

Fine roots of pedunculate oak (*Quercus robur* L.) in the Netherlands seven years after liming

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Abstract

Liming of poor and acidic forest stands has often proved to improve soil chemical status, to alleviate nutritional imbalances and as a result, to improve health and growth of the forest stand. In this study, an equivalent dose of $1.6 \text{ t ha}^{-1} \text{ CaO}$ was applied to a young and an old *Quercus robur* L. stand on acidic sandy soils in the southeast of the Netherlands. Seven years after the lime application the effects on soil and roots were intensively studied. Prior to liming, the youngest stand suffered from a deficiency in five nutrients, whereas in the older stand only two elements were inadequate. Results indicate a consistent improvement in cation availability and soil pH seven years after lime application. Regarding the roots, the two stands show a different reaction in response to liming. In the young stand, liming increased specific root length and number of apices with mycorrhizae per cm of fine root length in most of the profile, whereas in the old stand, liming stimulated fine root biomass and length, but only in the top soil. The leaf nutrient status was most improved in the youngest and poorest stand, where lime had greatest impact on the soil exploration system (roots, mycorrhizae).

Keywords: CaCO_3 , fine root biomass, fine root length, liming, pedunculate oak, *Quercus robur* L., roots, specific root length.

Introduction

Fine roots are a useful tool for the evaluation of site conditions (Clemensson-Lindell & Persson, 1993). Adverse site conditions can limit fine root growth (Rost-Siebert, 1983; Raspe, 1992), or may result in a higher allocation of total net primary production to fine roots in order to be able to fulfil the needs of the stand in terms of nutrients and water (Olsthoorn & Tiktak, 1991). Soil acidification may lead to changes in root branching, root elongation and specific root length (SRL), the ratio of length per unit root mass in m g^{-1} (Rost-Siebert, 1983; Persson & Ahlström, 1990/1991; Clemensson-Lindell & Persson, 1993) and to avoidance strategies of growing roots. After longer exposure time to severe soil acidification and serious subsoil acidification this can result in shallow root systems and low root biomass (Persson & Ahlström, 1990/1991; Marschner, 1991).

Lime and fertilizer trials were begun in the 1960's and 1970's to improve tree growth on poor sites and interest was renewed in the 1980's, when soil acidification appeared to be an imminent threat to forest vitality. Generally liming has a positive effect on soil chemical properties characterized by increases in topsoil pH, exchangeable Ca and base saturation (Derome, 1990/1991; Belkacem, 1993). Despite the improvement of soil conditions, the effects on fine root development appear to be rather site specific. Effects of liming varied depending on initial stand fertility (principally availability of Ca, Mg, K, P and N) and were time-dependent (Persson & Ahlström, 1990/1991; Hagen, 1992; Raspe, 1992). For the site studied here, Van Den Burg (1994) did not find very clear treatment responses of soil chemical status and tree growth, but observed some improvement of the leaf nutritional status, three years after liming. A study of the fine roots of Scots pine (Hagen 1992) in the Peel region on a poor sandy soil, showed that moderate liming increased fine root biomass and fine root length density without affecting the root distribution over depth. This beneficial effect of liming was probably related to the initially poor Ca levels in the soil (Hagen, 1992).

This paper describes the effects of liming on soil chemical composition and fine root development in two stands with pedunculate oak in St. Anthonis forest, situated in the Peel region in the southeast of the Netherlands. The goals are to determine the lime-induced modifications of fine root development and to answer the questions (1) how these developed with time and (2) what the influence of stand (age) is. The present two stands had been limed seven years before sampling and have a different age (a young and an old stand).

Site description

Two lime trials were established in 1988 in a young (parcel 46a) and an old stand (35c) of pedunculate oak (*Quercus robur* L.) in the state forest of St. Anthonis in the Peel region in the southeast of the Netherlands. The stands were planted in 1980 and 1953, respectively. The mean heights of the trees prior to liming were 3.4 and 14.7 m. Both stands were on poor acidic (pH-KCl 3.3 and 3.6, respectively, for the top 25 cm) sandy soils suffering from high N deposition ($67 \text{ kg ha}^{-1} \text{ yr}^{-1}$), which was among the highest for the Netherlands. Organic matter ranged from 4.5 to 2.8%, respectively. Prior to liming, the young stand suffered from deficiencies in N, P, Mg, Zn and Fe and the old stand had low levels of Mg and Zn (Van Den Burg, 1994).

Materials and methods

In 1988 several doses of dolokal (containing 3% Mg) were used as lime application and were applied to the surface manually (Van Den Burg, 1994). For the present fine root study the 0 (control) and $1.6 \text{ t equivalent CaO ha}^{-1}$ (liming) doses were selected and were sampled in early October 1995. The young and old stand have three and two replicate blocks, respectively. The samples for soil chemical composition were

collected in the middle: only one sample per replicate block (in total two for the old and three for the young stand) with the objective to link the root observations with the soil chemical status. Per treatment and layer 16 samples were taken for fine roots, distributed as follows: 8 per replicate bloc for the old stand (2 blocs; plot size either 30×30 m or 25×36 m) and 6, 5, 5 per bloc for the young stand (3 blocs, plot size 20×20 m). Sampling was carried out throughout the whole of each single plot, not completely at random, but avoiding the immediate vicinity of the trees (not at < 2 m in the old stand and < 1 m in the young stand) and other localities considered inappropriate (for instance where soil vegetation like heather was abundant or the soil profile clearly disturbed). Both fine root and soil samples were collected using a soil corer (\varnothing 8.0 cm, length 15 cm). The number of 16 samples per treatment and layer was based on pilot study calculations (Bakker, 1998) and was considered sufficient for the 0–5, 5–15, 15–30, 30–45, and 45–60 cm layers. This number is of the same order as those used by Vogt *et al.* (1986), Olsthoorn (1991) and Burke & Raynal (1994). For the 60–75 cm layer only two samples were taken for descriptive purposes (no effects of liming expected; low fine root density). The samples were wrapped in plastic bags and transported to the laboratory.

Soil samples were air-dried and then sieved at 2 mm. 0.5 M NH_4Cl -exchangeable Al, Ca, Mg, K, Mn and Na were determined by ICP (emission spectrometry), exchangeable acidity by automatic titration, and pH-KCl and pH- H_2O on a 1:2.5 dilution basis with pH-electrodes. Concentrations were expressed on oven-dried (105°C) weight basis. Cation Exchange Capacity (CEC) was defined as the sum of exchangeable Mn, Mg, Ca, Na, K, plus titratable Al^{3+} and H^+ . Base saturation was defined as the proportion of $^{\circ}\text{C}$ exchangeable Mn, Mg, Ca, Na and K in relation to total CEC.

On the 16 field samples for the fine root studies the following parameters were assessed: weight and length of live roots (sample $n = 16$), mycorrhizae ($n = 4$) weight and length of dead roots, nutrient element concentrations of live fine roots and fraction very fine roots (one per replicate block, thus $n = 2$ or 3, respectively, for the old and the young stand). The determination of dead root matter and nutrient element concentrations was always done on samples processed between the first day on return from the field and the third day at the latest. The remainder of the samples were stored at -1°C for a maximum of 2–3 months until being processed. All 16 root samples were wet sieved with tap water over a 4 and 2 mm sieve and root length was estimated by the line intersect method (Tennant, 1975). Root dry weight was assessed after drying at 105°C to constant weight.

Dead roots were separated from living roots using general visible criteria: resilience, brittleness, colour of bark and xylem (Vogt & Persson, 1991). This distinction was fairly clear, as confirmed by observations under a binocular microscope, which were used to calibrate the method (Bakker, 1998). From the live fraction of the same individual sample, sub-samples were selected at random and were used for total chemical analysis. These sub-samples were further treated separately and cleaned more intensively with tapwater and small brushes. Pollution by adhering soil particles was considered of negligible importance, as both observations under magnification and one of the tests used for the corrections factors (Bakker, 1998) based on stepwise ignition up to 650°C (Vogt & Persson, 1991) did not indicate that this

would be very important. The chemical analysis consisted of digestion by hydrogen-peroxyde (H_2O_2), then $HClO_4$ and analysis by ICP. The very fine fraction of roots (<0.5 mm) was counted on only a small number of samples as it was very time consuming.

Van Noordwijk & Floris (1979) and Vogt & Persson (1991) stressed the importance of correcting for the losses occurring during processing the root samples as well as potential inclusion of soil particles into the weight calculations. Therefore, a series of tests has been established to account for the most important potential error sources. This was primarily done on basis of material from the Ardennes sites (Bakker, 1998), but it appeared from verifications on several other sites, that the correction needed, depended rather of the processing method than on the site, so that these corrections were applied also for this study. The final corrections used were + 20% for weight of live fine roots (< 2 mm in diameter), + 10% for weight of dead fine roots and + 25% for length of both dead and live fine roots. The measured values of weight and length were corrected and then converted into fine root biomass ($kg\ ha^{-1}$), fine root length ($10^6\ m\ ha^{-1}$), fine root density ($cm\ cm^{-3}$), and specific root length (SRL, in $m\ g^{-1}$).

Counts of apices with mycorrhizae were established on four individual samples (distributed regularly over the replications: 2, 2 for in the old stand and 2, 1, 1 in the young stand). These counts were carried out under a binocular microscope ($4\times$ magnification) after a method developed by Voiry (1981), and a distinction was made between the main ectomycorrhizal morphotypes (Bakker & Garbaye, *in prep.*). This distinction covers two 'hairy' types (A1 and A2) having abundant mycelium, three 'smooth' types (C1, C2-Cenococcum, C2other) having no mycelium or only limited outgrowths and one intermediate type (B) having rhizomorphs (rounded strings of hyphae together in root-like structures). Such a distinction in morphotypes is relevant, as the influence and importance for uptake by mycorrhizae may vary according to their structure (Voiry 1981, Marschner 1991).

Means are tabulated using the real sampling depth (0–5, 5–15 cm etc.) and in the figures the values corresponding to these real sampling layers are represented in the middle of each single soil layer (at 2.5, 10 cm etc.). Before statistical tests were carried out, values of weight and length were standardized to 10 cm layers in order to enable the comparison of the effect of soil depth on fine roots. For fine root length, specific root length, total number of mycorrhizae and number of mycorrhizal tips per cm of root length, as well as absolute numbers of mycorrhizal morphotypes, no transformation of the values was applied prior to statistics, as these had shown to have a fairly normal distribution. The fine root parameters biomass, length and specific root length were tested for treatment, and soil depth effects by ANOVA, and the Student-Newman-Keuls test (with the statistical package Unistat 4.0) was used to determine the significantly different soil layers. The effect of liming on the relative proportion of ectomycorrhizal morphotypes was tested after arcsinus transformation of the proportion of each morphotype (Dagnélie 1970) and the effect on absolute number ectomycorrhizal morphotypes was tested as for fine roots: by using ANOVA followed by the Student-Newman-Keuls test to separate individual different soil layers. For the other parameters (concentrations in soil and fine roots, dead root matter,

very fine root fraction) similar statistical analyses seemed on forehand not appropriate due to a low sample number per layer. It was considered important, however, in order to improve the interpretation of the lime effects on fine root and mycorrhizal development, to discuss the effect of lime on these parameters also. Therefore, for these parameters the overall effect of liming was tested by ANOVA for all soil layers together, and only for soil and fine root concentrations ANOVA was carried out for individual soil layers (with low sample n) to reinforce the general interpretation.

Results

Soil

The soil chemical characteristics in October 1995, 7 years after liming, are presented in Table 1. This table shows that the effect of liming, which was limited to the organic Oh horizon in 1991 (Van Den Burg, 1994), extended to greater depths in October 1995. Although sample number was low, nevertheless, overall significant increases of Mg and Ca concentrations, base saturation, pH-H₂O and pH-KCl occurred in both stands, while H⁺ concentrations significantly decreased. These changes were in the whole profile, but reached significant levels only in the top 15 cm (young stand) or 30 cm (old stand), with the exception of some pH effects occurring in the young stand at 30–60 cm. Effects on CEC, Mn, Na and K were minor and limited to some increases in the old stand in the surface layers. To illustrate the effect on CEC: the overall values in the old stand increased from 2.15 in the control to 2.81 cmol_c kg⁻¹ after liming (top 0–5 cm layer 2.88 to 5.23 cmol_c kg⁻¹, respectively). Likewise, base saturation increased from 18 to 41% on overall basis (38 to 77% in top 0–5 cm layer). In the young stand this was less pronounced: CEC increased on overall basis from 3.01 to 3.29 cmol_c kg⁻¹ (4.84 to 6.47 in top 0–5 cm layer) and base saturation from 10 to 22% on overall basis (26 to 72% in the top 0–5 cm layer).

Fine roots

The fine root results are presented in Figure 1. With regards to the effects of liming on fine root matter and distribution, in the young stand total fine root biomass (0–75 cm) ranged from 5360 to 5046 kg ha⁻¹ for control and liming, respectively, whereas these figures were 6543 and 6897 kg ha⁻¹ in the old stand. Multiple comparisons (Student-Newman-Keuls interval) revealed no significant effect in the young stand, and a significant gain in fine root biomass in the top 0–5 cm (Figure 1) in the old stand. Total fine root length (0–75 cm) was between 67.2 and 78.7 · 10⁶ m ha⁻¹ for the control and the lime treatment in the young stand and between 104.9 and 112.2 · 10⁶ m ha⁻¹ in the old stand. No significant differences were detected in the young stand, but in the old stand liming significantly enhanced fine root length for the 0–5 cm, whereas values were significantly lower in the 45–60 cm layer after liming. Specific root length increased significantly in the top 30 cm (Figure 1) in the young stand, but no significant effects occurred in the old stand. The fractionation of the fine roots

Table 1 Soil composition: Exchangeable cations with 0.5 M NH₄Cl (cmol_c kg⁻¹) in a young and an old oak stand (*Quercus robur* L.) in October 1995, 7 years after application of a 1.6 t ha⁻¹ equivalent CaO dosis (small a and b indicate significant differences between the control and lime treatment at P<0.05 for a given layer and L and C indicate significant differences on overall basis (total profile: 0-60 cm) with L=lime, C=control and ns = not significant)

Treatment	Depth cm	pH H ₂ O	pH KCl	Mn cmol _c kg ⁻¹	Mg	Ca	Na	K	H ⁺	Al ³⁺	Ca/Al ³⁺ molar
<i>Young stand</i>											
Control	0-5	3.74	2.59	0.01	0.19a	0.98a	0.06	0.11	2.25	1.25	0.78a
Lime	0-5	4.13	3.18	0.02	0.58b	3.58b	0.08	0.13	1.02	1.06	3.4b
Control	5-15	4.01	2.66	0	0.02	0.15a	0.01	0.04	0.83	1.35	0.11
Lime	5-15	4.03	3.14	0	0.06	0.34b	0.02	0.06	0.86	1.85	0.18
Control	15-30	3.93	3.08	0	0.01	0.15	0.01	0.04	1.04	2.46	0.06
Lime	15-30	4.04	3.34	0	0.04	0.21	0.01	0.04	0.71	2.04	0.10
Control	30-45	4.05	3.50a	0	0.01	0.07	0.01	0.03	0.70	2.03	0.03
Lime	30-45	4.27	3.83b	0	0.01	0.06	0.02	0.03	0.30	2.06	0.03
Control	45-60	4.37a	3.94a	0	0	0.02	0	0.03	0.16b	1.05	0.02
Lime	45-60	4.59b	4.14b	0	0	0.03	0	0.03	0.10a	1.09	0.03
overall effect:		L>C	L>C	ns	L>C	L>C	ns	ns	C>L	ns	L>C
<i>Old stand</i>											
Control	0-5	4.07	3.08	0.03a	0.17	0.77a	0.05	0.07	0.68	1.09	0.71a
Lime	0-5	4.11	3.47	0.10b	0.47	3.33b	0.11	0.05	0.35	0.82	4.1b
Control	5-15	4.00	3.41	0.01a	0.05a	0.18a	0.05	0.03	0.41	1.47	0.12
Lime	5-15	4.13	3.58	0.01b	0.12b	0.56b	0.12	0.10	0.34	1.54	0.36
Control	15-30	4.12	3.71	0.01	0.04a	0.13a	0.05a	0.03	0.26	1.51	0.09
Lime	15-30	4.40	3.94	0.01	0.12b	0.59b	0.09b	0.06	0.17	1.30	0.45
Control	30-45	4.14	3.80	0.00	0.04	0.10	0.08	0.02	0.22	1.48	0.07
Lime	30-45	4.48	3.97	0.01	0.09	0.37	0.09	0.03	0.13	1.32	0.28
Control	45-60	4.27	3.94	0.00	0.03	0.09	0.05	0.02	0.13	1.41	0.06
Lime	45-60	4.68	4.12	0.01	0.06	0.26	0.09	0.04	0.10	1.10	0.24
overall effect:		L>C	L>C	L>C	L>C	L>C	L>C	ns	C>L	ns	L>C

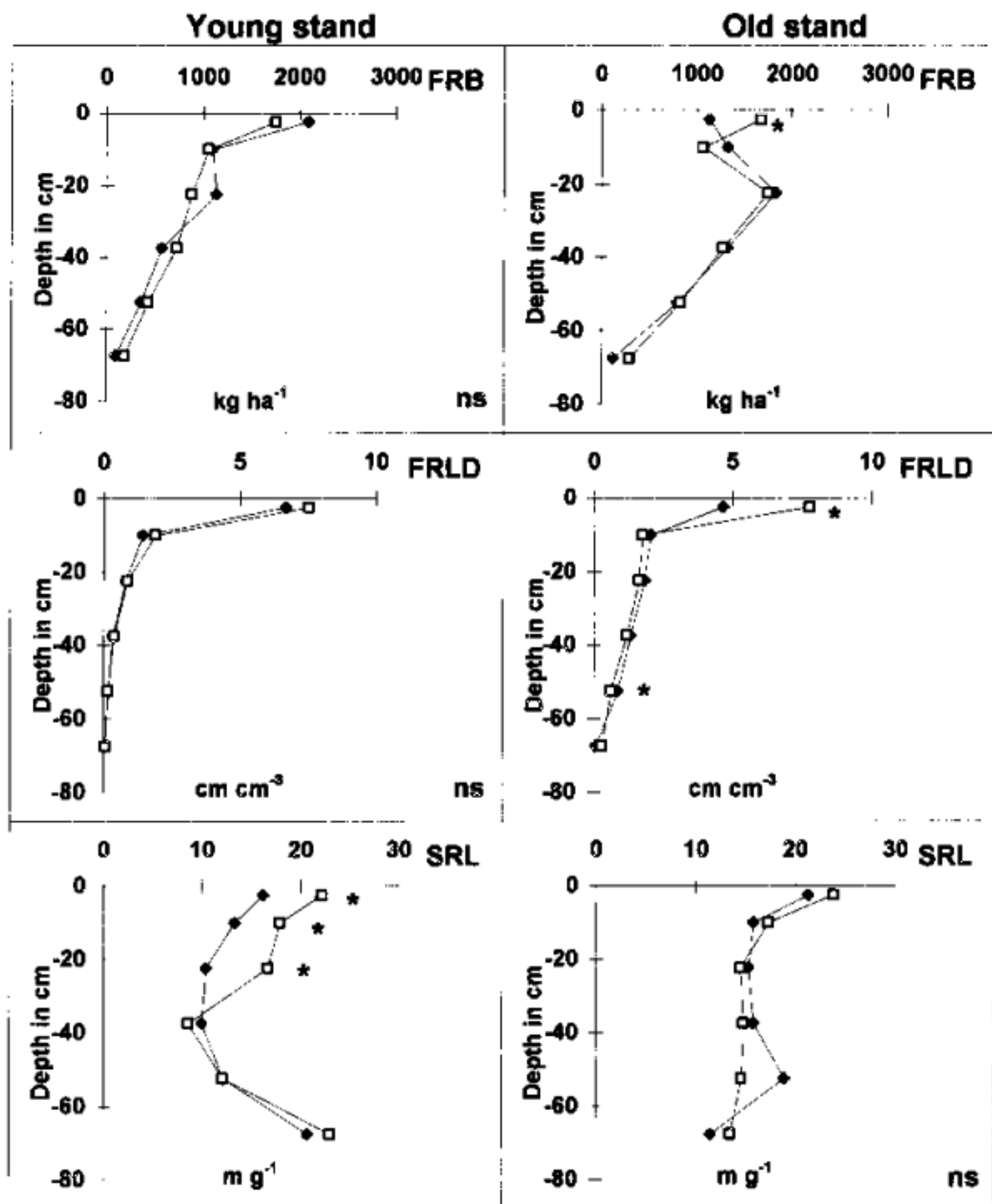


Figure 1. Vertical distribution of fine root biomass (FRB), fine root length density (FRLD), and specific root length (SRL) for the young and old stand. Mean depths of the soil layers were used to represent the values. Filled symbols are for the control and open squares for the lime treatment (sample number = 16, ns = no significant difference, * = significant for this layer at least at $p < 0.05$).

into two size classes (<0.5 mm and 0.5–2.0 mm) was carried out on only two samples per treatment and layer. The results indicate that after liming the proportion of the very fine class, based on mass data, tends to be smaller than in the control. This

suggests, that fine roots in the liming treatment are on average thicker than in the control plots.

The concentration of some elements in the fine roots as presented in Table 2, was tested statistically on an overall basis (all layers lumped). Tests per layer revealed hardly any significant difference, due to the limited sample number per layer, small absolute differences in concentrations and high variation. The only significant overall effects consisted of increases of Mg (both stands) and Ca (old stand) in the fine roots. This was especially the case in the toplayers. The comparison of the figures suggests no marked effects on S, P, Mn and K concentrations in the roots after liming. The Mn values seem higher in the old stand than in young stand, which was also observed by Van den Burg (1994) for the foliage and attributed to the differences in ground water table and Mn disponibility. Al concentrations seem lower in the topsoil and higher in the subsoil in the young stand, whereas in the old stand the differences are small.

Dead root pools

Total fine root necromass for 0–75 cm ranged from 2906 kg ha⁻¹ for the liming treat-

Table 2 Mass mineral content (g kg⁻¹) of fine roots of oak (*Quercus robur* L.) in a young and an old stand in October 1995, 7 years after application of a 1.6 t ha⁻¹ equivalent CaO dosis (small a and b indicate significant differences between the control and lime treatment at P<0.05 for a given layer and L and C indicate significant differences on overall basis (total profile: 0–60 cm) with L=lime, C=control and ns = not significant).

Treatment	Depth	n	S	P	Mn	Mg	Al	Ca	K	Ca/Al
<i>Young stand</i>										
Control	0–5	3	1.5	0.69	0.06	1.0	1.1	5.8	2.3	5.3
Lime	0–5	3	1.4	0.71	0.04	1.5	0.91	6.3	2.1	7.0
Control	5–15	3	1.3	0.68	0.02	0.74a	4.1	4.2	1.7	1.0
Lime	5–15	3	1.1	0.54	0.03	1.1b	2.4	5.6	2.2	2.3
Control	15–30	3	1.1	0.67	0.02	0.63	5.2	3.2	2.9	0.62
Lime	15–30	3	1.1	0.63	0.02	0.83	5.2	3.9	2.1	0.75
Control	30–45	3	1.0	0.61	0.01	0.47	7.3	2.0	2.1	0.27
Lime	30–45	3	1.0	0.56	0.01	0.73	9.1	2.4	2.4	0.26
Control	45–60	3	0.8	0.50	0.01	0.31	8.1	1.0	1.8	0.12
Lime	45–60	3	1.4	0.48	0.00	0.31	11.3	0.38	2.1	0.04
overall effects:			ns	ns	ns	L>C	ns	ns	ns	ns
<i>Old stand</i>										
Control	0–5	2	1.4	0.70	0.14	1.1a	1.1	4.9	2.0	4.5
Lime	0–5	2	1.8	0.95	0.20	1.3b	1.5	6	1.8	4.0
Control	5–15	2	1.5	0.87	0.18	1.0	3.5	4.6	2.0	1.3
Lime	5–15	2	1.3	1.2	0.27	0.92	4.4	3.6	1.7	0.82
Control	15–30	2	1.7	0.80	0.16	0.88	5.1	3.3	2.3	0.65
Lime	15–30	2	1.3	0.80	0.26	1.0	5.0	4.7	2.2	0.94
Control	30–45	2	1.4	0.62	0.13	0.65	4.9	2.6a	2.3	0.53
Lime	30–45	2	1.4	0.71	0.14	1.0	5.5	5.6b	1.8	1.0
Control	45–60	2	1.7	0.49	0.08	0.56a	6.5	1.8	2.4	0.28
Lime	45–60	2	2.1	0.44	0.06	0.83b	8.5	4.0	1.5	0.47
overall effects:			ns	ns	ns	L>C	ns	L>C	ns	ns

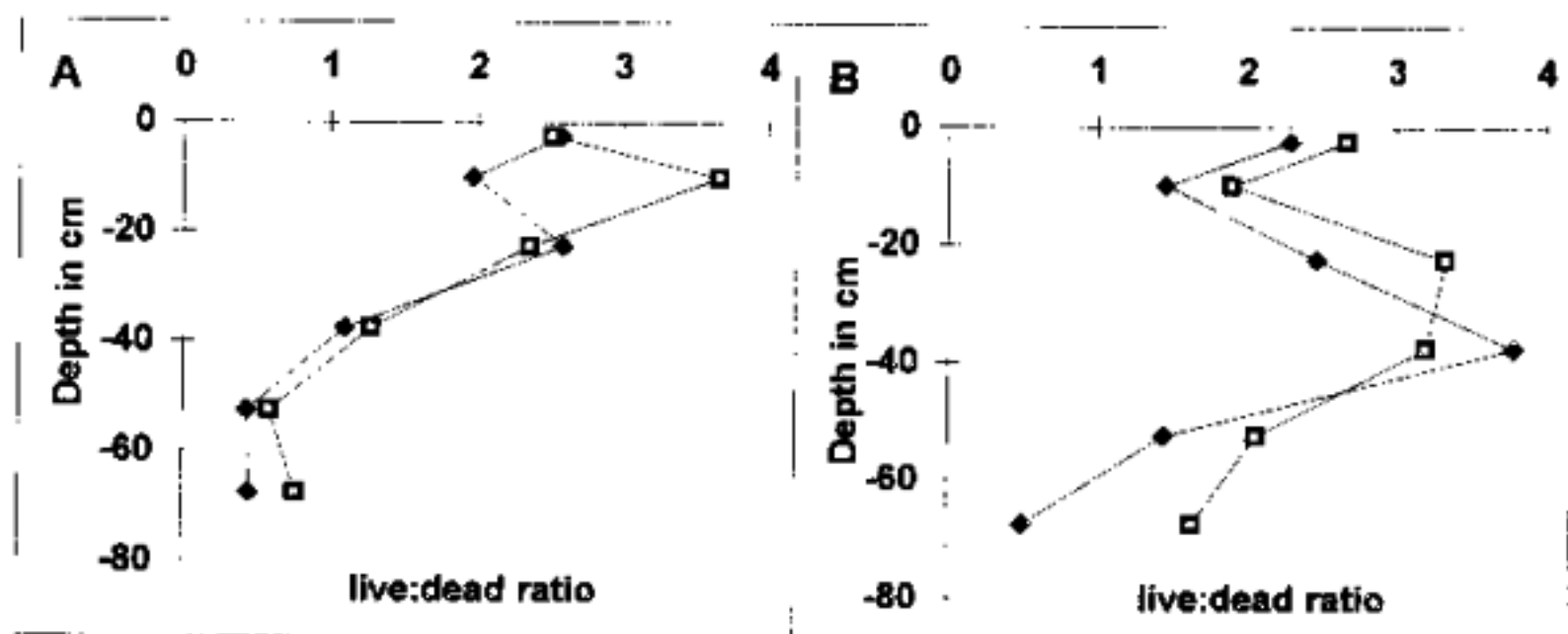


Figure 2. Live:dead ratio of fine root mass for the young (A) and the old stand (B). Mean depths of the soil layers were used to represent the values. Filled symbols are for the control and open squares for the lime treatment (sample number = 2 for the old stand and 3 for the young stand, no statistics applied).

ment and 3345 kg ha^{-1} for the control plots in the young stand and from 2691 to 3283 kg ha^{-1} in the old stand. Similarly, total fine dead root length ranged from 39.2 to 40.5 (liming and control plots, respectively, for the young stand) to 65.2 to $80.2 \cdot 10^6 \text{ m ha}^{-1}$ (respectively, in the old stand). Therefore, the amount of fine root necromass or -length, was consistently lower in both trials in the limed treatments as compared with the control plots. Figure 2 presents the live:dead ratio of fine root mass. It shows that the control plots seem to have a somewhat lower live:dead ratio than the lime treatment. This appears most pronounced in the old stand and only for one layer (5-15 cm) in the young stand.

Mycorrhizae

Counts of ectomycorrhizal morphotypes are presented in Figure 3. It illustrates that liming in the old stand did not significantly affect the number of mycorrhizal apices, whereas in the young stand it did. Expressed as number of apices with mycorrhizae or as number per cm root length, liming appears to enhance mycorrhizae fairly consistently down to 30 or even 45 cm in the young stand, although this is significant only at 5-15 cm for the total number of apices due to low sample number and high variation. Concerning the morphotypes, hairy types (A1-A2) seem to profit from liming in both stands (not significant increase in relative proportion but significant increase in absolute number), whereas the relative importance of the smooth types as a total (sum of C1, C2-Cenococcum and C2other) significantly decreased (only in the young stand), though not their absolute number. The stands vary between the different morphotypes, type B showing both negative (old stand) and positive (young stand) responses to liming. Furthermore, shifts from the C1 type to the C2-Cenococcum type occurred in the young stand, whereas this was absent in the old stand. Overall effects of liming on mycorrhizae will be dealt with in Bakker & Garbaye (*in prep.*).

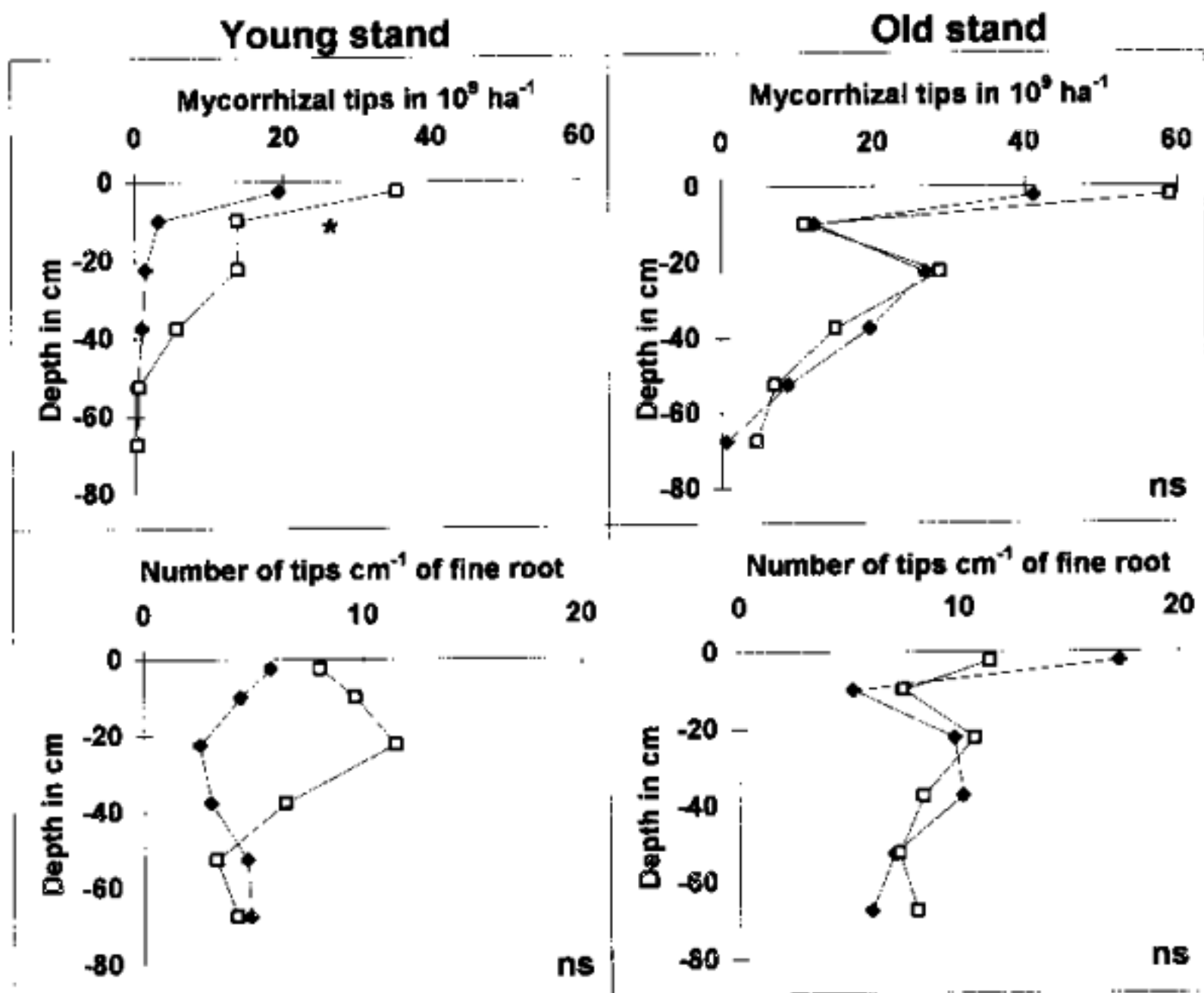


Figure 3. Number of mycorrhizal root tips per ha (upper half) and number of mycorrhizal tips per cm of fine root (lower half) for the young and the old stand. Mean depths of the soil layers were used to represent the values. Filled symbols are for the control and open squares for the lime treatment (sample number = 4, ns = no significant difference, * = significant for this layer at least at $p < 0.05$).

Discussion

Compared to the effects on the mineral horizon (0-25 cm) after three years in 1991 (Van Den Burg, 1994), arithmetical means of the 1995 data for this depth, showed that Mg and Ca concentrations were doubled for the limed plots, whereas the control plots showed slightly lower values. In general, the lime applied on topsoil had reached deeper soil horizons in 1995, 7 years after its application, as compared to 1991. This delay effect of liming probably is related to its solubility (Belkacem, 1993) and to the way the lime has been applied to the soil (dispatching manually on the top of the soil, no labouering of the soil), which avoids a too fast mineralization of the top organic layers (Van Den Burg, 1994).

The slight increase of CEC by liming was also observed in a liming experiment in the French Ardennes (Bakker *et al.*, 1998). This increase in CEC after liming or gypsum addition may be related to the pH-dependent character of the CEC

(Shamshuddin *et al.*, 1991). It could also be the result of an accumulation of organic matter (Derome, 1990/91) related to a short term decrease in N-mineralization together with additions of dead plants from the forest floor, or to an interference with undissolved lime and gypsum particles. Generally, however, liming stimulates mineralization of organic matter (Hüttl & Zöttl, 1993). Here, some accumulation seems to be true for the upper 10 cm in the young stand three years after liming according to the study by De Boer *et al.* (1993) in the same stands. Although interference by undissolved lime particles in the correct measurement of the CEC can not be ruled out completely, this has been proven very unlikely in the case of the liming experiment in the French Ardennes, four years after lime application (Bakker *et al.*, 1998).

The fine root responses of the young and old stands to liming appear to be different. In the young stand, where foliar concentrations of some elements (N, P, Mg, Zn, Fe) were insufficient, low or only close to sufficient prior to liming, the tree root system response to liming was an increase in specific root length in the top 30 cm, a higher occupation by mycorrhizae and more apices with mycorrhizae per cm of fine roots in the top 30 to 45 cm, and an increase in the proportion of hairy morphotypes. As all root tips were infected by fungi, the increased number of apices with mycorrhizae per cm of fine root implies a higher fine root branching. In contrast, in the old stand where foliar concentrations were at a more acceptable level (except for Zn), a slight increase of fine root biomass and fine root length occurred after liming in the top layers, without any increase in the number of mycorrhizae. This difference may reflect the slightly more acidic soil in the young stand, which impedes stimulation of root growth, or regulates the absorption surface of the root system by allocating photosynthates to the mycorrhizae. As a result, the leaf nutrient status was most affected in the young stand, where Ca, Mg and Zn levels were significantly improved three years after liming, while Mn decreased (Van Den Burg, 1994). In the old stand the effects were similar but less pronounced.

De Boer *et al.* (1993) carried out a study on nitrogen mineralization in the same stands and found on an overall basis (both control and liming) much lower absolute N concentrations in the top 10 cm in the young stand as compared to the old stand. Liming increased net N mineralization and the relative proportion of $\text{NO}_3\text{-N}$ in the old stand, whereas in the young stand this was not so. They explained this difference in terms of the effects of liming on bacterial biomass, which immobilized part of the nitrogen. In the young stand where a clear liming effect on net N mineralization was lacking, they expected an increase in bacterial, relative to fungal decomposition. However, the counts of mycorrhizae on root tips in this study, suggest that there was an increase of fungal activity (at least of ectomycorrhizal fungi) in the young stand after liming. This corresponds well with current theory, that fungal relative to bacterial biomass and respiration are higher for the type of humus and pH range in the young stand (Mangenot, 1980). Therefore, it seems more likely that fine roots and/or mycorrhizae are responsible for this difference in N concentrations. It may be expected that due to their abundant mycelium, the hairy types are more beneficial for uptake than the smooth types (Marschner, 1991; Bakker & Garbaye, *in prep.*). Effects of liming on saprophytic fungi and their effect on mineralization, were not

accounted for, but probably this is of importance considering the site conditions (Mangenot, 1980).

Solution culture experiments (Keltjens & Van Loenen 1989) showed *Quercus robur* to have an extreme NH_4^+ preference despite an ability to switch instantaneously to NO_3^- . This kind of experiment cannot be generalized to the field (e.g. Olsthoorn *et al.*, 1991), because of differences in mobility in soil between NH_4^+ and NO_3^- . In response to the dominant form of nitrogen uptake by the roots, with NO_3^- resulting in an increase and NH_4^+ in a decrease of rhizosphere pH (Gijssman, 1990), inhibition of cell elongation due to low pH can either be enhanced or alleviated, and as a result specific root length decreases or increases. The lower pH range and lower overall specific root length in the young stand as compared to the old stand, suggest that inhibition of cell elongation caused by soil acidity is of importance there. This would explain why, in response to direct alleviation of this stress (higher bulk soil pH and increased supply of NO_3^- , Ca, Mg) root cell elongation and mycorrhizal infection are stimulated by liming in the young stand. In contrast, in the old stand, which suffers less from soil acidity and root growth inhibition, liming acted as some kind of 'luxury' fertilization, significantly increasing root length and biomass in the top soil, with a tendency towards decreased specific root length in the subsoil layers. There, a lower specific root length would then reflect more storage in the thicker fraction of the fine roots.

Negative effects of liming on the trees, as observed for sites with high N deposition (e.g. Persson & Ahlström, 1990/1991), did not occur in this study. Liming did not cause a shallower rooting profile in either of the two stands. After liming fine root necromass and fine root necrolength were lower than in the control, thus, the live:dead ratio was higher in the liming treatments. Generally necromass was lower than biomass, with the exception of the deepest layers in the young stand, where biological processes are slower than at the surface. The effects of liming on fine root biomass and necromass appear very similar to those observed in the Ardennes study area (cf Bakker, 1998) where subsequent sampling over a two year period permitted to infer that fine root turnover was lower and longevity higher in the liming treatments. The same may apply in this study. A somewhat higher Al concentration in the fine roots corroborates this suggestion, as Al may accumulate during the lifetime of the roots (Murach & Schünemann, 1985).

For increasing site fertility, soil exploration density by roots and mycorrhizae was observed to decrease (Blaise & Garbaye, 1983). Perhaps, the lime-induced stimulation of soil exploration by roots and or mycorrhizae of this study in the young stand, will not last in the long-term and shift to a lower but more efficient soil exploration system. And, whereas the effects on leaf mineral status are positive for the moment, effects on tree growth were not consistent (Van Den Burg, 1994), suggesting that it would worthwhile to resample fine roots, leaf mineral status and tree growth in a few years.

Conclusions

Liming improved soil, fine root and foliar chemical status in both stands and the effects on fine roots and mycorrhizae were the clearest in the young stand with lowest

initial pH and where nutrient conditions were most insufficient. The effect on fine roots in the old stand was limited to some stimulation of fine root biomass and length in the topsoil whereas in the young stand total uptake volume was stimulated (increase in specific root length, number of mycorrhizae per cm root length). Further, in both stands, liming resulted in an increase of the relative proportion of hairy morphotypes. So, the effect of liming on the uptake system was largest in the stand featuring worst nutrient conditions prior to liming.

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