f] (%)	5.71±0.08	51.63±1.07	70.00±0.52	57.03±0.61	37.65±0.98
Carbon[g] (%)	17.94±0.28	1.62±0.04	0.98±0.02	0.60±0.02	0.83±0.01
Nitrogen[h] (%)	0.61±0.03	0.12±0.00	0.08±0.00	0.05±0.01	0.06±0.00
C/N ratio	28.4	14.0	11.7	11.9	12.7
pH (H_2O)(1:2.5)	3.4±0.01	3.5±0.02	3.7±0.01	3.9±0.00	4.3±0.01

[a]Horizon nomenclature follows Hodgson (1997)
[b]Cations and Al were measured by ICP/OES
[c]Exchangeable acidity (Al^{3+}+H^{+}) – determined by a titration to pH 6.8 in KCl extract (Rowell, 1994)
[d]CEC- Effective cation exchange capacity calculated as sum of acidity and base cations extracted with 1 M KCl
[e]Base saturation (%)=100 × exchangeable cations / CEC
[f]Al saturation (%)=100 × exchangeable Al^{3+} / CEC
[g]Organic carbon-analysed by Carbon elemental analyser
[h]Total N-analysed by Mass Spectroscopy

Soil solution sampling and analysis

Soil solution was collected by ceramic cups, 1.2 μm pore size, 4.8 cm o.d. and 7.3 cm in length (Soil Moisture Equipment Corp., USA). Prior to installation, the porous cups were washed with 5% HCl. Five porous cups were installed at 10, four at 30 and three at 60 cm depths. A vacuum of 70 kPa was applied once a week using a portable vacuum pump. Soil solution samples were collected weekly and the first three samples were discounted in order to allow the cups to equilibrate with the soil/substrate. Soil solution pH was measured by conventional pH meter. The soil solution was filtered through 0.45 μm membrane filter and analysed for: Al, Ca, Mg, K, Na, Mn, Fe, P, S and Si by ICP/OES, mineral anions: NO_3, SO_4, Cl and F by ion chromatography (Dionex DX-500), NH_4-N colorimetrically by flow injection analyser and DOC by carbon analyser (Shumatzu 500, TC analyser, Osaka, Japan). Speciation of Al was modelled by the chemical equilibrium program MINEQL+ (Version 4.0 for Windows, Environmental Research software, Edgewater, MD, USA), (Schecher and McAvoy, 1999). The inputs for the MINEQL+ calculations, the stoichiometric reactions and equilibrium constants used are described in Vanguelova (2002). Soil moisture was measured by Theta probes (Delta-T Devices Ltd., Cambridge, England) at four soil depths (10, 30, 50 and 70 cm) and temperature using thermocouples at three soil depths (10, 50 and 70 cm). The Theta probes measure changes in the apparent dielectric constant of soil, which is proportional to its moisture content. Readings are taken in voltages that given adequate calibration information can be subsequently converted into measures of volumetric soil moisture content.

Statistical analysis

Multi-factorial analysis of variance was carried out to compare the root parameters, soil solution chemistry, soil moisture and temperature at each sampling event, year and with depth. Factors were depth (roots: five levels: 0–5, 5–15, 15–30, 30–45 and 45–60; soil solution: three levels: 10, 30 and 60; soil moisture: four levels: 10, 30, 50 and 70; soil temperature: three levels: 10, 50 and 70), season (two levels: May and October) and year (two levels: 2000 and 2001). Differences among means were evaluated with the LSD-test.

Data which did not match the normality assumption were tested with non parametric analyses. When factors had more than two levels, the Kruskal-Wallis ANOVA was used, and when factors had two levels, the Kolmogorov-Smirnov two-sample test and the Mann-Whitney U-test were used.

Results

Fine roots

At the beginning of the first growing season (May 2000), the mean fine root density in the soil profile was 0.26 cm cm^{-3} and total biomass was 1070 kg ha^{-1}. These decreased to 0.02 cm cm^{-3} and 739 kg ha^{-1}, respectively, by the end of the growing season (October 2000) (Table 3). During the same periods in 2001, there was a significant increase ($P < 0.05$) in fine root biomass (1479 kg ha^{-1} in May and 1383 kg ha^{-1} in October) and fine root density ($P < 0.001$) (0.33 cm cm^{-3} in May and 0.37 cm cm^{-3} in October) (Table 3). There were significantly ($P < 0.001$) less dead roots in 2000 compared to 2001 and in both years a significantly ($P < 0.01$) smaller root necromass in May compared with October.

Root biomass ($P < 0.05$) and density ($P < 0.001$) decreased significantly with depth and approximately 30% of the root biomass was allocated in the organic layer (F) (Table 3). A different vertical distribution was found only in October 2001, when the biomass shifted from shallower to deeper mineral soil layers. Root necromass was generally significantly greater ($P < 0.05$) in the mineral soil (from 5 to 30 cm) than the organic layer (0–5 cm) and the subsoil (from 30 to 60 cm), with an exception in October 2001, where there was a significant increase in dead roots in the whole soil profile (Table 3). It was more difficult to determine the root necromass in the organic layer than the mineral soil due to high amount of organic debris. Thus, the root necromass in the organic layer may have been underestimated. The specific root length (SRL, m g^{-1}) was generally significantly ($P < 0.01$) higher in the organic than in the mineral layers. Seasonal variations of mean profile root diameter were not found except in October 2000 when root diameter increased significantly from that in May ($P < 0.05$) (Figure 1).

Root Al (g kg^{-1}) concentration increased significantly ($P < 0.001$) while Ca (g kg^{-1}) ($P < 0.001$) and Mg (g kg^{-1}) ($P < 0.01$) concentrations decreased

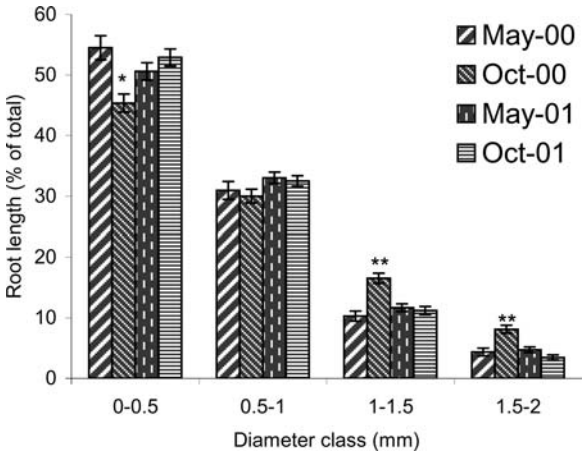

Figure 1. Root length distribution per diameter class. Values are means of all depths in the soil profile of live root length. Vertical bars indicate standard errors of the mean. Significant differences within sampling occasion at $P < 0.05$ (*) and $P < 0.01$ (**) are shown.

from May to October (Table 4). As a result, the fine root Ca/Al and Mg/Al molar ratio decreased significantly ($P < 0.001$) from May to October. In addition, in 2000 mean root Al was lower ($P < 0.01$) and Ca and Mg higher ($P < 0.001$) compared to 2001, corresponding to significantly lower ($P < 0.001$) root Ca/Al and Mg/Al molar ratios in the second year (Table 4). Root Al content increased with depth and was lowest in the organic layer, except in October 2001 when there was more Al in the roots in the organic layer. Root Ca and Mg generally decreased with depth and therefore the Ca/Al molar ratio also decreased with depth (Table 4).

Soil solution

Soil moisture and soil solution chemistry changed considerably during the two years of observations. Soil moisture content was significantly higher ($P < 0.001$) in the whole profile during the second year (Figure 2a), which was probably a result of the intensive rainfall during the previous autumn and winter (Figure 3). Soil solution pH decreased in 2001 (from June to November) compared with the previous summer (Figure 4a) and this was accompanied by a significant ($P < 0.01$) increase in soil solution Al (Figure 4b), Ca and Mg (Figure 4c and d). The soil solution Ca/Al molar ratio was generally higher at 30 cm depth compared to 10 cm depth during 2000, but this was reversed in 2001. At 30 cm depth, the

Table 3. Vertical and seasonal distribution of fine root (< 2 mm) biomass, necromass, density and specific root length (SRL). Values are means (May 2000, $n = 70$ and others $n = 30$) ± se of the mean. Multifactorial ANOVA analysis results, with LSD (p=0.05) and significant level at $P < 0.05$ (*), $P < 0.01$ (**), $P < 0.001$ (***) and not significant-ns are shown

Time of sampling	Depth (cm)	Biomass (kg ha^{-1})	Necromass (kg ha^{-1})	Density (cm cm^3)	SRL (m g^{-1})
May	0-5	375±35	41±7	0.83±0.07	12.82±1.36
2000	5-15	242±22	121±15	0.25±0.02	15.03±1.84
	15-30	186±25	84±13	0.09±0.01	7.98±0.71
	30-45	142±17	54±9	0.07±0.01	8.44±0.69
	45-60	125±20	40±8	0.07±0.01	8.11±1.15
Total	0-60	**1070**	**340**		
Average	0-60			**0.26**	**10.48**
October	0-5	292±49	111±22	0.08±0.01	11.57±1.26
2000	5-15	116±26	169±24	0.01±0.001	9.61±1.69
	15-30	140±28	134±30	0.01±0.001	8.17±1.02
	30-45	112±28	101±20	0.01±0.001	6.10±1.02
	45-60	78±22	77±31	0.01±0.001	8.67±2.12
Total	0-60	**739**	**591**		
Average	0-60			**0.02**	**8.82**
May	0-5	401±51	33±12	0.96±0.11	12.41±1.03
2001	5-15	391±45	195±34	0.32±0.03	8.64±0.79
	15-30	333±54	108±25	0.17±0.02	6.92±0.76
	30-45	189±29	96±21	0.11±0.01	8.27±1.16
	45-60	164±27	62±18	0.11±0.02	9.96±1.31
Total	0-60	**1479**	**495**		
Average	0-60			**0.33**	**9.24**
October	0-5	389±45	75±26	0.90±0.22	9.45±1.14
2001	5-15	299±36	234±46	0.34±0.10	7.59±1.40
	15-30	151±24	191±23	0.12±0.04	5.40±1.47
	30-45	264±34	226±28	0.24±0.06	9.20±1.64
	45-60	281±29	214±21	0.25±0.12	6.32±1.71
Total	0-60	**1383**	**941**		
Average	0-60			**0.37**	**7.55**
Source of variation					
Depth		101.2*	63.31*	0.17***	2.36**
Season		ns	40.21**	0.11*	ns
Year		64.6*	40.41*	0.11***	ns
Interactions					
Depth × Season		ns	ns	ns	ns
Depth × Year		ns	ns	ns	ns
Season × Year		ns	ns	*	ns

Table 4. Vertical and seasonal distribution of fine root (< 2 mm) elemental concentration. Values are means ($n = 5$) ± se of the mean. Multifactorial ANOVA analysis results with LSD ($P = 0.05$) and significant level at $P < 0.05$ (*), $P < 0.01$ (**), $P < 0.001$ (***) and not significant-ns are shown

Depth (cm)	Al (g kg^{-1})	Ca (g kg^{-1})	Mg (g kg^{-1})	Ca/Al (mol mol^{-1})	Mg/Al (mol mol^{-1})
May 2000					
0-5	0.56±0.03	6.58±0.34	0.73±0.03	7.96±0.35	1.46±0.07
5-15	1.23±0.05	5.13±0.18	0.65±0.01	2.79±0.05	0.59±0.01
15-30	2.02±0.01	3.60±0.02	0.55±0.001	1.20±0.01	0.30±0.001
30-45	2.92±0.05	3.08±0.03	0.44±0.01	0.71±0.01	0.17±0.001
45-60	3.61±0.05	3.12±0.04	0.41±0.01	0.58±0.001	0.13±0.001
Total	**10.34**	**21.50**	**2.78**		
Average				**2.65**	**0.53**
October 2000					
0-5	0.69±0.01	3.80±0.01	0.50±0.001	3.70±0.05	0.80±0.01
5-15	1.90±0.05	2.67±0.06	0.55±0.01	0.94±0.01	0.32±0.001
15-30	2.91±0.03	2.08±0.02	0.40±0.01	0.48±0.0001	0.15±0.001
30-45	3.94±0.03	2.00±0.01	0.32±0.001	0.34±0.0003	0.09±0.001
45-60	4.77±0.42	5.54±0.96	0.48±0.03	0.78±0.07	0.11±0.003
Total	**14.21**	**16.09**	**2.25**		
Average				**1.25**	**0.30**
May 2001					
0-5	0.83±0.17	3.48±0.16	0.36±0.01	2.88±0.41	0.49±0.08
5-15	1.89±0.66	2.53±0.21	0.32±0.02	0.96±0.29	0.20±0.05
15-30	2.56±0.65	2.22±0.22	0.28±0.03	0.61±0.15	0.13±0.03
30-45	3.34±0.96	2.23±0.19	0.24±0.01	0.48±0.14	0.08±0.02
45-60	4.67±0.20	2.57±0.81	0.33±0.13	0.37±0.13	0.08±0.03
Total	**13.29**	**13.03**	**1.52**		
Average				**1.06**	**0.20**
October 2001					
0-5	3.42±0.10	3.41±0.12	0.40±0.02	0.67±0.0001	0.13±0.001
5-15	1.77±0.02	1.82±0.03	0.24±0.001	0.69±0.001	0.15±0.001
15-30	4.29±0.02	1.51±0.06	0.25±0.01	0.24±0.01	0.07±0.0001
30-45	4.41±0.09	1.61±0.03	0.22±0.01	0.25±0.01	0.06±0.002
45-60	4.90±0.01	2.05±0.01	0.25±0.0001	0.28.±0.0003	0.06±0.0001
Total	**18.79**	**10.40**	**1.36**		
Average				**0.43**	**0.09**
Source of variation					
Depth	3.84***	3.19***	0.39***	0.16***	0.34***
Season	ns	2.03***	0.25**	0.10***	0.02***
Year	ns	2.04***	0.25***	0.11***	0.02***
Interactions					
Depth × Season	* * *	* * *	ns	* * *	* * *
Depth × Year	* * *	* * *	* * *	* * *	* * *
Season × Year	**	**	**	* * *	* * *

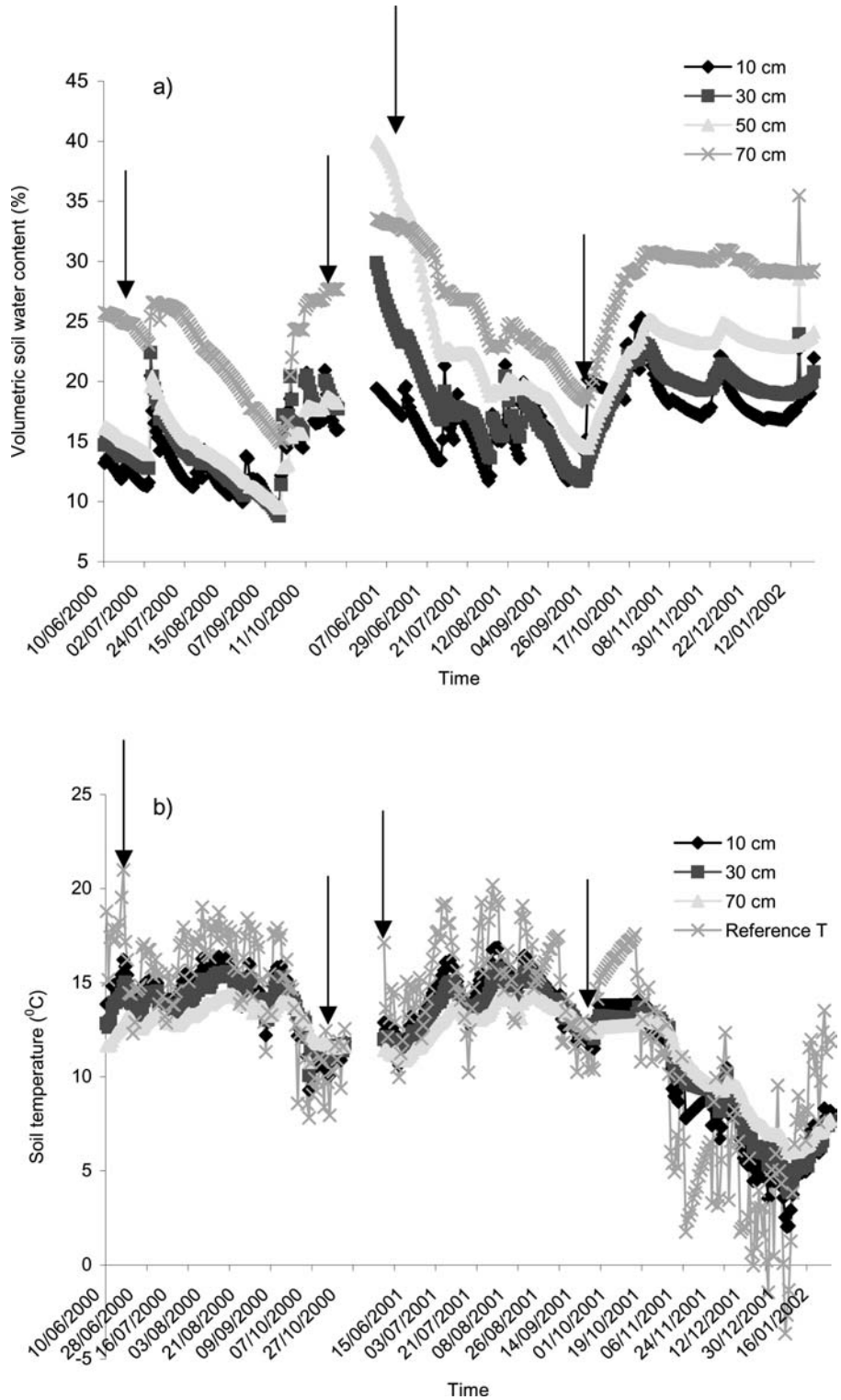

Figure 2. Average daily seasonal and vertical variations in (a) soil moisture and (b) soil temperature. Readings were taken every hour. The arrows indicate the period of root sampling. The reference temperature readings (b) were recorded in the Data-logger's box, used for data collection and storage. Measurements were not carried out between November 2000 and May 2001.

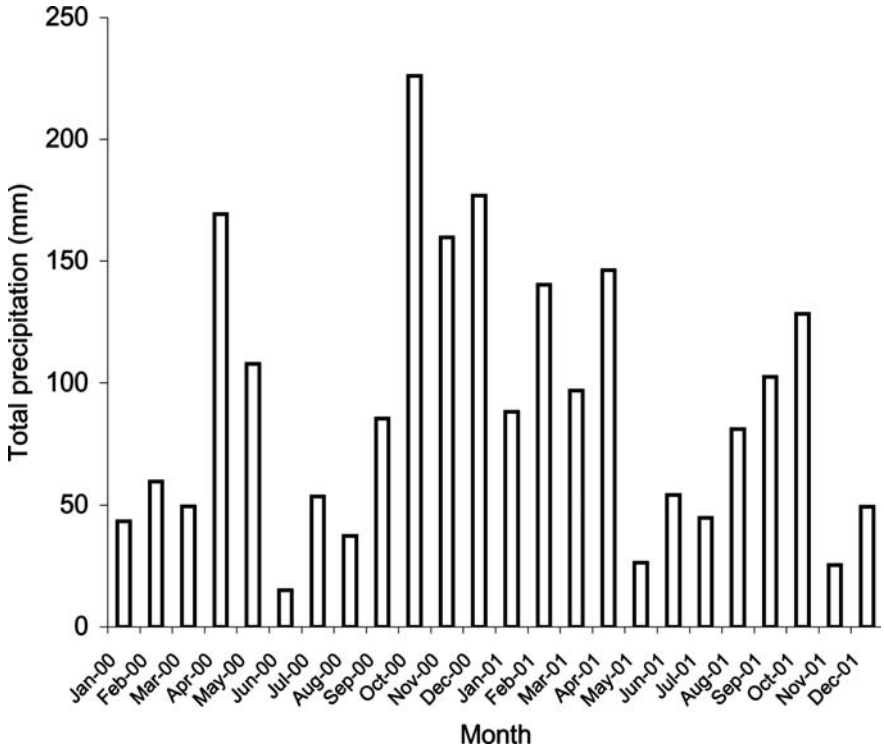

Figure 3. Total monthly precipitation during 2000 and 2001. Data were obtained from the Alice Holt, Forest Research Meteorological Station, about 4 km from the experimental site in Headley Park.

ratio was in the range of 1.75 to 2.27 during the summer 2000 in comparison to summer 2001 where Ca/Al ratio decreased and it was in the range of 0.63 to 1.25 (Figure 4e). Soil solution NO_3-N, NH_4-N and DOC also increased significantly ($P < 0.001$) during 2001 (Figure 4f, g and h) possibly as a result of increased nitrification and decomposition due to the higher soil moisture content. The changes in Al were most likely to be caused by changes in soil solution pH. However, the seasonal variation of Al was also related to NO_3 ($n = 150$, $r^2 = 0.79$, $P < 0.001$), but not to SO_4, suggesting the importance of the nitrification in the mobilisation of Al. This was also reported by others (van Breemen and Jordens, 1983; Mulder, 1988). Soil solution Al^{3+} also increased in 2001 compared with 2000. In 2000, the mean percentages Al^{3+} of the total Al were 35% at 10 cm depth, 36% at 30 cm and 13% at 60 cm depth while in 2001 these increased to 58%, 75% and 37% respectively with depth (Figure 5). The changes in soil solution chemistry have been related entirely to naturally occurring processes since the precipitation chemistry in the area did not differ between the two years of observation (Figure 6).

Discussion

Fine root changes in relation to seasonal fluctuation of soil moisture and temperature

At Headley, very dry soil conditions started at the end of July and continued until the end of September 2000, when the mean soil water content was as low as 9% at 10 cm, 8.8% at 30 cm and 9% at 50 cm depth for a 2 week period (Figure 2a). In our soil (Humo-ferric podzol, with sand content of 80–90%), a soil water content of about 7–8% is associated with the 'permanent wilting point' (Jarvis et al., 1984), but root growth may be inhibited before this point is reached. For example, the root elongation rate and number of new grown root tips of Scots pine were severely inhibited, and growth ceased after a 15 day-long dry period with soil moisture in the range of 8% to 12% (Bartsch, 1987). A highly significant negative relationship between the soil water potential and root elongation intensity was also observed in a mature oak stand (Joslin et al., 2001). Many other investigations have noted that fine tree roots die almost immediately in local dry areas.

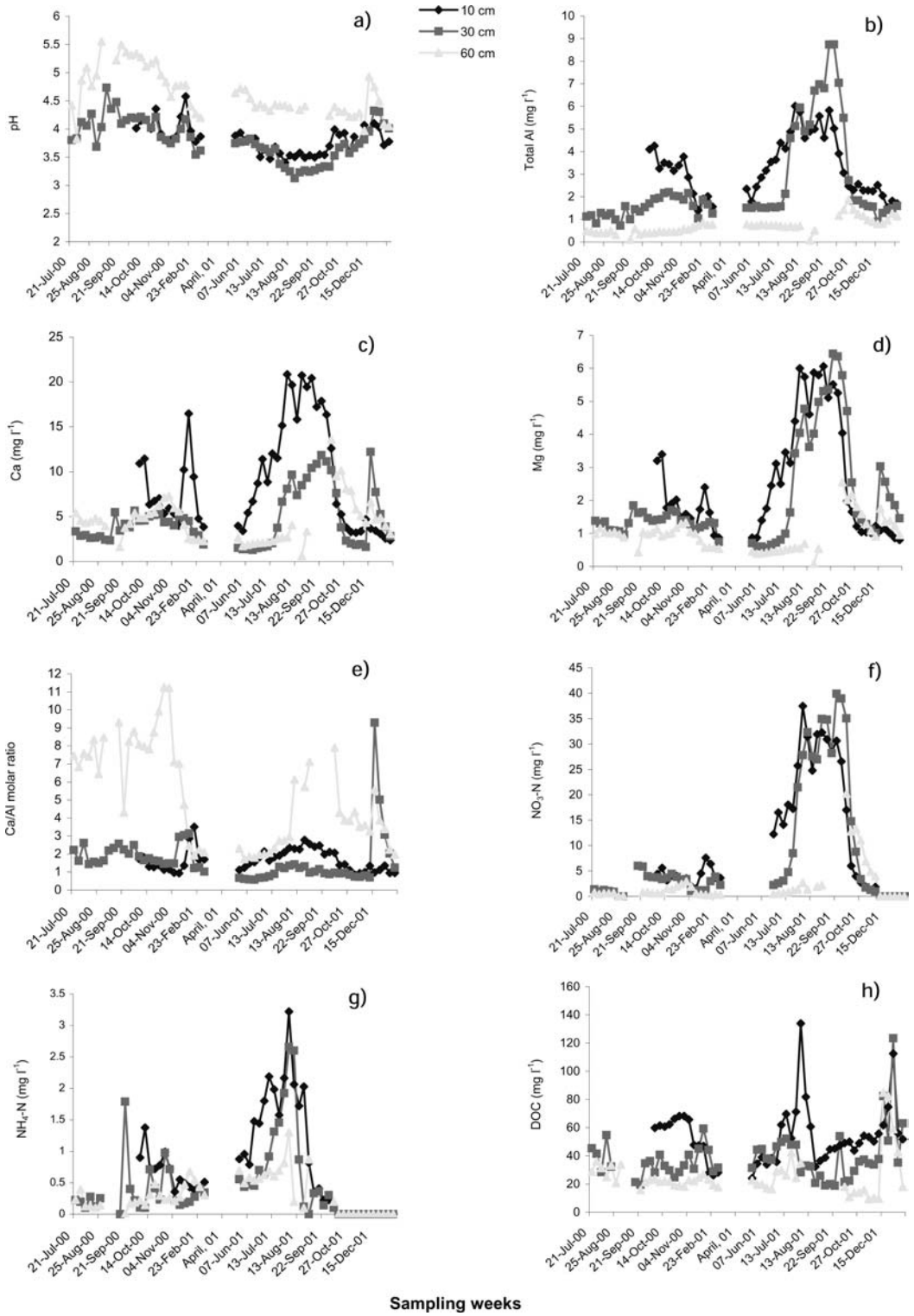

Figure 4. Average weekly seasonal and vertical variations in soil solution (a) pH, (b) Al, (c) Ca, (d) Mg, (e) Ca/Al molar ratio, (f) N-NO_3, (g) N-NH_4 and (h) DOC. Values are means of 5 at 10 cm, 4 at 30 cm and 3 at 60 cm depth. Data are missing where soil solution could not be collected.

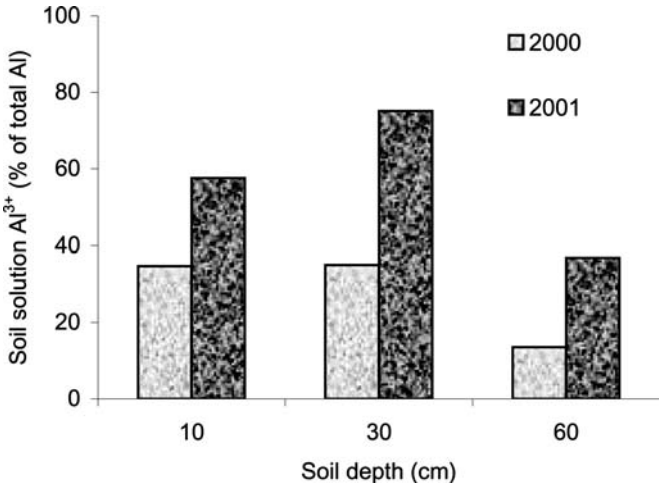

Figure 5. Mean modelled soil solution Al^{3+} (as % of the total Al in soil solution) at different depths in 2000 and 2001. Data are averaged from June until October in both years. Al^{3+} = Total Al − (Organically bound Al + Al-SO_4 complexes + Al-F complexes).

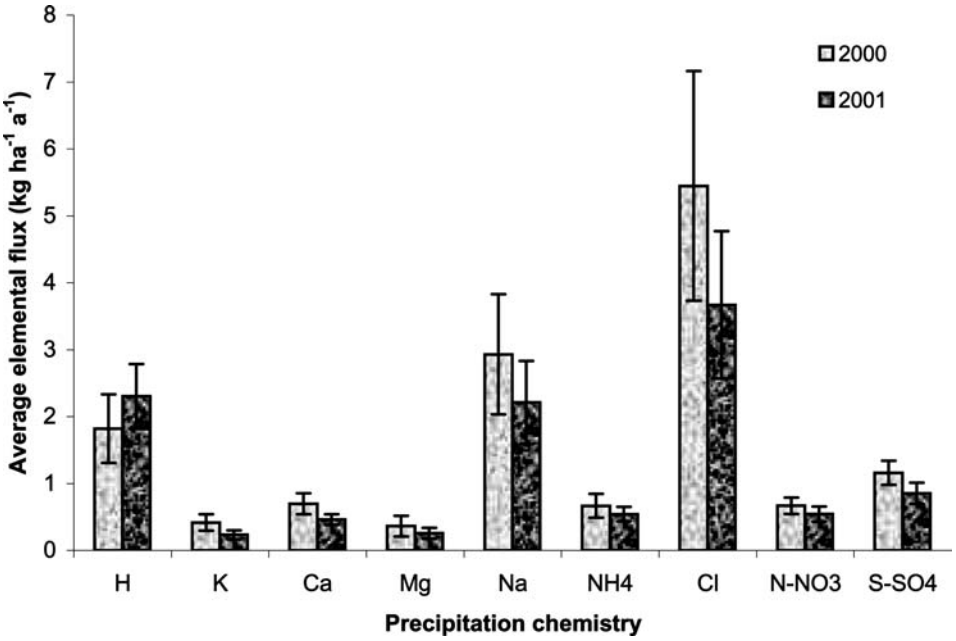

Figure 6. Average yearly precipitation chemistry in the area. The units for H are $H \times 10^{-5}$. The vertical bars indicate the standard error of the mean ($n = 12$). Data were obtained using open collectors located in grassland, about 6 km from the experimental site in Headley Park. Samples were analysed by methods described for soil solution.

For example, fine tree root mortality under drought conditions has been demonstrated in field experiments where throughfall was prevented from entering the soil (Holstener-Jorgensen and Holmsgaard, 1994). Similarly, after a summer period of large soil water deficits, *Fagus* fine root necromass in the organic soil layer nearly doubled in a study of *Fagus-Quercus* mixed forest (Hertel and Leuschner, 2002). Drawing from these studies, it seems likely that the dry period during summer 2000 caused the ten fold decrease in root density and the increase in root mortality. When drought causes fine root mortality, the fine root density can decrease rapidly over days or weeks (Olsthoorn, 1991). During a dry period, the fraction of the thicker fine roots have a greater chance of survival, which explains the larger mean diameter (Figure 1) and smaller

value of the SRL observed in October compared to May 2000 (Table 3).

The decrease in fine root biomass and the increase in root necromass was significantly greater in the organic and top mineral layer (up to 30 cm) than the deeper soil (Table 3). This was not surprising since the drought reaches first the organic and upper mineral layers of the soil, where the abundancy of fine roots was found. Similarly, the relation to water availability seemed to be the most likely cause of the sudden fine-root decline of Scots pine fine roots in the humus layer in a study by Makkonen and Helmisaari (1998). At Headley, however, although fine roots in upper soil were mostly affected, the root vertical distribution was not altered. Shallow roots are usually responsible for the majority of annual fine root production and mortality, but that deep roots are important during periods of water stress (Hendrick and Pregitzer, 1996). The trees at Headley did not compensate for the reduced soil water by allocating more fine roots deep into the soil profile, and thus tree water uptake might have been inhibited.

In the second year (2001), fine root biomass and density were significantly higher in both sampling events compared to 2000. The mean soil moisture content was positively related to the total root biomass in the soil profile (Figure 7a) and the mean profile density (Figure 7b). In October 2000, the significantly higher root necromass compared to May 2000 could have been caused by the prolonged drought during this summer. However, the same causal interpretation for the significant increase in root necromass in 2001 compared to 2000 (Table 3) is difficult since the soil moisture did not appear to limit root functioning during 2001. Another important determinant of the longevity of fine roots is soil temperature. The maximum difference in the soil temperature between the four root sampling events at Headley was about 3 °C (Figure 2b), and there was no significant correlation between biomass or root density with soil temperature. Therefore, the significant increase in root mortality in 2001 (highest in October) could have been caused by other factors, such as soil solution chemistry.

Fine root changes in relation to seasonal fluctuation in soil solution chemistry

In this investigation, root biomass was higher (Table 3) where soil solution Ca/Al ratio was lower (Figure 4e).

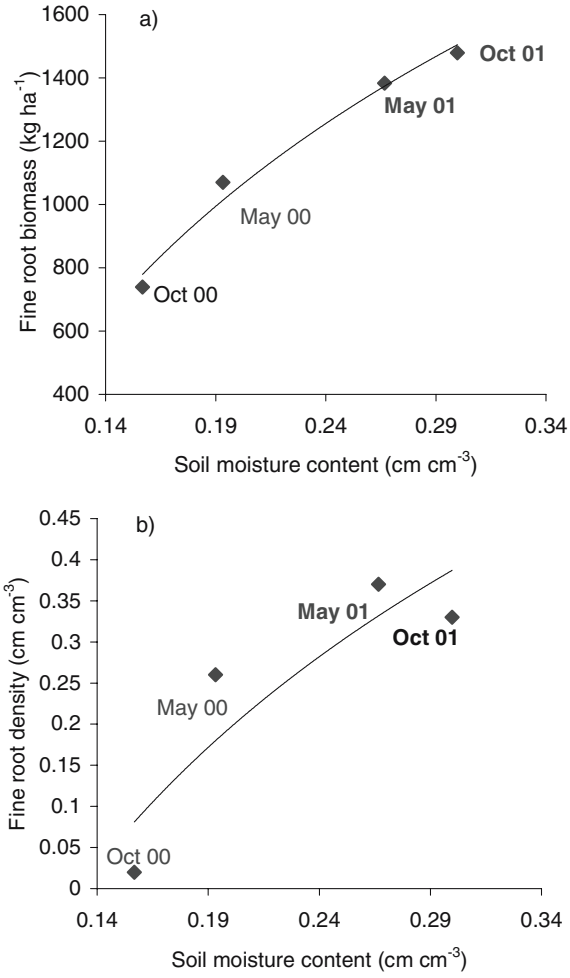

Figure 7. Relationships between soil moisture content and (a) root biomass (< 2 mm) and (b) root density (< 2 mm). The values represent mean soil moisture content, total root biomass and mean root density in the soil profile during the four sampling events. Relationship trends are presented with solid lines.

However, the positive relationship found between soil moisture and fine root biomass and density (Figure 7) showed that there was an effect of soil moisture on root production and therefore in spite of the less favourable soil conditions in the second year, there was more root biomass. In addition, the higher soil water content in 2001 was accompanied with higher soil solution NO_3-N and NH_4-N. This may give an additional explanation for the higher root biomass during 2001 compared to 2000. Dahlgren et al. (1991) compared seasonal patterns of fine root growth and mortality

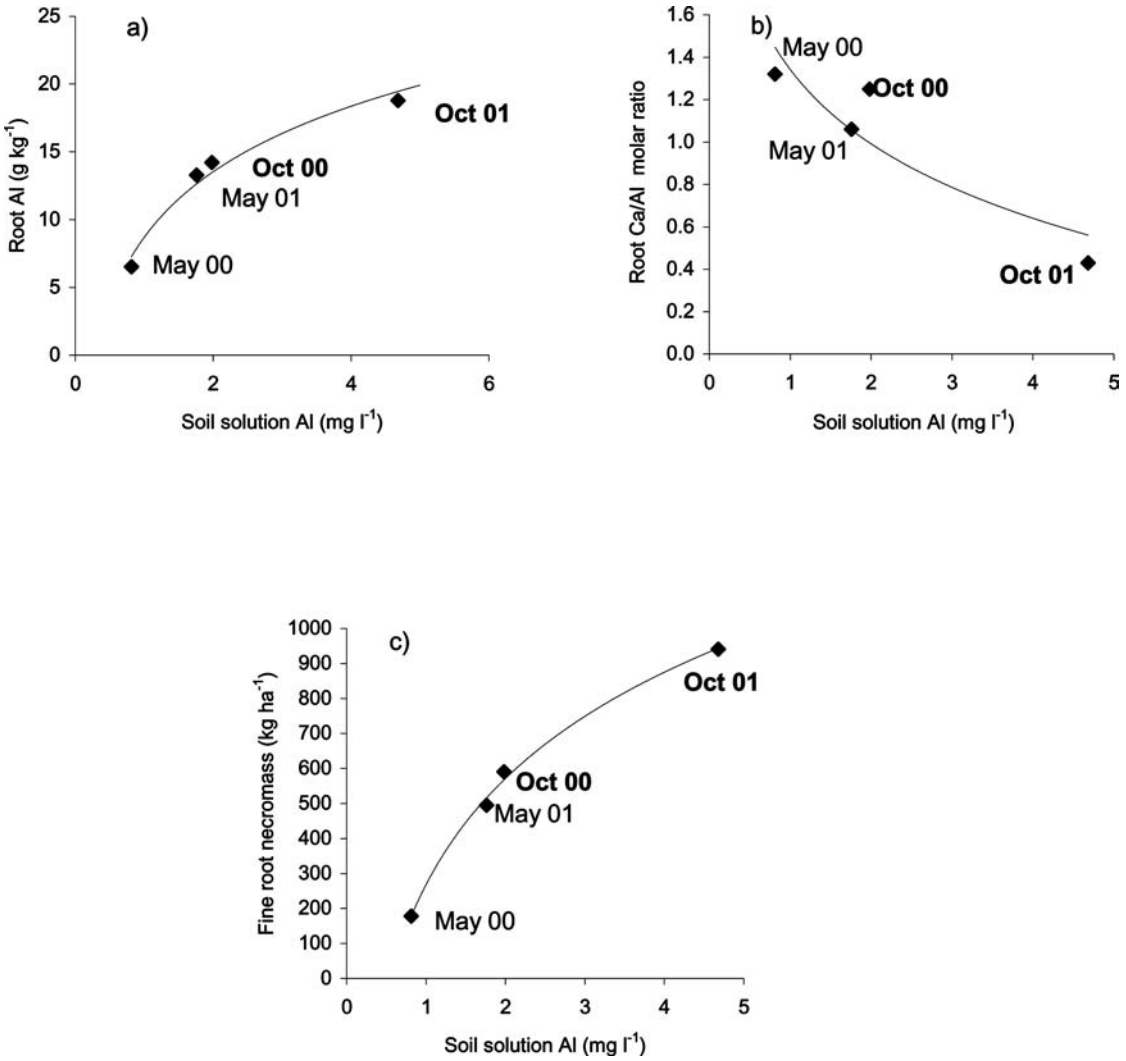

Figure 8. Relationships between soil solution Al and (a) root Al, (b) root Ca/Al molar ratio and (c) fine root necromass. The values represent mean soil solution Al and root Ca/Al molar ratio and total root Al and necromass (< 2 mm) in the mineral soil profile during the four sampling events. Relationship trends are presented with solid lines.

in mature *Abies amabilis* stands in the northwestern USA with the seasonal fluctuation of Ca/Al ratios in soil solution. In contrast to our study, they showed that root growth was highest when Ca/Al ratios were highest and root mortality highest when Ca/Al ratio was lowest. However, causal interpretation is difficult as other factors like temperature, soil moisture or shoot-root interactions may have also been responsible for the seasonal pattern of fine root demography observed (Dahlgren et al., 1991).

There were significantly more dead roots in October 2001 where soil solution total Al as well as Al^{3+} were higher (during the whole summer prior to root sampling), Ca/Al ratio lower, root Al higher and root Ca/Al ratio lower (around and < 1) compared to 2000 (Tables 3 and 4). Changes in root biomass and density between seasons and years should result in changes in root necromass. However, it is difficult to interpret the cause of these differences, since dead roots represent a changing pool, depending not only on root growth and mortality but also on the decomposition rate (Schneider et al., 1989). As the soil moisture was significantly higher during the growing season in 2001 compared to 2000, soil solution DOC increased, which suggests that the decomposition rate and possibly root exudation also increased in this period. On the other

hand, an increase of soil solution Al was related to an increase in Al in the roots (Figure 8a), decrease in root Ca/Al and Mg/Al molar ratio (Figure 8b) and higher fine root necromass (Figure 8c). In addition, in 2001 compared with 2000, much higher percentage of the total Al in the soil solution was present in its most toxic form (Al^{3+}) (Figure 5) (Kinraide, 1991). Thus it seems likely that Al could have caused the increase in root mortality in October 2001, since the soil moisture was not a limiting factor, the decomposition and soil solution mineral nitrogen were high during this period and Al antagonism on root Ca and Mg was apparent. At Headley, during May in both years, the percentages of dead roots of the total root system were 24% in 2000 and 25% in 2001 while during October these values were 44% and 41% for 2000 and 2001, respectively. The greater necromass in October may restrict nutrient uptake for the trees during this period with consequent effects on health and growth.

We found good evidence that an accumulation of Al in the roots blocks the root exchange sites and prevent Ca and Mg uptake (Figure 9a). Despite the higher concentrations of Ca and Mg in the soil solution available for uptake during summer 2001 (Figures 4c and d), root Ca and Mg concentrations decreased significantly compared to 2000 (Table 4). The high Al and low Ca and Mg accumulation in the roots resulted in low root Ca/Al and Mg/Al molar ratios. These ratios were negatively related to the total root necromass in the soil mineral profile in the different sampling events (Figure 9b). Only in October 2001 was there more Al accumulated in the roots in the organic layer than the mineral soil (Table 4). Nevertheless, the fine root biomass in the organic layer did not decrease, suggesting that Al may not be toxic to roots in this layer due to complexation with organic matter. The adverse soil condition (low pH and high soil solution Al concentration) in the mineral soil, between 5 and 30 cm, might have caused the change in the vertical root distribution observed in October 2001.

While Al accumulation may contribute to high root mortality, other factors are likely to have also influenced fine root growth and function, for example, root-shoot relationships, different tree phenological phases, fine root turnover, and tree carbon allocation and uptake. The pattern of higher fine root density and biomass in May compared to October during the first year coincides with the typical seasonal pattern for root growth in some temperate forests (Hendrick and Pregitzer, 1992). However, during the second year of investigation, this pattern was

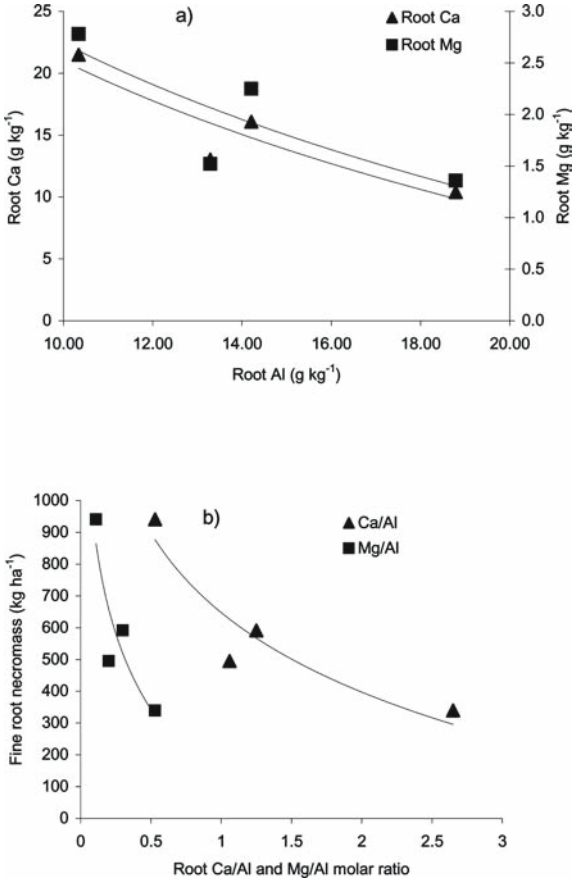

Figure 9. Relationship between (a) root Al and Ca and Mg and (b) root Ca/Al and Mg/Al molar ratios and fine root necromass (<2 mm). The values represent total root Al, Ca and Mg concentrations and fine root necromass and mean root Ca/Al and Mg/Al molar ratios in the soil profile during the four sampling events. Relationship trends are presented with solid lines.

not observed. Scots pine has also not shown any periodity of root growth in other investigations (Persson, 1980; Makkonen and Helmisaari, 1998), suggesting that the changes in soil moisture and soil solution chemistry observed in Headley were likely to have played a major role in the dynamics of fine roots of Scots pine.

Conclusions

Soil moisture was identified as an important factor in fine root growth and production, and accounted for some of the changes in the soil solution observed in this study. Scots pine fine roots grew rather well in different fertility conditions when the soil moisture was not a limiting factor and nitrogen supply was high.

However, seasonal acidification in the soil (soil solution pH < 4.2 and Al concentration > 3–10 mg l^{-1}) negatively affected the fine roots and cation uptake of Scots pine by increasing root mortality and root Al accumulation at the expense of Ca and Mg. This is likely to have reduced the capacity of the tree to take up water and nutrients and increased the risk tree functioning being compromised. If soil acidification is accompanied by dry soil conditions, the effects may be even more pronounced.

Overall, this study showed that the seasonal fluctuations of soil factors such as moisture and chemistry strongly influence the dynamics of fine roots of Scots pine. When cause-effects relationships are investigated, the seasonal fluctuations should be taken into account.

Acknowledgements

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