Annexe A (Papier I) : *Plant and Soil* **00**: 1-10, 1998
Reçu le 25 mai 1998 ; accepté en version révisée le 27 octobre 1998.
Repris dans cet oeuvre avec la permission de l'editeur Kluwer academic publishers

The effects of liming and gypsum applications on a sessile oak (*Quercus petraea* (M.) Liebl.) stand at La Croix-Scaille (French Ardennes) I. Site characteristics, soil chemistry and aerial biomass.

M.R. Bakker, C. Nys & J-F. Picard

Abstract

In a former 45 to 50 year old sessile oak (*Quercus petraea* (M.) Liebl.) coppice mixed with birch (*Betula pubescens* Ehrh.) and rowan (*Sorbus aucuparia* L.) on a poor acidic forest soil at la Croix-Scaille in the French Ardennes, several liming amendments were applied in 1990 and 1994. Data on soil and soil solution composition, as well as stand growth and foliar composition were collected between 1994 and 1997. All treatments, containing 1.4 t ha^{-1} equivalent of CaO supplied as lime, gypsum or a mixture of the two, resulted in an increase of cation exchange capacity and base saturation down to 15 cm and for $CaSO_4$ treatments down to 30 to 45 cm, increases of soil pH and Ca concentration at the surface and a decrease of Al concentration in the soil and soil solution in the surface layers. No negative effects like increased nitrate or cation leaching were observed. Although Mg nutrition was not improved by the treatments (not containing Mg), a relative and maintained gain of radial increment of sessile oak in the order of 40% for both lime and gypsum applied, was observed immediately from the first year on, after the application (1991).

Key-words: cation exchange capacity, gypsum, lime, *Quercus petraea*, sessile oak

Introduction

Soil acidification, either natural or by management or acid deposition, can have serious negative effects on the sustainability of forest ecosystems in terms of production and vitality (Andersson and Persson 1988; Weissen *et al.* 1988; Hüttl 1989). Soil acidification can lead to phytotoxic levels of aluminium and may disturb or inhibit nutrient uptake, leading to deficiencies of some elements (e.g., Mg, K, Ca, P) or excesses (e.g., N) of others (Roelofs *et al.* 1985; Rost-Siebert 1985; Göransson and Eldhuset 1987; Godbold *et al.* 1988; Hüttl and Zöttl 1993; Boudot *et al.* 1994; Ericsson *et al.* 1995; Ljungström and Nihlgård 1995).

Liming and fertilization may be applied as a means of increasing stand productivity and vitality of forest ecosystems. They have often proved to be adequate to raise pH, Ca concentration, cation exchange capacity and base saturation, and to lower the Al concentration, in spite of a slight initial acidification which may occur in deeper soil horizons (Hüttl and Zöttl 1993). Nutritional imbalances related to impaired nutrient uptake can be alleviated by liming (Heilman and Ekman 1973; Hüttl 1989; Joslin and Wolfe 1989; Derome 1990/91; Fehlen and Picard 1994; Belkacem and Nys 1997; Ranger *et al.* 1994). As a result, stand health and growth can be improved considerably, though some studies did not report such an improvement (Hüttl and Zöttl 1993; Clemensson-Lindell and Persson 1993). Liming may sometimes induce deficiencies of other elements (K, Zn, P, B, Mg) as observed in aerial parts of the tree due to antagonistic interactions with other elements in plant uptake or to dilution effects on sites where the soil is already relatively poor in these elements (Glatzel et al. 1986; Derome 1990/91).

This paper focuses on the site characteristics and the effects of liming on soil and aerial biomass at the 'La Croix-Scaille' site. The objectives of this study were to determine the modifications brought about by liming in the rooting zone of oak. It was hypothesized that liming and gypsum amendments would improve soil and soil solution chemistry, foliar nutrition and stimulate stand growth, the effect of gypsum being more rapid due to its higher solubility. The aim of Part I is to describe the effects on soil, solution, nutrition and growth, in order to explain the effects on fine roots, which will be discussed in a Part II.

Materials and Methods

The site

The "La Croix-Scaille" site, in the state forest of Château-Regnault, is located in the primary chain of the French Ardennes. The average altitude is 480 m a.s.l, the site being on top of a plateau. Average annual precipitation has a relatively even distribution throughout the year and ranges from 1100 to 1300 mm. The mean annual temperature is 8 °C, with the monthly averages ranging from -1.1 °C in January to 14.5 °C in August. During the experimental period 1994-1996 a high ground water-table was observed locally in March 1995, probably related to thawing of snow.

The soil developed in a loamy layer, overlying slates of the Upper Revinien, and is classified as an "acidic brown forest soil" (FAO: Dystric Cambisol; USDA: Dystrochrept), with acid moder humus types (Belkacem and Nys 1995). In the profile, a shallow litter and humus layer of 2.5 to 3.5 cm may be found, followed by an A11 (from 0 to 5 cm), a transition layer A1(B) (5 to 15 cm), a B horizon (15 to 45 cm), a transitional horizon (B)C (45 to 60 cm) and a C (60 to 75 cm) before the bedrock is reached. Locally podzolic stagnogley properties may occur. Generally the soil texture is loamy and down to 45 cm the presence of gravels is below 15%, but may increase to a mean of 25% at 45-60 cm. Before liming, average pH-H_2O was 3.6 in topsoil (A11) and 4.4 to 4.7 in the B-layers. The soil is strongly desaturated (on average base saturation < 10%), except for slightly higher values in the topsoil. The relative abundance of available P contrasts with low levels of exchangeable K and extremely low levels of exchangeable Ca and Mg (Bouchon *et al.* 1985).

The liming treatments were applied in 1990 and 1994 in an old coppice with standards, 45-50 years since the last cut. Sessile oak (*Quercus petraea* (M.) Liebl.) is the main coppiced species with birch (*Betula pubescens* Ehrh.) and rowan (*Sorbus aucuparia* L.), and the standards are oak (90%) and beech (*Fagus sylvatica* L.; 10%). Average total standing crop was estimated to be 161 t ha^{-1} (range 102-179 t ha^{-1}), based on equations given by Kestemont (1975) for similar stands nearby in Belgium, and it is comparable to the estimates of 94 to 135 t ha^{-1} for similar sites in the same forest. The mean yearly production was estimated at 2.3 to 3.2 t ha^{-1} yr^{-1}, or 5.1 m^3 ha yr^{-1} (Ranger *et al.* 1981; Bouchon *et al.* 1985).

Experimental treatments

Two trials were established: an old (plot size 15 x 15 m) and a new trial (plot size 10 x 15 m). Treatments consisted of a control, and additions of 1.4 t.ha^{-1} CaO as $CaCO_3$ (lime), 1.4 t.ha^{-1} CaO as $CaSO_4$ (gypsum) and a mix of 1.4 t.ha^{-1} CaO as $CaCO_3$ (80%) and $CaSO_4$ (20%). The old trial (established in spring 1990) consisted of 2 blocks with each one control, one lime (old lime), and one gypsum (old gypsum) treatment (all treatments replicated once in each of the 2 blocks). The new trial (established in September 1994) consisted of two blocks with each one

lime (new lime), one gypsum (new gypsum) and one mix (mix 80/20) treatment (all treatments replicated once in each of the 2 blocks). The control of the old trial was shared by the new trial. Analysis of soil and fine roots in June 1994 before liming justified the use of the same control plots. All treatments were applied to the soil surface and distributed manually.

Sampling procedure

Site production was estimated by diameter measurements (DBH) in June 1995 and March 1997 completed by ring analysis in March 1997 for the old trials. Height measurements were carried out in May 1996. Foliar samples were collected by shooting branches from the top of dominant trees at the end of summer in 1992, 1993 and 1996.

Soil samples were collected either as bulked samples from soil pits (September 1994), using small soil density cylinders (June 1994; length 5 to 8 cm, ∅ 6.4 cm) or by a soil corer in 1995 and 1996 (length 15 cm, ∅ 8.0 cm). Samples were taken at depths of 0-5, 5-15, 15-30 and 30-45 cm.

Soil solution was sampled from March 1995 using rhizon soil moisture samplers (Eijkelkamp BV, Giesbeek, The Netherlands, reference 19.21.05). The rhizons (length 10 cm, outer ∅ 2.3 mm) were installed horizontally in one soil pit per experimental plot at different depths (3, 10, 20 and 35 cm). Small vacuum-tubes (usually applied for blood samples) were connected on the outer edge of the rhizons by injection needles and were left overnight. Sample volume was generally between 2 to 7 ml. As the samples were taken using only a low vacuum, it is assumed that the quality of the soil solution sampled is between gravity water and weakly bound capillary water. After overnight sampling, the pits were closed by a plastic bag filled with soil until the next sampling period. The rhizons were installed in March 1995, and solute samples were collected in March, June and September 1995.

Sample processing

Soil samples were air-dried and then sieved at 2 mm. 0.5 *M* NH_4Cl-exchangeable Al, Ca, Mg, K, Mn and Na (Trüby 1989) were determined by ICP (emission spectrometry), exchangeable acidity by automatic titration (Trüby 1989), and pH-KCl and pH-H_2O following standard procedures with KCl-electrodes. Concentrations were expressed as oven-dried weights (determined after 48h at 105°C). Cation Exchange Capacity (CEC) was defined as the sum of exchangeable Mn, Mg, Ca, Na, K, plus titrable Al^{3+} and H^+ (Espiau and Pedro 1980). Base saturation was defined as the proportion of exchangeable Mn, Mg, Ca, Na and K in relation to total CEC. Soil solution analysis was performed by ICP (S, Mn, Mg, Al, Ca, Na, K) and colorimetry (Technicon Autoanalyzer) for nitrate and ammonium. Foliage samples were pretreated with hydrogen-peroxide (H_2O_2), then mineralized with $HClO_4$ and analysed by ICP for N, S, P, K, Mg, Ca and Mn.

Data analysis

All statistics were calculated with Unistat 4.0 software (Unistat Ltd 1995). Distribution was tested for normality and wherever necessary values were log transformed to improve the distribution. Soil and solution parameters were tested for treatment, season and soil depth effects by ANOVA, mainly on the total set of data (all periods), and the Student-Newman-Keuls test was used to separate group means. Only June 1994 permitted also individual analyses of significance for the soil data (4 replicates). The total set of data was compiled by merging the individual data-sets (number of sample replicates 2 to 4 for soil and soil solution per layer and treatment) to obtain a larger number of replicates (8 to 14 according to

treatment; some treatments not sampled at each period). Foliar composition and tree growth were evaluated similarly for treatment effects but for individual periods.

Results

Soil chemical properties

The soil chemical properties showed variations throughout the study period (June 1994 - March 1996). These seasonal variations were most pronounced in top soil and were similar in all treatments (data not shown). Alltogether, besides these seasonal variations, concentrations of exchangeable elements in the soil were fairly stable throughout the study period and similar to those described for an adjacent site (Belkacem and Nys 1997). Analysis of variance, applied to the total of all periods, showed that liming had a greater impact on the soil than gypsum. In the old trial, lime increased CEC by 50% in the 0 to 5 cm layer compared to a 20% increase for the gypsum treatment. Base saturation was increased from 19% to 60 - 75% for lime, and to 40% for gypsum and the mixed treatment. The new trials finally had the same effect on the soil as the old trials, relative to the control. The gypsum treatments had the fastest downward reaction but the liming treatments had a longer lasting reaction, the mixed treatments being intermediate. Table 1 illustrates these changes in soil chemistry for September 1995. The analyses of variance for all periods are summarized below.

Table 1 Description of soil chemistry for September 1995, five years after application of 1.4 t ha^{-1} of CaO as $CaCO_3$ ($CaCO_3$-old) or as $CaSO_4$ ($CaSO_4$-old), and one year after application of 1.4 t ha^{-1} of CaO as $CaCO_3$ ($CaCO_3$-new), as $CaSO_4$ ($CaSO_4$-new) or as a mixture of 80 % $CaCO_3$ and 20 % $CaSO_4$. CEC = Sum of 0.5 M NH_4Cl exchangeable Mn^{2+}, Mg^{2+}, Ca^{2+}, Na^+, K^+ plus titrable Al^{3+} and H^+ . BS= Base saturation of CEC. Layers are standard depths of 0-5 cm (A11), 5-15 cm (A1(B)), 15-30 cm (B) and 30-45 cm (B). (means of 2 values with standard errors in italic).

Treat-ment	Depth cm	pH (H_2O)		Mg^{2+}		Ca^{2+}		Al^{3+}		H^+		CEC	BS (%)	Ca/Al^{3+}
				cmol$_c$ kg^{-1}										
Control	0-5	3.77	*0.01*	0.28	*0.05*	0.61	*0.16*	5.43	*0.20*	1.60	*0.10*	8.2	14.1	0.17
	5-15	4.06	*0.17*	0.09	*0.02*	0.12	*0.02*	5.42	*0.08*	0.73	*0.28*	6.6	7.0	0.03
	15-30	4.34	*0.08*	0.04	*0.02*	0.10	*0.05*	3.37	*0.12*	0.18	*0.01*	3.9	8.3	0.05
	30-45	4.39	*0.02*	0.03	*0.01*	0.08	*0.03*	2.91	*0.46*	0.12	*0.03*	3.3	8.5	0.05
$CaCO_3$	0-5	4.78	*0.31*	0.86	*0.07*	15.7	*1.91*	0.48	*0.35*	0.21	*0.21*	18.0	96.2	49.1
old	5-15	4.36	*0.01*	0.16	*0.01*	2.38	*0.83*	4.95	*0.75*	0.65	*0.02*	8.4	33.5	0.72
	15-30	4.48	*0.04*	0.04	*0.01*	0.18	*0.03*	3.57	*0.46*	0.15	*0.02*	4.1	8.8	0.08
	30-45	4.47	*0.02*	0.03	*0.01*	0.11	*0.03*	2.67	*0.12*	0.13	*0.03*	3.1	8.2	0.06
$CaSO_4$	0-5	3.90	*0.08*	0.45	*0.08*	3.45	*0.48*	3.17	*0.01*	0.92	*0.75*	8.7	52.9	1.63
old	5-15	3.80	*0.09*	0.16	*0.06*	0.91	*0.06*	5.04	*0.00*	1.50	*0.29*	7.9	17.0	0.24
	15-30	4.30	*0.07*	0.03	*0.01*	0.27	*0.03*	3.42	*0.15*	0.21	*0.02*	4.1	10.8	0.12
	30-45	4.34	*0.06*	0.02	*0.01*	0.14	*0.01*	2.74	*0.09*	0.14	*0.02*	3.2	9.2	0.08
$CaCO_3$	0-5	3.80	*0.15*	0.45	*0.13*	2.74	*0.60*	8.67	*3.53*	1.89	*0.20*	14.5	27	0.48
new	5-15	4.02	*0.14*	0.08	*0.02*	0.21	*0.00*	6.46	*2.04*	0.58	*0.38*	7.6	6.9	0.05
	15-30	4.31	*0.08*	0.03	*0.01*	0.06	*0.00*	3.16	*0.08*	0.14	*0.03*	3.5	6.0	0.03
	30-45	4.40	*0.07*	0.01	*0.00*	0.03	*0.01*	2.32	*0.73*	0.14	*0.04*	2.6	5.0	0.02
$CaSO_4$	0-5	3.77	*0.02*	0.47	*0.22*	4.51	*0.45*	5.51	*2.19*	2.12	*0.25*	13.4	43.2	1.23
new	5-15	3.85	*0.10*	0.25	*0.14*	1.73	*0.51*	5.70	*0.54*	1.40	*0.35*	9.6	25.7	0.45
	15-30	4.16	*0.04*	0.05	*0.00*	0.22	*0.07*	4.72	*0.52*	0.39	*0.08*	5.6	8.1	0.08
	30-45	4.36	*0.03*	0.04	*0.01*	0.20	*0.10*	2.66	*0.97*	0.13	*0.04*	3.1	11.2	0.12
mix	0-5	4.01	*0.12*	0.25	*0.09*	3.23	*0.17*	4.09	*0.24*	1.26	*0.38*	9.3	42.5	1.20
80/20	5-15	4.05	*0.09*	0.11	*0.00*	0.68	*0.03*	5.34	*0.04*	0.87	*0.25*	7.3	14.9	0.20
	15-30	4.43	*0.07*	0.03	*0.00*	0.09	*0.03*	3.16	*0.79*	0.19	*0.06*	3.7	9.5	0.05
	30-45	4.40	*0.06*	0.02	*0.01*	0.08	*0.01*	2.27	*0.34*	0.12	*0.02*	2.7	12.5	0.06

In the mineral soil, increases in CEC were about 20% in 5-15 cm (both lime and gypsum), 10% in 15-30 cm and not significant below 30 cm. In contrast to this pattern, base saturation in the 5-15 cm layer featured important increases in the order of 60 to 270% (new versus old lime), 90% (gypsum) and 40% (mixed treatment), respectively. Below 15 cm the effects were very different relative to time. For the old trials both lime and gypsum increased base saturation by 10 to 30% in 15-45 cm layer, whereas in the new trials only gypsum caused a small increase of 5% for the 15-45 cm layer. More generally the effects of lime and gypsum may be summarized as being greater and having a longer lasting effect in the lime-applied plots, but a faster and deeper reacting effect for the gypsum-applied plots. The difference in reactivity between the different products related to their solubility, agrees with the work of Ponette *et al.* (1997).

The treatments had no effect on exchangeable Mn (0.01 to 0.15 $cmol_c\ kg^{-1}$), Na (0.02 to 0.10 $cmol_c\ kg^{-1}$) and K (0.10 to 0.60 $cmol_c\ kg^{-1}$) concentrations in the soil, although liming seemed to increase their concentrations in the 0 to 5 cm layer (significant in one period for Na). pH-H_2O values were significantly increased by the old lime application in the upper 5 or 15 cm, whereas they were not significantly affected (0 to 5 cm) or even decreased at 5 to 15 cm (significant at $p<0.05$) for the old gypsum treatment. The effect was lower for the new trials and intermediate for the mixed application. Exchangeable Ca (significant at $p<0.01$) increased considerably and also Mg to a lesser extent (sign. at $p< 0.05$), in both lime and gypsum treatments in the top 0 to 5 or 0 to 15 cm layer, contrasting with a decrease in Al ($p<0.001$) and H^+ ($p<0.05$). Ca/Al molar ratio increased significantly in top 0 to 5 cm after liming (Table 1) and this was significant down to 45 cm in June 1994.

Soil solution composition

Soil solution composition varied between the seasons, but the old treatment effects were consistent throughout all seasons, while the effects of the new treatments increased with time. Table 2 shows the main characteristics of the soil solution for March 1995, which may be considered as representative for the treatment effects, despite slightly lower pH values and the inversed importance of Ca and Al in June and September. Consequently, Ca/Al ratios were lower in June and September than in March. The solution is dominated by nitrate and sulphate (not shown), with important contributions in some months for Ca in March and Al in June and September (data not shown).

Analysis of variance was applied to all of the periods. It revealed that Mn (0.01-0.05 $mmol_c\ l^{-1}$), Mg (0.03-0.10 $mmol_c\ l^{-1}$) Na (0.05 to 0.20 $mmol_c\ l^{-1}$), K (0.02-0.10 $mmol_c\ l^{-1}$) and NH_4^+ (0.00 to 0.03 $mmol_c\ l^{-1}$) showed no consistently significant treatment response (data not shown), and no seasonal pattern, although there was a tendency towards a decrease in the treated plots as compared to the control for Mn, Na and NH_4^+, which was only significant at the 0.05 level in September. Increase of S was only significant in the treatments containing sulphate, and increase of Ca was significant for the mix 80/20 and old lime treatment, as compared to the control. Overall solution Al concentrations tended to decrease in all treatments as compared to the control, but this was significant only in September. As a result, overall Ca/Al molar ratios of the soil solution, ranging from 0.17 to 0.45 at some depths in June and September in the control, were enhanced by the treatments for all depths. This increase was significant for the old gypsum, old lime and mix 80/20 treatments. Nitrate appeared significantly lower on an overall basis for old lime, old gypsum and the mix 80/20 treatment as compared to the control. The pH value of the soil solution was only increased significantly by the lime treatments as compared to the control.

Table 2 Description of soil solution for March 1995, five years after application of 1.4 t ha^{-1} of CaO as $CaCO_3$ ($CaCO_3$-old) or as $CaSO_4$ ($CaSO_4$-old), and one year after application of 1.4 t ha^{-1} of CaO as $CaCO_3$ ($CaCO_3$-new), as $CaSO_4$ ($CaSO_4$-new) or as a mixture of 80 % $CaCO_3$ and 20 % $CaSO_4$. Samples taken in the middle of soil layers at 3 cm (A11). 10 cm (A1(B)), 20 cm (B) and 35 cm (B) (means of 4 values with standard error in italic).

	Depth	pH	Ca		Al		NO_3^-		Ca/Al	
	cm	(H_2O)	$mmol_c\ l^{-1}$		$mmol_c\ l^{-1}$		$mmol_c\ l^{-1}$		molar ratio	
Control	0-5	4.66	0.12	0.03	0.07	0.03	0.20	0.14	2.6	0.63
	5-15	5.28	0.21	0.05	0.06	0.00	0.17	0.04	5.3	1.4
	15-30	5.35	0.19	0.07	0.05	0.02	0.18	0.08	5.7	4.6
	30-45	5.24	0.15	0.03	0.03	0.01	0.08	0.01	7.5	7.5
$CaCO_3$	0-5	5.58	0.34	0.10	0.07	0.02	0.10	0.03	7.4	1.3
old	5-15	5.75	0.20	0.02	0.04	0.00	0.09	0.02	7.5	0.35
	15-30	5.79	0.18	0.02	0.03	0.01	0.08	0.02	9.0	2.6
	30-45	5.70	0.20	0.02	0.01	0.01	0.05	0.02	30	2.4
$CaSO_4$	0-5	4.64	0.20	0.03	0.03	0.00	0.03	0.02	10	2.4
old	5-15	5.59	0.23	0.04	0.06	0.01	0.08	0.01	5.7	0.72
	15-30	5.51	0.30	0.06	0.03	0.00	0.10	0.03	15	3.1
	30-45	5.14	0.29	0.07	0.06	0.05	0.06	0.00	7.2	10
$CaCO_3$	0-5	5.48	0.24	0.10	0.05	0.01	0.19	0.14	7.2	3.9
new	5-15	5.13	0.12	0.02	0.11	0.04	0.19	0.07	1.7	1.1
	15-30	5.28	0.16	0.01	0.10	0.03	0.22	0.06	2.4	1.1
	30-45	5.43	0.18	0.01	0.06	0.02	0.15	0.05	4.5	1.8
$CaSO_4$	0-5	5.04	0.17	0.04	0.06	0.02	0.06	0.02	4.2	2.4
new	5-15	4.98	0.30	0.11	0.04	0.00	0.03	-	11	5.8
	15-30	4.78	0.42	0.02	0.12	0.01	0.16	0.01	5.3	0.68
	30-45	5.00	0.28	0.05	0.07	0.04	0.14	0.00	6.0	2.8
mix	0-5	5.09	0.29	0.10	0.03	0.01	0.04	-	15	6.7
80/20	5-15	5.06	0.18	0.04	0.04	0.01	0.09	0.06	6.8	1.1
	15-30	4.95	0.24	0.04	0.08	0.04	0.10	0.05	4.5	3.4
	30-45	4.72	0.27	0.03	0.04	0.01	0.07	0.03	10	4.2

Stand growth

The results expressed in 'radial increment index %' (Ic %) showing the radial growth, are presented in Figure 1. The period of 1970 - 1989 was used to adjust the three curves. The figure shows an almost immediate significant increase in radial growth after both $CaCO_3$ and $CaSO_4$ applications as compared to the control. These increases relative to the control were significant for both treatments at the 5% level (at times1%) throughout the 1991-1996 period. As an average over 1991-1996 as compared to the control, this gain of radial growth (relative value) was 39% for the carbonate and 44% for the gypsum application.

Foliar nutrition

The analyses of 1992 indicate increases in S, P, Mn, Mg and N contents for the gypsum application as compared to the control and the lime application (Table 3), although no analysis of significance could be performed. Analyses after 3 years (1993) for the old treatments revealed no significant treatment effects for any of the elements analyzed, although differences in Ca content were close ($P = 0.052$). Foliar analysis in 1996 confirmed this Ca effect in the old plots, where the concentration in the control (2.8 ± 0.3 g kg^{-1}) is low and not even half that of

the old $CaCO_3$ and $CaSO_4$ treatments (6.0 to 6.7 g kg^{-1}). In the new plots, no significant effects appeared, showing that the effects on Ca nutrition were delayed.

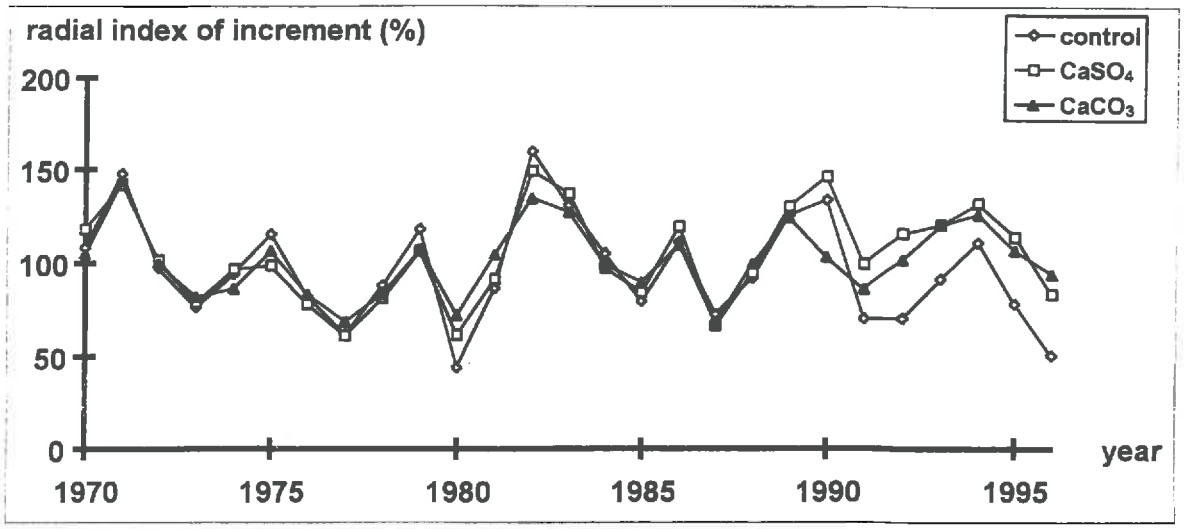

Figure 1 Tree growth: radial increment of *Quercus petraea* based on relative index values (%)

Table 3 Foliar composition in 1992, 1993 and 1996, 2 to 6 years after the applications (1990 for old; 1994 for new), replicated twice. Values are means of two blocks of pooled samples of 5 trees each. The mean is of one block for 1992 (no statistics) and of two blocks plus st. error (italic figures) in 1993 and 1996 (significant differences at $p<0.05$ level indicated by different letters).

treatment	year	1 *M* $HClO_4$ mineralized elements (g kg^{-1})						
		N	S	P	K	Ca	Mg	Mn
Control	1992	17	1.4	1.6	5.2	3.9	0.68	0.60
$CaCO_3$-old	1992	13	1.2	1.0	4.3	5.6	0.95	1.1
$CaSO_4$-old	1992	23	1.7	1.9	4.9	6.7	2.1	2.7
Control	1993	23	1.4	1.5	7.1	2.8	0.84	0.94
		0.88	*0.01*	*0.03*	*0.34*	*0.87*	*0.10*	*0.65*
$CaCO_3$-old	1993	22	1.4	1.3	7.2	4.3	0.86	0.82
		0.62	*0.06*	*0.17*	*0.45*	*0.28*	*0.14*	*0.10*
$CaSO_4$-old	1993	22	1.4	1.5	8.3	6.1	0.86	1.2
		1.2	*0.14*	*0.16*	*0.38*	*0.13*	*0.03*	*0.48*
Control	1996	26a	1.5	1.6	7.3	2.8b	0.92	0.76
		0.45	*0.05*	*0.11*	*0.08*	*0.30*	*0.08*	*0.47*
$CaCO_3$-old	1996	24ab	1.4	1.4	8.3	6.7a	1.0	0.53
		0.58	*0.03*	*0.10*	*0.39*	*0.66*	*0.19*	*0.03*
$CaSO_4$-old	1996	26a	1.6	1.6	8.4	6.0a	1.0	1.0
		1.20	*0.08*	*0.09*	*0.53*	*0.80*	*0.10*	*0.23*
$CaCO_3$-new	1996	23b	1.4	1.5	6.0	3.9b	1.3	0.77
		0.65	*0.03*	*0.07*	*1.3*	*0.53*	*0.11*	*0.39*
$CaSO_4$-new	1996	26a	1.5	1.8	7.0	4.6b	1.0	0.94
		0.93	*0.05*	*0.09*	*1.7*	*0.16*	*0.26*	*0.53*
Mix 80/20	1996	24ab	1.5	1.8	8.0	4.7b	1.1	0.67
		0.85	*0.12*	*0.02*	*0.37*	*0.67*	*0.06*	*0.08*

Discussion

Soil chemistry

The increase in CEC after liming or gypsum addition may be related to the pH-dependent character of the CEC (Pavan *et al.* 1984; 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, additions of dead plants from the forest floor, or to an interference with undissolved lime and gypsum particles. The latter possibility is unlikely in this study due to the fact that the increase in CEC is smaller in the new trial as compared with the old trial (Table 1). An increase of organic matter (higher litter fall, accumulation of humus) was not observed, either. On the contrary, the increases in pH-H_2O and base saturation, and the stimulation of mineralization in the litter and humus layers, as indicated by the higher nitrate concentrations in the soil solutions, after lime in this study and in another study on the same site (Belkacem and Nys 1995, 1997), support the concept that the increase of CEC is due to an increase in pH and the related dissociation of organic matter (André 1976).

The observed increases in exchangeable Mg and Ca, due to both lime and gypsum, together with decreases of Al, H^+ and Mn agree well with those of Haynes and Ludecke (1981), Reiter *et al.* (1986), Andersson and Persson (1988), Ranger *et al.* (1994) and Belkacem and Nys (1997). Affinity of soil exchange sites for the different cations (Haynes and Ludecke 1981) increases in the order Al < Ca < Mg < K < Na. Therefore, with time and for increasing lime rate, 'overliming stress' may cause exchangeable Mg, K and Na to decrease (Edmeades and Judd 1980; Haynes and Ludecke 1981; Grove and Sumner 1985; Myers *et al.* 1988; Belkacem and Nys 1997; Hüttl and Zöttl 1993). This time and dose dependent effect will differ according to soil depth and also depends on the dissolution rate of the product, which can be considerably lowered if applied on top of the humus layers (Derome 1990/91). In the present work, such an effect of the humus and litter layers on the dissolution rate of the products seems of minor importance, as these were only a few centimeters thick. Some elements can leach from top layers to accumulate in subsoil layers. Especially when liming induces increased N-mineralization, nitrate will be linked with the mobilization of cations into the mineral soil or subsoil horizons (Curtin and Smillie 1983; Hüttl and Zöttl 1993). However, such nitrate leaching was not observed in trials in the Ardennes and Vosges (Laudelout 1993; Ranger *et al.* 1994), nor in this study. Presumably, this is related to soil type (filtering effect) and the increased uptake by the above-ground biomass. Derome (1990/91) reports that lime affected the tree growth less on coarse substrates. Hüttl and Zöttl (1993) observed that in damaged stands, higher leaching losses occurred after lime application than in healthy stands where the elements liberated by liming were taken up by the trees.

Soil solution concentrations

Nitrate values were lower in the lime and gypsum plots as compared to the control. Leaching of nitrate after liming as observed by Matzner *et al.* (1983), Schierl and Kreutzer (1989) and Hüttl (1989), does not seem to occur for our site and lime conditions. If we compare the Ca/Al concentrations in the soil solution with values at which roots are damaged by Al (Cronan and Grigal 1995), it appears that in this study only the values in the control (Ca/Al ratios down to 0.24 and 0.50 in June and September) are in the range of the suggested toxicity limits of 0.2 to 0.5 commonly accepted (Rost-Siebert 1985; Cronan and Grigal 1995). However, toxicity maybe for certain species better related to absolute Al^{3+} concentrations or even to protons (Rost-Siebert 1985) and the Ca/Al ratio is poorly performing in many cases in predicting actual root mortality (Boudot et al. 1994). A more correct Al toxiticy index should comprise the

different forms and ionic strenghts of all the forms of Al and also incorporate the beneficial effects of other basic cations as Mg (Boudot et al. 1994). Tree species are more tolerant to Al than plant species (Keltjens and van Loenen 1989). Also, the relatively high pH values (at least in March) suggest that Al in the soil solution is not present in its most toxic forms. So, given the range of Ca/Al ratio and considering that other Al forms and cations are not accounted for, direct damage by Al to roots, may be possible in the control, but is improbable in the liming or gypsum treatments. Nevertheless, the slight increases of S (sulphate) and nitrate in the deeper soil horizons after liming and gypsum applications, together with a higher Al concentration, suggest that the applications resulted in some downward transport of Al in presence of sulphate and nitrate (Hendershot *et al.* 1991; Robinson 1994).

Effects on tree growth

The measurements of circumference (inventories 1995 and 1997) did not appear to be very sensitive when evaluating whether lime stimulated diameter growth. Therefore, a dendrochronogical approach was used instead. This corer based method of growth comparison provided a far better evaluation of the treatment responses and revealed that growth stimulation by the treatments based on annual increment (growth rings) was significant from the first year after application. It would probably have taken years for this effect to be shown as significant if circumference alone had been considered. Thus, it is possible that the effects in the new treatments - not sampled as growth responses were not expected yet - are already detectable. Such an increase of tree growth is more generally recorded, but does often occur after a few years (Derome 1990/91; Staaf et al. 1996). However, growth evaluations based on diameter measurements are far less accurate than dendrochronological measurements.

Mineral nutrition

An increase in foliar Ca and Mg after liming - especially if containing both Ca and Mg - may be expected (Hüttl and Zöttl 1993; Bonneau 1995) and a reduction in Mn, whereas effects on K, N and P seem variable. The relative increases found in 1992 but absent in 1993, suggest that the effect of gypsum was relatively fast but not lasting. The significant difference in N content between the $CaCO_3$ treatment and the others, either old or new, shows the effect of liming on organic matter mineralization (Hüttl and Zöttl 1993; Belkacem and Nys 1995). Our values compared with the critical levels (Bonneau 1995) of foliar content suggest that the supply of N, P, Mn and K is satisfactory and that Mg is poor in all trials, whereas the supply of Ca is poor for the control plots, but sufficient for the plots with lime or gypsum. This relative richness in P and poorness in Mg and Ca agrees with the nutritional status of the soil material, as stated previously.

Conclusions

The lime, gypsum or mixed applications resulted in an increase in CEC down to 30 cm, in base saturation down to 45 cm, increases in soil pH and soil exchangeable Ca at the surface and decreases in Al in the surface layers. Soil solution concentrations mainly showed increases in Ca and pH and decreases in Al and nitrate after treatments. Effects on solute sulphate were related to the sulphate applications and Mg concentrations were higher in the old than in the new plots (block effect rather than treatment response). Although there was no clear leaching of nitrate after the treatments, soil solution concentrations of sulphate, nitrate and Al suggest that the excess of Ca in the top soil causes ion exhange and subsequently some transport of Al to deeper horizons together with sulphate and nitrate. Ca/Al molar ratios indicating Al toxicity, were reached in the control but were alleviated by the doses applied in this study, and no overliming stress (decrease of other cations) was observed. Tree nutrition was improved for

Ca, but the poor Mg nutrition was not resolved. Tree growth was increased by about 40% as a result of old lime and old gypsum amendments; the extent to which this is similar for the new amendments is not yet known. The difference between the old and new trials seems to be merely a question of time, since the tendencies in the new trials are similar.

The question, whether increased tree growth and foliar biomass is due to an increased fine root biomass or an increased efficiency of the fine root biomass, will be dealt with in Part II.

Acknowledgments
We would like thank Jacques Ranger and several anonymous reviewers for their useful comments on earlier versions of this manuscript. Serge Didier is acknowledged for his technical assistance in the field. This research was supported by grants of INRA Paris and the Dutch Ministry of Agriculture, Nature Management and Fisheries, Directorate of Science and Knowledge Dissemination.

References

Andersson F and Persson T 1988 Liming as a measure to improve soil and tree conditions in areas affected by air pollution: results and experiences of ongoing research programme. Naturvårdsverket Report 3518, Sweden.131 p.

André J P 1976 Les propriétés d'échangeur cationique de la tourbe de sphaignes: échanges bicationiques entre le proton et un cation métallique. Ann. Agron. 27, 17-31.

Belkacem S and Nys C 1995 Consequences of liming and gypsum top-dressing on nitrogen and carbon dynamics in acid forest soils with different humus forms. Plant Soil 173, 79-88.

Belkacem S and Nys C 1997 Effects of liming and gypsum regimes on chemical characteristics of an acid forest soil and its leachates. Ann. Sci. For. 54, 169-180.

Bonneau M 1995 Fertilisation des forêts dans les pays tempérés. Théorie, bases du diagnostic, conseils pratiques, réalisations expérimentales. ENGREF, Nancy. 366 p.

Bouchon J, Nys C and Ranger J 1985 Cubage, biomasse et minéralomasse: comparaison de trois taillis simples des Ardennes primaires. Acta Oecologica/Oecol. Plant. 6, 53-72.

Boudot J P, Becquer T, Merlet D and Rouiller J 1994 Aluminium toxicity in declining forests: a general overview with a seasonal assessment in a silver fir forest in the Vosges mountains (France). Ann. Sci. For. 51, 27-51.

Clemensson-Lindell A and Persson H 1993 Long-term effects of liming on the fine-root standing crop of *Picea abies* and *Pinus sylvestris* in relation to chemical changes in the soil. Scan. J. For. Res. 8, 384-394.

Cronan C S and Grigal D F 1995 Use of calcium/aluminum ratios as indicators of stress in forest ecosystems. J. Environ. Qual. 24, 209-226.

Curtin D and Smillie G W 1983 Soil solution composition as affected by liming and incubation. Soil Sci. Soc. Am. J. 47, 701-707.

Derome J 1990/91 Effects of forest liming on the nutrient status of podzolic soils in Finland. Water Air Soil Pollut. 54, 337-350.

Edmeades D C and Judd M J 1980 The effects of lime on the magnesium status and equilibria in some new Zealand topsoils. Soil Sci. 129, 156-161.

Ericsson T, Göransson A, Van Oene H and Gobran G 1995 Interactions between aluminium, calcium and magnesium - Impacts on nutrition and growth of forest trees. Ecol. Bull. 44, 191-196.

Espiau P and Pedro G 1980 Caractérisation du complexe d'échange des sols acides. Le taux d'acidité d'échange et sa signification pédogénètique sous climat tempéré. Ann. Agron. 31, 363-383.

Fehlen N and Picard J-F 1994 Influence de la fertilisation sur la végétation spontanée et la croissance radiale de l'épicéa commun (*Picea abies* L. [Karst.]) dans une plantation adulte des Ardennes Françaises. Ann. Sci. For. 51, 569-580.

Glatzel G, Kazda M and Sieghardt M 1986 Zur Frage der Melioration versauerter Boden aus schadstoffbelasteten Buchenwäldern durch Zufuhr von Kalk oder halbgebranntem Dolomit. Ein Gefassversuch mit Rotbuche (*Fagus sylvatica*). Z. Pflanzernähr. Bodenk. 149, 658-667.

Godbold D L, Dictus K and Hüttermann A 1988 Influence of aluminium and nitrate on root growth and mineral nutrition of Norway spruce (*Picea abies*) seedlings. Can. J. For. Res. 18, 1167-1171.

Göransson A and Eldhuset T D 1987 Effects of aluminum on growth and nutrient uptake of *Betula pendula* seedlings. Physiol. Plant. 69, 193-199.

Grove J H and Sumner M E 1985 Lime-induced magnesium stress in corn: Impact on magnesium and phosphorus availability. Soil Sci. Soc. Am. J. 49, 1192-1996.

Haynes R J and Ludecke T E 1981 Effects of lime and phosphorus applications on concentrations of available nutrients and on P, Al and Mn uptake by two pasture legumes in an acid soil. Plant Soil 62, 117-128.

Heilman P and Ekman G 1973 Response of Douglas-fir and Western Hemlock seedlings to lime. For. Sci. 19, 220-224.

Hendershot W H, Warfvinge P, Courchesne F and Sverdrup H U 1991 The mobile anion concept - Time of a reappraisal? J. Environ. Qual. 20, 505-509.

Hüttl R F 1989 Liming and fertilization as mitigating tools in declining forest ecosystems. Water Air Soil Pollut. 44, 93-118.

Hüttl R F and Zöttl H W 1993 Liming as a mitigation tool in Germany's declining forests - reviewing results from former and recent trials. For Ecol. Manage. 61, 325-338.

Joslin J D and Wolfe M H 1989 Aluminum effects on northern red oak seedling growth in six amended forest soil horizons. Soil Sci. Soc. Am. J. 53, 274-285.

Keltjens W G and van Loenen E 1989 Effects of aluminium and mineral nutrition on growth and chemical composition of hydroponically grown seedlings of five different forest tree species. Plant Soil 119, 39-50.

Kestemont P 1975 Biomasse, nécromasse et productivités aériennes ligneuses de quelques peuplements forestiers en Belgique. PhD Thesis, Université Libre de Bruxelles. 334 p.

Laudelout H 1993 Chemical and microbiological effects of soil liming in a broad-leaved forest ecosystem. For. Ecol. Manage. 61, 247-261.

Ljungström M and Nihlgård B 1995 Effects of lime and phosphate additions on nutrient status and growth of beech (*Fagus sylvatica* L.) seedlings. For. Ecol. Manage. 74, 133-148.

Matzner E, Khanna P K, Meiwes K-J and Ulrich B 1983 Effects of fertilization on the fluxes of chemical elements through different forest ecosystems. Plant Soil 74, 343-358.

Myers J A, McLean E O and Bingham J M 1988 Reductions in exchangeable magnesium with liming of acid Ohio soils. Soil Sci. Soc. Am. J. 52, 131-136.

Pavan M A, Bingham F T and Pratt F J 1984 Redistribution of exchangeable calcium, magnesium and aluminum following lime or gypsum applications to a Brazilian Oxisol. Soil Sci. Soc. Am. J. 48, 33-38.

Ponette Q, Dufey J E and Weissen F 1997 Downward movement of dolomite, kieserite or a mixture of $CaCO_3$ and kieserite through the upper layers of an acid forest soil. Water Air Soil Pollut. 95, 353-379.

Ranger J, Daldoum M A and Gelhaye D 1994 Effet d'un amendement calco-magnésien associé ou non à une fertilisation, sur le cycle biogéochimique des éléments nutritifs dans une

plantation d'épicéa commun (*Picea abies* Karst) dépérissante dans les Vosges. Ann. Sci. For. 51, 455-475.

Ranger J, Nys C and Ranger D 1981 Etude comparative de deux écosystèmes forestiers feuillus et résineux dans les Ardennes primaires françaises. I. Biomasse aérienne des taillis-sous-futaie. Ann Sci. For. 38, 259-282.

Reiter H, Bittersohl J, Schierl R and Kreutzer K 1986 Einfluß von saurer Beregnung und Kalkung auf auftauschbare und gelöste Ionen im Boden. Forstwiss. Cbl. 105, 300-309.

Robinson D 1994 The responses of plants to non-uniform supplies of nutrients. New Phytol. 127, 635-674.

Roelofs J E M, Kemper A J, Houdijk A L F M and Jansen J 1985 The effect of air-borne ammonium-sulphate on *Pinus nigra* var. maritima in the Netherlands. Plant Soil 84, 45 - 56.

Rost-Siebert K 1985 Untersuchungen zur H- und Al-Toxizität an Keimpflanzen von Fichte (*Picea abies* Karst.) und Buche (*Fagus sylvatica* L.) in Lösungskultur. Berichte Forschungszentrum Waldökosysteme, Universität Göttingen 12, 1-219.

Schierl R and Kreutzer K 1989 Dolomitische Kalkung eines Fichtenbestandes auf saurer Parabraunerde: Auswirkungen auf Bodenchemie und Vegetation. Kali-Briefe (Büntehof) 19, 417-423.

Shamshuddin J, Chefauziah I and Sharifuddin H A H 1991 Effects of limestone and gypsum applications to a Malaysian Ultisol on soil solution composition and yields of maize and groundnut. Plant Soil 134, 45-52.

Staaf H, Persson T and Bertills U (Eds.) 1996 Skogsmarkskalkning. Resultat och slutsatser från Naturvårdsverkets försöksverksamhet. Naturvärdsverket rapport 4559. Tryck Gotab, Stockholm.

Trüby P 1989 Eine Titrationsmethode zur simultanen Bestimmung von H^+ und Aluminium in NH_4Cl-Bodenextrakten. Z. Pflanzenernaehr. Bodenk. 152, 297-300.

Unistat Ltd 1995 Unistat version 4.0 for Windows.

Weissen F, van Praag H J, Marechal P, Delecour F and Fracy C 1988 Les causes de dégradatior sanitaire de forêts en Wallonie: le point de la situation. Bull. Soc. Roy. de Belgique 95, 57-68.

Annexe A (Paper II) : *Plant and Soil* **00**: 1-13, 1998
Reçu le 25 mai 1998 ; accepté en version révisée le 15 septembre 1998.
Repris dans cet oeuvre avec la permission de l'editeur Kluwer academic publishers.

The effect of lime and gypsum applications on a sessile oak (*Quercus petraea* (M.) Liebl.) stand at La Croix-Scaille (French Ardennes) II. Fine root dynamics.

M.R. Bakker

Abstract

Fine root distribution, quantities, dynamics and composition were studied in a sessile oak coppice stand in the French Ardennes on an acidic soil (< pH-H_2O 4.5), 1 to 5 years after lime or gypsum applications. Fine root biomass and length increased and specific root length decreased after lime or gypsum treatments. The treatment responses were strongest four to five years after the applications, but the tendencies after one year were similar. The effects were pronounced in the top 15 cm but also at 30-45 cm four to five years after liming. The latter effect suggests an indirect positive feedback from the aerial parts of the trees into the deeper soil layers. Sequential sampling for two years revealed large differences in total fine root length between the years, and also indicated that fine root turnover was lower after liming or gypsum applications than in the control. This seemed to be related to a lower fine root mortality and higher longevity rather than to increased fine root production. The improved nutrient status of the fine roots corroborates this and coincides with improved foliar nutrition and tree growth. Moderate doses of lime and gypsum appeared effective in enhancing root system uptake function, resulting in increased above ground growth.

Key-words: fine root biomass, fine root dynamics, fine root length, gypsum, lime, *Quercus petraea*.

Introduction

Fine roots with the function of nutrient and water uptake can fluctuate considerably in biomass throughout the season or between years, according to site events (Persson 1983; Olsthoorn 1991). Although uptake of water and Mg (Dieffenbach *et al.* 1997) is of importance in the suberised parts of fine roots, most of the nutrient uptake seems to occur in new roots in the zone immediately behind the apex of the root tips. Hence the need for continuous renewal, as suberization and nutrient depletion around the roots occur fairly quickly (Persson 1983). Consequently, fine root parameters are useful for the evaluation of site conditions (Squire *et al.* 1978; Clemensson-Lindell and Persson 1993) and for the understanding of their role in nutrient cycles in forest ecosystems.

Fine root biomass and fine root length density are highest in the top 15 cm of mineral soil or in the litter and humus, reflecting both the better physical environment and higher nutrient availability there (Deans 1979; Vogt *et al.* 1981). Fine roots in deeper horizons are far less numerous, but can be of importance for uptake, especially in dry periods. Fine root growth is often greatest in spring and early summer (Deans 1979; Van Praag et *al.* 1988; Kummerow *et al.* 1990), but climatic events like summer drought may lead to substantial differences between seasons or years (Persson 1983; Olsthoorn 1991).

Highly acidic and poor site conditions can limit fine root growth and acidification related to excess nitrogen or Al toxicity may lead to changes in root branching, root elongation and specific root length (Rost-Siebert 1985; Matzner *et al.* 1986; Fiskesjö 1989; Kruger and Sucoff

1989; Raspe 1992). Liming can counteract these effects, but acts slowly. Gypsum is more soluble and has an effect further down into the profile, but since a larger part of the product is transported downward in soil, the effects on pH and Ca availability in the surface layers are more limited and often do not last as long as those of liming.

This study focuses on a coppiced oak (*Quercus petraea*) stand on a nutrient poor acidic brown forest soil. The soil has a loamy texture and pH-H_2O values range from 3.6 in top soil layers about 4.4 to 4.7 in subsoil layers. Base saturation is generally below 10 % and levels of exchangeable K are low and of exchangeable Ca and Mg extremely low. The effects of liming on stand growth, foliar nutrition, soil and soil solution were detailed in Part 1. The effects of liming on below-ground phytomass (biomass and necromass) and nutrient availability are discussed in this paper. The aim of this study was to determine the effects of liming on fine root biomass, length, distribution, and the development of these effects with time. The hypothesis was that both liming and gypsum treatments would increase base saturation (and percentage occupation of the CEC by Ca and Mg) with a concomittant increase in base cation concentrations in the soil solutions, stimulating fine root development, biological acitivity (mineralization) and thereby improving tree growth and nutrition. The effect of gypsum would be faster and penetrate deeper into the soil layers than that of liming, related to the higher solubility of gypsum.

Methods

Experimental treatments

Treatments consisted of a control, and additions of 1.4 $t.ha^{-1}$ CaO as $CaCO_3$ (lime), 1.4 $t.ha^{-1}$ CaO as $CaSO_4$ (gypsum) and a mix of 1.4 $t.ha^{-1}$ CaO as $CaCO_3$ (80 %) and $CaSO_4$ (20 %). The old trial (established 1990) consisted of 2 blocks with each one control, one lime (old lime), and one gypsum (old gypsum) treatment (2 replicate blocks in total). The new trial (established in 1994) consisted of two blocks with each one lime (new lime), one gypsum (new gypsum) and one mix (mix 80/20) treatment (2 replicate blocks in total). The control of the old trial was shared by the new trial. More details are to be found in Part 1. Sampling of roots was carried out in June and September 1994, March, June and September 1995 and March 1996. Thus, the root data cover two growing seasons: 1994 and 1995.

Sampling procedure

Root samples were gathered by sequential core sampling using either small soil density cylinders (Ø 6.4 cm) hammered into the soil (1994) or a soil corer (Ø 8.0 cm) in 1995 and 1996, avoiding zones with abundant vegetation and the proximity of stems of oak trees. This was done to obtain comparable samples and to facilitate processing : close to the stem rooting is often too dense and separation of other than oak roots is not always easy and costs more effort. Each profile sampled was stratified into 5 layers per core: 0-5, 5-15, 15-30, 30-45 and 45-55 cm, corresponding to the soil profile (see also part I). Due to the low rooting intensity and higher stoniness, regular sampling was limited to 45 cm and few samples were taken at 45-55 cm (for description). Roots in the litter and humus were only sampled once (September 1995) on four areas of 0.10 m^2 per treatment.

Sample processing and measurements

In the laboratory the root core samples were wet sieved with tap water through 4 and 2 mm sieves and root length was estimated by counting intersections (Tennant 1975). One series of samples per block was processed within three days. On this series length and weight of dead roots were determined to estimate the proportion of root necromass. A sub-sample of the living

fine roots was cleaned more thoroughly and handled faster. After moderate drying, a second cleaning was performed with brushes, then the roots were further dried and used for total chemical analysis. These sub-samples were pre-treated with H_2O_2 and wet-digested by $1N$ $HClO_4$ (ratio 1/20 : g of root DW / ml of perchloric acid), then the aqueous solution was analysed by ICP. Dead roots were separated from living roots using general visible criteria: resilience, brittleness, colour of bark and xylem. This was calibrated and confirmed by observations under a binocular microscope. The very fine fraction of roots (<0.5 mm) was counted on only a small number of samples. Root dry weight was assessed after drying at 105 °C to constant weight. The rest of the samples not processed immediately, were stored at +1°C for a maximum of 2-3 months until being processed.

Sample number

The number of samples needed statistically per treatment is a function of soil conditions and management history, and is site-specific (Vogt & Persson 1991). Olsthoorn (1991) used 55 core-samples for Douglas-fir for calibration and found that below 10 samples, standard error increased fairly sharply. In June 1994, 30 fine root length samples per treatment and layer were taken to calibrate the following periods. Minimum sample number within 10 % of the arithmetic mean (Millier *et al.* 1986) per treatment and layer appeared to range from 8 to 12 in nearly all cases. Therefore, from September 1994, 12 samples per treatment and per horizon were taken, comparable to the number of 10 to 13 calculated in other studies (Vogt *et al.* 1986; Olsthoorn 1991; Burke and Raynal 1994).

Correction factors

Processing fine root samples induces losses of weight and smaller parts of roots. Van Noordwijk and Floris (1979) estimated this loss to be 20 to 48 %. Therefore, in this study, five correction factors accounting for both losses and overestimates (due to pollution with soil particles), were established on the basis of a series of tests carried out in 1994 and 1995.

(1) Losses through sieveing were estimated using very fine sieves under the two regular sieves in order to collect the mud with lost fine root particles and to separate these particles from the mud by washing small fractions of the effluent very carefully. Estimates were based on samples from all soil horizons and regardless of the amount of roots in the sample, the loss appeared to be a fairly constant proportion of the total sample. Weight and length losses of this type for fine roots were in the order of just over 10 % and 26.5 % respectively (for 28 samples).

(2) Loss of weight by washing and floating and (3) loss during average storage was evaluated on 15 samples of clean fine roots obtained from a nursery experiment. Three series of five samples were subjected to different treatments; immediate drying at 105°C to constant weight, average washing (washing 2 min., floating 10 min.) and then drying at 105°C to constant weight, or average storage and washing (storage at + 1°C for in soil for an average of 1.5 months) and then drying at 105°C to constant weight. These tests revealed that the loss by pure washing and floating during normal handling time was nearly negligible, but that storage and then washing of the roots caused losses in the order of 10 % as compared to immediate handling.

(4) A correction for adhering soil particles was assessed by comparing the ash-free content of clean roots and roots of regular samples after loss on ignition up to 650°C (Vogt & Persson 1991). The difference in content was attributed to the weight of the adhering soil particles, which formed the percentage of overestimation. Overestimates of this type (based on 18

samples) appeared to be 1% of weight. (5) Counts of the occupation of apices by mycorrhizas under magnification revealed small quantities of dead root tips. Five soil samples from different depths on which dead and live roots had been separated according to normal procedure, were taken for observation under a binocular microscope and dead roots were removed from the living sample and vice versa. It appeared that the net inclusion of dead roots accounted for only 0.4 % of weight and 1.5 % of length of fine roots. Clearly, the occurrence of dead root tips was not limited to dead roots, but was also observed on parts of live roots.

Final correction terms were evaluated at + 20 % for weight of living fine roots (< 2 mm in diameter) , + 10 % for weight of dead fine roots (no storage losses accounted for as the determination of root necromass proportion was carried out upon return from the field) and + 25 % for length of both dead and living fine roots.

Data processing

Bulk values of weight and length, standardized to 10 cm layers, were converted - including the estimated correction terms - 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} dry matter). Results after chemical analyses of root contents were calculated relative to 105° C oven-dry weights (Burke and Raynal 1994). The parameters were tested for treatment, season and soil depth effects by ANOVA, and the Student-Newman-Keuls test (Unistat 4.0) was used to separate the group means. Of the six complete data sets of both seasons, only the most representative and complete data-sets of June 1994 and September 1995 are presented. It was judged that June 1994 was better than September 1994, since number of replicates (30) was higher than that of September (12). Logically, these data compare better with data from the same season (June or September 1995) than of another season (March 1995 or 1996). Since September 1995 comprised all treatments (old and new trials entirely sampled), the data-set of September 1995 was preferred.

Calculation of fine root turnover

Estimates of fine root production in forests are generally derived from comparisons of changes between live or both live and dead fine roots, sampled periodically throughout at least 1 year (Santantonio *et al.* 1977; Keyes and Grier 1981, McClaugherty & Aber 1982; Fogel 1983; Persson 1983; Nadelhoffer *et al.* 1985), and limited sampling is considered sufficient (McClaugherty and Aber 1982; Vogt *et al.* 1986) in case of a unimodal peak of root biomass as shown for the Belgian Ardennes (Van Praag *et al.* 1988). Fine root production (P) was defined as the fine root biomass formed during the interval; mortality (M) as the dead root biomass formed during the interval; and decomposition (D) as the shift of root material to the organic matter pools. These values were calculated on the basis of all increments and decrements of both live and dead fine root matter (McClaugherty and Aber 1982). Turnover rate (Tr) was expressed as the ratio of ((P + M)/2) / (mean live pool).

Results

Fine root distribution

In the control plots about 60 % of total fine root biomass for the profile down to 55 cm, occurred in the top 15 cm with only about 7 % below 45 cm (Figure 1). Fine root matter in humus and litter layers (September 1995 data) was not taken into consideration in this figure, as it appeared negligible: 11 to 56 kg ha^{-1} with a length of 0.2 to 0.5 10^6 m ha^{-1}, corresponding to a maximum of 2% of total fine root matter.

Table 1 Fine root biomass (FRB in kg ha^{-1}), fine root length density (FRLD in cm cm^{-3}), specific root length (SRL in m g^{-1}) and fine root length (FRL in 10^6 m ha^{-1}) of Oak (Quercus petraea) in June 1994 and September 1995 (st.error in italic and significant differences on basis of ANOVA and Student-Newman-Keuls test at $p<0.05$ level indicated with different letters; statistics applied to 0-45 cm only)

		FRB		FRLD		SRL	
		June '94	Sep '95	June '94	Sep '95	June '94	Sep '95
depth cm	treatment	kg ha^{-1} n = 30	kg ha^{-1} n = 12	cm cm^{-3} n = 30	cm cm^{-3} n = 12	m g^{-1} n = 30	m g^{-1} n = 12
0-5	Control	799 *87*	990 *120*	3,22 *0,28*	1,64 *0,21*	23,5 *1,52* **a**	8,66 *0,74*
	$CaCO_3$-old	1142 *153*	987 *147*	3,32 *0,31*	2,06 *0,32*	18,1 *1,43* **b**	11,3 *1,24*
	$CaSO_4$-old	942 *67*	1283 *255* **a**	3,68 *0,20*	2,33 *0,32* **a**	20,8 *1,03*	11,3 *1,39*
	$CaCO_3$-new		572 *76* **a**		1,13 *0,13* **b**		11,4 *1,74*
	$CaSO_4$-new		653 *140*		1,38 *0,19*		12,6 *1,77*
	Mix 80/20		938 *161*		1,82 *0,22*		12,6 *1,94*
5-15	Control	1046 *105* **b**	755 *59*	1,67 *0,14* **b**	0,54 *0,06*	18,4 *1,63*	7,16 *0,54*
	$CaCO_3$-old	975 *102*	508 *87*	1,34 *0,11* **b**	0,46 *0,08*	16,2 *1,24*	9,6 *1,19*
	$CaSO_4$-old	1370 *121* **a**	642 *136*	2,25 *0,15* **a**	0,58 *0,10*	18,0 *1,23*	10,2 *0,90*
	$CaCO_3$-new		797 *136*		0,52 *0,08*		7,25 *0,99*
	$CaSO_4$-new		544 *117*		0,68 *0,16*		23,3 *11,9*
	Mix 80/20		933 *189*		0,58 *0,08*		8,69 *1,46*
15-30	Control	854 *78*	544 *118*	1,19 *0,07*	0,45 *0,07*	24,0 *1,86*	15,3 *2,35*
	$CaCO_3$-old	1093 *144*	572 *107*	1,28 *0,12*	0,51 *0,13*	22,6 *1,62*	14,4 *1,71*
	$CaSO_4$-old	1102 *209*	547 *114*	1,27 *0,09*	0,45 *0,07*	22,6 *1,85*	15,1 *1,91*
	$CaCO_3$-new		675 *165*		0,46 *0,07*		14,9 *2,42*
	$CaSO_4$-new		814 *117*		0,53 *0,07*		10,6 *1,00*
	Mix 80/20		794 *183*		0,52 *0,11*		11,0 *1,22*
30-45	Control	487 *55* **b**	224 *62* **c**	0,68 *0,04*	0,23 *0,05* **b**	26,1 *2,09* **a**	19,2 *2,45* **a**
	$CaCO_3$-old	738 *90* **a**	734 *160* **a**	0,83 *0,07*	0,56 *0,10* **a**	19,0 *1,07* **b**	13,5 *1,29*
	$CaSO_4$-old	556 *40*	413 *86* **bc**	0,82 *0,04*	0,38 *0,05*	24,8 *1,59* **a**	17,7 *2,10*
	$CaCO_3$-new		374 *73*		0,24 *0,03*		11,7 *1,52* **b**
	$CaSO_4$-new		500 *112*		0,42 *0,09*		16,8 *2,81*
	Mix 80/20		657 *99* **ab**		0,40 *0,07*		10,4 *1,53* **b**
45-55	Control	269 *162*	228 *101*	0,72 *0,41*	0,30 *0,02*	29,1 *4,16*	16,8 *8,14*
	$CaCO_3$-old	251 *84*	528 *380*	0,46 *0,10*	0,43 *0,11*	22,0 *3,83*	13,9 *8,00*
	$CaSO_4$-old	215 *116*	242 *51*	0,48 *0,19*	0,49 *0,01*	39,4 *14,8*	21,3 *4,26*
	$CaCO_3$-new		377 *217*		0,23 *0,08*		7,51 *2,25*
	$CaSO_4$-new		828 *191*		0,58 *0,09*		7,67 *2,87*
	Mix 80/20		101 *60*		0,21 *0,06*		26,2 *9,57*

	Totals:	FRB		FRL	
		kg ha^{-1}	kg ha^{-1}	10^6 m ha^{-1}	10^6 m ha^{-1}
0-55	Control	3455	2741	68,0	26.8
	$CaCO_3$-old	4199	3329	66.3	35.2
	$CaSO_4$-old	4185	3127	77.1	34.9
	$CaCO_3$-new		2795		23.6
	$CaSO_4$-new		3339		33.9
	Mix 80/20		3423		30.7

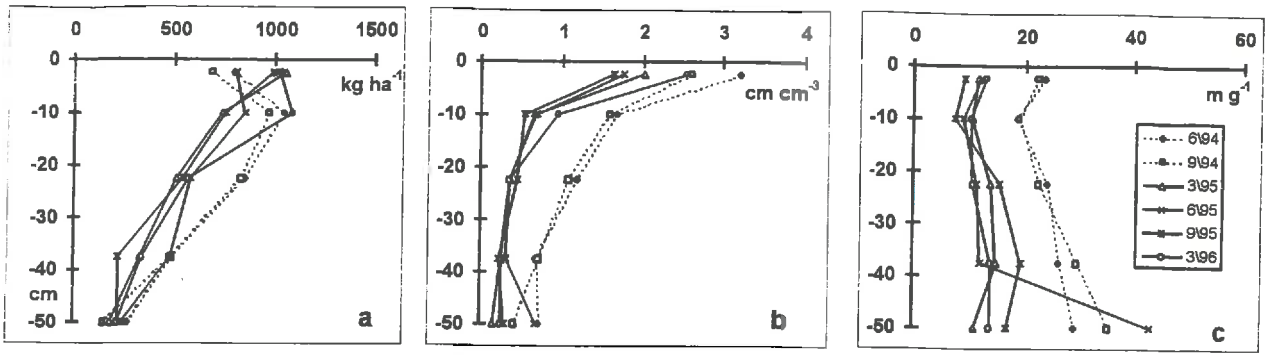

Figure 1 Distribution in the control of fine root biomass in kg ha^{-1} (a), fine root length density in cm cm^{-3} (b) and specific root length in m g^{-1} (c) through the profile for all six sampling periods (June 1994 to March 1996)

Fine root changes within and between seasons

Fine root biomass and length in the control down to 55 cm totalled 3.1 to 3.5 t ha^{-1} and 60 to 68 10^6 m ha^{-1} from June (Table 1, Figure 2) to September 1994. Total fine root biomass in March 1995, when the water-table reached sub-surface layers in some areas by the end of the winter, fell non-significantly to nearly 2.8 t ha^{-1}, whereas total fine root length showed a significant decrease and was only 28 10^6 m ha^{-1} (Figure 2). After the spring growth of 1995, total fine root biomass and length were higher in June 1995, but the mid-summer drought caused another non-significant decrease in fine roots from June to September (Table 1 and Figure 2). Finally, autumn rain and a moderate winter enabled fine root production, increasing the total fine root biomass and fine root length from September 1995 to March 1996. Specific root length (SRL) was in the order of 20-25 in 1994 for the top 30 cm, significantly increasing to 30 to 40 towards the 45-55 cm layer (Figure 1). The SRL values were significantly lower in '95 and '96 (10-15 for the upper 30 cm and 10-20 for 30-55 cm), with slight but significant increases in September 1995 in the deepest layer.

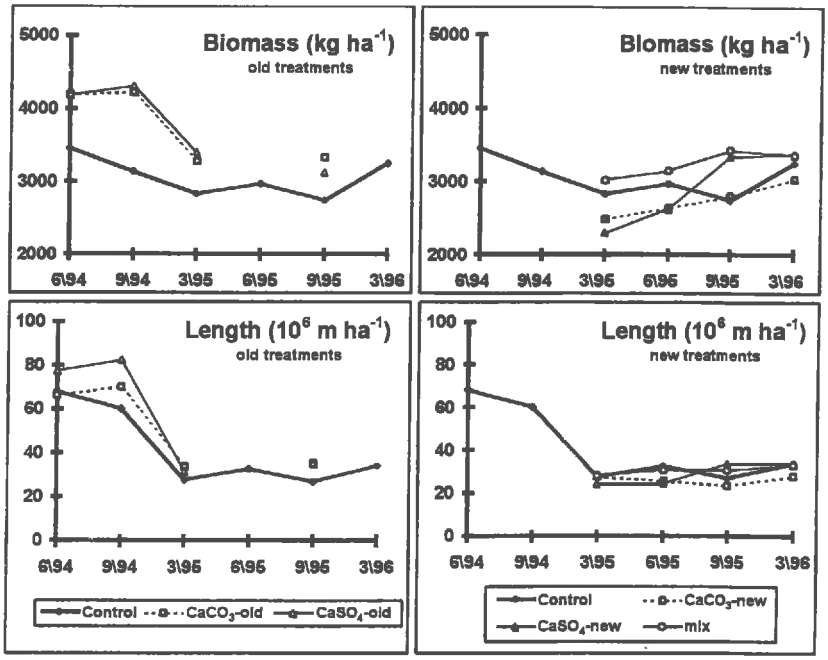

Figure 2 Total fine root biomass (kg ha^{-1}) and fine root length (10^6 m ha^{-1}) for old (left side) and new treatments (right side) from June 1994 to March 1996.

Effect of lime and gypsum on fine roots

Both lime and gypsum stimulated fine root amount four to five years after application (Table 1), although this was significant only in some layers and not in all six periods. The old lime treatment stimulated total fine root biomass and length down to 55 cm by 24 and 17 %, respectively (Figure 2), as compared to the control for the growing seasons of 1994 and 1995. Similarly, old gypsum increased both total fine root biomass and length by 23 % on average, but the gain decreased for 1995 as compared to 1994. This gain in fine root matter by the old treatments occurred mainly at two depths: at 0-5 and 30-45 cm for the limed trees and at 5-30 cm for the gypsum plots (Figure 3). In the upper 5 cm fine root biomass increased and SRL decreased in the old liming treatment as compared to the control; the old gypsum treatment showing intermediate values. For 5-30 cm, the old gypsum treatment showed a significantly higher fine root biomass and fine root length density as compared to the other treatments; this is in accordance with its higher solubility. In the subsoil 30-45 cm, only the old liming treatment showed significantly higher fine root biomass, without an increase in root length, so that SRL decreased (Figure 3). The percentage of fine root biomass below 30 cm in the old lime treatment was 24 to 38 % of the total fine root biomass, which is higher than in the control (16 to 22 %) and the old gypsum (19 to 23%) treatments.

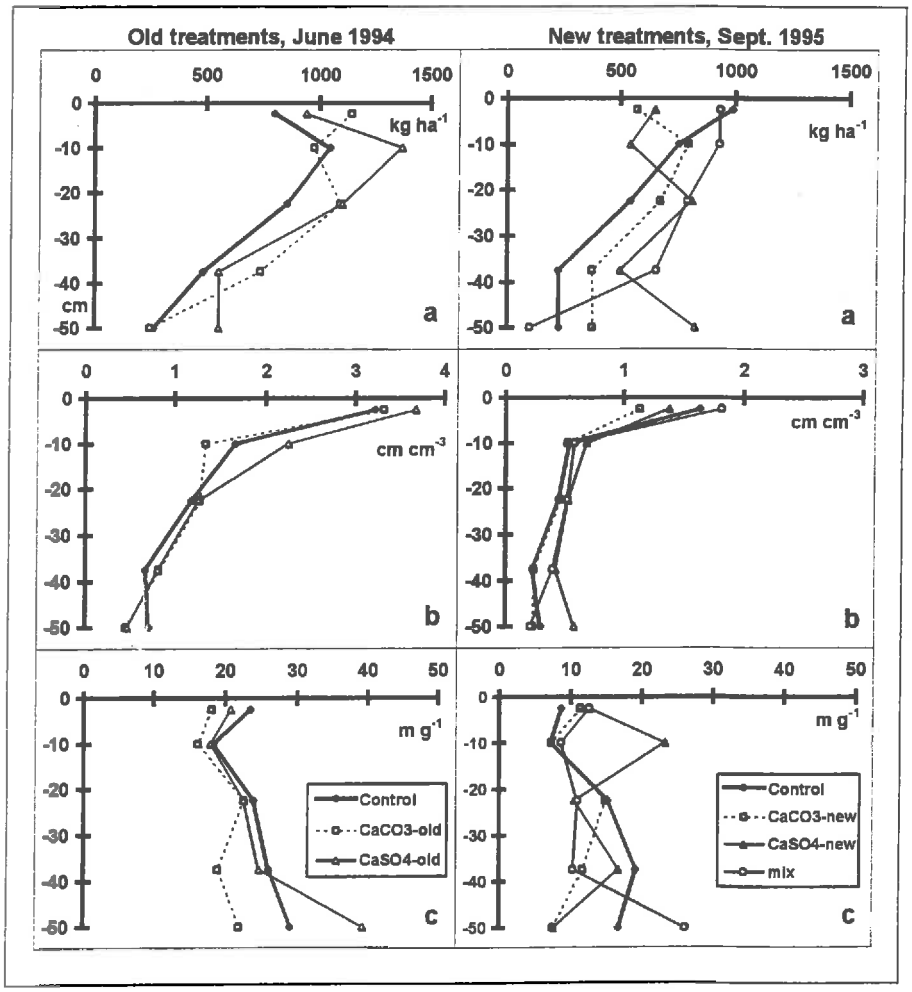

Figure 3 Fine root biomass in kg ha^{-1} (a), fine root length density in cm cm^{-3} (b) and specific root length in m g^{-1} (c) in old (4 years) and new (one year since application) treatments

Before the treatments were applied in the new trial, fine root biomass and length were similar to control values (June 1994). The initial effects of the new treatments were not significant in March 1995, but appeared to increase fine root biomass and to a lesser degree fine root length in the period March 1995 to March 1996. In September 1995 these increases, relative to the control, were between 22 to 25 % for fine root biomass and 15 to 26 % for fine root length for the new gypsum and mix 80/20, respectively. This was only significant for the mix 80/20 treatment and not for the new gypsum, whereas the new lime treatment remained unaffected. This reflects the difference in reactivity in the short term between the treatments containing more solube gypsum as compared to the liming treatment. This suggests, that more consistent and positive effects will occur in the mid-term for all new treatments, similar to the effects observed in the old trial (Figure 2 and 3).

Fine root necropools

Total fine root necromass ranges from 0.6 to 1.9 t ha^{-1} and fine root necrolength from 11 to 39 10^6 m ha^{-1}. Fine root necromass is a more or less stable proportion of total live root matter, fluctuating with time, showing no clear treatment effects between 1994-1996. Compared to live pools, the proportion of dead root matter to total phytomass was 15 to 40 %, being 25 to 55 % of total phytolength. In half of the plots live to dead ratios increased in September 1995 in the deepest horizons.

Fine root dynamics and turnover

Table 2 presents the estimates of fine root production, turnover, decomposition and turnover rate. The 1994 growing season suggests a lower mortality and turnover rate for the old liming and old gypsum treatments as compared to the control. The 1995 growing season, affected by summer drought, indicates slightly higher production figures and turnover rates for the three new treatments and again a lower turnover rate in the old treatments as compared to the control. Averaging both growing seasons, fine root production on this site ranges from 0.3 to 2.1 t.ha^{-1}.yr^{-1}, and the turnover rate from 0.24 to 0.90.

Table 2 Fine root dynamics: production (P), mortality (M) and decomposition (D) estimates and the comparison with the pool of live roots (turnover rate) by the average of P and M divided by mean live standing crop

treatment	year	Fine root dynamics			average pool of live roots	turnover rate
		P	M	D		
		kg ha^{-1} yr^{-1}	kg ha^{-1} yr^{-1}	kg ha^{-1} yr^{-1}	kg ha^{-1}	times yr^{-1}
Control	1994	1532	4252	5208	3208	0.90
$CaCO_3$-old		388	3250	2696	3752	0.48
$CaSO_4$-old		1962	2328	2850	3621	0.59
Control	1995	1576	1188	1190	2727	0.51
$CaCO_3$-old		1018	1182	986	2842	0.39
$CaSO_4$-old		286	1224	1584	3120	0.24
$CaCO_3$-new		1600	1197	1498	2572	0.54
$CaSO_4$-new		2149	1238	1335	2587	0.65
Mix		1874	1671	1972	3058	0.58

Fine root composition

Table 3 shows that the treatments significantly affected only Mn, Mg and Ca content and the Ca/Al molar ratio of the fine roots. Mean contents (g kg^{-1}) for S (1.5), P (0.6), Al (6.5) and K (3.5) and molar Mg/Al ratio (0.15) were not significantly affected by liming. P and Ca content of fine roots and the ratios Ca/Al and Mg/Al were significantly higher in the top soil and decreased with depth, whilst conversely the Al content increased significantly with depth. As can be seen in Table 3, liming essentially decreased the Mn content of fine roots, while increasing the Ca content. The differences in total mineral pools in fine roots between the treatments were greater (Table 4), since biomass acted as a multiplier. This is especially pronounced for Ca with almost twice the amount stored in the old lime plot as compared to the control, and to a lesser extent the same applies for Mg, Al and K.

Table 3 Fine root composition in g kg^{-1} of mass for the 0-45 cm layers of 1995 (3 periods) pooled (with st. error between brackets and significant differences based on ANOVA and Student-Newman-Keuls test indicated by different letters).

treatment	sample n	g kg^{-1} Mg	g kg^{-1} Ca	g kg^{-1} Mn	molar Ca/Al
Control	24	0.9 (0.1)	2.1 (0.2) **b**	0.3 (0.0) **a**	0.28 (0.05)
$CaCO_3$-new	24	0.8 (0.1) **b**	2.5 (0.2) **b**	0.2 (0.0) **b**	0.30 (0.08)
$CaCO_3$-old	16	1.0 (0.0)	3.8 (0.7) **a**	0.1 (0.0) **bc**	0.46 (0.12) **a**
$CaSO_4$-new	24	0.8 (0.0)	2.7 (0.3) **b**	0.2 (0.0) **b**	0.23 (0.03) **b**
$CaSO_4$-old	15	1.0 (0.1) **a**	2.7 (0.2) **b**	0.3 (0.0) **a**	0.35 (0.15)
Mix 80/20	24	0.9 (0.1)	2.4 (0.2) **b**	0.1 (0.0) **c**	0.29 (0.05)

Table 4 Average amount of minerals in live fine roots in kg/ha in 1995

	S	P	Mn	Mg	Al	Ca	K
Control	4.50	1.49	0.69	2.42	16.36	5.68	8.62
$CaCO_3$-old	3.78	1.31	0.24	2.73	18.02	10.40	9.85
$CaSO_4$-old	4.15	1.75	0.85	3.19	25.66	8.32	13.13
$CaCO_3$-new	4.32	1.25	0.42	1.93	18.43	6.28	8.76
$CaSO_4$-new	3.65	1.49	0.46	2.01	17.70	6.80	9.38
Mix	4.97	2.09	0.28	2.69	16.36	7.99	9.96

Discussion

Fine root distribution and total biomass

The vertical fine root distribution pattern observed in this study matches those stated generally (Meyer 1967; Vogt *et al.* 1981; Olsthoorn 1991), although some authors (Büttner and Leuschner 1994) reported a much shallower root system with half of all fine roots in the litter and humus layers in a mixed beech - oak forest on a very acid soil. Hence, the relative importance of the humus layer for fine roots in this study is rather limited. Specific root length was lowest in the 5-15 cm layer, possibly related to the fact that the 5-15 cm layer is a transition zone from the A to the B horizon (impeding easy penetration). The increasing SRL with increasing soil depth suggests either root proliferation from early spring onward (growth of small roots), or a different textural environment. In accordance with this, Makkonen (1995) differentiated fine root growth

of Scots pine per soil layer and found root amount to peak earlier at 0-10 cm (in July) than at 10-20 cm (September), indicating growth of fine roots out into the profile during the growing season. In 'cold-temperate' climates root length growth of perennial plants may occur also during the winter, provided soil is not frozen.

The total fine root biomass of this study compares fairly well with 1.45 t/ha for sessile oak and 4.09 t/ha for European beech in a mixed Oak-Beech forest (Büttner and Leuschner 1994), 6 t/ha for *Quercus robur* stand (Santantonio *et al.* 1977) and values ranging generally between 1 and 6 t/ha for several forest species or ecosystems (McClaugherty and Aber 1982; Santantonio and Hermann 1985; Van Praag et al. 1988; Burke and Raynal 1994). The much lower amount of fine root matter in the second year corresponds with observations on drought-induced summer mortality (Deans 1979; Olsthoorn 1991). This variation between the two seasons emphasizes the importance of multiple rather than single observations. The slight increases in SRL observed in the deepest layers in September 1995 is due to the period of drought in summer 1995, leading to fine root mortality in the topsoil and an increase of the fraction of fine root biomass below 30 cm (from around 15-24 % toward 16-40 %), suggesting stimulation of root growth for water uptake.

Effects of lime and gypsum on fine roots

In the short term, the effects of lime on fine root development are reported to be positive (Safford 1974; Squire *et al.* 1978; Gehrmann 1984; Rost-Siebert 1985; Murach and Schünemann 1985; Matzner *et al.* 1986; Glatzel *et al.* 1986; Persson and Ahlström 1991; Schüler and Zwick 1992; Raspe 1992; Clemensson-Lindell and Persson 1993). However, liming may induce deficiencies of other elements (K, Zn, P, B, Mg) in aerial parts of the tree due to antagonistic interactions in uptake or dilution effects on sites where the soil is already relatively poor in these elements (Glatzel *et al.* 1986; Derome 1991).

As the percentage of fine root biomass below 30 cm in this study is higher in the limed than in the control treatment, these results contradict reports of root shallowing after liming (Murach and Schünemann 1985; Hüttl and Zöttl 1993). This would suggest a sufficient downward distribution of the applied material, e.g. highly pulverized lime or more water-soluble or liquid fertilizers (Schüler and Zwick 1992; Hüttl and Zöttl 1993; Persson *et al.* 1995; Majdi and Nylund 1996), or an indirect fertilizer response (Raspe 1992). Majdi and Nylund (1996) reported that due to liquid fertilization, fine root production increased at a depth of 41-85 cm, leading to an increase in above ground production of 57%, in spite of a decline in fine root production at 0-20 cm. Raspe (1992) describes this phenomenon in terms of direct and indirect fertilizer response, eg. a direct chemotropic impulse of fine root growth by dissolution of Mg fertilizer dependent on its depth followed by an indirect root stimulation by higher photosynthetic production and translocation of assimilates. The latter would then correspond to the observed stimulation of fine root growth in deeper layers in this study.

Persson and Ahlström (1991) and Clemensson-Lindell and Persson (1993) showed an increase in fine root development for Norway Spruce and Scots pine 2 - 3 years after application of moderate doses of crushed dolomite (1.55 t ha^{-1}), and a tendency towards an increased SRL (thinner fine roots) 5-18 years after the application. However, 8 to 10 years after the application, effects of liming on fine root development decreased of disappeared in their study. Also, higher doses of lime did not enhance fine root development, and there were negative effects of liming in combination with high N deposition. Squire *et al.* (1978) postulated that reduced root elongation and thickening of fine roots may occur, resulting in an overall decrease of fine roots. In this study

the treatments seem to have no effect or a positive effect on fine root length, but a significant positive effect on fine root biomass. As a result, SRL decreased (thicker roots). Thus, the fine roots in the lime or gypsum treatments were in the thicker fraction within the size class of fine roots (< 2 mm). This suggests more storage of photosynthates and nutrients and corroborates the observation of increased longevity (lower turnover) in the liming and gypsum treatments as compared to the control. In the control, the trees need to invest more in root proliferation, developing a lot of very fine roots. Such an investment (in very fine roots) in the control plots could be related to toxic or mechanical constraints. It can also be seen as an adaptation to soil exploration. Mou *et al.* (1997) showed that fine roots adapt to local nutrient patches by producing thinner fine roots and increasing root elongation. Compared to the old treatments, the new treatments show the same tendencies, and are expected to give the same result after some years. The faster reaction of the treatments containing gypsum compared to lime only, reflects its higher solubility.

Fine root necropools

In unhealthy stands in case of root damage, the live/dead ratio may be expected lower than in healthy stands (Persson and Ahlström 1991; Clemensson-Lindell and Persson 1995; Persson *et al.* 1995). Liming is reported to increase the live/dead ratio (Matzner *et al.* 1986; Schüler and Zwick 1992) and to decrease fine root mortality (Murach and Schünemann 1985). This study featured no marked differences in live/dead root ratio between the treatments. In general, in this study, dead fine root pools were lower than live fine root pools, but in the deeper horizons where decay and mineralization processes are slower than at the soil surface, dead root pools were of the same order or even larger than live pools. In half of the plots increases in live to dead ratios were observed in September 1995 in the deepest horizons, suggesting a relationship between drought and roots exploring the soil for water.

Fine root turnover

In agreement with McClaugerty and Aber (1982) and Fogel (1983), estimates were based on all increments and decrements of fine root biomass, considering that only in case of frequent sampling statistical tests are needed to distinguish between random variations and real changes (Vogt *et al.* 1986). The estimated fine root production and turnover are in the lower range when compared with other studies. For oak species estimates ranged from 2 to 6 $t.ha^{-1}.yr^{-1}$ (Nadelhoffer *et al.* 1985; Joslin and Henderson 1987; Kummerow *et al.* 1990; Vogt *et al.* 1996). Turnover rates for deciduous species ranged from 0.8 to 2.2 (McClaugherty and Aber 1982; Nadelhoffer *et al.* 1985; Van Praag *et al.* 1988; Burke and Raynal 1994). The low values in this study can be explained at least partly by the size class of fine roots (< 2 mm compared to < 5 mm in some of the cited studies) and the limited sampling scheme, generally leading to underestimates (Kurz and Kimmins 1987; Publicover and Vogt 1993; Majdi and Nylund 1996).

Turnover rate is lower in the old lime and old gypsum treatments as compared with the control and this was more pronounced in 1994 than in 1995. Such a lower turnover rate is in agreement with the observations of Matzner *et al.* (1986) that the percentage of dead roots in ingrowth cores was only 25% in limed as compared to 60-70% in unlimed soil, indicating that longevity was higher and turnover rate lower. Murach and Schünemann (1985) found accumulation of Al in fine roots of unlimed stands, leading to unfavourable Ca/Al ratios (Cronan and Grigal 1995) in the fine roots followed by higher fine root mortality (lower longevity) in these stands. Such a high Al accumulation was hypothesized to increase root senescence and root turnover (Vogt *et al.* 1987). Eissenstat (1991) described an investment in opportunistic root growth of lower tissue density and higher specific root length on nutrient-

poor sites, to explore the soil patches rich in water and nutrients. According to his work, these fast growing small diameter roots would have a higher turnover, but they would be more successful for competition of limited resources. However, the costs of construction may be substantial. Depending on the trade-off between these extra costs and the improved accessibility of soil resources, a higher turnover can be a good adaptation for successful competition for limited soil resources. Others (Keyes and Grier 1981; Eissenstat and Yanai 1997) also observed higher fine root production on lower quality sites.

The new treatments may have a turnover rate which is slightly higher than the control treatment in 1995. This agrees well with the relative increment of fine root biomass in the new treatments (Figure 2) as a short-term response to lime-induced changes in soil fertility.

Element contents of fine roots

The mean concentrations of elements in fine roots in this study are within the range of concentrations reported (Gehrmann 1984; Murach and Schünemann 1985; Kelly and Joslin 1989; Raspe 1992; Persson *et al.* 1995; George *et al.* 1997). The effect of lime and gypsum applications on the fine root concentrations of Mn, Ca, Mg and Ca/Al ratio are comparable with those described by Safford (1974), Gehrmann (1984) and Murach and Schünemann (1985), although effects on Mg and Ca/Al ratio are significant only in few cases. Ca/Al ratios were close to the range for which a 50 % risk of Al stress is likely (Cronan and Grigal 1995) and these ratios were in general higher in the lime treatments than in the control. George *et al.* (1997) pointed out that as a response to local nutrient enrichment, fine root biomass or length increased and seemed to be better indicators of pre-existing nutrient deficiencies than increases in root nutrient concentrations.

The total mineral pools in fine roots (Table 4) are comparable with those stated by Raspe (1992), with the exception of P which was lower in this study. Safford (1974), Kelly and Joslin (1989), Vogt *et al.* (1987) report much higher mineral pools in fine roots, but this is due to the definition of 'fine roots' (including roots > 2 mm) and thus a higher root biomass. Ca/Al ratios in the fine roots increased slightly as a result of liming, but less than Ca/Al ratios in the soil solutions (see part I). This phenomenon has been described by Murach and Schünemann (1985), who suggest a stronger selectivity for Al by the acid components of the outer cell structures of fine roots. In consequence, with a lime-induced increase of fine root longevity, the Al content also increases in these fine roots, leading in time to a smaller increase of Ca/Al ratio in fine roots as compared to the soil solution. In spite of low Ca/Al molar ratios in the fine roots in the control, which occurred in the deeper soil layers throughout most of the study period, no direct root damage related to Al toxicity could be observed. However, the higher fine root mortality and turnover observed in the control treatments, leading to the formation of new roots, may obscure such visual root damage.

Conclusions

On this type of poor forest soil, the doses of lime and gypsum applied increased fine root biomass and length four to five years after its application. The initial effects follow the same trend but are less apparent one year after the application. The effects are less marked in the winter season. The difference in effect between lime and gypsum on fine roots at these doses is limited to a faster and deeper effect of the more soluble gypsum in the short term. Lime stimulated fine root growth both at 0-5 and as deep as 30-45 cm, so that vertical fine root distribution was not negatively affected. The observed increase in tree growth, suggests that this stimulation of root growth in the deeper layers is an indirect response to increased

photosynthesis. Lime and gypsum decreased the specific root length significantly four to five years after application. The tendency was the same in the new treatments. This is not due to root thickening in relation to a hostile rooting environment, but an effect of storage within these roots related to a longer longevity than in the control. Liming reduced fine root turnover rate, although it initially stimulated fine root production, leading to a higher live fine root pool. Then, fine root production, but especially mortality and turnover rate, decreased. As a consequence, root necromass was only a small proportion of total root mass and the higher amount of fine root biomass in the limed plots in the mid-term are a result of lower fine root mortality rather than higher fine root production. The effects of lime on soil and soil solution chemistry led to a concomitant amelioration of fine root composition, and thus an improved nutritional status and a stimulation of tree growth. Both the enhancement of the root system function and the size of the root system seemed to be responsible for this growth stimulation, at least in the short term.

Acknowledgements

I would like to acknowledge C. Nys and J. Ranger for their useful comments on earlier versions of this manuscript and S. Didier for his technical assistance in the field. This research was supported by grants of INRA Paris, the Dutch Ministry of Agriculture, Nature Management and Fisheries, Directorate of Science and Knowledge Dissemination, and the MEAC company.

Literature cited

Burke M K and Raynal D J 1994 Fine root growth phenology, production, and turnover in a northern hardwood forest ecosystem. Plant Soil 162, 135-146.

Büttner V and Leuschner C 1994 Spatial and temporal patterns of fine root abundance in a mixed oak-beech forest. For. Ecol. Manage. 70, 11-21.

Clemensson-Lindell A and Persson H 1993 Long-term effects of liming on the fine-root standing crop of *Picea abies* and *Pinus sylvestris* in relation to chemical changes in the soil. Scand. J. For. Res. 8, 384-394.

Clemensson-Lindell A and Persson H 1995 Fine-root vitality in a Norway spruce stand subjected to various nutrient supplies. Plant Soil 168-169, 167-172.

Cronan S and Grigal D F 1995 Use of calcium/aluminum ratios as indicators of stress in forest ecosystems. J. Environ. Qual. 24: 209-226.

Deans J D 1979 Fluctuations of the soil environment and fine root growth in a young Sitka spruce plantation. Plant Soil 52, 195-208.

Derome J 1991 Effects of forest liming on the nutrient status of podzolic soils in Finland. Water Air Soil Pollut. 54, 337-350.

Dieffenbach A, Göttlein A and Matzner E 1997 In-situ soil solution chemistry in an acid forest soil as influenced by growing roots of Norway spruce (*Picea abies* [L.] Karst.) Plant Soil 192, 57-61.

Eissenstat D M 1991 On the relationship between specific root length and the rate of root proliferation: a field study using citrus rootstocks. New Phytol. 118, 63-68.

Eissenstat D M and Yanai R D 1997 The ecology of root lifespan. Adv. Ecol. Res. vol 27, 1-60.

Fiskesjö G 1989 Aluminium toxicity in root tips of *Picea abies* L. Karst., *Fagus sylvatica* L. and *Quercus robur* L. Hereditas 111, 149-157.

Fogel R 1983 Root turnover and productivity of coniferous forests. Plant Soil 71, 75-85.

Gehrmann J 1984 Einfluß von Bodenversauerung und Kalkung auf die Entwicklung von Buchenverjüngungen (*Fagus sylvatica* L.) im Wald. Berichte des Forschungszentrum Waldökosysteme/Waldsterben Göttingen, Band 1.

George E, Seith B, Schaeffer C and Marschner H 1997 Responses of Picea, Pinus and Pseudotsuga roots to heterogeneous nutrient distribution in soil. Tree Physiol. 17, 39-45.

Glatzel G, Kazda M and Sieghardt M 1986 Zur Frage der Melioration versauerter Boden aus schadstoffbelasteten Buchenwäldern durch Zufuhr von Kalk oder halbgebranntem Dolomit. Ein Gefassversuch mit Rotbuche (*Fagus sylvatica*). Z. Bodenk. Pflanzernähr. 149, 658-667.

Hüttl R F and Zöttl H W 1993 Liming as a mitigation tool in Germany's declining forests - reviewing results from former and recent trials. For Ecol. Manage. 61, 325-338.

Joslin J D and Henderson G S 1987 Organic matter and nutrients associated with fine root turnover in a white oak stand. For. Sci. 33, 330-346.

Kelly J M and Joslin J D 1989 Mass and chemical composition of roots in two second-growth Oak forests in Eastern Tennessee. For. Ecol. Manage. 27, 87-92.

Keyes M R and Grier C C 1981 Above- and below-ground net production in 40-year old Douglas-fir stands on low and high productivity sites. Can. J. For. Res. 11, 599-605.

Kruger E and Sucoff E 1989 Growth and nutrient status of *Quercus rubra* L. in response to Al and Ca. J. Exp. Bot. 40, 653-658.

Kummerow J, Kummerow M and Trabaud L 1990 Root biomass, root distribution and the fine root growth dynamics of *Quercus coccifera* L. in the garrigue of southern France. Vegetatio 87, 37-44.

Kurz W A and Kimmins J P 1987 Analysis of some sources of error in methods used to determine fine root production in forest ecosystems: a simulation approach. Can. J. For. Res. 17, 909-912.

Majdi H and Nylund J-E 1996 Does liquid fertilization affect fine root dynamics and lifespan of mycorrhizal short roots? Plant Soil 185, 305-309.

Makkonen K 1995 Seasonal variation of fine-root biomass in *Pinus sylvestris* (L) stand. In Roots, mycorrhizas and rhizosphere microbes. Eds. H-S Helmisaari, A Smolander and A Suokas. pp 89-94. The Finnish Forest Research Institute, Research papers 537.

Matzner E, Murach D and Fortmann H 1986 Soil acidity and its relationship to root growth in declining forest stands in Germany. Water Air Soil Pollut. 31, 273-282.

McClaugherty C A and Aber J D 1982 The role of fine roots in the organic matter and nitrogen budgets of two forested ecosystems. Ecology 66, 1377-1390.

Meyer F H 1967 Feinwurzelverteilung bei Waldbäumen in Abhängigkeit vom Substrat. Forstarchiv 38, 286-290.

Millier C, Nys C and Ranger J 1986 L'échantillonnage dans l'étude de la minéralomasse forestière: l'example des taillis ardennais. Ann. Sci. For. 43, 165-178.

Mou P, Mitchell R J and Jones R H 1997 Root distribution of two tree species under a heterogeneous nutrient environment. J. Applied Ecol. 34, 645-656.

Murach D and Schünemann E 1985 Reaktion der Feinwurzeln von Fichten auf Kalkungsmassnahmen. Allgemeine Forstzeitschrift 40, 1151-1154.

Nadelhoffer K J, Aber J D and Melillo J M 1985 Fine roots, net primary production, and soil nitrogen availability: a new hypothesis. Ecology 66, 1377-1390.

Noordwijk M van and Floris J 1979 Loss of dry weight during washing and storage of root samples. Plant Soil 53, 239-243.

Olsthoorn A F M 1991 Fine root density and root biomass of two Douglas-fir stands on sandy soils in the Netherlands. 1. Root biomass in early summer. Neth. J. Agric. Sci. 39, 49-60.

Persson H 1983 The distribution and productivity of fine roots in boreal forests. Plant Soil 71, 87-101.

Persson H and Ahlström K 1991 The effects of forest liming and fertilization on fine-root growth. Water Air Soil Pollut. 54, 363-375.

Persson H, Majdi H and Clemensson-Lindell A 1995 Effects of acid deposition on tree roots. Ecol. Bull. 44, 158-167.

Praag H J van, Sougnez-Remy S, Weissen F and Carletti G 1988 Root turnover in a beech and spruce stand of the Belgian Ardennes. Plant Soil 105, 87-103.

Publicover D A and Vogt K A 1993 A comparison of methods for estimating forest fine root production with respect to sources of error. Can. J. For. Res. 23, 1179-1186.

Raspe S 1992 Biomasse und Mineralstoffgehalte der Wurzeln von Fichtenbeständen (*Picea abies* Karst.) des Schwarzwaldes und Veränderungen nach Düngung. Freiburger Bodenkld. Abh. 29, 1-197.

Rost-Siebert K 1985 Untersuchungen zur H- und Al-Toxizität an Keimpflanzen von Fichte (*Picea abies* Karst.) und Buche (*Fagus sylvatica* L.) in Lösungskultur. Berichte Forschungszentrum Waldökosteme, Universität Göttingen 12, 1-219.

Safford L O 1974 Effect of fertilization on biomass and nutrient content of fine roots in a beech-birch-maple stand. Plant Soil 40, 349-363.

Santantonio D, Hermann R K and Overton W S 1977 Root biomass studies in forest eocsystems. Pedobiologia 17, 1-31.

Santantonio D Hermann R K 1985 Standing crop, production and turnover of fine roots on dry, moderate, and wet sites of mature Douglas-fir in western Oregon. Ann. Sci. For. 42, 13-142.

Schüler G and Zwick N 1992 Die Beeinflussung von Feinwurzelmasse und -vitalität eines Kiefernbestandes (*Pinus sylvestris* L.) mit unterständiger Buche (*Fagus sylvatica* L.) durch pflanzenverfügbare Elemente, sowie Veränderungen nach unterschiedlichen Kalkungsmaßnahmen. Mitt. Forst. Versuchsanstalt Rheinland-Pfalz 21, 69-98.

Squire R O, Marks G C and Craig F G 1978 Root development in a *Pinus radiata* D. Don plantation in relation to site index, fertilizing and soil bulk density. Austr. For. Res. 8, 103-114.

Tennant D 1975 A test of a modified line intersect method of estimating root length. J. Ecol. 63, 995-1001.

Vogt K A, Edmonds R L and Grier C C 1981 Seasonal changes in biomass and vertical distribution of mycorrhizal and fibrous-textured conifere fine roots in 23 and 180 years old subalpine *Abies amabilis* stands. Can. J. For. Res. 11, 223-229.

Vogt K A, Grier C C, Gower S T, Sprugel D G and Vogt D J 1986 Overestimation of net root production: a real or imaginary problem? Ecology 67, 577-579.

Vogt K A, Dahlgren R, Ugolini F, Zabowski D, Moore E E and Zasoski R 1987 Aluminium, Fe, Ca, Mg, K, Mn, Cu, Zn and P in above- and belowground biomass. II. Pools and circulation in a subalpine *Abies amabilis* stand. Biogeochemistry 4, 295-311.

Vogt K A and Persson H 1991 Measuring growth and development of roots. *In* Techniques and approaches in forest tree ecophysiology. Ed. J P Lassoie and T M Hinckley. pp 477-502. CRC Press, Boca Raton.

Vogt K A, Vogt D J, Palmiotto P A, Boon P, O'Hara J and Asbjornsen H 1996 Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. Plant Soil 187, 159-219.

Annexe A (Paper III) : *For. Ecol. Manage.* à apparaître

Reçu 20 novembre 1997 ; accepté en version révisée le 28 octobre 1998

Fine-root parameters as indicators of sustainability of forest ecosystems

Mark R Bakker

Abstract

The potential of fine-roots as indicators of forest sustainability is discussed. In ten oak (*Quercus petraea, Q. robur*) trials where moderate doses of lime had been applied up to 27 years ago, the effects on soil, root and foliar chemical parameters were compared with above- and below-ground growth. The effects of liming on growth appeared positive and sustained for about 25 years after application, whereas effects on soil, root, and foliar chemical parameters only lasted for 10 to 25 years. Fine-root biomass or length appeared to be significantly increased by liming and comparable to the effects on above-ground tree growth, but were considered too time-consuming for use as indicators of ecosystem function. A combination of soil and root chemical parameters predicted fine-root mass and length best, and thus tree growth, with foliar chemical parameters being of minor importance. When this best fitting linear regression model was applied, separately for both the lime treatment and the control, the contribution of root chemical parameters in the model decreased in the lime treatment as compared to the control, while that of foliar chemical parameters increased. Consequently, root as well as soil chemical parameters appeared to be more sensitive to changes in the chemical status of the site.

In general it is recommended, that studies aiming to define useful indicators, should start with a feasibility study (e.g. comparing the utility of soil, root and foliar chemical parameters) before defining a smaller set of most sensitive parameters. For the sites examined, a combination of parameters such as fine-root Ca, Al, Mg, Ca/Al, Mg/Al, soil exchageable Ca, Al, and Mg gave a good insight into the actual uptake capacity of roots or constraints on that capacity.

key-words: fine-roots, soil chemistry, fine-root chemical contents, foliar nutrition, indicators, liming, oak, *Quercus petraea, Quercus robur*

Introduction:

Recently, there have been important international efforts (eg. Montreal Process 1995) to define social, economic and environmental criteria for ecologically sustainable forest management and the indicators to evaluate these criteria (Raison *et al.* 1997). However, at present, much work still needs to be carried out on the choice of proper indicators, as they are site-dependent and may vary according to the scale at which the criteria are to be evaluated.

For the purpose of forest productivity and vitality, and their relationship with soil resources, the interface between soil nutrient pools and tree roots as uptake organs to sustain above-ground growth, is of utmost importance. Foliar analysis may detect deficiencies for certain elements, but only if these deficiencies are major (Helmisaari 1997), and the element concentrations in fine-roots may be better indicators of nutritional conditions (Persson *et al.* 1995). Soil analysis can describe growth potential, especially if a proper speciation of chemical forms is carried out, distinguishing forms free for uptake from those that are bound structurally. However, uptake of Mg^{2+} or Ca^{2+} can be strongly depressed by other cations such as K^+, NH_4^+, Al^{3+} or H^+ (Raspe

1997), so that there may not be uptake of all the potentially available soil nutrients by tree roots (Rost-Siebert 1985). It is relevant to evaluate the usefulness of root parameters as indicators of growth potential and actual nutrient acquisition.

This work focuses on the soil and rooting environment. In 10 oak stands, ranging in age from 15 to 80 years, lime was applied up to 27 years ago. Generally these stands were situated on relatively poor soil substrates and showed deficiencies for one or more base cations. Consequently, it was assumed that, in terms of nutrient cycling and tree growth, these sites were unsustainable, i.e. under current forestry practice some nutrients are deficient in the nutrient balance and forest productivity is declining (Nys 1989). In this situation, liming can be seen as a 'compensation amendment' restoring the sustainability and productivity of the system, whereas the untreated control sites represent an unsustainable situation. This paper does not describe the effects of lime on soils, roots or foliage in detail. It discusses the impact of lime relative to the control in terms of its effect on soil and plant parameters that are sensitive indicators of productivity, focusing mainly on the potential use of fine-root parameters as indicators.

Material and methods:

Between June 1994 and March 1996 a total of 10 different oak (*Quercus petraea* M. Liebl. and *Q. robur* L.) sites were sampled for soil, fine-root, foliage and above ground growth parameters (Tables 1 and 2). Eight of these stands are situated in France and two are in the southeast of the Netherlands (sites 9 and 10). After a detailed study of sites 1 and 2 (Bakker 1998), it was shown that humus and litter layers contained negligible proportions of fine-roots and were not further included in this study. In the soil, soil and fine-roots were sampled with a soil corer (length 15 cm, ∅ 8.0 cm) down to a maximum of 75 cm (Tables 1 and 2) and different soil layers were separated on sampling and processed independently. Generally, this resulted in a separation into 0 to 5 cm and 5 to 15 cm layers for the first core, whereas the subsequent cores were processed entirely (15 to 30 cm etc.). Foliage was sampled in August close to the top of the crown of five dominant trees in each experiment plot and above ground tree growth was evaluated by means of diameter measurements and analysis of ring width on stem wood cores.

Table 1 Characteristics of the 10 limed oak stands

Site	Site	Species	Stand age (year)	Soil texture	Eq CaO dose (t. ha^{-1})	Time since liming (years)	Soil profile (cm)
Ardennes-old	1	Q. petraea	48	silty clay	1.4	4	0-55
Ardennes-new	2	Q. petraea	48	silty clay	1.4	1	0-55
Fontainebleau	3	Q. petraea	25	sand	1.25	25	0-75
Trembles	4	Q. petraea	76	silt	1.5	26	0-75
Gaie Mariée	5	Q. petraea	55	silt	1.5	27	0-75
Rond du May	6	Q. petraea	50	sandy silt	1.5	27	0-75
Bertranges	7	Q. petraea	24	silt	1.25	24	0-45
Tronçais	8	Q. petraea	44	silty sand	0.8	14	0-60
St. Anthonis 35c	9	Q. robur	42	sand	1.6	7	0-75
St. Anthonis 46a	10	Q. robur	15	sand	1.6	7	0-75

Soil samples were air-dried and then sieved (< 2 mm). Soils were extracted with 0.5 *M* NH_4Cl and exchangeable Al, Ca, Mg, K, Mn and Na (Trüby 1989) were determined by ICP (emission spectrometry), exchangeable acidity by automatic titration (Trüby 1989), and pH-KCl and pH-H_2O following standard procedures with KCl-electrodes. Concentrations were expressed on an oven-dried (105°C) weight basis. Prior to processing, fine-root core samples were stored for ≤ 3 months at + 1°C. The fine-roots (< 2 mm in diameter) were separated from the soil by wet

sieving over 4 and 2 mm sieves followed by short flotation to clean the roots. Dead roots were separated from living roots using general visible criteria: resilience, brittleness, colour of bark

Table 2 Soil characteristics of the 10 limed oak stands

Site	Site	CEC ($cmol_c\ kg^{-1}$) 0-5 cm	BS (%) 0-5 cm	pH-H_2O 0-5 cm	CEC ($cmol_c\ kg^{-1}$) 30-45 cm	BS (%) 30-45 cm	pH-H_2O 30-45 cm
Ardennes-old	1	7.60	14	3.99	2.43	13	4.48
Ardennes-new	2	8.20	14	3.77	3.30	9	4.39
Fontainebleau	3	7.66	100	6.36	11.07	100	7.08
Trembles	4	5.55	43	3.73	3.00	15	4.40
Gaie Mariée	5	5.45	56	3.92	4.91	20	4.47
Rond du May	6	5.03	25	3.97	3.21	11	4.44
Bertranges	7	5.75	81	4.97	-	-	-
Tronçais	8	2.13	34	4.84	2.33	41	4.72
St. Anthonis 35c	9	2.86	38	4.07	1.94	12	4.14
St. Anthonis 46a	10	4.85	28	3.74	2.85	4	4.05

and xylem (Vogt and Persson 1991), the reliability of which was confirmed by observations under a binocular microcope. Length and weight of live roots were assessed for all samples and for dead roots only on a small number of samples. Root length was estimated 'manually' by counts of intersections of roots and lines (Tennant 1975). The fine-root biomass (dry weight) was obtained by drying at 105°C to a constant weight. This 'manual' procedure for assessing root weight and length was corrected for five sources of error and these error terms appeared to be a fairly constant proportion of total weight (net loss of 20%) and length (net loss of 25%) for the manual processing method applied, regardless of the site. The five sources of error accounted for, were: losses of root particles through the sieve by washing, losses of weight by washing and floating for average handling time, losses of weight during average storing time, overestimates of weight due to incomplete cleaning, and bias related to incorrect identification of live and dead roots by verification under magnification (Bakker 1998). For the chemical analyses of foliage and live fine-roots, subsamples were pretreated with peroxide (H_2O_2), then mineralized with $HClO_4$ and analysed by ICP.

Fine-root biomass and length were expressed as kg ha^{-1} and 10^6 m ha^{-1}, respectively. They were summed as totals for the whole soil depth sampled (0-45 or 0-75 cm), so that they could be compared more directly with foliar and above ground growth data. Specific root length (SRL, m/g), soil chemical data and the chemical contents of fine-roots, were expressed separately for each layer. Means per stratum were calculated using Unistat 4.0 software (Unistat Ltd 1995). Fine-root biomass, fine-root length, specific root length, fine-root chemistry and soil chemistry parameters were tested for treatment, season and soil depth effects using ANOVA, and the Student-Newman-Keuls test was used to separate the means. For foliar and above ground growth data, treatment effects were tested using ANOVA. The effects of lime were evaluated for four groups of parameters: 1) root properties (fine-root biomass, fine-root length, specific root length, ratio live/dead of fine-roots); 2) soil chemistry (exchangeable Al, Ca, Mg, K, Mn, Na, titrable Al^{3+} and H^+, ratios of Ca/Al^{3+} and Mg/Al^{3+} , pH-H_2O and pH-KCl); 3) fine-root chemistry (total content of S, P, Mn, Mg, Al, Ca, and K and Ca/Al ratio); and 4) foliar chemistry (total content of N, S, P, Mn, Mg, Ca, and K). These effects are discussed in relation to the time since liming. After logtransformations on some of the parameters to normalize their distributions, linear regressions were calculated to illustrate the relations between the sets of parameters and the impact of lime on these relationships in order to estimate the importance of the parameters considered.

Table 3 Effects of lime as compared to the control on above-ground tree growth (average of height and diameter growth; * sign. at least at p<0.05 level), fine root biomass (FRB), fine root length (FRL), specific root length (SRL) and live/dead ratio of fine-roots (L/D) based on weight or length for the total profile (symbols indicating significant increases (+) and decreases (-) (when not significant between brackets) of values after liming)

Site nr	Above-ground growth (%)	FRB	FRL	SRL	L/D Weight	L/D Length
1	+ 39 *	+	(-)	-	+	+
2	?	(+)	-	-	-	-
3	+28 *	+	+	-	-	Same
4	+ 10 *	+	(-)	-	-	+
5	+ 12 *	(-)	+	+	-	-
6	+ 23 *	-	-	+	+	Same
7	0	+	+	-	-	-
8	+ 15 *	+	(+)	(-)	-	-
9	- 8	+	+	(-)	+	+
10	+ 32	(+)	+	+	+	+

Results

In Table 3 the effects of lime on above-ground tree growth are presented as averages of effects on heigth and diameter and the figures are expressed as the difference in growth in the limed stands as compared to those in the control stands. It was chosen to present the average effect on height and diameter growth, as height data were lacking for some sites. The 'stand age time scale' appeared far less interesting than the 'time since liming' axis, so that the latter was used throughout the presentation of the data (Figures 1 to 6). Wherever data were present for different soil layers (soil chemistry, specific root length, fine-root chemistry) without the possibility of summing these values eg. for total fine-root biomass, average values were given, one or two parameters selected or the general features were described without presenting all the data.

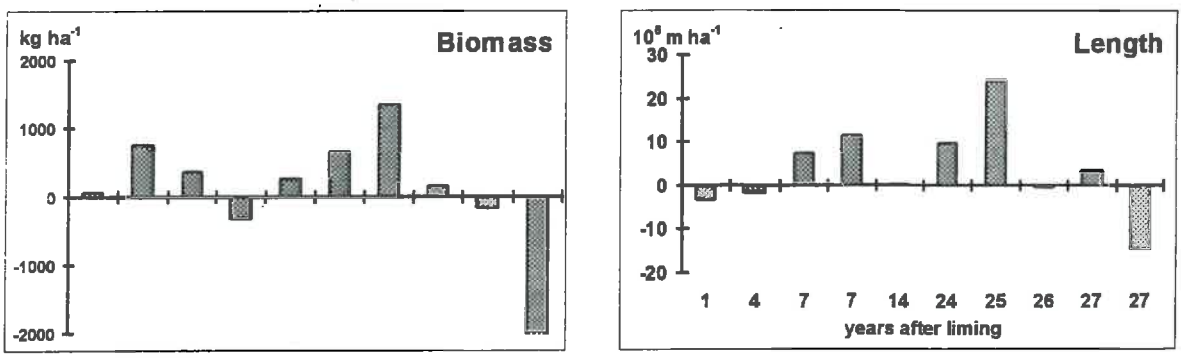

Figure 1 Lime-induced change in total fine-root biomass and length as a function of time since liming.

Effects of liming on total fine-root biomass and total fine-root length were generally positive and still detectable after 20-25 years (Figure 1; Table 3). The effect on weight seems to occur sooner after liming, than that for length. On an overall basis, specific root length decreased as a result of liming, with the exception of two older lime trials and one new lime trial. However, this depends on the soil layer (data not presented separately). Both in surface layers (0 to 15 cm) and in the deeper layers (60 to 75) an increase of SRL was observed, whereas the tendency in between (30 to 60 cm) was towards a decreased SRL. Lime-induced stimulation of fine-root growth was

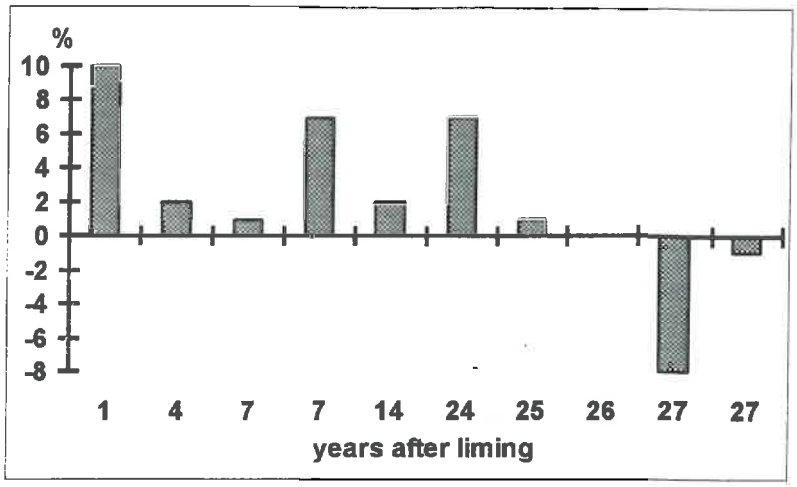

Figure 2 Lime-induced change in percentage of total profile fine-root biomass occurring below 30 cm as a function of time since liming.

greatest in the deeper layers, so that a higher percentage of fine-root mass occurred below 30 cm in the limed plots as compared to the control (Figure 2). The live/dead ratio of fine-roots based on the whole profile was increased by liming in the first few years after liming. The opposite was true in the older trials (Figure 3).

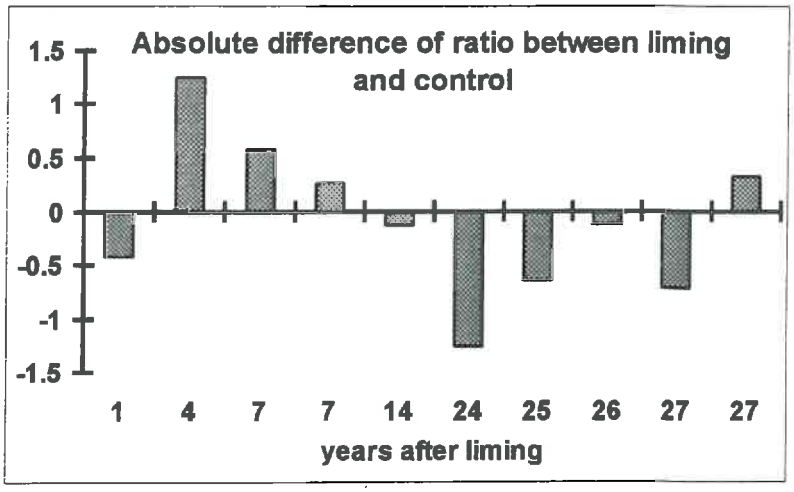

Figure 3 Lime-induced change in live/dead ratio of fine-roots (dry weight basis) as a function of time since liming.

Table 4 Effects of lime on element concentrations in soil ($cmol_c\ kg^{-1}$), fine roots ($g\ kg^{-1}$) and foliage ($g\ kg^{-1}$); data are the averages of all 10 sites for all soil layers (with standard error in brackets); in soil Al^{3+} instead of Al

Sample	Treatment	Mg	Ca	K	Mn	Al	Ca/Al	Mg/Al
Soil	Control	0.20 (0.03)	0.33 (0.04)	0.15 (0.01)	0.07 (0.01)	3.91 (0.22)	0.22 (0.05)	0.11 (0.02)
	Lime	0.22 (0.02)	0.88 (0.15)	0.13 (0.01)	0.08 (0.01)	3.11 (0.18)	1.06 (0.49)	0.22 (0.08)
Fine-root	Control	0.95 (0.04)	2.3 (0.22)	0.93 (0.06)	0.10 (0.01)	5.5 (0.36)	0.53 (0.08)	0.27 (0.03)
	Lime	0.98 (0.03)	2.6 (0.27)	0.87 (0.05)	0.10 (0.01)	5.8 (0.54)	0.63 (0.09)	0.28 (0.03)
Foliage	Control	1.6 (0.08)	6.3 (0.39)	7.6 (0.24)	2.8 (0.39)			
	Lime	1.7 (0.08)	7.6 (0.33)	7.5 (0.26)	2.4 (0.37)			

Table 4 shows the most important soil, fine-root, and foliar chemical changes presented as means of the ten sites. Table 5 presents the foliar data for all ten sites. Overall, lime increased exchangeable Ca, Ca/Al^{3+} ratio, base saturation, CEC, pH-H_2O and pH-KCl, but decreased soil Na, Al^{3+} and H^+ (Figure 4). These effects were, however, not significant on all sites, nor in all layers. Most of the changes were only significantly detectable in top soil.

Table 5 Foliar composition (g kg^{-1}) in control and limed stands (¤ = missing data)

Element	Treatment	Site number										
		1	2	3	4	5	6	7	8	9	10	Average
N	Control	22.7	25.9	20.7	19.5	19.8	19.6	19.8	22.1	28.1	21.0	21.8
	Lime	21.6	22.5	20.6	19.9	21.8	20.6	21.9	23.1	28.2	21.2	22.3
S	Control	1.4	1.5	1.4	1.4	1.3	1.5	1.4	1.5	¤	¤	1.4
	Lime	1.4	1.4	1.4	1.5	1.4	1.4	1.4	1.6	¤	¤	1.4
P	Control	1.5	1.6	0.82	1.2	1.0	1.0	1.2	1.3	1.8	1.3	1.3
	Lime	1.3	1.5	0.77	1.0	0.94	1.0	1.2	1.7	1.8	1.2	1.2
Mn	Control	0.94	0.76	1.0	2.8	2.5	3.5	¤	3.9	5.3	3.8	2.8
	Lime	0.82	0.77	0.65	3.0	2.5	2.7	¤	2.8	6.5	1.8	2.4
Mg	Control	0.84	0.92	1.5	1.6	1.7	1.4	1.7	1.7	1.9	2.0	1.6
	Lime	0.86	1.3	1.6	1.7	1.6	1.6	1.8	1.9	2.2	2.4	1.7
Ca	Control	2.8	2.8	7.8	7.9	6.8	6.8	7.5	7.4	5.6	5.6	6.3
	Lime	4.3	3.9	9.5	7.9	7.0	6.7	8.8	8.9	7.3	8.6	7.6
K	Control	7.1	7.3	5.7	7.9	7.0	9.0	8.4	9.0	8.1	7.1	7.6
	Lime	7.2	6.0	5.9	7.1	7.4	7.1	9.2	8.9	8.4	6.7	7.5

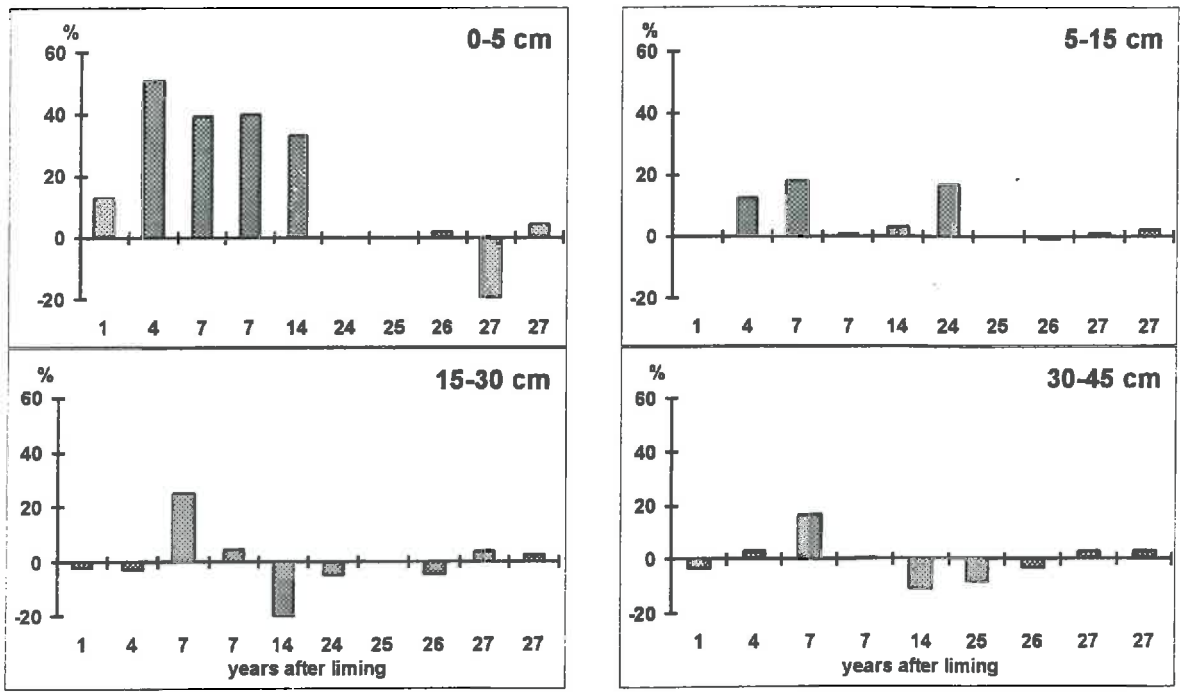

Figure 4 Lime-induced change (absolute difference) in base saturation in different soil layers as a function of time since liming.

Analysis of total fine-root content indicated that concentrations decreased in the order Al>Ca>Mg>K>S>P>Mn (5.6, 2.4, 0.97, 0.90, 0.80, 0.51 and 0.10 g kg^{-1} biomass, respectively) and these concentrations compare well with those given by Persson and Ahlström (1994). Liming had significant effects on the Ca content (2.6 versus 2.3 g kg^{-1} for liming and control, respectively), the Ca/Al molar ratio, but no significant effects on the other elements (data not further shown). Liming significantly enhanced Ca/Al ratio in most of the stands and for most of the soil profile, but was most consistent for the 15-30 cm layer (Figure 5).

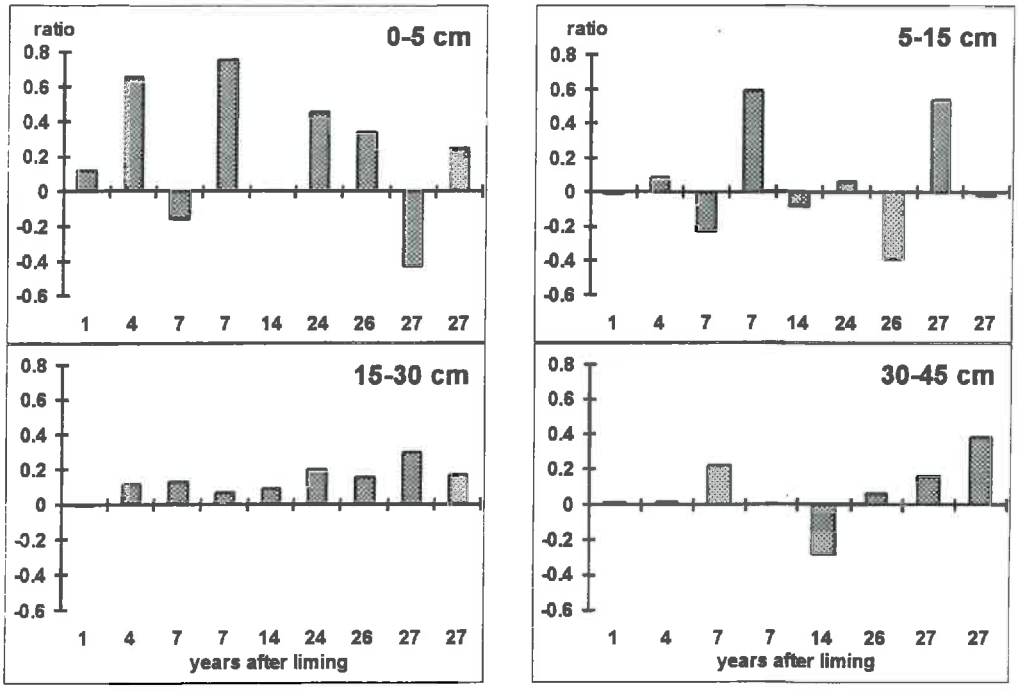

Figure 5 Lime-induced change (absolute difference) in Ca/Al molar ratio of fine- roots at four soil depths as a function of time since liming.

Foliar analysis showed that liming significantly increased foliar Ca and Mg content, and decreased foliar P and Mn content, but the latter was not significant (Table 5; Figure 6). Furthermore, liming initially decreased foliar N, but this then increased over time. The other elements (data not shown), were not significantly affected by liming.

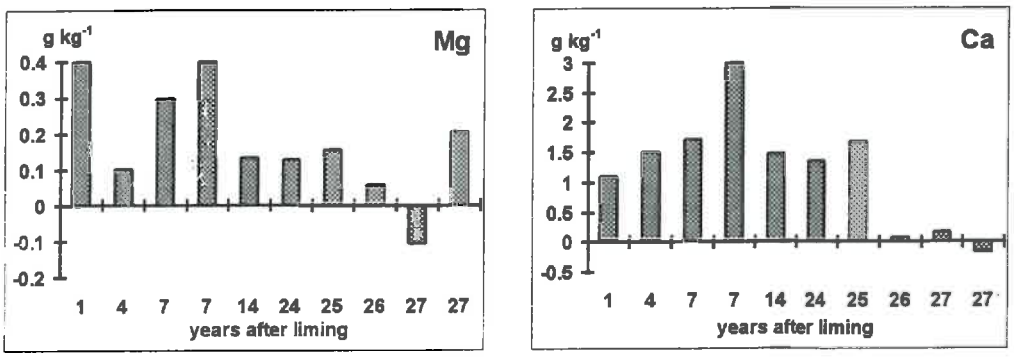

Figure 6 Lime-induced change (absolute difference) in foliar Mg and Ca content as a function of time since liming.

Discussion

Although the procedure of growth appraisal based on diameter measurements (most sites) is not as robust and sensitive as the dendrochronological method applied at Site 1, the comparison in statistical terms revealed significant increases for six sites. For Site 2 an evaluation based on diameter measurements was judged to be too early, 1 year after sampling, but growth increase is expected to be similar to that observed at site 1, since the sites are very close to each other. At Site 9 frost caused dieback of topshoots, and site 10 was not clearly interpretable when compared with the effects of other (higher) lime doses (Van den Burg 1994). So, in 6 sites (but probably 9) the effects on above-ground growth seem positive, which justifies the comparison with the other parameters studied.

For a parameter to be of relevance as an indicator, it should be scientifically sound (interpretable), sufficiently sensitive to detect the effects of forest management, and be fairly simple to apply (Raison *et al.* 1997). The data for ten sites indicate that lime has had a positive effect on above-ground tree growth. Here, this stimulation of above-ground tree growth is related to a stimulation of fine-root biomass and fine-root length, which lasted for 20-25 years after liming. Other parameters like specific root length, rooting depth distribution, live/dead ratio of fine-roots and fine-root chemistry also showed consistent responses to liming, and are thus all potentially good indicators. However, a lime-induced stimulation of tree growth is not necessarily linked to a higher fine root development as shown in many Scandinavian studies (Clemensson-Lindell and Persson 1993; Persson *et al.* 1995), so that such relationships need to be established for each site.

Assessing the total amount of fine-roots is very laborious and from this point of view cannot be used as a simple indicator. In addition, root changes need to be assessed to considerable soil depth, as liming increased root growth in the deeper layers. Also, the total amount of fine-roots present in a forest stand did not vary very clearly with the confounding effects of stand age or soil fertility. For situations where root growth is hampered by acidification of the mineral soil - e.g. a Mg or Ca deficiency - an improvement of fertility and alkalinity (by lime) may increase fine-root growth (Hüttl 1991), but more generally allocation of assimilates to fine-roots is higher at poor sites (Olsthoorn and Tiktak 1991). With N, P or S deficiency, root growth is stimulated relative to shoot growth by intensified translocation of carbohydrates (Hüttl 1991), so that a stimulation or inhibition of root growth is not, in itself, easily interpretable. Therefore, it is difficult to interprete change in fine-root amount, in isolation, in a given ecosystem.

Specific root length was related to the fine-root biomass distribution. Agreeing well with a decreased SRL ('thicker roots') at 30-60 cm, the vertical root distribution pattern was slightly altered and the relative proportion of total profile fine-root mass below 30 cm was higher in the lime treatments (Figure 2). Although SRL and also the vertical root distribution can be of interest for detecting changes at a local level - here consistently linked to above-ground tree growth - their dependence on soil texture, soil depth and water table induces considerable variation between sites or layers (Clemensson-Lindell and Persson 1993, 1995). Also, both increases in SRL, meaning the necessity to invest in root elongation for nutrient acquisition (Eissenstat 1991), and decreases in SRL, suggesting mechanical or chemical impedance and damage (Rost-Siebert), could indicate an unfavourable root environment. The practical use of SRL and vertical root distribution as indicators with absolute threshold values may, thus, be limited. Similarly to fine-root biomass and length, these data are very difficult to obtain.

The live/dead ratio of fine-roots was increased by liming during the first few years after liming, improving the low live/dead ratios of fine-roots reported for poor or acidified sites (Persson 1993). Here, liming shifted the system towards a somewhat higher live root biomass and lower necromass. This indicates that fine-roots either live longer, are decomposed faster, or both. A detailed study at site 1 and 2 (Bakker 1998) suggests that it is due to higher longevity rather than a faster turnover after liming. In agreement with this (Helmisaari 1997) described increased turnover in response to Al toxicity, and Persson *et al.* (1995) stated that additions of ammonium sulphate increased fine-root production (turnover) while decreasing the life-time of fine-roots. Fertilizers without N had the opposite effect (Persson *et al.* 1995). As a consequence, the live/dead ratio of fine-roots can be a parameter of interest for assessing the way the forest ecosystem functions.

The fine-root chemistry data showed that fine-root content differs from both soil and foliar content for several elements. This means that the overall effect of liming on the soil chemistry is found also in the two other compartments, but can be reinforced or reduced. The size of lime-induced change in concentration is larger in foliage for Mg (+) and Mn (-) than in the soil, while the changes in Ca (+), Al (-) and K(-) are greater in the soil than in foliage. K and Mn show opposite uptake patterns, K being lower in the soil after liming but present in equal concentrations in foliage and Mn being more abundant in soil after liming but lower in foliage. This reflects the difference in uptake and upward transport of the different elements and suggests preferential uptake and allocation to foliage for Mg and K; and the inverse: a retention in fine-roots of Al and Mn, or an uptake below potential (Ca). Also, crown dilution may mask smaller deficiencies that occur if only foliar nutrition is examined.

With increasing Al concentrations in soil solution, Al becomes more important in the exchange complex and competitively reduces the concentration of basic cations at the root CEC and their uptake potential (Rengel 1992). Since basic cations like Ca and Mg may alleviate Al stress, the latter is often expressed in terms of Ca/Al molar ratios in soil solution or fine-root tissue (Rost-Siebert 1985; Cronan and Grigal 1995). The fine-root Ca/Al molar ratio is potentially a good environmental indicator, reflecting Al stress. In this study, toxic Ca/Al ratios of 0.10-0.20 (Puhe *et al.* 1986; Cronan and Grigal 1995) were alleviated by liming down to a depth of 30 or even 45 cm. This Ca/Al molar ratio in the fine-roots was most markedly enhanced in the somewhat deeper layers, corresponding to the relatively 'thicker' roots there (lower SRL), sequestering less toxic Al than the finer roots in the control stands. This is interesting, as the most 'vital' fine-roots according to Ca/Al ratio are usually found in the upper organic soil due to the binding of Al to organic matter (Rost-Siebert 1985). As fine-root element concentrations often reflect concentrations of the soil solution (integrating them more or less), the evaluation of fine-root chemical parameters for several layers (separating top soil from subsoil, often more sensitive to acidification) would offer the possibility of avoiding most of the transitory seasonal effects of soil solute analysis. The Ca/Al molar ratio of fine-roots seems valuable as an indicator because it reflects uptake potential. Other potential parameters like root vitality (Clemensson-Lindell and Persson 1995) or fine-root N content (Persson *et al.* 1995) also merit consideration when evaluating ecosystem functioning, but were not within the scope of this study. It has been demonstrated that fine-root N content especially (ratios of N:cations) gives good additional information on nutrient status and mineral nutrient requirements of forest trees (Persson *et al.* 1995).

A combination of root, soil and foliar parameters predicted fine-root biomass, fine-root length and specific root length best (Table 6). Whereas total adjusted R^2 was similar for the tree root

Table 6 Linear regressions between total fine root biomass (FRB), total fine root length (FRL), mean specific root length (SRL) and root (r), soil (s) and foliar (f) composition parameters in limed and unlimed oak stands

FRB	=	$-1375 - 4154*\log Al_r - 3196*Ca/Al_r + 10168*Mg/Al_r - 3327*Mg_s + 1783*\log Ca_s - 5695*K_s + 5374*K_f - 3227*Ca_f + 18268*Mg_f$ R^2-adjusted: 0.70
FRL	=	$-114 - 93*\log Ca_r + 141*Mg/Al_r - 72*Mg_s - 9*Al_s + 36 \log Ca_s + 74*N_f - 359*P_f$ R^2-adjusted: 0.69
SRL	=	$19 - 161*Mg_r + 27*K_r + 7*Ca/Al_r + 4*\log Mn_s - 31*Mg_s + 47*Na_s + 1*Al^{3+}_s - 3*\log Ca/Al^{3+}_s + 56*Mg/Al^{3+}_s + 10*N_f - 89*P_f$ R^2-adjusted: 0.73

parameters tested, the contribution of the different parameters in these models differed. Root chemical parameters explained about a third of the variance for fine-root biomass and soil and foliar parameters also approximately a third. In the model for fine-root length these figures were 32, 43 and 25 %, and for specific root length 25, 58 and 17 %, respectively. When comparing these models for control and lime treatments separately, the fraction of the variance explained by root chemical parameters decreased in all three cases, while as a consequence, the contribution of foliar parameters increased. This shows that as a result of liming the root chemical parameters show the most sensitive reaction. This was confirmed by a comparison of the new versus the old lime trials (less than 20 and more than 20 years ago). In the old lime trials, where the effect of lime has become small or absent, the contribution of root variables is again much higher for all three models.

Conclusions

The above findings suggest, that it would be worthwhile investing effort in the exploration of fine-root based parameters to complement soil and foliar indicators to evaluate site conditions or sustainability (cf Clemensson-Lindell and Persson 1995). An evaluation and definition of threshold values for these parameters is required. Such studies would aid design of cost-effective monitoring approaches, and provide an important basis for interpretating temporal data. For evaluation of soil and fine-roots as indicators of sustainability, a 2-tier approach is advocated. Initially the study should sample a limited number of fine-roots down to 50 or 100 cm (depending on rooting depth), assess the live/dead ratio of these fine roots, conduct analyses of the fine-root chemistry (N, P, K, Ca, Mg, Al, Ca/Al), of foliage (N, P, K, Ca, Mg) and measure tree growth. The relationship between these parameters and forest growth should be explored so as to define the best parameters for future monitoring. This study suggests that fine-root Ca/Al (and maybe P or N) for at least one surface and one subsoil level, together with foliar Ca, Mg, P, K, and Mg are useful indicators of forest nutrition and productivity.

References

Bakker M R, Nys C and Picard J-F 1998 The effects of liming and gypsum applications on a sessile oak (*Quercus petraea* (M.) Liebl.) stand at La Croix-Scaille (French Ardennes) I. Site characteristics, soil chemistry and aerial biomass. Accepted (Plant and Soil **00**, 1-10).

Bakker M R 1998 The effects of liming and gypsum applications on a sessile oak (*Quercus petraea* (M.) Liebl.) stand at La Croix-Scaille (French Ardennes). II Fine root dynamics. Accepted (Plant and Soil **00**, 1-13).

Burg J van den (1994) Verslag van het landelijk bemestingsonderzoek in bossen 1986 t/m 1991. Deelrapport 4. De effecten van bekalking op vitaliteitskenmerken en groei van zes opstanden

in de boswachterij St. Anthonis (1988 t/m 1991). IBN-rapport 104, Instituut voor Bos- en Natuuronderzoek, Wageningen. 89 pp.

Clemensson-Lindell A and Persson H 1993 Long-term effects of liming on the fine-root standing crop of *Picea abies* and *Pinus sylvestris* in relation to chemical changes in the soil. Scand. J. For. Res. 8, 384-394.

Clemensson-Lindell A and Persson H 1995 Fine-root vitality in a Norway spruce stand subjected to various nutrient supplies. Plant and Soil 168-169, 167-172.

Cronan C S and Grigal D F 1995 Use of calcium/aluminium ratios as indicators of stress in forest ecosystems. J. Environ. Qual. 24, 209-226.

Eissenstat D M 1991 On the relationship between specific root length and the rate of root proliferation: a field study using citrus rootstocks. New Phytol. 118, 63-68.

Helmisaari H-S 1997 Vitality of trees and forest ecosystems - concepts and criteria. In: F Andersson, F Braekke and L Hallbäcken (Eds.) Imbalanced forest nutrition - vitality measures. A SNS-project 1993-1996. Final and work report, Section of Systems Ecology, Swedish University of Agricultural Sciences. p 158-175.

Hüttl R F 1991 Die Nährelementversorgung geschädigter Wälder in Europa und Nordamerika. Freib. Bodenkl. Abh. 28. University of Freiburg, Germany. 440 p.

Nys C 1989 Fertilisation, dépérissement et production de l'épicéa commun (*Picea abies*) dans les Ardennes. Revue Forestière Française 41, 336-347.

Olsthoorn A F M and Tiktak A 1991 Fine root density and root biomass of two Douglas-fir stands on sandy soils in the Netherlands. 2. Periodicity of fine root growht and estimation of belowground carbon allocation. Neth. J. Agr. Sci. 39, 61-77.

Persson H 1993 Factors affecting fine root dynamics of trees. Suo 43, 163-172.

Persson H and Ahlström K 1994 The effects of alkalizing compounds on fine-root growth in a Norway spruce stand in southwest Sweden. J. Environ. Sci. Health, A29(4), 803-820.

Persson H, Majdi H and Clemensson-Lindell A 1995 Effects of acid deposition on tree roots. Ecol. Bull. 44, 158-167.

Puhe J, Persson H and Börjesson I 1986 Wurzelwachstum und Wurzelschäden in Skandinavischen Nadelwäldern. Allg. Forst. Zeitschr. 20, 488-492.

Raison R J, McCormack R J, Cork S J, Ryan P J and McKenzie N J 1997 Scientific issues in the assessment of ecologically sustainable forest management, with special reference to the use of indicators. In: E P Bachelard and A G Brown (Eds.) Preparing for the 21st Century: proceedings of the 4th Joint Conference of the Institute of Foresters of Australia and the New Zealand Institute of Forestry, 21-24 April 1997, Canberra ACT Australia.

Raspe S 1997 Fine root development. In: R F Hüttl and W Schaaf. Magnesium deficiency in forest ecosystems. Kluwer Academic Publishers. p 309-332.

Rengel Z 1992 Role of calcium in aluminium toxicity. New Phytol. 121, 499-513.

Rost-Siebert K 1985 Untersuchungen zur H- und Al-Toxizität an Keimpflanzen von Fichte (*Picea abies* Karst.) und Buche (*Fagus sylvatica* L.) in Lösungskultur. Berichte Forschungszentrum Waldökosteme, Universität Göttingen 12, 1-219.

Tennant D 1975 A test of a modified line intersect method of estimating root length. J. Ecol. 63, 995-1001.

Trüby P 1989 Eine Titrationsmethode zur simultanen Bestimmung von H^+ und Aluminium in NH_4Cl-bodenextrakten. Z. Pflanzenernähr. Bodenk. 152, 297-300.

Unistat Ltd 1995. Unistat Version 4 for Windows. London, UK.

Vogt K A and Persson H 1991 Measuring growth and development of roots. *In* Techniques and approaches in forest tree ecophysiology. Ed. J P Lassoie and T M Hinckley. pp 477-501. Boca Raton.

Annexe A (Paper IV) : à soumettre aux Annales des Sciences Forestières

Fine roots and mineral nutrition of Oak in response to lime-induced differences in site fertility

M R Bakker et C Nys

Abstract

Fine roots are a function of both site fertility and the demand of trees for uptake to support growth. Differences between sites may lead either to changes in amount or functioning of fine roots. This study focuses on the effects of liming on site fertility. The objectives are to evaluate what the effects of these lime-induced differences in site-fertility are on fine roots and mineral nutrition. Lime was applied in ten oak (*Quercus petraea* and *Q. robur*) stands, 2 to 27 years before fine root core sampling. All sites but one were situated on acidic soils with low base saturation. They showed deficient nutrient levels according to soil exchangeable nutrient pool, fine root- and foliar composition. Results indicate a higher fine root biomass in the limed stands with a concomitant increase in above-ground standing crop. Fine root distribution was enhanced both in top-soil and in deeper horizons. Overall fertility and nutrition were improved by the lime applications for Ca and Mg. However, the poor nutrition of K and P in a part of the stands was not improved and the higher fine root development may be an adaptation to low levels of these elements. As a conclusion this suggests that liming in moderate doses on acidic sites showing nutrient deficiencies may stimulate the absorbing capacity of the tree root system by enlarging fine root standing crop and thereby improve mineral nutrition and stand growth, but one should keep in mind that resolving a deficiency for some elements may be less favorable for others.

key-words: fine roots, liming, mineral nutrition, *Quercus*, soil

Introduction

For the purpose of evaluating forest productivity, vitality, and soil resources, the interface between soil nutrient pools and tree roots as uptake organs to sustain above-ground growth, is of utmost importance. A sufficient level of nutrient resources in the soil (in plant-available form or liberated by weathering) is needed to ensure a sustained productivity and vitality of the forest stands. Uptake of Mg^{2+} or Ca^{2+} can be strongly depressed by other cations such as K^+, NH_4^+, Al^{3+} or H^+ (Raspe 1997), so that due to this antagonistic uptake not all of the potentially available soil nutrients are actually accessible to tree roots (Rost-Siebert 1985). Further, allocation of nutrients to the canopy often is preferential relative to allocation of nutrients to the roots, so that fine roots can be good indicators of nutritional conditions (Persson *et al.* 1995). They can be very useful as stress indicators at an early stage (Vogt *et al.* 1993) before major deficiences can be detected at foliar level (Helmisaari 1997). Ten oak stands situated on poor acidic forest soils were included in this study. They featured deficiencies for one or more nutrients (amongst which in general Ca). Lime as a 'compensation amendment' was expected to increase fertility and productivity of these stands. In a previous paper (Bakker 1998) the effects of liming on soil chemistry, element concentrations in roots and foliage, fine root development and stand growth were described. Here the focus is more on general site fertility and nutrition. The objective of this paper is to: « Determine the lime-induced changes in soil fertility and total mineral nutrition and their relation with fine root development ».

Materials and methods

Between June 1994 and March 1996 a total of 10 different sites with Oak (*Quercus petraea* and *Q. robur*) were sampled for soil-, fine root-, foliage- and above ground growth parameters. For two of the trials, sampling was sequential over a 21 month period. Eight of the trials are situated in France and two in the southeast of the Netherlands (site 9 and 10). Soil and fine roots were sampled by soil coring down to 75 cm at maximum (Table 1). Foliage was sampled in August close to the top of the crown of five dominant trees per experimental plot and above ground tree growth was evaluated by means of height, Dbh and analyses of ring width on wood cores.

Table 1 Site characteristics of 10 limed oak stands

site nr	age of stand yr	year since liming	soil profile cm	eq CaO dose t. ha^{-1}	Quercus species	soil texture	BS % 0-5 cm	pH-H_2O 0-5 cm	BS % 30-45 cm	pH-H_2O 30-45 cm
1	c. 48	4	0-55	1.4	petraea	silty clay	13.9	3.99	12.8	4.48
2	c. 48	1	0-55	1.4	petraea	silty clay	14.1	3.77	8.5	4.39
3	25	25	0-75	1.25	petraea	sand	100	6.36	100	7.08
4	c. 76	26	0-75	1.5	petraea	silt	42.9	3.73	15.0	4.40
5	c. 55	27	0-75	1.5	petraea	silt	55.6	3.92	20.2	4.47
6	c. 50	27	0-75	1.5	petraea	sandy silt	24.7	3.97	10.9	4.44
7	24	24	0-45	1.25	petraea	silt	80.9	4.97	-	-
8	44	14	0-60	0.8	petraea	silty sand	33.8	4.84	40.8	4.72
9	42	7	0-75	1.6	robur	sand	38.1	4.07	12.4	4.14
10	15	7	0-75	1.6	robur	sand	27.8	3.74	4.2	4.05

1 = Croix-Scaille ancient; 2 = Croix-Scaille recent; 3 = Fontainebleau; 4 = Trembles; 5 = Gaie Mariée; 6 = Rond du May; 7 = Bertranges; 8 = Tronçais; 9 = St. Anthonis 35c ; 10 = St. Anthonis 46a.

Soil samples were air-dried and then sieved at 2 mm. 0.5 *M* NH_4Cl-exchangeable Al, Ca, Mg, K, Mn and Na (Trüby 1989) were determined by ICP (emission spectrometry), exchangeable acidity by automatic titration (Trüby 1989), and pH-KCl and pH-H_2O following standard procedures with KCl-electrodes. Concentrations were expressed at an oven-dried (105°C) weight basis. The fine roots (< 2 mm in diameter) were separated from the soil by wet sieving above a 4 and 2 mm sieve followed by short flotation to rinse the roots and root length was estimated by the line intersection method (Tennant 1975). The fine root biomass was obtained by drying at 105°C until constant weight. Correction factors for losses due to stocking, passing through the sieve and so on were established and evaluated at +20% for biomass and at +25% for length. For the chemical analyses of foliage and fine roots, subsamples were pretreated with peroxyde (H_2O_2), then mineralized with $HClO_4$ and analysed by ICP. Mycorrhizae were characterized by counting and classifying apices with ectomycorrhizae over main ectomycorrhizal morphotypes (Bakker *et al.* 1999). For more information on the methods used see also Bakker (1998).

The amounts of exchangeable nutrients in the soil were calculated by multiplying the concentration determined on soil samples by the average soil density of the layer. These soil densities were either known or estimated using general site characteristics like texture and soil density values for similar sites in the RENECOFOR sites (Brêthes & Ulrich 1997). The amounts of nutrients in fine roots were calculated by multiplying the concentrations of these nutrients in the fine roots by the mass of fine roots per soil layer, before summing these values to a hectare and profile basis. As the deepest layer was sampled only in limited number, the calculated summed values were not tested for treatment effects. In stead, treatment effects

were established by analysis of variance within individual horizons. The Student-Newman-Keuls test was used to establish significant differences between group means with Unistat 4.0 software (Unistat Ltd 1995).

Table 2 Amounts of exchangeable elements in kg ha^{-1} ; soil fertility evaluated as poor or very poor for Ca (< 600 and < 415 kg CaO ha^{-1} resp.), for Mg (< 220 and < 150 kg MgO ha^{-1} resp.), for K (< 400 and < 290 kg K_2O ha^{-1} resp.) and for P (< 760 and < 280 kg P_2O_5 ha^{-1} resp.); values are sums of the profile (* = limed stands not assessed for P) and threshold values are derived from Bonneau (1995).

site	CaO		MgO		K_2O		P_2O_5	
	Control	Liming	Control	Liming	Control	Liming	Control	Liming
1	303	1233	113	127	551	505	875	*
2	294	422	94	75	515	433	875	*
3	22440	13252	385	563	283	268	*	*
4	362	414	614	535	632	564	231	*
5	2058	1187	1691	1479	626	650	720	*
6	269	252	300	622	370	331	254	*
7	1869	1757	583	491	695	602	561	*
8	598	529	554	260	839	488	611	*
9	360	1341	78	191	108	210	324	*
10	298	701	28	81	157	165	206	*

Results

The quantities of exchangeable elements are presented in Table 2 and Figure 1. These show that the quantity of exchangeable Ca and Mg have been increased by liming, but this is noticeable only in the most recently limed stands. All together, based on individual horizons, this increase in Ca is significant for the most recently limed stands. An apparent decrease of exchangeable Ca at sites 3 and 5 is due to a lime rich layer in the the subsoil, explaining the high sum values of Ca in the control fields; in the toplayers liming increased the total amount of Ca. Effects on K were less clear; maybe that the total amount of K is slightly declining as a result of liming. Data on P were incomplete to evaluate the effect of liming. As compared with the threshold levels (Bonneau 1995)for soil fertility, 7 stands were poor or very poor in Ca, 4 stands were very poor in Mg, 4 poor or very poor in K and 6 (probably 7) poor or very poor in P. Liming improved this clearly for Ca (4 sites with a poor nutrition in Ca left after liming) and a little bit for Mg.

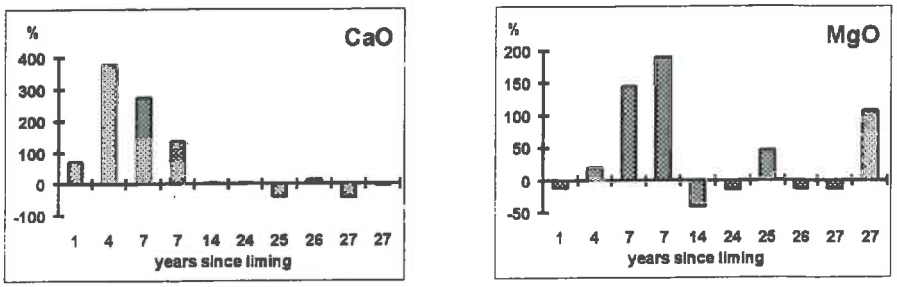

Figure 1 Lime-induced change (in %) of soil Ca or Mg (expressed in kg CaO or MgO ha^{-1} as a function of time since liming (sum of profile).

The amounts of nutrients in the fine roots are presented in Table 3. The total amount of Mg and Ca in the fine roots was increased in a general way (for 7 out of 10 sites higher values), although this failed a significant level in most stands due to the limited sample number; effects

Table 3 Total amount of four macroelements in the fine roots as a function of liming; values are sums for the total profile (kg ha^{-1})

site	Ca		Mg		K		P	
	Control	Lime	Control	Lime	Control	Lime	Control	Lime
1	14.86	11.17	4.89	5.41	5.63	6.51	2.98	1.34
2	3.65	4.47	2.49	2.53	3.46	2.95	2.15	1.89
3	29.81	57.11	3.69	5.47	1.91	7.13	0.50	0.51
4	4.77	5.36	3.44	3.52	2.80	2.80	1.43	2.15
5	4.46	7.98	3.25	3.09	2.42	2.18	1.02	1.24
6	9.69	9.20	8.08	5.94	7.98	5.08	2.90	1.89
7	5.48	9.35	2.75	4.11	1.98	2.14	1.06	1.04
8	8.53	7.80	5.08	4.79	5.08	5.11	1.79	3.44
9	11.38	16.95	4.62	5.91	3.67	3.23	4.53	5.45
10	10.94	11.18	3.41	4.28	3.07	2.69	3.44	2.98

on P and K were not conclusive. The concentrations of these elements in the fine roots showed to be increased marginally as shown by the overall mean values (± standard errors) for Ca (2.3 ±0.22 and 2.6 ±0.27 g kg^{-1} dry weight for control and liming, respectively), whereas concentrations of Mg (0.95 ±0.04 and 0.98 ±0.03), of K (0.93 ±0.03 and 0.87 ±0.05) and P (0.51 ±0.03 and 0.51 ±0.03) were not clearly affected (Bakker 1998). The root function, that is root health and thus uptake potential, may be best evaluated on the basis of Ca/Al ratio in the tissue of fine roots (Cronan and Grigal 1995; Bakker 1998); Ca/Al ratios below the threshold levels indicating potential toxicity and physiological disturbance. The parts below these thresholds in the control and lime treatments and the net effects of liming are presented in Table 4. It shows that in most of the sites fine root Ca/Al ratios occur in at least a part of the soil profile that are in the critical range (Cronan and Grigal 1995), and that liming increased this Ca/Al ratio in many soil layers.

Table 4 Fine root tissue Ca/Al molar ratios as a function of liming: presented are the soil horizons in cm where these ratios are below the general toxicity threshold levels < 0.2 and < 0.5; the treatment effects are summarized in italic in the two colums at the right (* = missing data).

site nr	part below threshold in the control		part below threshold in the lime treatment		net positive effect	net negative effect
	root Ca/Al < 0.2	root Ca/Al 0.2-0.5	root Ca/Al < 0.2	root Ca/Al 0.2-0.5	on root Ca/Al	on root Ca/Al
1	5-55	0-5	5-55	-	*0-30*	
2	5-55	0-5	5-55	0-5	*0-5*	
3	*	*	*	*	*	*
4	15-60	5-15	5-15/30-60	15-30	*15-45*	*5-15/45-60*
5	15-30/45-60	5-15/30-45	-	15-45	*0-60*	
6	15-60	5-15	45-60	5-45	*0-5/15-60*	
7	0-5	5-30	-	0-30	*0-30*	
8	-	0-45	30-45	0-30	*15-30*	*30-45*
9	30-60	5-30	45-60	5-45	*15-60*	*0-15*
10	15-60	5-15	30-60	15-30	*0-30*	

The deficiencies according to foliar analysis and foliar concentrations relative to N are presented in Table 5. It shows that according to absolute nutrient levels (Bonneau 1995; Van den Burg & Olsthoorn 1996), liming only succeeded in improving foliar nutrition out of the critical range for Ca, and more occasionally for Mg. Such a lime-induced increase in foliar Ca and Mg was shown to be consistent throughout all liming trials, only slightly lowered for the

Table 5 Deficiencies and alleviation by liming according to foliar composition thresholds (poor = < 2 % N, < 0.13% P for *petraea* and < 0.14% for *robur*, < 0.60% K, < 0.30% Ca for *petraea* and < 0.50% for *robur*, and <0.15% Mg for *petraea* and <0.16% for *robur*; based on Bonneau 1995 and on Van den Burg & Olsthoorn 1996); further expressed relative to nitrogen (100 x nutrient %DW/N % DW)

site	foliage	foliage	Ca:N		Mg:N		K:N		P:N	
nr	Control	Lime	Control	Lime	Control	Lime	Control	Lime	Control	Lime
1	Ca,Mg	Mg	12.3	18.9	3.5	4.0	31.3	31.7	6.6	5.7
2	Ca,Mg	Mg	10.8	15.1	3.5	5.0	28.2	23.2	6.2	5.8
3	Mg,P,K	P,K	37.9	46.0	7.2	7.9	27.4	28.4	4.0	3.7
4	N,P	N,P	40.3	40.7	8.4	8.7	40.6	36.2	6.0	5.2
5	N,P	P	34.2	35.1	8.7	8.2	35.3	37.3	5.2	4.8
6	Mg,N,P	P	34.9	34.1	7.3	8.4	46.1	36.3	5.2	4.9
7	N,P	P	37.6	44.4	8.6	9.3	42.1	46.2	5.9	6.1
8	-	-	33.5	40.2	7.9	8.5	40.9	40.2	6.1	7.8
9	-	-	19.9	26.0	6.8	7.8	28.8	29.9	6.4	6.4
10	P	P	26.7	41.0	9.5	11.4	33.8	31.9	6.2	5.7

sites with the greatest time lapse since liming. This picture is very similar for the values relative to nitrogen: the Ca:N and Mg:N values show the same lime-induced stimulation and consistency over time. However, for P and K, the values relative to N were less positive than were absolute foliar levels. Absolute levels showed some decrease of P level (6 sites decrease, 1 increase, 3 no effect) and no clear effect on K (5 sites increase, 5 sites decrease). The values relative to N indicated a decrease in 8 out of 10 for P:N and some changes in K:N ratios for in particularly the oldest lime trials. For one of the sites were an increase in P:N occurred, P was also supplied together with the lime treatment. Compared to the values given by Boxman *et al.* (1994), most of the values relative to N are normal (Mg:N $\geq$ 5, K:N $\geq$ 25 and P:N $\geq$ 5) or close to normal with low values at site 3 (P:N) and 1 and 2 (Mg:N).

Table 6 Ratios of root elements:foliar N (100 x nutrient % DW of root / N % DW of foliage); root element values are average values of all soil layers (standard errors in italic).

site	Ca:N		Mg:N		K:N		P:N	
	Control	Lime	Control	Lime	Control	Lime	Control	Lime
1	19.1 (*1.8*)	12.4 (*0.6*)	6.5 (*0.5*)	6.6 (*0.9*)	8.0 (*1.2*)	7.8 (*0.3*)	4.2 (*0.7*)	1.3 (*0.3*)
2	4.9 (*0.5*)	7.2 (*0.9*)	3.5 (*0.1*)	4.0 (*0.2*)	4.9 (*0.4*)	4.6 (*1.7*)	2.8 (*0.7*)	3.0 (*0.2*)
3	41.5 (*9.5*)	56.2 (*8.8*)	4.8 (*0.5*)	5.3 (*0.7*)	2.7 (*0.5*)	7.0 (*0.2*)	0.5 (*0.4*)	0.6 (*0.4*)
4	5.3 (*0.8*)	5.4 (*1.1*)	3.9 (*0.4*)	3.8 (*0.2*)	3.4 (*0.2*)	3.2 (*0.8*)	1.5 (*0.3*)	2.4 (*0.8*)
5	6.7 (*0.9*)	11.0 (*0.3*)	4.6 (*0.3*)	4.3 (*0.3*)	3.7 (*0.2*)	3.1 (*0.2*)	1.4 (*0.2*)	1.6 (*0.3*)
6	6.7 (*1.1*)	9.0 (*0.8*)	5.9 (*0.4*)	5.7 (*0.2*)	5.9 (*0.5*)	5.1 (*0.1*)	2.1 (*0.2*)	1.8 (*0.2*)
7	9.8 (*1.1*)	12.4 (*1.3*)	5.1 (*0.3*)	5.4 (*0.2*)	3.7 (*0.4*)	2.8 (*0.2*)	2.0 (*0.2*)	1.4 (*0.1*)
8	10.8 (*1.0*)	8.8 (*0.9*)	6.4 (*0.2*)	5.4 (*0.2*)	6.5 (*0.5*)	5.7 (*0.2*)	2.3 (*0.1*)	3.8 (*0.3*)
9	6.1 (*1.1*)	8.5 (*0.8*)	2.5 (*0.3*)	3.0 (*0.2*)	2.0 (*0.1*)	1.6 (*0.2*)	2.4 (*0.2*)	2.8 (*0.4*)
10	7.6 (*2.0*)	8.7 (*2.6*)	2.5 (*0.5*)	3.5 (*0.8*)	2.6 (*0.3*)	2.5 (*0.8*)	2.9 (*0.2*)	2.7 (*0.2*)

The fine root concentrations relative to foliar N are presented in Table 6, as the dataset for root N was not complete. Such a comparison of root to foliar levels might indicate early deficiency levels (Vogt *et al.* 1993). Here the values are in general positive for root Ca and Mg as compared to foliar N (increase by liming), showing no nutritional disturbances (Vogt *et al.* 1993, Boxman *et al.* 1994). The decrease in Ca:N and Mg:N ratios for site 8 perhaps is due to the fact that N was also added on that particular site. So, the effect of lime on the values of root Ca and root Mg : foliar N closely ressemble those for the ratios of foliar:foliar levels (Tab. 5). For the P:N and K:N ratios this was different (Figure 2). As can be seen in this Figure, for

the P:N ratios, the effect of liming (expressed as nutrient level relative to N) is not much affected in the fine roots (no clear tendency), but in the foliage the P:N ratios (indicated by the symbols) tend to decrease after liming. This can indicate a retention of P in the fine roots, rather than transport to the foliage, relative to N. For the K:N ratios the opposite is true: the foliar:foliar ratio is not clearly affected by liming (indicated by the symbols), while the root:foliar ratios tend to decrease. This would indicate a preferential transport to the foliage relative to N.

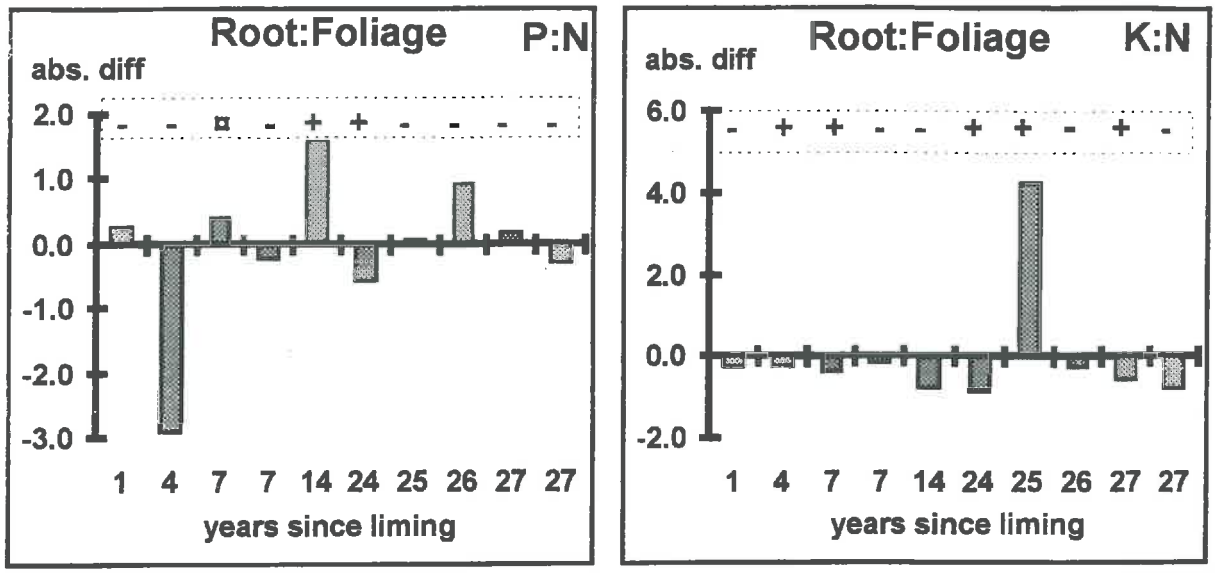

Figure 2 Lime-induced change (absolute difference) of nutrition ratios of root P and K : foliar N as a function of time since liming; the symbols in the upper part of the figure present the effects of lime on the foliar P:N and K:N nutrient ratios (+ = lime increased this value; - = lime decreased this value and ¤ = lime did not change this value).

Discussion

The adaptation of root systems to acidic soils can be achieved either by a highly efficient uptake, or utilization of nutrients or both (Marschner 1995). At poor sites allocation of assimilates to fine roots in general is higher (Olsthoorn and Tiktak 1991), for example when N, P or S are deficient (Hüttl 1991). Conversely, when subsoil acidification enhances a Mg or Ca deficiency due to imbalanced uptake, an improvement of fertility and alkalinity (by lime) may increase fine root growth (Hüttl 1991). In the ten oak stands included in this work, liming generally stimulated fine root development and stand growth and these effects were detectable at least until 20-25 years after the lime treatments (Bakker 1998). Whether this stimulation is the result of a resolved deficiency or on the contrary an investment optimizing uptake of nutrients that are most deficient (Eissenstat and Yanai 1997), depends on the general soil fertility and the way these nutrients are transported to the roots (Yin *et al.* 1991).

The soil chemical status was improved by liming, as described more in detail in a previous paper (Bakker 1998). Liming increased exchangeable Ca, Ca/Al^{3+} ratio, base saturation, CEC, pH-H_2O and pH-KCl, and inversely decreased soil Na, Al^{3+} and H^+; effects on Mg, K, S and Mn were negligible. When considering the total amount of exchangeable elements (sum of profile) as presented in Tab 2 and Fig 1, the poor availability of Ca and Mg appears to be improved the first years after liming, but availability of K (poor on 4 sites) and of P (poor on 7

sites) was not improved. Of course, observations on total P availability were incomplete, but were infered by the foliar analyses (Tab. 5).

Root health appeared to be improved by liming, as was shown by the increase of Ca/Al ratio (Cronan and Grigal 1995), a higher live/dead ratio of fine roots in the first years after liming and indications of a higher root lifespan (Bakker 1998). The Ca/Al molar ratio in the fine roots can express the ability or inability to take up nutrients, due to presence or absence of Al-stress. In this study toxic Ca/Al ratios of 0.10-0.20 (Puhe *et al.* 1986; Cronan and Grigal 1995) were alleviated by liming down to a depth of 30 or even 45 cm, and concomittantly root growth was not only stimulated in topsoil but also in the deeper layers.

So, the higher Ca availability improved fine root health, amount of fine roots, tree growth and Ca nutrition (in fine root tissue and in foliage), whereas Mg was also stimulated to a smaller extent. Effects on N nutrition were a decrease of foliar N by lime at first, followed by and increase over time. Contents of P showed a decrease in fine roots in the most recently limed plots and a general decrease in foliage. To evaluate disequilibria in nutrition, values should be expressed relative to nitrogen (Boxman *et al.* 1994) and the comparison of foliar to root levels is another means of detecting potential stress (Vogt *et al.* 1993). Changes in root concentrations may occur before those in foliage, so that fine root chemical analyses may be powerful indicators of mineral deficiencies at an early stage. These comparisons showed no nutritional desequilibria for Ca or Mg after liming (Tables 5 and 6), but in contrast indicated that P and K nutrition may become deficient in term (Tables 5 and 6, Fig. 2). P seems to be retained more in the fine roots whereas K was transported preferentially to the leaves (measured in top of the crown), suggesting that a part of the crown and the root system may be low already on K, possibly due to dilution effects.

Since Ca and Mg are less limiting now, the observed higher fine root mass after liming could be an adaptation to low P and K levels. Accidently, these are both elements that are principally transported by diffusion processes, so that an increase of the soil volume explored by fine roots is directly related with a higher access to P and K sources (Yin *et al.* 1991). In accordance with this, Ca is important for cell extension (Marschner 1995), so that a resolved deficiency for this element may explain the higher ability for fine root growth. Also, a shift of ectomorphological morphotypes towards hairy morphotypes was observed (Bakker *et al.* 1999), which can be related to the fact that mycorrhizal associations have proven to be an important adaptation to acid mineral soils with low phosphorus availability (Marschner 1995), which is the case in most of the sites.

Conclusions

In the fertility range of sites subject of this study, moderate doses of lime resulted in a higher overall site fertility and nutritional status of the fine roots and leaves of oak. However, it is possible that the higher fine root amount observed in the limed stands is not necessarily an expression of a higher longevity and improved fine root health (as indicated by higher live/dead and Ca/Al ratios of fine roots). It could also be a response to low P and K levels, as shown by low total levels of these elements in the soil and the nutrient ratios in foliage:foliage and foliage:root relative to N.

References

Bakker M R 1998 Fine-root parameters as indicators of sustainability of forest ecosystems. Accepted for For. Ecol. Manage.

Bakker M R, Garbaye J and Nys C 1999 Effect of liming on the ectomycorrhizal status of oak. Accepted for For. Ecol. Manage.

Bonneau M 1995 Fertilisation des forêts dans les pays tempérés. Théorie, bases du diagnostic, conseils pratiques, réalisations expérimentales. ENGREF, Nancy. 366 p.

Boxman A W, Cobben P L W and Roelofs J G M 1994 Does (K+Mg+Ca+P) fertilization lead to recovery of tree health in a nitrogen stressed *Quercus rubra* L. stand? Environ. Pollut. 85, 297-303.

Brêthes A and Ulrich E 1997 RENECOFOR - Caractéristiques pédologiques des 102 peuplements du réseau. Office National des Forêts, Dép. Recherches Techniques. 573 pp.

Cronan C S and Grigal D F 1995 Use of calcium/aluminium ratios as indicators of stress in forest ecosystems. J. Environ. Qual. 24, 209-226.

Eissenstat D M and Yanai R D 1997 The ecology of root lifespan. Avances in Ecological Research 27, 1-60.

Helmisaari H-S 1997 Vitality of trees and forest ecosystems - concepts and criteria. In: F Andersson, F Braekke and L Hallbäcken (Eds.) Imbalanced forest nutrition - vitality measures. A SNS-project 1993-1996. Final and work report, Section of Systems Ecology, Swedish University of Agricultural Sciences. p 158-175.

Hüttl R F 1991 Die Nährelementversorgung geschädigter Wälder in Europa und Nordamerika. Freib. Bodenkl. Abh. 28. University of Freiburg, Germany. 440 p.

Marschner, H 1995 Mineral nutrition of higher plants. 2nd ed. Academic Press, London.

Olsthoorn A F M and Tiktak A 1991 Fine root density and root biomass of two Douglas-fir stands on sandy soils in the Netherlands. 2. Periodicity of fine root growth and estimation of belowground carbon allocation. Neth. J. Agr. Sci. 39, 61-77.

Persson, H 1993 Factors affecting fine root dynamics of trees. Suo 43, 163-172.

Persson H, Majdi H and Clemensson-Lindell A 1995 Effects of acid deposition on tree roots. Ecol. Bull. 44, 158-167.

Puhe J, Persson H and Börjesson I 1986 Wurzelwachstum und Wurzelschäden in Skandinavischen Nadelwäldern. Allg. Forst. Zeitschr. 20, 488-492.

Raspe S 1997 Fine root development. In: R F Hüttl and W Schaaf. Magnesium deficiency in forest ecosystems. Kluwer Academic Publishers. p 309-332.

Rost-Siebert K 1985 Untersuchungen zur H- und Al-Toxizität an Keimpflanzen von Fichte (*Picea abies* Karst.) und Buche (*Fagus sylvatica* L.) in Lösungskultur. Berichte Forschungszentrum Waldökosteme, Universität Göttingen 12, 1-219.

Shortle W C and Smith, K T 1988 Aluminium-induced calcium deficiency syndrome in declining red spruce. Science 240, 1017-1018.

Tennant D 1975 A test of a modified line intersect method of estimating root length. J. Ecol. 63, 995-1001.

Trüby P 1989 Eine Titrationsmethode zur simultanen Bestimmung von H^+ und Aluminium in NH_4Cl-bodenextrakten. Z. Pflanzenernähr. Bodenk. 152, 297-300.

Unistat Ltd 1995 Unistat Version 4 for Windows.

Van den Burg J, Olsthoorn A F M 1996 National research project on forest fertilisation. 1985/86 - 1991-92. IBN Research Report 96/10. IBN-DLO, Wageningen, The Netherlands. 43 p.

Vogt K A, Publicover D A, Bloomfield J, Perez J M, Vogt D J and Silver W L 1993 Belowground responses as indicators of environmental change. Envir. Exp. Bot. 33, 189-205.

Yin X, Perry J A and Dixon R K 1991 Temporal changes in nutrient concentrations and contents of fine roots in a *Quercus* forest. For. Ecol. Manage. 44, 175-184.

Annexe A (paper V) : *Neth. J. Agr. Sci.* **46**: 213-226, (1998)
Reçu le 2 février 1998 ; accepté le 1 juin 1998.
Repris dans cet oeuvre avec la permission de l'éditeur en chef de *Netherlands Journal of Agricultural Science* ; veuillez-bien utiliser la référence ci-dessus en cas de citation.

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

M.R. Bakker

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 dosis of 1.6 t ha^{-1} 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 developped 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 kg ha^{-1} 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 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 x 30 m or 25 x 36 m) and 6, 5, 5 per bloc for the young stand (3 blocs, plot size 20 x 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 (ø 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 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 x 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-H_2O 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 proncounced: 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).

Table 1 Soil composition: Exchangeable cations with 0.5 *M* NH_4Cl ($cmol_c\ kg^{-1}$) 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	pH	pH	Mn	Mg	Ca	Na	K	H^+	Al^{3+}	Ca/Al^{3+}
	cm	H_2O	KCl	$cmol_c\ kg^{-1}$							molar
Young stand											
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
Old stand											
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

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 $.10^6$ m ha^{-1} for the control and the lime treatment in the young stand and between 104.9 and 112.2 $.10^6$ 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 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.

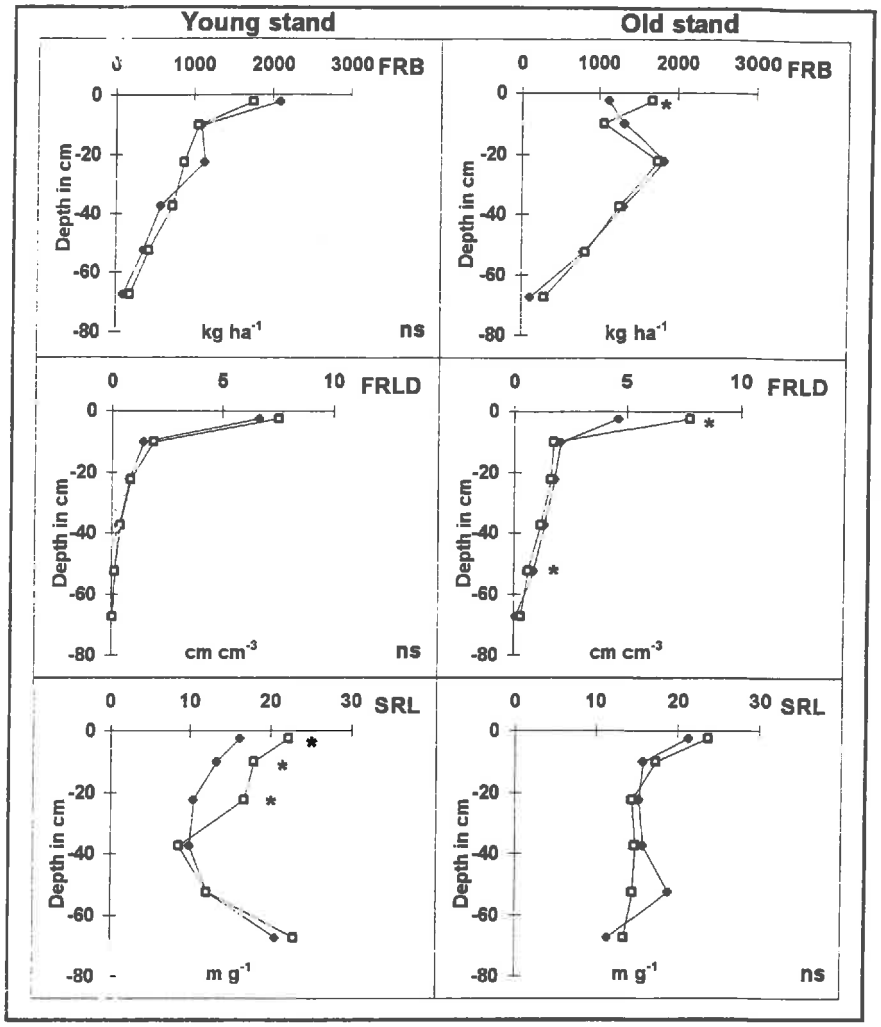

Figure 1 Vertical distribution of fine root biomass (FRB), fine root length density (FRLD), and specific root length (SRL) for the young and old stand. Mean depths of the soil layers were used to represent the values. Filled symbols are for the control and open squares for the lime treatment (sample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

The concentration of some elements in the fine roots as presented in Table 2, was tested statistically on an overal 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.

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
Young stand										
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
Old stand										
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

Dead root pools

Total fine root necromass for 0-75 cm ranged from 2906 kg ha^{-1} for the liming treatment 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 10^6 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

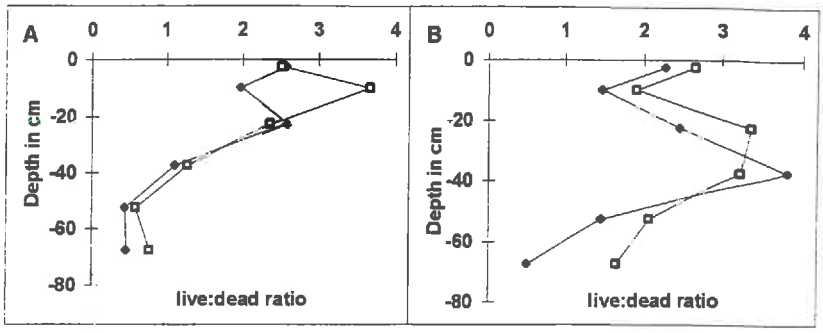

Figure 2 Live:dead ratio of fine root mass for the young (A) and the old stand (B). Mean depths of the soil layers were used to represent the values. Filled symbols are for the control and open squares for the lime treatment (sample number = 2 for the old stand and 3 for the young stand, no statistics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

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.*).

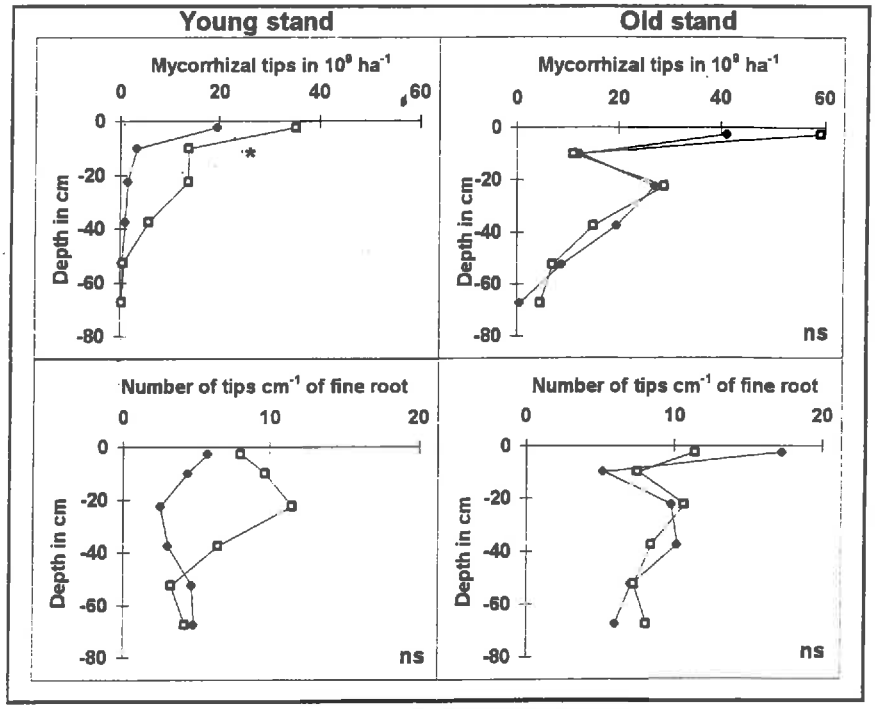

Figure 3 Number of mycorrhizal root tips per ha (upper half) and number of mycorrhizal tips per cm of fine root (lower half) for the young and the old stand. Mean depths of the soil layers were used to represent the values. Filled symbols are for the control and open squares for the lime treatment (sample 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 labouring 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 an 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 NO_3-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 (Gijsman, 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.

Acknowledgements

I would like to acknowledge C. Nys and J. Ranger for their useful comments on earlier versions of this manuscript, and S. Didier and D. Gelhaye (all working at INRA Nancy) for their technical assistance in the field. Furthermore, I would like to thank J. Van Den Burg and A.F.M Olsthoorn (IBN-DLO), and A.W.J. Bosman (SBB regio Rivierenland) for their permission to work in the experimental trial at St. Anthonis. This research was supported by grants of INRA Paris, and the Dutch Ministry of Agriculture, Nature Management and Fisheries, Directorate of Science and Knowledge Dissemination.

References

Bakker, M.R., 1998. The effect of lime and gypsum applications on a sessile oak (*Quercus petraea* (M.) Liebl.) stand at La Croix-Scaille (French Ardennes) II. Fine root dynamics. *Plant and Soil (accepted)*.

Bakker, M.R., C. Nys & J.-F., Picard, 1998. The effects of liming and gypsum applications on a sessile oak (*Quercus petraea* (M.) Liebl.) stand at La Croix-Scaille (French Ardennes) I. Site characteristics, soil chemistry and aerial biomass. *Plant and Soil (accepted)*.

Belkacem, S., 1993. Etude de la resaturation des sols acides soumis à de forts apports acides: effet des formes et doses d'amendements sur le fonctionnement d'un sol acide forestier. PhD-Thesis. University Nancy I, Nancy. 188 pp.

Blaise, T. & J. Garbaye, 1983. Effets de la fertilisation minérale sur les ectomycorhizes d'une hêtraie. *Acta Oecologica, Oecologia Plantarum* 4: 165-169.

Burke, M.K. & D.J. Raynal, 1994. Fine root growth phenology, production, and turnover in a northern hardwood forest ecosystem. *Plant and Soil* 162: 135-146.

Clemensson-Lindell, A. & H. Persson, 1993. Long-term effects of liming on the fine-root standing crop of *Picea abies* and *Pinus sylvestris* in relation to chemical changes in the soil. *Scandinavian Journal of Forest Research* 8: 384-394.

Dagnélie, P., 1970. Théorie et méthodes statistiques; applications agronomiques. Volume II Les méthodes de l'inférence statistique. Les presses agronomiques de Gembloux, ASBL; Editions J. Ducolot, S.A, Gembloux, Belgium, 451 pp.

De Boer, W., M.P.J. Hundscheid, J.M.T. Schotman, S.R. Troelstra & H.J. Laanbroek, 1993. In situ net N transformations in pine, fir, and oak stands of different ages on acid sandy soil, 3 years after liming. *Biology and Fertility of Soils* 15: 120-126.

Derome, J., 1990/1991. Effects of forest liming on the nutrient status of podzolic soils in Finland. *Water, Air and Soil Pollution,* 54: 337-350.

Gijsman, A.J., 1990. Nitrogen nutrition and rhizosphere pH of Douglas-fir. PhD-Thesis, Groningen University, Groningen, 132 pp.

Hagen, T., 1992. The effects of mineral supplies on fine root development of scots pine in a reafforestation stand on poor sandy soil (In Dutch). Student Dissertation. Agricultural University Delft (Agr. Hogeschool Delft) and Institute for Forest and Nature Research (IBN-DLO), Wageningen, 35 pp.

Hüttl, R.F. & H.W. Zöttl, 1993. Liming as a mitigation tool in Germany's declining forests - reviewing results from former and recent trials. *Forest Ecology and Management* 61: 325-338.

Keltjens, W.G. & E. Van Loenen, 1989. Effects of aluminium and mineral nutrition on growth and chemical composition of hydroponically grown seedlings of five different forest tree species. *Plant and Soil* 119: 39-50.

Mangenot, F., 1980. Les litières forestières; signification écologique et pédologique. *Revue Forestière Française* 32: 339-356.

Marschner, H., 1991. Mechanisms of adaptation of plants to acid soils. *Plant and Soil* 134: 1-20.

Murach, D. & E. Schünemann, 1985. Reaktion der Feinwurzeln von Fichten auf Kalkungsmassnahmen. *Allgemeine Forstzeitschrift* 40: 1151-1154.

Olsthoorn, A.F.M., 1991. Fine root density and root biomass of two Douglas-fir stands on sandy soils in the Netherlands. 1. Root biomass in early summer. *Netherlands Journal of Agricultural Science* 39: 49-60.

Olsthoorn, A.F.M., W.G. Keltjens, B. Van Baren & M.C.G. Hopman, 1991. Influence of ammonium on fine root development and rhizosphere pH of Douglas-fir seedlings in sand. *Plant and Soil* 133: 75-81.

Olsthoorn, A.F.M. & A. Tiktak, 1991. Fine root density and root biomass of two Douglas-fir stands on sandy soils in the Netherlands. 2. Periodicity of fine root growth and estimation of belowground carbon allocation. *Netherlands Journal of Agricultural Science* 39: 61-77.

Persson, H. & K. Ahlström, 1990/91. The effects of forest liming and fertilization on fine-root growth. *Water, Air and Soil Pollution* 54: 363-375.

Raspe, S., 1992. Biomasse und Mineralstoffgehalte der Wurzeln von Fichtenbeständen (*Picea abies* Karst.) des Schwarzwaldes und Veränderungen nach Düngung. *Freiburger Bodenkundliche Abhandlungen* 29, 197 pp.

Rost-Siebert, K., 1983. Aluminium-Toxizität und -Toleranz an Keimpflanzen von Fichte (*Picea abies* Karst.) und Buche (*Fagus silvatica* L.). *Allgemeine Forstzeitschrift* 38: 686-689.

Shamshuddin, J., I. Chefauziah & H.A.H. Sharifuddin, 1991. Effects of limestone and gypsum applications to a Malaysian Ultisol on soil solution composition and yields of maize and groundnut. *Plant and Soil* 134: 45-52.

Tennant, D., 1975. A test of a modified line intersect method of estimating root length. *Journal of Ecology* 63: 995-1001.

Van Den Burg, J., 1994 National research project on forest fertilization 1986 - 1991. Volume 4. The effects of liming on vitality and growth of six stands in the state forest of St. Anthonis, 1988 - 1991 (In Dutch). IBN-report 104 Institute for Forestry and Nature Research (IBN-DLO), Wageningen, 89 pp.

Van Noordwijk, M. & J. Floris, 1979. Loss of dry weight during washing and storage of root samples. *Plant and Soil* 53: 239-243.

Voiry, H., 1981. Classification morphologique des ectomycorrhizes du chêne et du hêtre dans le nord-est de la France. *European Journal of Forest Pathology* 11: 284-299.

Vogt, K.A., C.C. Grier, S.T. Gower, D.G. Sprugel & D.J. Vogt, 1986. Overestimation of net root production: a real or imaginary problem? *Ecology* 67: 577-579.

Vogt, K.A. & H. Persson, 1991. Measuring growth and development of roots. In: J.P. Lassoie & T.M. Hinckley (Eds.), Techniques and approaches in forest tree ecophysiology. CRC Press, Boca Raton, pp. 477-502.

Annexe A (Paper VI) : *soumis à For. Ecol. Manage.*

Effect of liming on the ectomycorrhizal status of oak

M. R. Bakker[1], J. Garbaye[2] and C. Nys[1*]

Abstract

The potential for nutrient uptake by forest trees is a function of site fertility, fine roots and mycorrhizal symbiants. This study focuses on the effects of moderate doses of liming on the mycorrhizal status of oak (*Quercus petraea* and *Q. robur*) roots. In ten *in situ* trials, where liming has been applied 1 to 27 years prior to sampling, the effects on fine roots and their mycorrhizal status were assessed in 1994-1996. All sites, except one, were situated on acidic soils with low base saturation. Fine roots were evaluated in terms of fine root biomass, length and specific root length. Mycorrhizal status was evaluated in terms of total number of mycorrhizal tips, number of tips per root length and main ectomycorrhizal morphotypes, both in absolute numbers and in relative proportion. At two of these sites, in close vicinity to each other, consecutive sampling was carried out during 4 periods between 1995 and 1996. The fact that some variation existed between the sampling seasons was verified, but lime-induced treatment effects were similar for all seasons. Data from all ten sites showed that liming resulted in an overall stimulation of the relative proportion of the hairy morphotypes to the detriment of the smooth types. Furthermore, within the smooth types, some changes occurred. Although fine root biomass and length were enhanced by liming, the number of mycorrhizal tips per root length unit was not stimulated. Hence, the absorption surface of the uptake system was enhanced by an increase in fine root length and a differential stimulation of hairy types of ectomycorrhizae. Soil pH explained part of the shift within the smooth types, but not the increase in the hairy types. In the present study, liming consistently modified the mycorrhizal status of the oak roots and stimulated fine root development.

key-words: fine roots, ectomycorrhizae, mycorrhizal morphotypes, *Quercus petraea*, *Quercus robur*, liming

Introduction

Liming is a forestry practice aimed at correcting soil acidity, rectifying calcium or magnesium deficiency and restoring the vigour of decaying forest stands (Hüttl and Zöttl 1993). As with any soil amendment or fertilisation, the overall effect of liming is complex: it acts directly by modifying the soil physical and chemical properties as well as indirectly by modifying root morphology, symbiotic status and absorption efficiency (Blaise & Garbaye, 1983). It is known that ectomycorrhizae — and especially their exploring extramatrical mycelium— play a major role in water and nutrient flow at the soil-root interface of all the social tree species in temperate areas, such as oaks, beech, pines, spruce, etc (Bolan, 1991; Marschner & Dell, 1991; Read, 1993; George & Marschner, 1996; Garbaye & Churin, 1997). It is therefore relevant to take the ectomycorrhizal status of the trees into account when attempting to interpretate the effect of liming on forest mineral nutrition.

This work describes the effect of liming on the populations of ectomycorrhizae in ten oak stands in France and the Netherlands, and at discusses the results in relation to other data sets collected in the same stands: fine root status and dynamics, tree growth and mineral nutrition. For the

same stands, Bakker (1998b) has shown that liming generally increased fine root biomass, fine root length and tree growth, and improved the mineral levels in the foliage. In this work, special attention was paid to the morphology of ectomycorrhizae, because of the importance of the extramatrical mycelium in absorption phenomena.

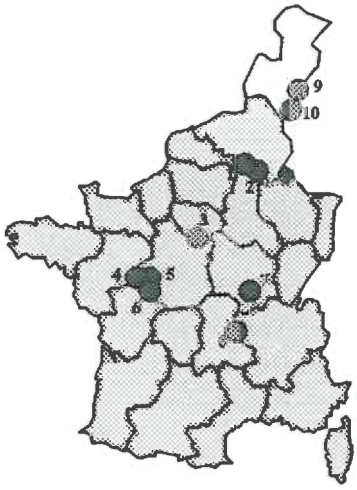

Figure 1 Location of the 10 study sites

Materials and Methods

Sites and experimental designs

Ten sites with oak stands of different ages (ranging from 15 to 76 yrs) were studied. Eight are situated in France (all with *Quercus petraea*) and two in the Netherlands with *Q. robur* (Fig. 1). Lime was applied 1 to 5 (Croix-Scaille), 7 (St. Anthonis), 14 (Tronçais) or even 24 to 27 years (the remaining sites) prior to sampling (Bakker 1998b). At all sites, one lime treatment (doses selected within a comparable range of CaO equivalents) was compared with an untreated control treatment (Table 1). In addition, at the two Croix-Scaille sites there were also two gypsum (one ancient 5 years old and one recent one year old) and a mixed treatment (80% $CaCO_3$ and 20 % $CaSO_4$). The lime treatments were in form of $CaCO_3$ or CaO. In addition to the liming amendment some complementary compounds were used: N (sites 4 to 6), N, P and K (site 8) and Mg (3.5 % in the lime product on sites 9 and 10). The levels of these additions were low, especially for the N which was only applied in the oldest sites (26-27 yrs ago), and it was assumed that it would not have an influence on the present tree response (Bonneau 1995) anymore. With the exception of Fontainebleau, all stands are on acidic, desaturated soils (Table 1). The pH values in the 30-45 cm layer were on average 0.3 to 0.5 higher than those of the 0-5 cm layer, where they range from 3.7 to 5.0. More details about the sites are to be found in Bakker (1998b).

Sampling and sample processing

Soil cores (Bakker, 1998a) were sampled (four replicates per site-treatment combination) on different dates depending on the site (in October 1994 at Fontainebleau and from March to October 1995 at the other sites). Generally, samples were taken from a 0-75 cm soil depth, but at la Croix-Scaille (0-55 cm), Bertranges (0-45 cm) and Tronçais (0-60 cm) sites the sampling depth was shallower due to stoniness or a hard clayey layer. More details about the sampling procedure are described in Bakker (1998a). In order to assess the seasonal variations of the

mycorrhizal status of the trees, sampling was performed four times at the two Croix Scaille sites in 1995 and 1996.

Table 1 Site characteristics of the 10 limed oak stands

site	nr	stand age (yr)	soil texture	eq CaO dose (t. ha^{-1})	pH-H_2O (0-5 cm)	BS % (0-5 cm)	BS % (30-45 cm)
Croix-Scaille (ancient)	1	48	silty clay	1.4	4.0	14	13
Croix-Scaille (recent)	2	48	silty clay	1.4	3.8	14	9
Fontainebleau	3	25	sand	1.25	6.4	100	100
Trembles	4	76	silt	1.5	3.7	43	15
Gaie Mariée	5	55	silt	1.5	3.9	56	20
Rond du May	6	50	sandy silt	1.5	4.0	25	11
Bertranges	7	24	silt	1.25	5.0	81	*
Tronçais	8	44	silty sand	0.8	4.8	34	41
St. Anthonis 35c	9	42	sand	1.6	4.1	38	12
St. Anthonis 46a	10	15	sand	1.6	3.7	28	4

BS = base saturation; * = not determined

Fine roots (diameter < 2 mm) from the soil cores were separated into five categories according to depth (0-5, 5-15, 15-30, 30-45 and 45-60 cm), stored at +1°C with adhering soil in air-tight plastic bags for at most three months, and washed on a sieve before assessing fine root length by the line intersect method (Tennant, 1975) and fine root biomass by drying at 105°C to constant weight. Fine roots were rarer in the deepest layers (either 45-60 or 60-75 cm) and the replicate number for this depth was generally only 1 or 2 instead of 4. The ectomycorrhizal status of the roots was determined with a stereomicroscope by observation of at least 200 tips on a randomly-picked subsample. A quick scan of the whole sample aimed at detecting any aberrant proportions of a given ectomycorrhizal morphotype in the subsample was made. In this case, more tips were observed. All samples were assessed by the same person.

Classification of the ectomycorrhizal morphotypes

The classification established by Voiry (1981) for oak and beech ectomycorrhizae in north-eastern France and used by Blaise & Garbaye (1983) and Garbaye *et al.* (1986) was used. Due to the large number of samples, description was limited to the higher level of the classification which does not require sectioning and observing the mantle structure with a microscope. Five morphotypes (A1, A2, B, C1 and C2) were distinguished according to the structure of the outer mantle and of the extramatrical mycelium (letters and indices refer to Voiry's groups):

A: thin, soft, fluffy outer mantle and abundant mycelium more or less loosely aggregated.
- A1: non-aggregated, web-like, cotton-like or woolly mycelium.
- A2: mycelium aggregated in wicks or loose cords.

B: thick mantle and mycelium fully aggregated into branched rhizomorphs with differentiated hyphae forming a dense cortex.

C: very dense mantle, smooth or with expansions of limited length.
- C1: smooth mantle, without any expansion.
- C2: mantle bearing cells, cystidia or ornamentations of different shapes.

From June 1995 and after, a sixth morphotype was distinguished within group C2: the typical, jet-black mycorrhizae with thick hairs formed by the ubiquitous Ascomycete *Cenococcum geophilum*. They were noted as C2x. In order to compare these results with results older than June 1995, within group C, the statistical analysis of the results considered either C1, Ctot (all C), C2tot (all C2, including *C. geophilum*), C2oth (C2 without *C. geophilum*) or C2x (*C. geophilum*). The percentage of ectomycorrhizal live fine root apices was always close to 100, as found by Blaise & Garbaye (1983) and Garbaye *et al.* (1986).

Data processing and statistical analyses

Four root-related parameters (M = total number of tips in 10^9 ha^{-1}; L = total fine root length in 10^6 m ha^{-1}; SRL = specific root length in m g^{-1}; and N/l = number of apices per cm of fine root length) and eight mycorrhiza-related parameters (A1, A2, B, C1, Ctot, C2tot, Coth and C2x) were evaluated in absolute numbers and in their relative abundancy. The parameters M and L were also evaluated for the sum of the soil profile studied, whereas SRL and N/l were only analyzed horizon by horizon. The arc sine transformation was used for the percentages of mycorrhizal morphotypes. For all other parameters, the large data-set from the two Croix-Scaille sites did not reveal any non-normality and no transformation was done. All statistics were done using Unistat 4.0 software (Unistad Ltd, 1995). The Croix-Scaille data (resulting from several sampling dates) were first used to assess seasonal effects by comparing 2 (ancient liming treatment) or 4 dates (recent treatment and control) by three-way ANOVA for treatment, soil depth and season. Then, all variables were individually tested for each site for treatment and soil-depth effects by two way ANOVA followed by one-way ANOVA for treatment effect at each soil depth. Whenever possible, similar tests were also carried out with the summed values of the whole soil profile. When more than two levels of a factor were involved, the Student-Newman-Keul's test was used to compare the group means if the design was not balanced, as was often the case due to the deepest soil layer with a smaller number of replicates. When the design was balanced or after excluding the deepest soil layer, Tukey's HSD test was used. The outcome of both tests was generally similar. Finally, an ANOVA on treatment effects with soil pH (H_2O) as a co-variate was applied to a balanced data-set of all ten sites without the deepest soil layer.

Table 2 Seasonal changes in the proportion of six ectomycorrhizal morphotypes at the two Croix-Scaille sites (1yr and 5yrs after the amendments) for the 0-15 cm soil layer. Roots were sampled four times during a 12 month period: in March, June and September 1995 and March 1996.

Treatment	Mycorrhizal types (% of total root tip number)					
	A1	A2	B	C1	C2tot	Ctot
Control	ns	ns	+	+	-	ns
Lime 5yrs	-	ns	ns	ns	ns	ns
Gypsum 5yrs	ns	ns	ns	ns	ns	ns
Lime 1yr	ns	ns	ns	+	-	ns
Gypsum 1yr	-	-	-	+	-	+
Mix 1yr	-	ns	ns	+	-	ns

Significant changes ($p<0.05$) over time; + = the corresponding parameter increases over time (at least one significant difference between two sampling dates); - = the corresponding parameter decreases over time (same criterion); ns = not significant (at $p<0.05$).

Results

Influence of sampling date

Because roots were not sampled at the same time in all sites, it was necessary to assess the effect of the sampling date on the root mycorrhizal status before comparing liming effects at the different sites. For this purpose, the two sites at Croix-Scaille (5yrs and 1yr since liming) were sampled four times during a 12 month period of time: in March, June and September, 1995, and in March, 1996. Table 2 shows that the relative proportions of the different mycorrhizal morphotypes are not stable during the period considered but it also reveals a consistent pattern: types C1 and Ctot tend to increase while types A1, A2 and C2tot tend to regress; type B behaves more irregularly. However, Figure 2, which illustrates the fluctuations of these parameters in the case of Croix-Scaille (recent liming: 1 yr since application), shows that all other morphotypes vary in the same way for all treatments. Note (Table 2) that the seasonal variation is more important for the most recently applied amendments (especially gypsum and the mixed treatment) and much less so for the treatments applied 5 years before the sampling. From this preliminary approach it can be concluded that, while comparing the average mycorrhizal status between the different sites would be hazardous, it is perfectly reasonable to assess the effect of liming within each site, which was the main objective of this work.

Compared effect of liming in the ten sites

Table 3 shows that all mycorrhiza-related parameters (relative proportions) analyzed significantly differentiate the ten sites (but we have seen that the sampling date contributes to these differences), while only two mycorrhizal morphotypes are significantly affected by the liming treatment: type A2 is favoured relative to type Ctot (this is illustrated in Fig. 3). The site x treatment interaction is significant for five parameters out of nine. In most cases this can be attributed to a few sites: Rond du May (lower fine root biomass after liming), Fontainebleau (different pH range) and St. Anthonis (having clearly more mycorrhizal tips per ha or a higher number per cm of root length). The overall average percentages in which the different ectomycorrhizal types occur are: 0.5-1.0 % (A1), 1-3 % (A2; liming 2-6 %), 1-4 % (B), 45-60 % (C1), 15-35 % (C2oth) and 15-25 % (C2x).

Table 4 analyses the site x treatment interaction in more detail. From this rather complex pattern only two trends emerge clearly: the stimulation of mycorrhizal morphotype A2 relative to type Ctot as a result of liming (already shown by the global analysis in Table 3) and the positive effect of liming on two parameters characterizing root growth and spatial development (M, and L). The effects on specific root length (SRL) are less conclusive (Bakker 1998b): depending on the site (and initial range of SRL values), liming increases this parameter (significant at three sites), or decreases it (significant at 2 sites, not significant at 5 sites). It depends whether root length is stimulated more than root biomass or not. It appears that the total amount of roots (weight or length basis) is affected more by liming than the number of ectomycorrhizal root tips per root length (N/l), so that the observed increase in total number of mycorrhizal tips per ha (M) should be attributed to the effect of the treatment on the roots, rather than a stimulation of root branching. This also implies that the effect of the fine root biomass weighed considerably in the appreciation of absolute numbers of mycorrhizal morphotypes. For instance, at the site Rond du May, where fine root biomass was lower, the increase in proportion of type A2 was completely overridden by the biomass effect (lower absolute number of type A2). Therefore, absolute numbers of morphotypes were not further considered.

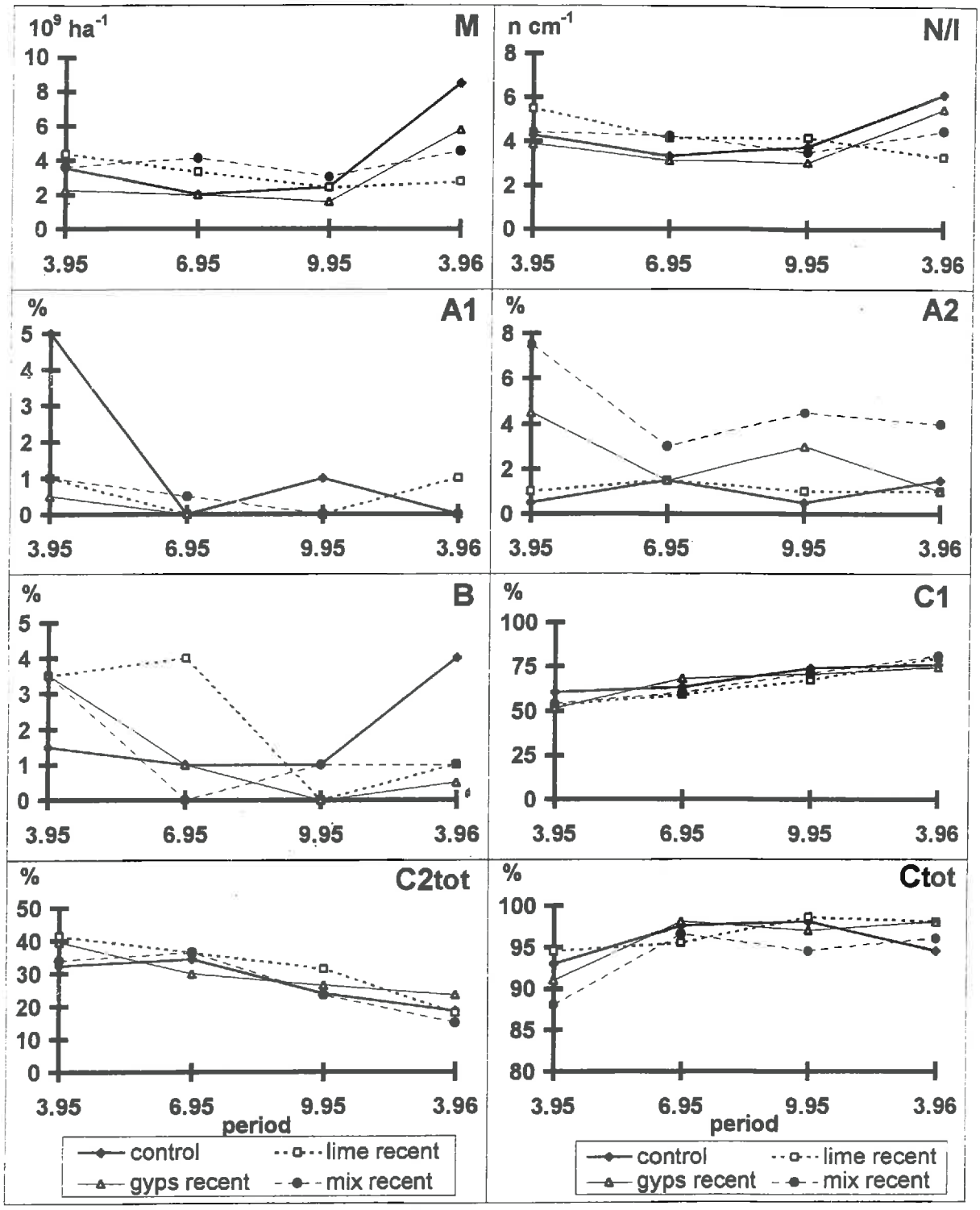

Figure 2 Seasonal variation in number of mycorrhizal tips (M), number of tips per cm root length (N/l) and relative proportion (%) of ectomycorrhizal morphotypes (based on the most recently limed Croix-Scaille site; values are for the 0-15 cm layer).

Table 3 Site and treatment (liming) effect on the total number of mycorrhizal root tips (M) and the relative proportion of the ectomycorrhizal morphotypes.

	M	Mycorrhizal types (% of total root tips)							
Factor	(10^9 ha^{-1})	A1	A2	B	C1	C2oth	C2x	C2tot	Ctot
Liming treatment	ns	ns	+	ns	ns	ns	ns	ns	-
Site	*	*	*	*	*	*	*	*	*
Treatment * site	ns	ns	ns	*	*	*	ns	*	*

* = significant at p<0.05 (+ = positive effect; - = negative effect); ns = not significant

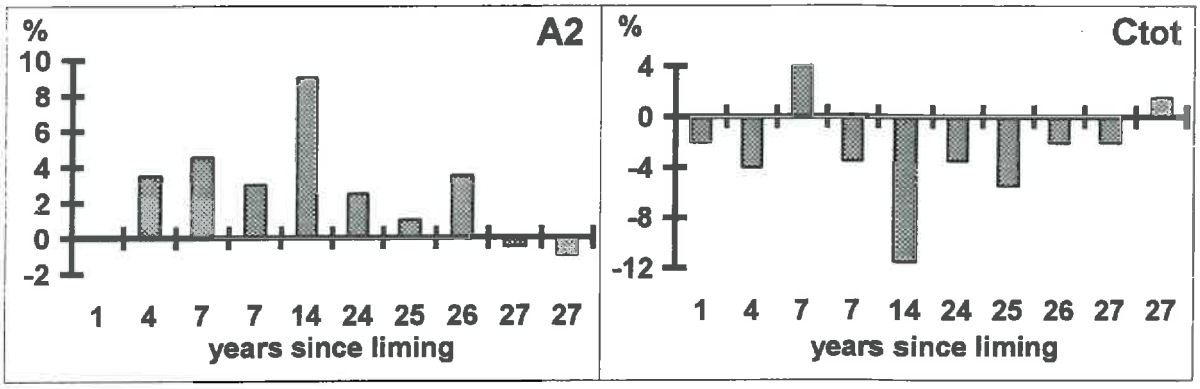

Figure 3 Lime-induced change (absolute difference) in relative proportion of type A2 or type Ctot mycorrhizae as a function of time since liming.

Table 4 Effect of liming on root parameters and mycorrhizal status of the ten oak stands (M = total number of mycorrhizal tips ha^{-1}, L = total fine root length per ha^{-1}, N/l = number of mycorrhizal tips per cm of fine root length and A2-Ctot are the different ectomycorrhizal morphotypes.

Site	roots			mycorrhizal types (% of total root tips)						
	M	L	N/l	A2	B	C1	C2oth	C2x	C2tot	Ctot
	10^9 ha^{-1}	10^6 m ha^{-1}	n cm^{-1}	(%)						
Croix-Scaille 5yrs	ns	+	ns	ns	ns	-	+	ns	+	ns
Croix-Scaille 1yr	+	ns	+	ns	ns	ns	ns	ns	ns	ns
Fontainebleau	ns	+	ns	ns	ns	-	¤	¤	ns	-
Trembles	ns	+	-	+	ns	ns	ns	-	ns	ns
Gaie Mariée	ns	+	ns	ns	ns	ns	-	ns	-	ns
Rond du May	ns	ns	ns	ns	ns	+	+	ns	ns	ns
Bertranges	ns	ns	ns	+	ns	-	+	ns	+	ns
Tronçais	ns	ns	ns	+	ns	ns	-	ns	ns	-
St Anthonis 35c	ns	+/-	ns	ns	-	ns	+	ns	ns	ns
St Anthonis 46a	+	ns	ns	ns	ns	-	ns	+	ns	-

Significant effects at p<0.05 in at least one layer, indicated by + (increase), - (decrease) or +/- (increase in one and decrease in another layer); ns = not significant; ¤ = not determined. (A1 type not presented: not significantly affected at any site).

Figure 4 graphically presents the data which were analyzed statistically in the columns M and N/l of Table 4. In the control plots, the total number of ectomycorrhizal root tips per hectare vary widely from about 10^{10} (Gaie Mariée, Croix Scaille 1yr, Tronçais) to ten times this value in St. Anthonis 35c, while the number of mycorrhizae per cm root length in the top 5 cm of the soil generally remains around 5 except in St. Anthonis 35c where it reaches a value of 17. This parameter tends to decrease in the deeper layers of the soil except in Tronçais, St. Anthonis 46a, Rond du May and Croix Scaille (5yr). The effect of liming on this parameter is erratic and no significant pattern emerges, except in St Anthonis 46a where, consistently with Table 4, liming dramatically increased the root mycorrhizal density in the upper 40 cm of the soil profile. However, it should be remembered that the sampling date may have biased these data when the sites are compared: only the biggest differences can be interpreted safely. Figure 4 also shows that in general the total number of mycorrhizal root tips per ha (M) was stimulated by liming (6 sites out of 10), but that important changes in this absolute number can be affected by liming either positively (St Anthonis, Croix Scaille ancient, Gaie Mariée) or negatively (Les Trembles, Rond du May).

Effect of soil pH

Table 5 shows that soils with high pH (either because of the site or because of liming) clearly favour mycorrhizal morphotypes C2 (including *C. geophilum*) against type C1. The significant (positive) effects on other parameters are only due to the high soil pH in the Fontainebleau site and are meaningless in general.

Table 5 Effect of soil pH-H_2O on total number of mycorrhizal tips per ha (M), number of root tips per cm of root length (N/l) and the mycorrhizal status of these tips (presence of ectomycorrhizal morphotypes A1 - Ctot).

Depth	Roots		Mycorrhizal types (% of total root tip number)							
(cm)	M	N/l	A1	A2	B	C1	C2oth	C2X	C2tot	Ctot
	10^9 ha^{-1}	n cm^{-1}	(%)							
0-5	ns	ns	ns	ns	ns	-	ns	+*	+	ns
5-15	ns	ns	ns	ns	ns	-	ns	+	+	ns
15-30	ns	ns	ns	ns	ns	-	+	+	+	ns
30-45	ns	ns	ns	ns	+ (F)	-	+	+	+	ns
45-60	+ (F)	+ (F)	ns	ns	ns	-*	+	ns	+	ns

Significant relationships at $p<0.05$: + = an increase of the parameter for increasing pH value and - a decrease of the parameter for increasing pH (F = denoting that the significant effect is due to the high pH of the Fontainebleau soil; * = significant at $p<0.06$).

Discussion

In spite of a wide variability of the recorded parameters, depending on the site, stand age, type and time of the liming treatments, sampling time and sampling depth, oak trees react significantly to liming by modifying their root systems. The morphology of fine roots is affected: in the limed plots, they tend to be longer (Bakker 1998b). Generally, the specific root length tends to decrease, although in some stands this parameter increased after liming (Bakker 1998b). This is probably related to the initial SRL value; liming directing the fine roots to an optimal size, integra-

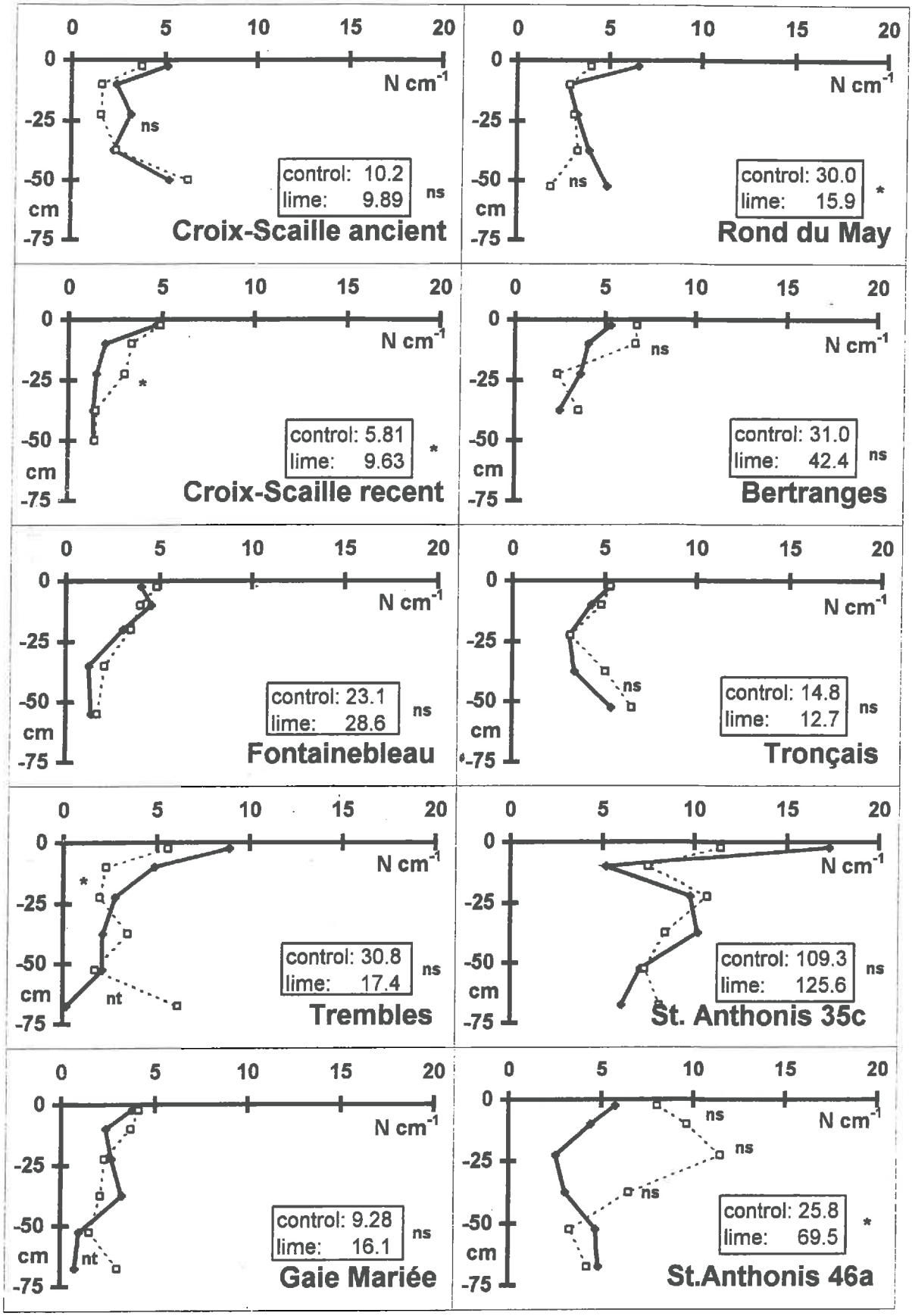

Figure 4 Number of mycorrhizal tips per cm root length (N/l) with a limed (dotted line) and a control (continuous line) soil profile for 10 experimental sites. Number of total mycorrhizal tips in 10^9 ha^{-1} is indicated below in the right corner (the symboles indicate a significant treatment effect at $p<0.05$ (*), a non significant effect (ns) or that it was not tested (nt) in at least one horizon).

costs and benefits for uptake and maintenance (Bakker 1998a). In case of low initial SRL values, the SRL would increase and in case of relatively high initial SRL values, it would decrease as a result of liming.

In addition, the ectomycorrhizal morphotype A2 (with long mycelial wicks and loose cords) is favoured relative to all types of group C (with no extramatrical mycelium exploring the soil at long distances from the root). When the pH is added as a covariable to the statistical analysis (in control as well as in treated plots) the A2 vs Ctot effect does not appear any more; instead, increasing pH (within a range from 3.5 to 5.5) favours morphotypes of sub-group C2 (smooth mantle with only expansions of limited length) relative to morphotype C1 (smooth mantle with no expansion at all) within group C. Therefore, the effect of liming on the A2 and Ctot types cannot be explained by its effect on pH and must be attributed to a difference in nutrition (Ca, Al, NO_3^-?), whereas the effects on C1 and C2tot are not significantly related to the nutritonal component of the liming treatment, but are significantly dependent on pH.

In both cases (change of overall root morphology or shift in dominant ectomycorrhizal morphotypes), the root system reacts to liming by improving its ability to explore the soil and build an absorption-efficient soil-root interface: extensive fine root development and more mycorrhizal tips with extending cords or rough surface. This could explain why limed oak stands show improved mineral nutrition and better growth than the untreated control stands (Bakker, 1998ab). Recently, Le Tacon *et al.* (*in prep.*) found similar results in beech: liming also favoured hairy ectomycorrhizae against smooth ones. However, our results seem to contradict those of Vogt *et al.* (1983), Blaise & Garbaye (1983) and Lehto (1994) who found either higher soil exploration by roots and mycorrhizae in the less fertile stands or no stimulation of fine roots and mycorrhizae by fertilisation. Lehto (1994) established several experiments and found liming to decrease mycorrhizae. This could not be explained by the Ca^{2+} concentration only, and the author concluded that the increased ionic strength and pH were responsible for this. However, since in a part of the experiments the liming dose was very high (Lehto 1994) and / or evaluated after a relatively short period (one year), it is difficult to make a straightforward comparison with the present study. Blaise and Garbaye (1983) observed in a beech stand 9 years after comparable doses of Ca or NPKCa fertilisers (using the same classification, Voiry's ectomycorrhizal morphotypes, as in the present work) results, which were contradictory to ours: the same morphotypes (A2 and C1) reacted, but the opposite way.

This apparent contradiction disappears when some additional factors are considered. First, the literature reports many experimental results showing that factors regulating the establishment and stability of mycorrhizal symbioses can have response curves with an optimum value (Wallander, 1992); this is the case for pH, which is a relevant factor when liming is involved (Erland & Söderström, 1990; Aggangan *et al.*, 1996; Thomson *et al.*, 1996). Therefore, depending on the initial position relative to this optimum, sites may respond in opposite ways to the same kind of treatment. Second, the balance between different fungi within a mycorrhizal complex is determined by their differential response to environmental factors; because when results are given as percentage, when one type increases, another has to decrease. As the fungi forming smooth or hairy ectomycorrhizae apparently have contrasting responses to nutrient availability, and also to the pH depending on its level, this would explain the discrepancy between our results and those of the other authors discussed above. In addition, Kåren and Nylund (1996) suggested, that a relatively small change in the colonization capacity of a mycorrhizal fungus, would cause marked changes in the community structure over a relatively

short time, that is, an increase in relative proportion of the morphotypes having a higher colonization capacity.

Besides the obvious difference between smooth and or hairy mycorrhizae in terms of soil colonization, other aspects should be considered. Building a large amount of extramatrical mycelium and long extensions such as cords or wicks requires sufficient carbon allocation; Godbold *et al.* (1997) observed that the proportion of hairy types increased when the atmosphere was enriched in CO_2. This means that the morphological shifts we observe after liming could be indirectly due to the increased photosynthetic efficiency of the trees due to improved mineral nutrition. Different strategies of nitrogen acquisition could also be involved: Wallander *et al.* (1997) found a lime-induced shift in the ectomycorrhizal community on Scots pine roots, in favour of fungi which use inorganic nitrogen (mainly ammonium) rather than organic forms (amino-acids and proteins); in their study, liming resulted in the appearance of a mycorrhiza type with a high ammonium uptake rate. Such a shift towards inorganic nitrogen sources can be a good adaptation to the higher levels of nitrate (after liming) or ammonium (after the gypsum treatment) observed in the soil solution of the surface horizons at the Croix-Scaille site (Bakker *et al.* 1998). This compares well with the work of Boiffin (1997), who observed for increasing nitrogen nutrition to the roots, that 25 to 30 % more C was allocated to the fine roots when in symbiosis.

Conclusion

The present study revealed seasonal effects with regards to total number of mycorrhizal tips or mycorrhizal tips per root length, but also that effects on relative abundance of morphotypes were limited and that control and liming treatments featured the same seasonal patterns. Liming in general decreased the relative proportion of smooth mycorrhizae in favour of hairy types, and soil pH explained part of the shift within the smooth types. The increase of these hairy morphotypes possibly implies a change in nutrient availability and the use of nitrogen in other forms, or at other levels than in the control, in exchange for a higher carbon allocation. Fine root length was also enhanced by liming, therefore the absorbing surface of the uptake system increased as a result of liming, either by stimulation of the fine roots, of the mycorrhizae or both. However, the present study does not allow us to conclude, whether this stimulation is an active regulatory process, or a merely a reflection of soil chemical constraints (nutrients, pH).

Acknowledgements

We would like to thank Serge Didier for his technical assistance in the field. This research was supported by grants of INRA Paris and the Dutch Ministry of Agriculture, Nature Management and Fisheries, Directorate of Science and Knowledge Dissemination. The MEAC company is acknowledged for providing the liming products.

References

Aggangan, N.S., Dell, B. and Malajczuk, N., 1996. Effects of soil pH on the ectomycorrhizal response of *Eucalyptus urophylla* seedlings. New Phytol., 134: 539-546.

Bakker, M.R., 1998a. The effects of liming and gypsum applications on a sessile oak (*Quercus petraea* (M.) Liebl.) stand at La Croix-Scaille (French Ardennes) II Fine root dynamics. Plant and Soil, *in press*.

Bakker, M.R., 1998b. Fine root parameters as indicators of sustainability of forest ecosystems. For. Ecol. Manage., *in press.*

Bakker, M.R., Nys, C. and Picard, J.-F., 1998. The effects of liming and gypsum applications on a sessile oak (*Quercus petraea* (M.) Liebl.) stand at La Croix-Scaille (French Ardennes) I. Site characteristics, soil chemistry and aerial biomass. Plant and Soil, *in press.*

Blaise, T. and Garbaye, J., 1983. Effets de la fertilisation minérale sur les ectomycorhizes d'une hêtraie. Acta Oecologica, Oecol. Plant., 4: 165-169.

Boiffin, V., 1997. Contribution à l'étude de la régulation du métabolisme carboné de l'ectomycorhize d'*Eucalyptus globulus - Pisolithus trinctorius* ; caractérisation, clonage et expression de l'isocitrate déshydrogénase à NADP de la racine. PhD Thesis, University Paris-Sud. 115 pp.

Bolan, N.S., 1991. A critical review on the role of mycorrhizal fungi in the uptake of phosphorus by plants. Plant and Soil, 134: 189-207.

Bonneau, M., 1995. Fertilisation des forêts dans les pays tempérés. Théorie, bases du diagnostic, conseils pratiques, réalisations expérimentales. ENGREF, Nancy. 366 pp.

Erland, S. and Söderström, B., 1990. Effects of liming on ectomycorrhizal fungi infecting *Pinus sylvestris* L. I. Mycorrhizal infection in limed humus in the laboratory and isolation of fungi from mycorrhizal roots. New Phytol., 115: 675-682.

Garbaye, J., Menez, J. and Wilhelm, M.E., 1986. Les mycorhizes des jeunes chênes dans les pépinières et les régénérations naturelles du Nord-est de la France. Acta Oecologica, Oecol. Plant., 7: 87-96.

Garbaye, J. and Churin, J.-L., 1997. Growth stimulation of young oak plantations inoculated with the ectomycorrhizal fungus *Paxillus involutus* with special reference to summer drought. For. Ecol. Manage., 98: 221-228.

George, E. and Marschner, H., 1996. Nutrient and water uptake by roots of forest trees. Z. Pflanzenernaehr. Bodenk., 159: 11-21.

Godbold, D.L., Berntson, G.M. and Bazzaz, F.A., 1997. Growth and mycorrhizal colonization of three north American tree species under elevated atmospheric CO_2. New Phytol., 137: 433-440.

Hüttl, R.F. and Zöttl, H.W., 1993. Liming as a mitigation tool in Germany's declining forests - reviewing results from former and recent trials. For Ecol. Manage., 61: 325-338.

Kårén, O. and Nylund, J.-E., 1997. Effects of ammonium sulphate on the community structure and biomass of ectomycorrhizal fungi in a Norway spruce stand in south western Sweden. Can. J. Bot., 75: 1638-1642.

Lehto, T., 1994, Effects of soil pH and calcium on mycorrhizas of *Picea abies*. Plant and Soil, 163: 69-75.

LeTacon, F., LeTacon, Y., Moron, V., Rousseau, Y. and Bakker, M.R., *in prep.* Effect of mineral fertilisation on fine roots and mycorrhizal development in a mature beech (*Fagus sylvatica* L.) stand.

Majdi, H. and Nylund, J.-E., 1996. Does liquid fertilization affect fine root dynamics and lifespan of mycorrhizal short roots. Plant and Soil, 185: 305-309.

Marschner, H. and Dell, B., 1994. Nutrient uptake in mycorrhizal symbiosis. Plant and Soil, 159: 89-102.

Read, D., 1993. Appendix C: Mycorrhizas. In: J.M. Anderson and J.S.I. Ingram (Editors), Tropical soil biology and fertility, a handbook of methods. CAB International, Wallingford, United Kingdom, pp. 121-131.

Tennant, D., 1975. A test of a modified line intersect method of estimating root length. J. Ecol., 63: 995-1001.

Thomson, B.D., Grave, T.S., Malacjzuk, N. and Hardy, G.E.St.J., 1996. The effect of soil pH on the ability of ectomycorrhizal fungi to increase to growth of *Eucalyptus globulus* Labill. Plant and Soil, 178: 209-214.

Vogt, K.A., Moore, E.E., Vogt, D.J., Redlin, M.J. and Edmonds, R.L., 1983. Conifer fine root and mycorrhizal root biomass within the forest floors of Douglas-fir stands of different ages and site productivities. Can. J. For. Res., 13: 429-437.

Unistat Ltd., 1995. Unistat version 4 for Windows.

Voiry, H., 1981. Classification morphologique des ectomycorrhizes du chêne et du hêtre dans le nord-est de la France. European Journal of Forest Pathology, 11: 284-299.

Wallander, H., 1992. Regulation of ectomycorrhizal symbiosis in *Pinus sylvestris* L. seedlings. Influence of mineral nutrition. PhD-Thesis, Swedish University of Agricultural Science, Uppsala, Sweden.

Wallander, H., Arnebrant, K., Östrand, F. and Kårén, O., 1997. Uptake of 15N-labelled alanine, ammonium and nitrate in *Pinus sylvestris* L. ectomycorrhiza growing in forest soil treated with nitrogen, sulphur or lime. Plant and Soil, 195: 329-338.

Annexe A (Paper VII) : *soumis à Plant and Soil*

Effects of liming on rhizosphere chemistry and growth of fine roots and of shoots of sessile oak (*Quercus petraea*)

M R Bakker, R Kerisit, K Verbist, and C Nys

key words: fine roots, liming, *Quercus petraea* Liebl. M., rhizosphere, rhizotron, shoot:root

Abstract

Soil acidification can be detrimental to root growth and nutrient uptake, and liming may alleviate such acidification. In the following study seedlings of sessile oak (*Quercus petraea* Liebl. M.) were grown in rhizotrons and subjected to liming (L) or gypsum (G) treatments and compared with the control (C). In order to study and interpret the impact of these calcium rich treatments on fine root development and tree growth, the following parameters were assessed: fine root biomass, fine root length, seedling development (height, diameter, leaves), seedling biomass, nutrient content of roots and seedlings, bulk soil and soil solution chemistry and rhizosphere soil chemistry. The results show that liming increased bulk soil pH, exchangeable Mg, Ca and the Ca/Al molar ratio, and decreased exchangeable Al, mainly in the A-horizon. Gypsum had a similar but smaller impact on exchangeable Al, Ca, H^+ and the Ca/Al molar ratio in the A-horizon, but reacted with depth, so that exchangeable Mn, Mg and Ca were increased in the B-horizon. In the rhizosphere, the general pattern was determined by the treatment effects of the bulk soil. Most elements were more concentrated in the rhizosphere than in bulk soil, except for Ca that was less concentrated after liming or gypsum application. In the B-horizon rhizosphere pH was increased by the treatments (L>G,C) close to the root tips. Furthermore, the length of the zone with a positive root-induced pH increase was larger for the limed roots as compared with both the other treatments. Fine root growth was stimulated by liming (L>G,C) both in terms of biomass and length, whereas specific root length was not obviously affected apart from the indication of some stimulation after liming at the beginning. The live:dead ratio of fine roots was significantly higher in the limed rhizotrons as compared to the control (G not assessed), indicating lower mortality (higher longevity). Shoot growth showed greater lime-induced stimulation (L>G,C) as compared to root growth. As a result the shoot:root ratio was higher in the limed rhizotrons than in the control (L>G,C). Liming induced a higher allocation of P, S, Mg, Ca and K to the leaves, stem and twigs. Gypsum showed similar effects, but was only significant for S. Liming increased the foliar Ca/Al ratio by both increasing foliar Ca and decreasing foliar Al, whereas gypsum did not clearly improve foliar nutrition.

This study suggests that a moderate application of lime can be successful in stimulating seedling growth. Gypsum had no effect on seedling growth. It can be concluded that this lime-induced growth stimulation is directly related to the improved soil fertility status, and the alleviation of Al toxicity and acid stress, resulting in a better foliar nutrition. The impact of liming on fine roots, as a consequence, was not limited to a stimulation of the total amount of fine roots, but also improved the root uptake performance.

Introduction

Soil acidification has a negative effect on fine root development (Rost-Siebert 1983, Marschner 1991). High concentrations of Al, N or protons, and low cationic:Al and cationic:N ratios in the soil solution inhibit root growth, damage root tissues or lead to impaired uptake

(Rost-Siebert 1983, Göransson and Eldhuset 1987, Ljungström and Nihlgård 1995). A decrease in root growth results in a low specific root length (Olsthoorn *et al.* 1991) or even mortality of parts of the root system. Where acidification is stratified according to soil depth, roots are often concentrated in the upper organo-mineral layers (A horizons), reflecting avoidance of the acid subsoil layers (Marschner 1991) and the buffering of Al toxicity by organic matter. Liming has been advocated to counterbalance many of the undesirable effects of soil acidification (low pH, Ca and Mg concentrations, high Al concentrations) and their impact on fine root development (Hüttl and Zöttl 1993). Effects of liming on fine root development are reported to be positive (Murach and Schünemann 1985, Schüler and Zwick 1992, Gobran *et al.* 1993), although some state the contrary, depending on site, soil type, form and doses of liming and the time lapse since liming (Persson and Ahlström 1994, Persson *et al.* 1995, Staaf *et al.* 1996).

Earlier results from ten field sites on acidic soil, suggested that liming stimulated fine root development and tree growth of sessile oak (*Quercus petraea* Liebl. M.) (Bakker 1998). The present paper aims to link the *in situ* observations of these ten field sites with the lime-induced changes in the rhizosphere. For this a number of rhizotron experiments have been carried out and a two-tier approach was applied. In the first (indirect) series, the stock of nutrients at the beginning (soil, acorns, litter, lime treatments) and the amount of biomass formed during the experiment (leaves, branches, roots) were determined. In the second (direct) series, a chemical characterization of the rhizosphere soil was carried out at the end of the experiment, while measurements of rhizosphere pH were carried out during the experiment. It was expected that the lime or gypsum-induced changes in the bulk soil and bulk soil solution would react differently in the rhizosphere, thereby improving the uptake conditions, explaining the increased tree growth.

Materials and methods

Experimental treatments

Seedlings of sessile oak were grown in rhizotrons in four successive experiments. Rhizotrons, measuring 55 (length) x 40 (height) x 3.5 cm (width), were filled with an acid brown forest soil (FAO Dystric Cambisol; USDA Dystrochrept) collected in a field liming experiment at La Croix-Scaille (French Ardennes). The oak stand of that trial showed low foliar K and very low foliar Mg and Ca nutrition. The A-horizon (average pH-H_2O 3.8) of 15 cm was put on top of the B-horizon soil (average pH-H_2O 4.4) of 20 cm and both were re-constituted with a density equivalent to field conditions. A control (C) was compared with soils treated with doses of $CaCO_3$ (Lime, L) or $CaSO_4$ (Gypsum, G) equivalent to 1.4 t ha^{-1} CaO. In order to obtain a rapid effect of these applications on root growth, half of the dose of lime or gypsum was mixed with the top A-horizon soil before filling the rhizotrons. The other half was spread on top of a shallow litter-layer of oak leaves. This situation (half of the applied calcium in form of lime incorporated into the soil) corresponds to a period of 20 months after liming if applied to the surface as shown in previous studies on the same soil (Belkacem and Nys 1997).

Three of the experiments, each replicated 4 times, were carried out for 3 to 5 months, whereas the longest lasted 13 months (replicated twice only). The first three experiments (consisting of two short experiments and the long experiment) were carried out with small seedlings (age 4 months). For the fourth (short) experiment acorns (brought to simultaneous germination by a pre-treatment) were used, as seedlings were not available any more. Both the acorns and

seedlings have the same genetic origine (northeastern France). The seedlings from the laboratory nursery were also obtained by acorns and grown on a growth substrate that could easily be removed before replanting the seedlings in the rhizotrons. Before replanting nearly all roots were pruned. In all rhizotrons either three to four seedlings were planted or three to four acorns (average dry weight 1.5 g) sown.

The rhizotrons were placed at an angle of about 30°, so as to induce fine root growth preferentially along one side. All experiments were carried out in the greenhouse. A summary of the initial situation is presented in Table 1 (soil, litter and acorns).

Table 1 Composition of soil layers A and B, litter and acorns used for the experiments with sessile oak (*Quercus petraea*) seedlings, presented as averages over n repetitions, respectively (* = missing value).

stratum	n	pH H_2O	pH KCl	K	Ca	Mg	Na	Mn	H^+	Al^{3+}	BS
				$cmol_c\ kg^{-1}$							%
A-layer	3	3.79	2.88	0.22	0.91	0.27	0.06	0.14	1.58	4.23	21.6
B-layer	3	4.54	3.97	0.12	0.01	0.02	0.04	0.06	0.00	3.18	7.3
		S	P	K	Ca	Mg	Mn	Al			
		$mmol_c\ g^{-1}$									
litter	2	0.10	0.09	0.03	0.35	0.05	0.05	0.06			
acorns	10	0.02	*	0.22	0.04	0.04	0.00	0.00			

Sampling procedure

Seedling growth, root growth and soil analysis (bulk and rhizosphere) were determined at the end of each experiment. Seedlings were cut at the root collar and the following growth parameters were assessed: number of leaves, dry weight of leaves, stem diameter, stem weight and height of seedling. Sub-samples of leaves and stems were analysed for their element content. Dry weight was determined after drying at 65°C to constant weight. Roots were sampled destructively on opening the rhizotrons and they were collected separately for both soil layers. The roots were separated from the soil by wet sieving with tapwater over two consecutive sieves (4 and 2 mm mesh size), followed by floating the roots collected from the sieves in a bin filled with water. Dead roots were separated from living roots using general visible criteria: resilience, brittleness, colour of bark and xylem (Vogt and Persson 1991), the reliability of which was confirmed by observations under a binocular microcope. Roots were separated into fine (< 2 mm diameter) and coarse (> 2 mm) roots. Dry weight of roots was assessed by drying at 105°C to constant weight and length was determined by the line intersection method (Tennant 1975). The element contents of fine roots were analysed on subsamples of the live roots, dried at 65°C to constant weight.

Soil adhering to the roots was collected and formed the 'rhizosphere' soil fraction. For this, only roots of a comparable size (< 2 mm) were used. Rhizosphere soil was obtained by gently shaking the fine roots until only small amounts of soil remained adhered to the roots (Hendriks and Jungk 1981, Olsthoorn *et al.* 1991). Roots were air dried for some hours before the rhizosphere soil was brushed off. Bulk soil was sampled at random throughout every rhizotron, but not in the vicinity of roots. Soil solution was sampled during the experiment using rhizon soil moisture samplers (Eijkelkamp BV, Giesbeek, the Netherlands, reference 19.21.05). The rhizons (length 10 cm, outer diameter 2.3 mm) were inserted horizontally in both A and B-layers after boring small holes in the plexiglass. After installation and a contact time of several days, small vacuum-tubes were connected to the outer edge of the rhizons using injection

needles and were left overnight in order to collect a sufficient sample volume (generally between 2 to 7 ml). Rhizosphere pH was determined using micro-electrodes (outer diameter of the tip of the electrode and reference electrode 0.5 to 1.0 mm) with agar of a pH comparable to the soil pH (pH around 4) as a contact medium between the electrode and the soil. During the pH measurements, the selected rhizotron was placed horizontally and opened. On suitable roots (measurable over a 4 to 5 cm length) small pieces of agar (size approx. 4 x 4 mm, thickness about 2 mm) were put at regular distances from the root tip before measuring the pH at these localities, with the reference electrode placed in the vicinity of the measurement localities (Gijsman 1990).

Sample processing

Soil samples were air-dried and then sieved at 2 mm. 0.5 *M* NH_4Cl-exchangeable Al, Ca, Mg, K, Mn and Na (Trüby 1989) were determined by ICP (emission spectrometry), exchangeable acidity by automatic titration (Trüby 1989), and pH-KCl and pH-H_2O on a 1:2.5 dilution basis with pH-electrodes. Concentrations were expressed as oven-dried (105°C) weights. Cation Exchange Capacity (CEC) was defined as the sum of exchangeable Mn, Mg, Ca, Na, K, plus titrable Al^{3+} and H^+ (Espiau and Pedro 1980). Base saturation was defined as the proportion of exchangeable Mn, Mg, Ca, Na and K in relation to total CEC. Soil solution analysis was performed by ICP (S, Mn, Mg, Al, Ca, Na, K) and colorimetry (Technicon Autoanalyzer) for nitrate and ammonium. For chemical analyses of foliage, stems and live fine-roots, subsamples were pretreated with peroxide (H_2O_2), then mineralized with $HClO_4$ and analysed by ICP. The acorns were mineralized by HCl after consecutive ignition up to 500°C, then analysed by ICP.

Data analysis

All statistics were calculated with Unistat 4.0 software (Unistat Ltd 1995). Distribution was tested for normality and wherever necessary values were log transformed to improve the distribution. The three short experiments were regrouped prior to analysis while the long experiment was analysed separately if this was feasible according to number of repetitions. The one experiment for which acorns were used in stead of pruned seedlings, was not analysed separately, as the genetic origin was comparable and the amount of roots formed was not different from that in the other experiments. The above-ground parameters, seedling growth and foliar composition were analysed per seedling by a Two-Way ANOVA for treatment and experiment effects for both the short experiments and the long experiment, followed by an ANOVA for treatment effects per individual experiment. The below-ground parameters, soil, solution and roots were analysed per rhizotron by a Three-Way ANOVA for effects of treatment, soil layer and experiment for the set of data of the three short experiments. This was followed by a Two-Way ANOVA for treatment and soil layer for each single experiment. For the long experiment, treatment and soil layer effects were only tested for the soil and fine root mineral concentration data, as number of replications was too low elsewhere. As there was quite some variation in absolute mean values of the three short experiments with regards to shoot:root ratios and also the amount of mineral elements immobilized in the biomass of the plants (summed values per rhizotron), some further statistical analyses were carried out on weighted values. For this, the original values shoot:root values were divided by the mean value of the individual experiment. Similarly, for the total amount of elements immobilized per rhizotron, the values were weighted, dividing them by the number of trees, in order to avoid an effect due to the different number of seedlings. An ANOVA was then carried out on these standardized values (shoot:root and quantity of immobilized mineral elements). Wherever treatment effects were significant, the Student-Newman-Keuls test was used to determine the significantly different treatments.

Table 2 Effects of liming and gypsum treatments on seedling growth; presented are n = number of seedlings and mean values of seedling height (H in cm), seedling diameter (D in mm), number of leaves (Nl), dry weight of leaves (Wl in g seedling^{-1}), dry weight of stem and branches (Wst in g seedling^{-1}), total shoot dry weight (Wtot in g seedling^{-1}). The different letters indicate significant treatment effects at $p<0.05$ level (st.errors in italic).

Treatment	n	H		D		Nl		Wl		Wst		Wtot	
short experiments (3 to 5 months)													
Control	35	13.2**b**	*0.9*	3.7**b**	*0.2*	14**b**	*1.0*	0.70**b**	*0.1*	0.40**b**	*0.1*	1.1**b**	*0.2*
$CaCO_3$	34	17.3**a**	*1.4*	5.4**a**	*0.5*	21**a**	*1.6*	1.4**a**	*0.2*	0.74**a**	*0.1*	2.1**a**	*0.3*
$CaSO_4$	32	13.6**b**	*1.0*	3.7**b**	*0.2*	14**b**	*1.2*	0.76**b**	*0.1*	0.45**b**	*0.1*	1.2**b**	*0.1*
long experiment (13 months)													
Control	6	17.9	*4.0*	5.5	*0.3*	19	*3.1*	1.5	*0.3*	1.1	*0.3*	2.6	*0.6*
$CaCO_3$	6	19.2	*3.3*	6.2	*1.1*	28	*9.4*	1.7	*0.6*	1.2	*0.5*	2.9	*1.1*
$CaSO_4$	6	13.2	*0.8*	6.3	*0.3*	19	*5.5*	1.1	*0.3*	0.8	*0.2*	1.9	*0.5*

Results

Plant growth

Table 2 presents the overall treatment effects on above-ground growth. Generally, the limed seedlings grew significantly more in the short experiments than the seedlings in the control and gypsum treatments. This was also true for each single individual short experiment, and in the long experiment the tendency - although not significant - is the same. The lower seedling number in the $CaSO_4$ treatment is mainly the result of the experiment with acorns, and could suggest a lower seedling survival due to less favourable conditions for root development in the early stages of seedling establishment. Also, the seedling perfomance in the long experiment seems to decline for the $CaSO_4$ treatment as compared to the short experiments, but this is not significant. So, the lime treatment increased above-ground growth, whereas the gypsum treatment had no effect, or perhaps even a slightly negative effect.

Table 3 Effects of lime and gypsum applications on fine root biomass (FRB sum of A and B layer in g rhizotron^{-1}), fine root length (FRL sum of A and B layer in m rhizotron^{-1}) and specific root length (per layer in m g^{-1}); with standard errors in italic (no significant overall effects for the short experiments; the long experiment was not tested due to low sample number).

Treatment	n	FRB		FRL		SRL (A)		SRL (B)	
short experiments (3 to 5 months)									
Control	12	1.91	*0.33*	24.1	*3.5*	12.5	*1.8*	20.6	*3.7*
$CaCO_3$	12	2.24	*0.32*	34.5	*4.8*	15.0	*1.4*	20.5	*3.6*
$CaSO_4$	12	1.98	*0.39*	25.4	*3.7*	15.4	*2.9*	23.6	*4.8*
long experiment (13 months)									
Control	2	2.48	*0.18*	37.0	*0.4*	14.9	*4.6*	16.8	*3.4*
$CaCO_3$	2	3.02	*0.41*	42.7	*7.9*	16.2	*1.7*	12.9	*0.2*
$CaSO_4$	2	1.90	*0.05*	32.8	*3.8*	16.0	*0.5*	19.2	*3.4*

The root system was analysed per rhizotron, thereby decreasing the number of replicate samples, since it was not feasible to attribute the roots to each single seedling. Table 3 presents the overall means for fine root biomass, fine root length and specific root length for the short and long experiments. Liming seems to have stimulated fine root length and both liming and gypsum applications appear to have increased specific root length in the A-layer, but this was

not significant on an overall basis. Only in one of the short experiments this lime-induced stimulation of fine root length and specific root length was significant at $p<0.05$. Similar to the observations on seedling growth, the $CaSO_4$ treatment tends to fell back in the longest experiment as concerns fine root biomass and length. About half of all root biomass and root length was formed in the A-layer and half in the B-layer.

There were no treatment effects on coarse roots (data not presented). The live/dead ratio of the fine roots (Figure 1), based only on a few replicate samples in the long experiment (not assessed for gypsum), was significantly higher in the limed rhizotrons (7.2 ± 1.2) than in the control (3.6 ± 0.4) (values are means $\pm$ standard error).

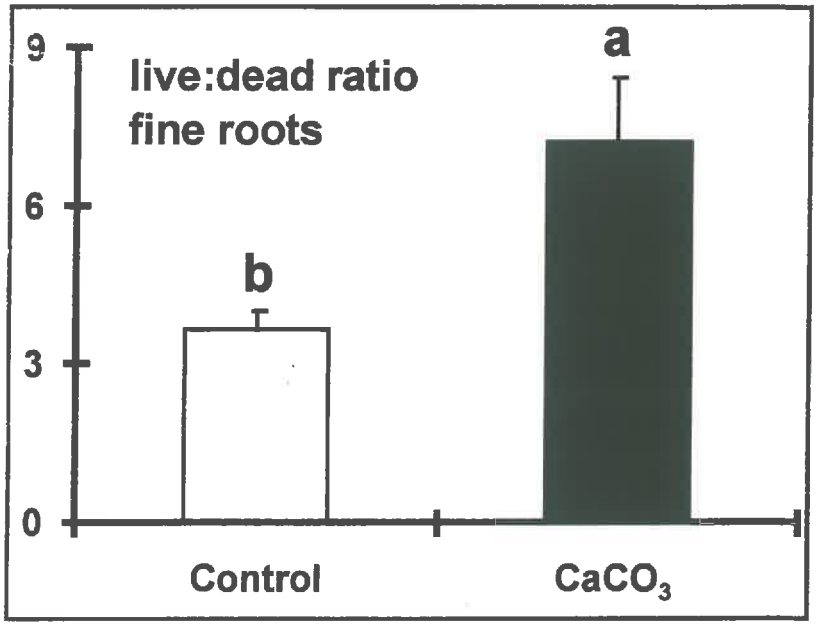

Figure 1 Live:dead ratio of fine roots (< 2 mm diameter) on a weight basis (after 13 months); the letters indicate a significant treatment effect at $p<0.05$).

In Table 4 the effects of the treatments on the foliar nutrition and fine root concentrations are presented. In the short experiments, liming significantly increased foliar Ca concentration, foliar Ca/Al ratio while lowering Al concentration. Gypsum significantly increased N nutrition while significantly lowering Mg nutrition. In the long experiment the only significant effect was an increase of the Mg concentration in the foliage by liming. The element concentrations in the fine roots did not show as many significant treatment effects. Liming significantly increased Ca concentration in the A-layer and the gypsum application resulted in significantly higher S concentrations in the B-layer and lower Mn concentrations in the fine roots of the A-layer. In the long experiments (data not shown) treatment effects were not tested (n=2), but mineral concentrations in the fine roots were in the same range as in the short experiments. The element concentrations of the coarse roots only revealed lower Al concentrations after liming and gypsum as compared to the control.

Table 4 Effect of lime and gypsum applications on foliar mineral concentrations (in the short experiments based on 11, 10 and 8 seedlings for C, L and G, respectively, and in the long experiment on 6, 6 and 5 seedlings, respectively) and root mineral concentrations (based on 4 rhizotrons each for the short experiments; the long experiment is not presented) in g kg^{-1} dry weight (letters indicating significant differences at $p<0.05$; st.errors in italic).

	N		S		P		K		Ca		Mg		Mn		Al		Ca/Al	
									g kg^{-1}								mol/mol	
Foliage: short experiments (3 to 5 months)																		
Control	23.8**b**	*1.1*	1.9	*0.2*	1.2	*0.3*	10.1	*1.7*	5.2**b**	*0.3*	1.5**a**	*0.1*	4.2	*0.5*	0.2**a**	*0.0*	22.7**b**	*2.2*
$CaCO_3$	23.5**b**	*0.7*	1.7	*0.1*	1.3	*0.1*	7.9	*0.3*	7.0**a**	*0.7*	1.3**a**	*0.1*	4.0	*0.2*	0.1**b**	*0.0*	39.9**a**	*5.2*
$CaSO_4$	27.2**a**	*1.5*	2.0	*0.1*	0.8	*0.1*	6.0	*0.4*	5.3**b**	*0.4*	0.9**b**	*0.1*	4.4	*0.4*	0.2**a**	*0.0*	18.5**b**	*1.1*
Foliage: long experiment (13 months)																		
Control	28.4	*1.1*	1.9	*0.1*	1.0	*0.3*	7.0	*0.3*	3.21	*0.5*	1.4**b**	*0.1*	1.9	*0.1*	0.1	*0.0*	75.8	*11.7*
$CaCO_3$	28.1	*1.2*	2.0	*0.1*	1.6	*0.1*	7.9	*0.4*	4.72	*0.4*	1.7**a**	*0.1*	2.1	*0.0*	0.1	*0.0*	107	*8.3*
$CaSO_4$	30.8	*1.7*	1.7	*0.2*	1.5	*0.3*	6.9	*0.7*	3.92	*0.4*	1.3**b**	*0.2*	1.8	*0.3*	0.1	*0.0*	73.8	*3.9*
Fine-roots, A-layer (short experiments only)																		
Control	12.1	*1.3*	1.79	*0.3*	1.3	*0.3*	7.3	*0.5*	3.1**b**	*0.5*	1.4	*0.1*	0.6**a**	*0.0*	4.3	*0.7*	0.54	*0.15*
$CaCO_3$	16.9	*2.5*	1.88	*0.4*	1.5	*0.3*	7.4	*0.5*	4.4**a**	*0.2*	1.6	*0.1*	0.5**ab**	*0.1*	7.6	*1.6*	0.45	*0.08*
$CaSO_4$			2.78	*0.3*	1.5	*0.2*	7.1	*0.5*	3.3**b**	*0.1*	1.6	*0.2*	0.4**b**	*0.1*	6.5	*0.9*	0.36	*0.04*
Fine-roots, B-layer (short experiments only)																		
Control	14.4	*1.4*	1.7**b**	*0.2*	0.8	*0.1*	7.4	*1.8*	2.3	*0.3*	1.5	*0.1*	0.8	*0.0*	8.8	*1.0*	0.18	*0.02*
$CaCO_3$	15.2	*0.9*	1.5**b**	*0.1*	0.9	*0.1*	4.3	*2.2*	3.0	*0.3*	1.4	*0.1*	0.8	*0.1*	10.7	*1.7*	0.20	*0.02*
$CaSO_4$	16.2	*0.5*	2.6**a**	*0.2*	1.2	*0.3*	7.1	*0.2*	3.0	*0.3*	1.6	*0.1*	0.7	*0.1*	10.1	*0.6*	0.21	*0.02*

Table 5 presents the total mineral element content in the seedlings (shoot + root) in the 4th, short, experiment only (4 rhizotrons each). Since the number of seedlings was different for the treatments, the summed content values were divided by the number of seedlings. An ANOVA on these summed content values per seedling per rhizotron, showed liming to significantly increase total content of P, Mg, Ca and K as compared to the control. Both liming and gypsum increased S content as compared to the control. The percentage allocation to the shoot is significantly increased by liming for S, P and K as compared to the control (Table 6). Mg allocation was significantly higher after liming when compared to the gypsum treatment.

Table 5 Total amount of elements in the seedlings in mg $seedling^{-1}$, after five months of growth as a function of lime or gypsum treatments based on only one of the short experiments (small letters denoting significant treatment effects).

treatment	S		P		K		Ca		Mg		Mn		Al	
Control	9.94**b**	*1.9*	9.29**b**	*2.5*	27.0**b**	*6.1*	16.0**b**	*4.1*	4.98**b**	*1.1*	8.69	*2.5*	8.91	*2.8*
$CaCO_3$	18.6**a**	*1.3*	24.5**a**	*2.0*	52.0**a**	*6.0*	42.3**a**	*5.4*	9.60**a**	*0.8*	15.2	*3.0*	14.2	*1.8*
$CaSO_4$	20.2**a**	*2.6*	13.3**b**	*2.6*	30.9**b**	*5.3*	23.4**b**	*4.4*	6.40**ab**	*1.2*	10.3	*2.2*	11.4	*2.8*

Table 6 Percentage allocation of nutrients to the shoot after five months of growth based on only one of the short experiments (values are averages over 4 rhizotrons; letters denoting significant differences).

treatment	S	P	K	Ca	Mg	Mn	Al
Control	0.43**b**	0.40**b**	0.42**b**	0.59	0.42**ab**	0.73	0.02
$CaCO_3$	0.56**a**	0.57**a**	0.53**a**	0.64	0.51**a**	0.79	0.02
$CaSO_4$	0.33**b**	0.43**b**	0.37**c**	0.51	0.32**b**	0.71	0.03

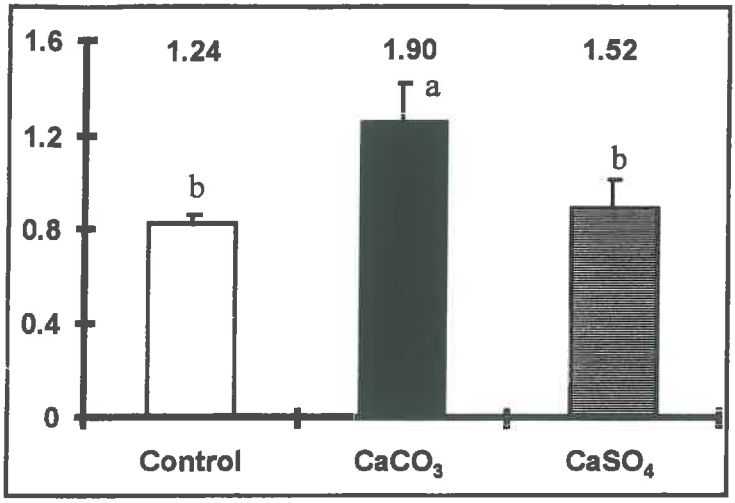

Figure 2 Shoot:root ratios summed for the three short experiments (standardized values); values indicated in the figure are the non-standardized means of the three experiments (the letters indicate significant treatment effects at $p<0.05$).

In Figure 2 the overall effects (for the three short experiments) on shoot:root (dry weight) ratio are presented (standardized values). For the non-standardized values, shoot:root ratios (means $\pm$ standard errors) ranged from 1.24 ± 0.17, 1.52 ± 0.39 to 1.90 ± 0.41 for the control, gypsum and liming treatments, respectively. The differences between the non-standardized values were not significant when regrouping the three short experiments, but in the last experiment (with acorns), liming had a significantly higher shoot:root ratio than the gypsum and the control treatment. Since variation between the experiments was considerable, perhaps related to the fact that the latter experiment was carried out with acorns, a standardization was applied by dividing the values by the mean of each experiment (Figure 2). On the basis of these standardized values, liming significantly ($p<0.05$) increased the shoot:root ratio.

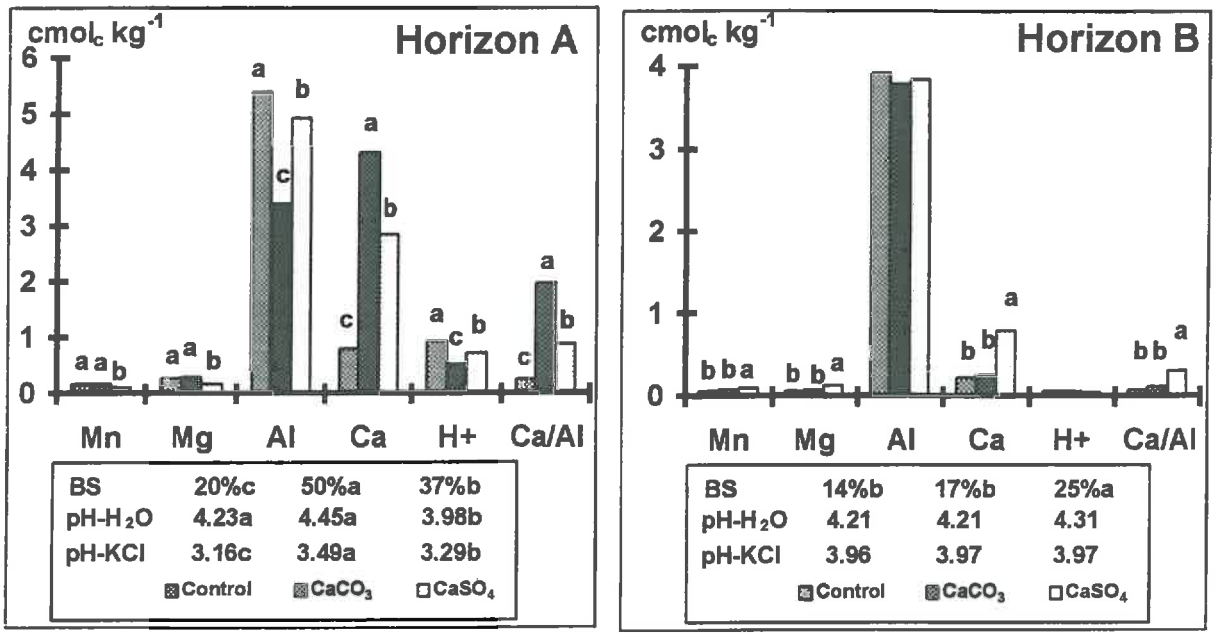

Figure 3 Effects of lime and gypsum applications on the bulk soil in the A and B-layers (letters indicating significant treatment effects at at least $p<0.05$; Na and K not presented).

The soil

Figure 3 presents the treatment effects for the bulk soil. Liming significantly enhanced exchangeable Ca concentration, CEC, base saturation and Ca/Al ratio in the A-layer, while significantly decreasing exchangeable Al and H^+. Gypsum significantly increased exchangeable Ca, base saturation and Ca/Al ratio in both A and B-layers. In the A-layer, gypsum significantly increased CEC and decreased exchangeable Mn, Mg and Al, while in the B-layer exchangeable Mn and Mg were significantly increased. Concentrations of Na (0.16 and 0.17 $cmol_c\ kg^{-1}$ in A and B, respectively) and K (0.32 and 0.25 $cmol_c\ kg^{-1}$, respectively) were not affected by the treatments. Effects on soil pH were limited to the A-layer, with gypsum showing a significantly lower pH-H_2O relative to both the other treatments, and for pH-KCl, significant increases for both applications ($CaCO_3$>$CaSO_4$>control). These results reflect the higher solubility of the gypsum product as compared to the lime product, resulting in a greater shock reaction and reactivity extending to a greater soil depth, displacing elements like Mn, Mg and Ca from the A to the B-layers. The effects of the treatments on the concentrations in the rhizosphere were similar, but weaker than those in the bulk soil.

Table 7 Effect of lime and gypsum applications on exchangeable elements in bulk and rhizosphere: the rhizospheric gradient based only on the short experiments (different letters denoting significant differences at $p<0.05$ between bulk and rhizosphere soil).

	K		Ca		Mg		Na		Mn		H^+		Al		Ca/Al	
	$cmol_c\ kg^{-1}$														mol/mol	
A-layer (short experiments only)																
Control bulk	0.31**b**	*0.01*	0.83	*0.03*	0.27	*0.01*	0.06**b**	*0.01*	0.16**a**	*0.00*	0.85	*0.04*	5.40**b**	*0.11*	0.23**a**	*0.01*
Control rhizo	0.41**a**	*0.03*	0.83	*0.10*	0.35	*0.06*	0.28**a**	*0.07*	0.13**b**	*0.01*	1.03	*0.13*	6.06**a**	*0.19*	0.17**b**	*0.02*
$CaCO_3$ bulk	0.29**b**	*0.01*	4.32**a**	*0.18*	0.30	*0.01*	0.09**b**	*0.01*	0.17	*0.02*	0.47**b**	*0.04*	3.44**b**	*0.15*	1.94**a**	*0.15*
$CaCO_3$ rhizo	0.38**a**	*0.04*	3.02**b**	*0.26*	0.35	*0.05*	0.25**a**	*0.04*	0.13	*0.01*	0.79**a**	*0.13*	4.95**a**	*0.22*	0.92**b**	*0.14*
$CaSO_4$ bulk	0.27**b**	*0.01*	2.84	*0.15*	0.17**b**	*0.02*	0.06**b**	*0.01*	0.11	*0.01*	0.68	*0.04*	4.97**b**	*0.15*	0.86**a**	*0.03*
$CaSO_4$ rhizo	0.40**a**	*0.04*	2.62	*0.15*	0.27**a**	*0.05*	0.18**a**	*0.03*	0.12	*0.01*	0.82	*0.16*	5.44**a**	*0.16*	0.66**b**	*0.03*
B-layer (short experiments only)																
Control bulk	0.17**b**	*0.01*	0.23	*0.04*	0.07**b**	*0.01*	0.07**b**	*0.02*	0.07**b**	*0.01*	0.06	*0.02*	3.95	*0.08*	0.09	*0.02*
Control rhizo	0.36**a**	*0.05*	0.34	*0.07*	0.20**a**	*0.05*	0.34**a**	*0.08*	0.11**a**	*0.01*	0.08	*0.03*	3.96	*0.10*	0.07	*0.01*
$CaCO_3$ bulk	0.17**b**	*0.01*	0.29**b**	*0.02*	0.08**b**	*0.01*	0.10**b**	*0.02*	0.07**b**	*0.01*	0.06	*0.02*	3.87	*0.05*	0.11	*0.01*
$CaCO_3$ rhizo	0.32**a**	*0.03*	0.48**a**	*0.06*	0.20**a**	*0.04*	0.27**a**	*0.04*	0.14**a**	*0.02*	0.08	*0.03*	3.91	*0.12*	0.14	*0.02*
$CaSO_4$ bulk	0.20**b**	*0.01*	0.85	*0.23*	0.13**b**	*0.01*	0.08**b**	*0.01*	0.10**b**	*0.01*	0.04	*0.02*	3.84	*0.14*	0.31	*0.06*
$CaSO_4$ rhizo	0.33**a**	*0.03*	0.86	*0.06*	0.27**a**	*0.05*	0.18**a**	*0.03*	0.14**a**	*0.01*	0.08	*0.03*	3.81	*0.13*	0.29	*0.02*

The differences between bulk and rhizosphere soil are presented in Table 7. As can be seen (and also in Figure 3) the liming and gypsum treatments affected overall concentrations in bulk and rhizosphere, but not that much the gradient between bulk and rhizosphere, meaning that these gradients were comparable for all three treatments for most elements. In a general way, most echangeable elements were more concentrated in the rhizosphere than in the bulk soil, regardless of treatment or soil layer (not significant everywhere). The most important exceptions to this are lower values in the rhizopshere of exchangeable Mn (significant only for the control) and Ca (significant only for liming), as well as the Ca/Al ratio (significant for both lime and gypsum treatment), in the A-layer as compared to the bulk soil. The CEC did not

differ significantly between bulk and rhizosphere soil, neither in the A nor in the B-layer. Base saturation was significantly lower in the rhizosphere in the A-layer after liming and higher in the B layer for the control and the liming treatment, as compared to the bulk soil. So, the liming and gypsum treatments mainly affected overall soil chemistry of the bulk soil and thereby the rhizosphere soil chemistry, whereas effects on the gradient between bulk and rhizosphere were limited to some effects on base saturation, exchangeable Ca and Ca/Al ratio in the A-layer. The significantly lower values of Ca in the liming treatment in the A-layer, could suggest a relatively high uptake of Ca here as compared to the other two treatments. This is confirmed by the observation of higher Ca tissue concentrations and contents (Tables 4 and 5).

Table 8 Effects of treatments on soil solution based only on the short experiments (standard errors in italic and significant differences indicated by different letters).

	n	pH	Ca		Mg		Mn		Al		NO_3^-		NH_4^+		Ca/Al
			mmol$_c$ l^{-1}												mol/mol
A-layer															
Control	18	3.85b	0.31c	*0.04*	0.19b	*0.03*	0.07b	*0.01*	0.29b	*0.01*	1.76b	*0.35*	2.68b	*0.27*	1.55c *0.17*
$CaCO_3$	17	4.12a	1.51b	*0.08*	0.32b	*0.02*	0.11b	*0.01*	0.20b	*0.01*	3.18a	*0.14*	2.75b	*0.14*	11.4a *0.51*
$CaSO_4$	16	3.46c	4.73a	*0.31*	0.69a	*0.08*	0.34a	*0.03*	1.07a	*0.11*	0.48c	*0.07*	4.06a	*0.24*	7.38b *0.56*
B-layer															
Control	17	3.98b	0.99b	*0.07*	0.53b	*0.03*	0.46b	*0.02*	0.88	*0.08*	3.83a	*0.05*	1.51b	*0.19*	1.80b *0.11*
$CaCO_3$	13	3.97b	1.25b	*0.06*	0.57b	*0.03*	0.46b	*0.03*	1.20	*0.13*	3.94a	*0.03*	1.33b	*0.18*	1.70b *0.12*
$CaSO_4$	15	4.06a	1.99a	*0.23*	0.87a	*0.06*	0.56a	*0.03*	1.10	*0.10*	3.36b	*0.23*	2.34a	*0.25*	2.97a *0.41*

The soil solution composition is presented in Table 8. Generally the gypsum application resulted in the highest solution concentrations (Mn, Mg, Ca, Al, NH_4^+) in both soil layers. The difference in the form of nitrogen is remarkable: a significant increase of NO_3^- by liming as compared to the control treatment (A-layer) and an overall decrease due to the gypsum treatment in both layers as compared to the other treatments. Conversely, gypsum significantly increased NH_4^+ concentration in both layers. Again the higher solubility (leading more immediately to higher solution concentrations to a greater depth) of gypsum as compared to the lime product, is very clear. Whereas $CaCO_3$ had more effect on pH and Ca/Al ratio in the A-layer, the opposite was true in the B-layer. S concentrations increased logically due to $CaSO_4$ application. Na (0.27 and 0.26 mmol$_c$ l^{-1} for A and B-layers, respectively) and K (0.43 and 0.35, respectively) were not significantly affected by the treatments.

In Figure 4 the effects of the treatments on the rhizosphere pH are shown, based on comparisons from measured pH values at the rhizoplane with values obtained in the bulk soil at 1 cm from the root. It can be seen that the pH at the root tip is higher (sign. at $p<0.05$) than the pH of bulk soil close to the tip for the control and liming treatment. Furthermore, liming affected the extent of the zone where these differences occur along the axis of the root. The increase of the pH in the rhizosphere was significant ($p<0.05$) even at 2 cm from the root tip. The gypsum treatment had no significant effect on the rhizosphere pH at all. These observations suggest a different uptake balance of cations and anions according to the treatments, perhaps more favourable uptake conditions (over a greater part of the root length) after liming.

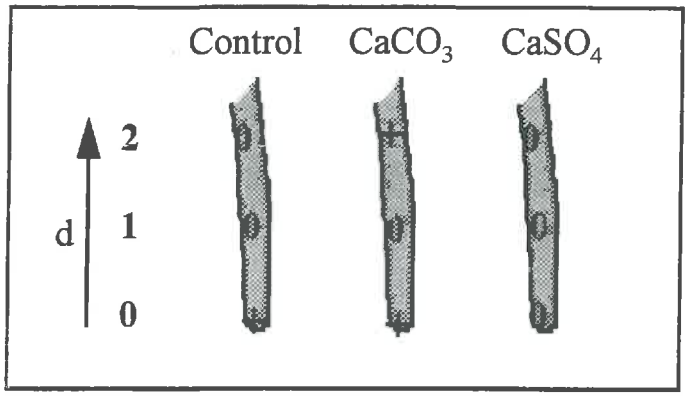

Figure 4 Effects of liming and gypsum applications on the pH at the rhizoplane of fine roots of the B horizon as a function of the distance 'd' from the root apex in cm (presented only up to 2 cm from the apex) Indicated with are pH values that were significantly higher at $p<0.05$ at the rhizoplane as compared to the bulk soil at that particular point (+) or not significantly different (0) between the rhizoplane and bulk soil.

Discussion

Plant growth

In the present work liming consistently and significantly stimulated seedling growth throughout the experiments. Considering the very low levels of Ca^{2+} and Mg^{2+}, and low levels of K^+ in the soil used for the experiments, an addition of Ca, a limiting nutrient, was expected to increase shoot growth. Liming, especially when it also affects the N availability, is known to stimulate seedling growth (Hürtl and Zöttl 1993, Gobran *et al.* 1993, Belkacem and Nys 1995). In the present study, root growth also appeared to be stimulated by lime (Table 3), but less so than the stimulation of shoot growth. Effects on fine root length were more consistent than those on fine root weight, so that specific root length tended to be increased by liming. Due to this higher stimulation of the shoot compared to the root, shoot:root ratio increased as a result of liming. This is similar to the observations by Gobran *et al.* (1993) and Tagliavini *et al.* (1995), but must be considered in relation to the lime-induced stimulation of N-mineralization occurring on the same soil (Belkacem and Nys 1995, 1997), which is known to increase shoot:root ratio (Seith *et al.* 1996, Beck 1996).

In contrast to the stimulation of growth by liming, gypsum did not stimulate shoot nor root growth clearly, in spite of the similar doses of Ca added. Gypsum even seems to result in a lower survival in the one experiment where seedlings were grown directly from acorns, or to decrease (not-significantly) above- and below-ground seedling growth in the longest experiment (13 months). This would suggest a more hostile rooting environment, perhaps leading to a higher mortality of roots and a lower growth over time. Unfortunately, the amount of dead roots was not assessed in the gypsum application, so this could not be verified in this rhizotron experiment. In the field trial on the same substrate, fine root mortality did not significantly differ between the gypsum and the liming treatment (Bakker 1998) and both had a lower mortality than the control. Other studies indicated that ammonium-sulphate increased fine root necromass (Majdi and Rosengren-Brinck 1994) or lowered fine root vitality (Clemensson-Lindell and Persson 1995), and that low live/dead root ratios are a result of high Al concentrations and root damage (Gobran *et al.* 1993, Persson *et al.* 1995). The observed higher levels of NH_4^+ (Table 8) and SO_4^{2-} (by means of the application of gypsum) in the soil solution for the gypsum treatment in this work, would agree with these studies.

The observed lime-induced stimulation of live/dead ratios of fine roots (Fig. 1), should thus be interpreted in terms of better health and higher survival. Such an increase in survival can be accompanied by lower fine root production, as observed after N-free fertilization (Persson *et al.* 1995), but higher survival can also be the result of nutrient rich patches, where root longevity is higher (Robinson 1994). One may speculate about the origin of this apparently higher mortality in the gypsum and control treatments relative to the liming treatment. Higher mortality of fine roots could be an adaptation to high Al toxicity, leaving behind large amounts of Al in the dying roots. The absence of growth stimulation by $CaSO_4$ in this work is in contrast with the work of Carvalho and Van Raij (1997), who reported equal or slightly higher growth stimulation by $CaSO_4$ than $CaCO_3$ of shoot and root growth for maize as compared to the control. This difference could be related to the fact that maize, a plant species, has more difficulties in growing into an acid subsoil as compared to oak seedlings, so that the beneficial effect of $CaSO_4$ (higher Ca activity, Al complexation by sulfate) is more important in their work.

The observed concentrations of nutrients in foliage (Keltjens and Van Loenen 1989, Ljungström and Nihlgård 1995) and fine roots (Yin *et al.* 1991, Majdi and Rosengren-Brinck 1994, Persson *et al.* 1995) in this study are in the range of values commonly reported for other tree species, despite the fact that part of the fine root values in these studies are based on coniferous species. Only the foliar levels of Ca, Mg and P are somewhat low, especially for gypsum in the case of Mg, and P (Bonneau 1995). The significant increases of Ca in fine roots and foliage by liming and of S in roots by gypsum, were expected. Such increases of foliar levels of Ca after lime and Mg in the case of dolomitic lime, are commonly observed (Ljungström and Nihlgård 1995, Van Praag *et al.* 1997). The fact that gypsum did not improve Ca, but increased N while decreasing Mg nutrition, was more unexpected. This probably reflects the higher concentrations of Al^{3+} and NH_4^+ in the soil solution or at the adsorption sites of the root apoplasm, reducing uptake of Ca^{2+}, Mg^{2+} and K^+ (Keltjens and Van Ulden 1987, Keltjens and Van Loenen 1989, Majdi and Rosengren-Brinck 1994, Ljungström and Nihlgård 1995, Kölling *et al.* 1997).

Liming significantly enhanced total uptake of S, P, Mg, Ca and K, and percentage allocation of S, P and K to the shoot. In contrast, gypsum only stimulated total S uptake, but not percentage allocation to the shoot. This higher allocation to the shoot by liming confirms other observations on increased allocation of nutrients such as P to the shoot (Gobran *et al.* 1993), or a general increase in biomass (carbon) allocation to the shoot when nutrient availability increases (Ericsson 1995). In the present study, despite a significantly higher proportion of biomass allocated to the roots in the control and gypsum treatment as compared to the liming treatment, uptake (total content) was higher in the liming treatment, except for S in the gypsum treatment. On the contrary, liming significantly increased uptake of nutrients (Table 5) as compared to gypsum and in particular the control treatment. Plants with a fertilizer supply in the immediate locality in nutrient limiting soils, have been shown to have very high uptake rates (Robinson 1994). Apparently, availability and accessibility of most cations in sufficient quantities in the liming treatment, permits the seedlings to allocate more of their biomass to shoot growth. Since the gypsum treatment added the same amounts of Ca to the soil, an explanation for the absence of a positive effect on growth, shoot:root and uptake, has to be sought in the difference in bulk and rhizosphere chemistry of soil and solution, impeding uptake and reducing root function.

The soil

The effects of liming and gypsum on the bulk soil and bulk soil solution are comparable to those more generally observed (Belkacem and Nys 1995, 1997). In the soil, the slight increase of CEC is thought to be related to the pH dependent character of the CEC (Bakker *et al.* 1998). The lower concentrations of exchangeable Mn, Mg and Al in the A-layer compared with a significant increase of Mn and Mg in the B-layer, supports the evidence of displacement of these cations by gypsum. The method used for separating rhizosphere from bulk soil may be criticized as being rather approximate, levelling the existing differences between bulk and rhizosphere soil. Nevertheless, the concentration effect of most elements in the rhizosphere is in accordance with the observations by Guan (1997). Such a concentration of nutrients in the rhizosphere is related to higher concentrations of exudates, bacteria and organic matter, but also depends on the rate of uptake and release, the mobility of the ions in the soil and the rate of conversion between available and unavailable forms (Darrah 1993). In the liming treatment, Ca concentration was significantly lower in the rhizosphere, suggesting that uptake was higher than diffusion plus mass flow to the roots.

The solution was affected much more by gypsum than liming as compared to the control. Although Ca concentrations also increased and should have increased Ca availability even more than the liming treatment, gypsum had a negative influence on the soil solution chemistry. First, for Mg and Ca, a shift of the exchangeable ions from the A into the B-layer can be observed, indicating potential leaching losses, and, second, the increase of solution concentrations in both layers of Mn^{2+}, NH_4^+ and Al^{3+}, increases the risk of phytotoxic levels of these ions (Keltjens and Van Ulden 1987, Keltjens and Van Loenen 1989). Aluminium toxicity, but also high acidity, are known to have a detrimental effect on root elongation and can lead to deficiencies of nutrients like Mg as a result of impaired uptake (Marschner 1991). A treatment with ammonium sulphate in Scandinavia (Majdi and Rosengren-Brinck 1994) also resulted in high NH_4^+ concentrations and a reduced Mg and Mn uptake. This antagonism between Mg and NH_4^+ is confirmed by the higher N and lower Mg levels in the foliage of the gypsum treatment in this study.

The effects on root pH confirm the earlier observations on solution, seedling nutrition and plant growth. The liming treatment has the largest effect on root-induced pH increase and the length of the zone where this increase occurs, is larger for the liming treatment. As ammonium and nitrate weigh heavily in the cation/anion uptake balance, this pH increase means a higher NO_3^-/NH_4^+ uptake ratio, or that more OH^-/HCO_3^- ions are excreted into the soil (Darrah 1993, Gijsman 1990, Keltjens and Van Ulden 1987). Gijsman (1990) concluded that the proportion of N taken up as NO_3^- was very important for root growth and the function of Douglas-fir. When the proportion $N\text{-}NO_3^-$ is greater than 65%, there was favourable root growth due to carboxylate and OH^- excretion, between 20 and 65 % alkalinization only occurred at the root tip, and below 20 % physological disturbances occurred (Gijsman 1990). This beneficial effect of NO_3^- uptake compared to NH_4^+ uptake was also reported by Seith *et al.* (1996), who found increased uptake of the cations Ca^{2+}, Mg^{2+} and Mn^{2+} with higher NO_3^- uptake.

In the present work, fine root length was only moderately stimulated by liming, but uptake rate was greatly improved. If mass flow is sufficient to fulfil the needs for uptake of the seedlings, an increased fine root system is expected not to increase uptake. For nutrients that are more generally present in insufficient quantities (or having a limited mobility) in the soil solution such as P, K, NH_4^+ (Yin et al. 1991), an increase of the fine root system, may be effective for increasing uptake. This suggests that the uptake conditions at the uptake sites of the root (root

tips) have improved considerably in the liming treatment, as total amount taken up of nearly all elements was significantly increased, much more than the small increase in fine root length can explain.

Conclusions

Soil chemistry and development of the oak seedlings were affected differently by the control, liming and gypsum treatments. Although both liming and gypsum added the same quantities of Ca to the Ca poor soil, liming was much more effective than gypsum in improving soil and plant fertility status and seedling growth as compared to the control. Whereas liming had more gradual effects, gypsum had a larger and deeper reaching effect on soil and soil solution. It is concluded that the stimulation of seedling growth and nutrition, the higher immobilization and percentage allocation of biomass and nutrients to the shoot by liming, are the result of an improved root environment and function. Nutrient availability is improved and Al toxicity alleviated as a result of liming. Gypsum improved nutrient availability to some extent, but also increased aluminium and ammonium activity, inhibiting the improvement of root function and seedling development.

Acknowledgments
This research was supported by grants of INRA Paris and the Dutch Ministry of Agriculture, Nature Management and Fisheries, Directorate of Science and Knowledge Dissemination. The authors also acknowledge the valuable comments of two anonymous referees to an earlier version of this manuscript.

References

Bakker M R, Nys C, Picard J-F 1998 The effect of liming and gypsum applications on a sessile oak (*Quercus petraea* (M.) Liebl.) stand at La Croix-Scaille (French Ardennes). I. Site characteristics, soil chemistry and aerial biomass. Plant Soil **00**, 1-10.

Bakker M R 1998 The effect of lime and gypsum applications on a sessile oak (*Quercus petraea* (M.) Liebl.) stand at La Croix-Scaille (French Ardennes). II. Fine root dynamics. Plant Soil **00**, 1-13.

Belkacem S and Nys C 1995 Consequences of liming and gypsum top-dressing on nitrogen and carbon dynamics in acid forest soils with different humus forms. Plant Soil 173, 79-88.

Belkacem S and Nys C 1997 Effects of liming and gypsum regimes on chemical characteristics of an acid forest soil and its leachates. Ann. Sci. For. 54, 169-180.

Beck E H 1996 Regulation of shoot/root ratio by cytokinins from roots in *Urtica dioica*: Opinion. Plant Soil 185, 3-12

Bonneau M 1995 Fertilisation des forêts dans les pays tempérés. Théorie, bases du diagnostic, conseils pratiques, réalisations expérimentales. ENGREF, Nancy. 367 p.

Carvalho M C S and Van Raij B 1997 Calcium sulphate, phosphogypsum and calcium carbonate in the amelioration of acid subsoils for root growth. Plant Soil 192, 37-48.

Clemensson-Lindell A and Persson H 1995 Fine-root vitality in a Norway spruce stand subjected to various nutrient supplies. Plant Soil 168/169, 167-172.

Darrah P R 1993 The rhizosphere and plant nutrition: a quantitative approach. Plant Soil 155/156, 1-20.

Ericsson T 1995 Growth and shoot:root ratio of seedlings in relation to nutrient availability. Plant Soil 168/169, 205-214.

Espiau P and Pedro G 1980 Caractérisation du complexe d'échange des sols acides. Le taux d'acidité d'échange et sa signification pédogénètique sous climat tempéré. Ann. agron. 31, 363-383.

Gijsman A J 1990 Rhizosphere pH along different root zones of Douglas-fir (*Pseudotsuga menziesii*), as affected by source of nitrogen. Plant Soil 124, 161-167.

Gobran G R, Fenn L B, Persson H and Al Windi I 1993 Nutrition response of Norway spruce and willow to varying levels of calcium and aluminium. Fertilizer Research 34, 181-189.

Göransson A and Eldhuset T D 1987 Effects of aluminum on growth and nutrient uptake of *Betula pendula* seedlings. Physiol. Plant. 69, 193-199.

Guan X 1997 Nutrient availability in forest soils. Rhizospheric and sequential leaching studies. PhD-Thesis. Acta Universitatis Agriculturae Sueciae Silvestria 36. Uppsala, Sweden.

Hendriks L and Jungk A 1981 Erfassung der Mineralstoffverteilung in Wurzelnähe durch getrennte Analyse von Rhizo- und Restboden. Z. Pflanzenernähr. Bodenk. 144, 276-282.

Hüttl R F and Zöttl H W 1993 Liming as a mitigation tool in Germany's declining forests - reviewing results from former and recent trials. For Ecol. Manage. 61, 325-338.

Keltjens W G and Van Loenen E 1989 Effects of aluminium and mineral nutrition on growth and chemical composition of hydroponically grown seedlings of five different forest tree species. Plant Soil 119, 39-50.

Keltjens W G and Van Ulden P S R 1987 Effects of Al on nitrogen (NH_4^+ and NO_3^-) uptake, nitrate reductase activity and proton release in two sorghum cultivars differing in Al tolerance. Plant Soil 104, 227-234.

Kölling C, Pauli B, Häberle K-H and Rehfuess K E 1997 Magnesium deficiency in young Norway spruce (*Picea abies* [L.] Karst.) trees induced by NH_4NO_3 application. Plant Soil 195, 283-291.

Ljungström M and Nihlgård B 1995 Effects of lime and phosphate additions on nutrient status and growth of beech (*Fagus sylvatica* L.) seedlings. For. Ecol. Manage. 74, 133-148.

Majdi H and Rosengren-Brinck U 1994 Effects of ammonium sulphate application on the rhizosphere, fine-root and needle chemistry in a *Picea abies* (L.) Karst. stand. Plant Soil 162, 71-80.

Marschner H 1991 Mechanisms of adaptation of plant roots to acid soils. Plant Soil 134, 1-20.

Murach D and Schünemann E 1985 Reaktion der Feinwurzeln von Fichten auf Kalkungsmassnahmen. Allgemeine Forstzeitschrift 40, 1151-1154.

Olsthoorn A F M, Keltjens W G. Van Baren B and Hopman M C G 1991 Influence of ammonium on fine root development and rhizosphere pH of Douglas-fir seedlings in sand. Plant Soil 133, 75-81.

Persson H and Ahlström K 1994 The effects of alkalizing compounds on fine-root growth in a Norway spruce stand in southwest Sweden. J. Environ. Sci. Health, A29(4), 803-820.

Persson H, Majdi H and Clemensson-Lindell A 1995 Effects of acid deposition on tree roots. Ecol. Bull. 44, 158-167.

Praag H J van, Weissen F, Dreze P and Cogneau M 1997 Effects of aluminium on calcium and magnesium uptake and translocation by root segments of whole seedlings of Norway spruce (*Picea abies* Karst.). Plant Soil 189, 267-273.

Robinson D 1994 The responses of plants to non-uniform supplies of nutrients. New Phytol. 127, 635-674.

Rost-Siebert K 1983 Aluminium-Toxizität und -Toleranz an Keimpflanzen von Fichte (*Picea abies* Karst.) und Buche (*Fagus sylvatica* L.). Allgemeine Forstzeitschrift 38, 686-689.

Schüler G and Zwick N 1992 Die Beeinflussung von Feinwurzelmasse und -vitalität eines Kiefernbestandes (*Pinus sylvestris* L.) mit unterständiger Buche (*Fagus sylvatica* L.) durch pflanzenverfügbare Elemente, sowie Veränderungen nach unterschiedlichen Kalkungsmaßnahmen. Mitt. Forst. Versuchsanstalt Rheinland-Pfalz 21, 69-98.

Seith B, George E, Marschner H, Wallenda T, Schaeffer C, Einig W, Wingler A and Hampp R 1996 Effects of varied soil nitrogen supply on Norway spruce (*Picea abies* [L.] Karst.). I. Shoot and root growth and nutrient uptake. Plant Soil 184, 291-298.

Staaf H, Persson T et Bertills U (Eds.) 1996 Skogsmarkskalkning. Resultat och slutsatser från Naturvårdsverkets försöksverksamhet. Naturvärdsverket rapport 4559. Tryck Gotab, Stockholm.

Tagliavini M, Masia A and Quartieri M 1995 Bulk soil pH and rhizosphere pH of peach trees in calcareous and alkaline soils as affected by the form of nitrogen fertilizers. Plant Soil 176, 263-271.

Tennant D 1975 A test of a modified line intersect method of estimating root length. J. Ecol. 63, 995-1001.

Trüby P 1989 Eine Titrationsmethode zur simultanen Bestimmung von H^+ und Aluminium in NH_4Cl-Bodenextrakten. Z. Pflanzenernaehr. Bodenk. 152, 297-300.

Unistat Ltd 1995 Unistat version 4.0 for Windows.

Vogt K A and Persson H 1991 Measuring growth and development of roots. *In* Techniques and approaches in forest tree ecophysiology. Ed. J P Lassoie and T M Hinckley. pp 477-502. CRC Press, Boca Raton.

Yin X, Perry J A and Dixon R K 1991 Temporal changes in nutrient concentrations and contents of fine roots in a Quercus forest. Forest Ecol. Manage. 44, 175-184.

Annexe A (Papier VIII) : *soumis à Plant and Soil*

Soil solution chemistry in the rhizosphere of roots of Sessile oak (Quercus petraea) as influenced by lime

Bakker M R, Dieffenbach A and Ranger J

Key words: liming, micro lysimetry, rhizosphere, rhizotron, sessile oak, soil solution chemistry

Abstract

This study describes the soil solution chemistry in the rhizosphere of fine roots of sessile oak (*Quercus petraea* (M.) Liebl.) grown in rhizotrons. A control was compared with soils treated with an equivalent $CaCO_3$ of 1.4 t ha^{-1} CaO. Solution samples were extracted from the B-horizon using micro suction cups with a suction of ~400 hPa. Two series of experiments were carried out: one irrigated with rain water (age of seedling 2 to 4 months) and one irrigated with demineralized water (age of seedlings 1.5 to 2 months). Half of the sampling points were choosen close to the roots and half in the bulk soil. In both experiments there was generally no rhizospheric gradient after liming. In contrast, in the control, depletion in the rhizosphere occurred for most of the ions studied (Mg, Ca, Al, K, NO_3^-, NH_4^+, Cl^-) in the demineralized water experiment, but this was different when rainwater was used. The latter effect is probably due to the higher solution concentrations in the rainwater experiment but could also be a result of root damage due to low Ca/Al ratios in the rhizosphere solution. It was concluded, that liming improved the chemical composition in the rhizosphere soil solution by increasing overall solute concentration to levels enabling sufficient and easier nutrient uptake by roots.

Introduction

The rhizosphere differs in many aspects from the bulk soil due to higher microbial and fungal activity. Soil solution in the vicinity of the roots is often more favourable than bulk soil (Callot *et al.* 1982, Gobran and Clegg 1996). Some elements are taken up preferentially (more than by mass flow alone) whilst others are taken up less, leading to either depletion or concentration gradients close to the roots (Häussling *et al.* 1988, Marschner *et al.* 1991, Gobran and Clegg 1996, Dieffenbach *et al.* 1996). Exudation and activity of mycorrhizae close to the roots can stimulate biological weathering (Hinsinger *et al.* 1992, Paris *et al.* 1995, Hinsinger and Gilkes 1997, Jongmans *et al.* 1997, Courchesne and Gobran 1997). Often a pH change in the rhizosphere can be attributed to a change in NO_3^-/NH_4^+ uptake ratio (Keltjens and Van Ulden 1987; Gijsman 1990). Root-induced pH changes in the rhizosphere can affect the solubility of Al and thereby its phytotoxicity in the rhizosphere. Aluminium can be complexed by excretion of organic ligands, like citrate (Gahoonia 1993) or malate that are ascribed an Al detoxification effect (Jones and Darrah 1994). Anions also decrease the phytotoxicity of Al in acidic solutions through complexation; Grauer (1993) ranked anions for ameliorative effectiveness as $OH^- > F^- > SO_4^{2-} > Cl^-$. A separate evaluation of bulk and rhizosphere soil and soil solution chemistry, and even further of apical and basal root zones of the rhizosphere, is indispensable for an appropriate prediction of the nutritional status or the risk of Al toxiticity of trees (Marschner *et al.* 1991).

Therefore, the characterization of concentration or depletion gradients in the soil solution of the rhizosphere, caused by nutrient uptake and root exudation, is of importance when

addressing to root function issues. In this study, the objectives were to assess the root function in the rhizosphere of sessile oak (*Quercus petraea* (M.) Liebl.) by using micro suction cups, and to examine the effect of liming on this root function.

Materials and methods

Rhizotrons, 55 (l) x 40 (h) x 3.5 (w) cm, were filled with an acid brown forest soil (FAO Dystric Cambisol; USDA Dystrochrept) collected in a liming experiment in the French Ardennes (Belkacem and Nys 1997). Soil was air-dried and sieved at ~4 mm. The A-horizon (average pH-H_2O 3.8) of 15 cm was put on top of the B-horizon soil (average pH-H_2O 4.4) of 20 cm and both were re-constituted with a density equal to field conditions. A control (Control, C) was compared with soils treated with $CaCO_3$ (Lime, L) at a dosis equivalent to 1.4 t ha^{-1} CaO. In order to obtain a rapid effect of these applications on root growth, half of the dose of lime was mixed with the top A-horizon soil before filling the rhizotrons. The other half was spread on top of a small litter-layer of Oak leaves. This situation (half of the applied calcium in form of lime incorporated into the soil) corresponds to a period of 20 months after liming if applied to the surface as shown in previous studies on the same soil (Belkacem and Nys 1997). After a re-wetting period, 3 to 4 acorns (*Quercus petraea* (M.) Liebl.) were planted and rhizotrons were put at an angle of about 30°, as to induce fine root growth along one of the two sides. The rhizotrons were then covered to the height of the soil profile with black plastic to prevent light effects on root development.

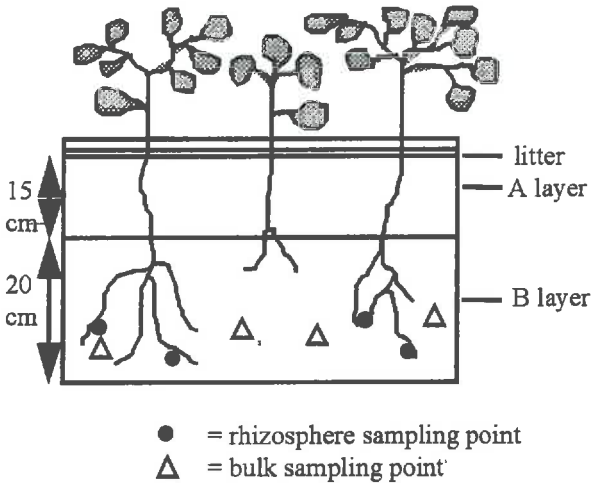

Figure 1 Position of the micro cups in the rhizotrons

Once sufficient root growth had occurred into the B-layer, little holes were bored into the side with preferential root growth. Half of these holes were choosen close to the roots and half in the bulk soil (Figure 1). Small metal pins of dimensions equal to the micro suction cups were used to prepare holes of a depth of a few mm under the plexiglass into the soil. The micro suction cups consisted of a ceramic cell glued into a small rigid tube of polyetheretherketone, PEEK (Göttlein *et al.* 1996, Göttlein and Stanjek 1996, Dieffenbach *et al.* 1997). The ceramic side was inserted in the hole and glue was used to fix the cups to the plexiglass, to keep them in place and to close the hole. The other side, glued into the PEEK, was then attached to flexible tubes, which had been rinsed previously with HCl and destilled water. At the outer end, these flexible tubes were connected again to a small PEEK tube and glued onto a vacuum

collecting device, similar to the one described by Göttlein *et al.* (1996). Likewise, to minimize the evaporation of sample droplets hanging at the capillary outlet, the bottom of the collecting device was filled with destilled water to produce a water-vapour saturated atmosphere (Göttlein *et al.* 1996). After a contact time of a few days, pumping sessions were started with help of a vacuum-pump connected to the collecting device creating a suction of ~400 hPa.

Table 1 Overview of experiments with microsuction cups (C = Control; L = lime)

experiment number	number of rhizotrons	sample number bulk	sample number rhizosphere	seedling age in months	irrigation
1	3 C, 2 L	16 C, 10 L	10 C, 5 L	2-4	rainwater
2	2 C, 2 L	42 C, 58 L	40 C, 33 L	1.5-2	demineralized water

The first experiment (Table 1) was conducted in 1996 and rainwater was used for irrigation, whereas the second experiment was carried out in 1997 with demineralized water. Although rainwater had a higher load in nutrients than demineralized water, concentrations of nutrients in the rain water were generally negligible (0.01 to 0.03 mmolc l^{-1}) when compared to bulk and rhizosphere solute concentrations, except SO_4^{2-} and Ca^{2+} with concentrations of 0.04 ($\pm$0.001) and 0.06 ($\pm$0.01) mmol l^{-1}, respectively, being about 20% of soil solution concentrations. The first experiment was conducted with only four replicate micro cups (bulk versus rhizosphere) according to the following protocol: pumping 5 to 6 hours, break of circa 18 hours, pumping 5 to 6 hours etc. After completion of a pumping series for a rhizotron, micro cups were removed, cleaned and installed likewise in a next rhizotron. Connecting tubes were cleaned as before. First samples ('dead volume', generally several hundreds of µl) and samples below 200 µl ('small' volume samples) were excluded from further analysis. In the second experiment two rhizotrons were sampled simultaneously (12 replicates for control bulk and rhizosphere and lime bulk and rhizosphere) and this was done twice (part 1 and 2). Besides the exclusion of 'small' volume samples, some devices did not collect solution due to breaking during installation or to bad contact with the soil solid phase (see Table 1 for final sample number).

Solute samples were analysed by ICP (Mg, Al, Ca, K), ion chromatography (F^-, Cl^-, NO_2^-, NO_3^-, SO_4^{2-}, HPO_4^{2-}) and TRAACS (NH_4^+). All statistics were carried out using Unistat 4.0 software (Unistad Ltd 1995). Analysis of variance based on the test and first experiment, revealed no significant difference between consecutive samples from the same micro cup, so that all separate samples were used for further analysis. Means for all parameters were tabulated and distributions were plotted to judge for normality or not. Whenever necessary, log transformations were carried out prior to statistics. A three-way ANOVA for treatment (C and L), solution type (bulk and rhizosphere) and experiment (1 and 2) was carried out. Finally, two-way ANOVA's were carried out per experiment separately to test for treatment and bulk versus rhizosphere effects.

Results

Cationic charge was largely dominated by ammonium and anionic charge by nitrate for both control and liming treatment (Figure 2). Concentrations of F^- were negligible and of NO_2^- and HPO_4^{2-} very low and often below detection limit (data not presented). Concentrations were often higher in the first experiment as compared to the second experiment, especially

concentrations of Ca and Al. In contrast, concentrations of SO_4^{2-} and Cl^- were lower in the first experiment as compared to the second.

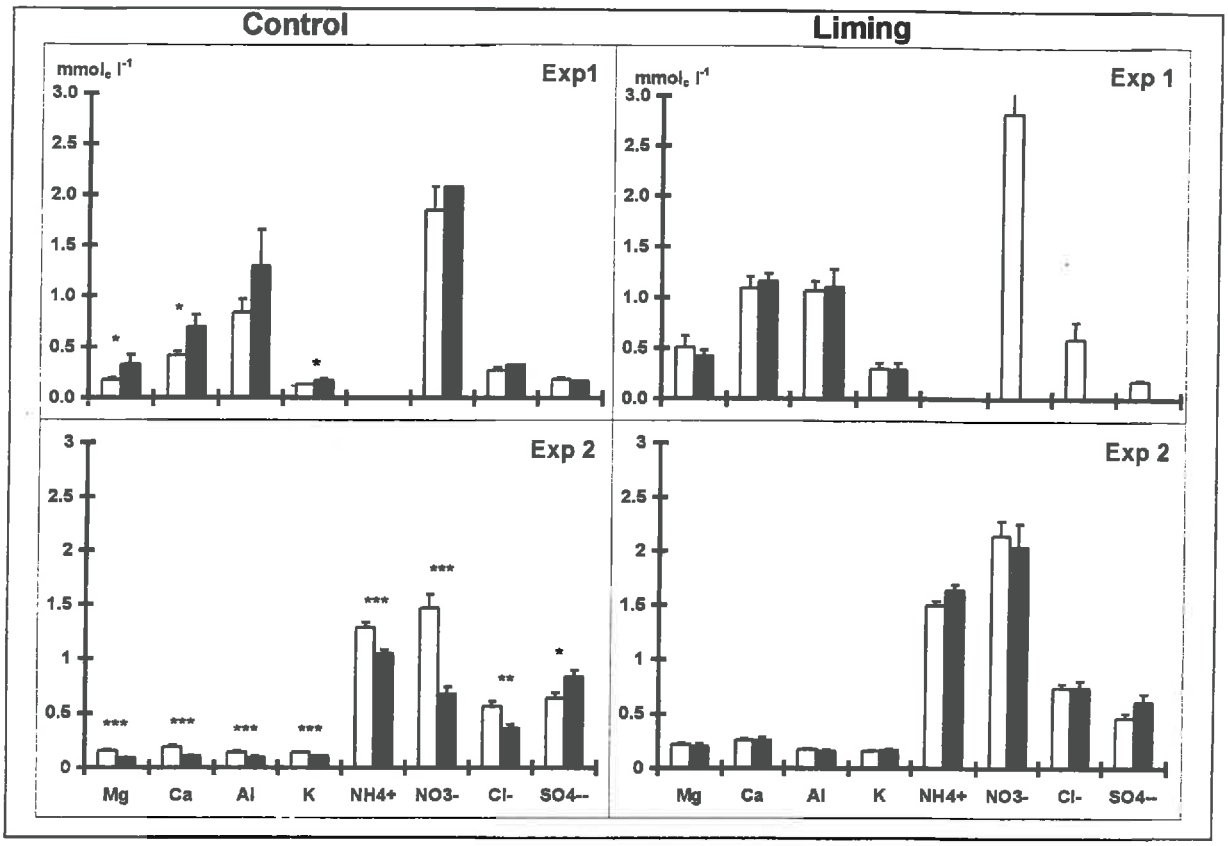

Figure 2 Comparison of the rhizosphere (black) with the bulk (white) solution for the control and the liming treatment (significant differences indicated by *, **, and *** for $p<0.05$, 0.01 and 0.001, respectively)

In the control, numerous significant differences between bulk and rhizosphere soil solution appeared (Figure 2). In experiment 1, all examined nutrients showed to be more concentrated in the rhizosphere, and this was significant for Mg, Ca and K. In experiment 2, overall concentration levels in the solutions were lower, and a significant depletion occurred in the rhizosphere solution for all nutrients studied, except for SO_4^{2-}, which was significantly concentrated in the rhizosphere.

Considering the rhizospheric gradients in the soil solution, liming basically levelled these gradients, and no significant difference between bulk and rhizosphere soil solution persisted (Figure 2). In the limed rhizotrons, charge of nitrate always exceeded charge of ammonium, whereas in the control the opposite holds, with the exception of the bulk solution in experiment 2. As shown in Figure 3, presenting the data for experiment 2 (first experiment comparable as concerns lime effects), liming significantly increased concentrations of Ca, Mg, K, NO_3^-, NH_4^+ and Cl^- both in bulk and rhizosphere, although this was not necessarily significant in each individual experiment. In contrast, SO_4^{2-} was significantly lower. The Ca/Al ratio was only significantly enhanced by lime in the rhizosphere of the second experiment. The Ca/Al ratio was always lower in the rhizosphere of the control, and higher in the rhizosphere of the lime

treatment, as compared to the bulk soil (Fig 4), but this was not significant due to high variation between samples.

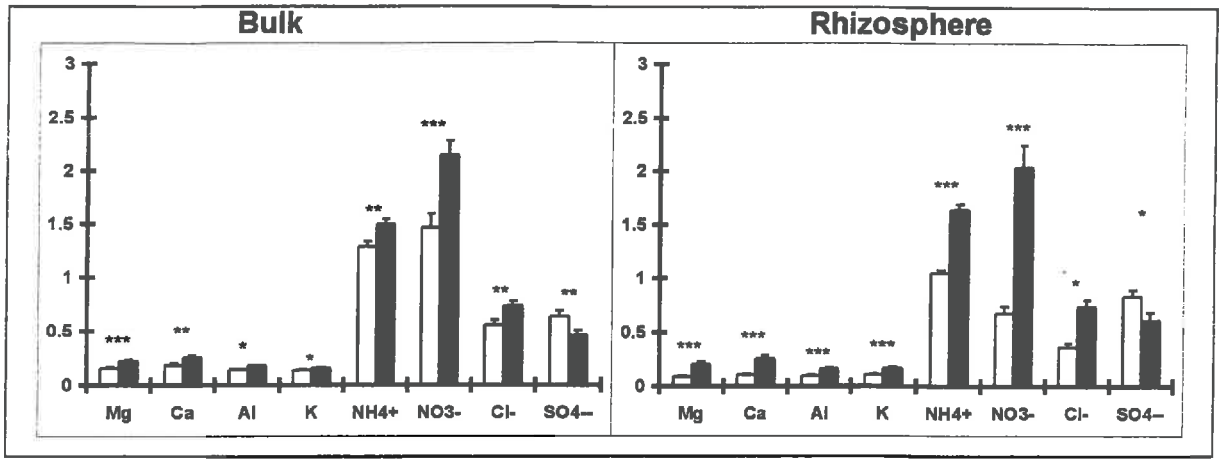

Figure 3 Effects of liming (black bars) as compared to control (white bars) for the soil solution in bulk or rhizosphere soil in experiment 2 (significant liming effects indicated by *, **, and *** for $p < 0.05$, 0.01 and 0.001, respectively)

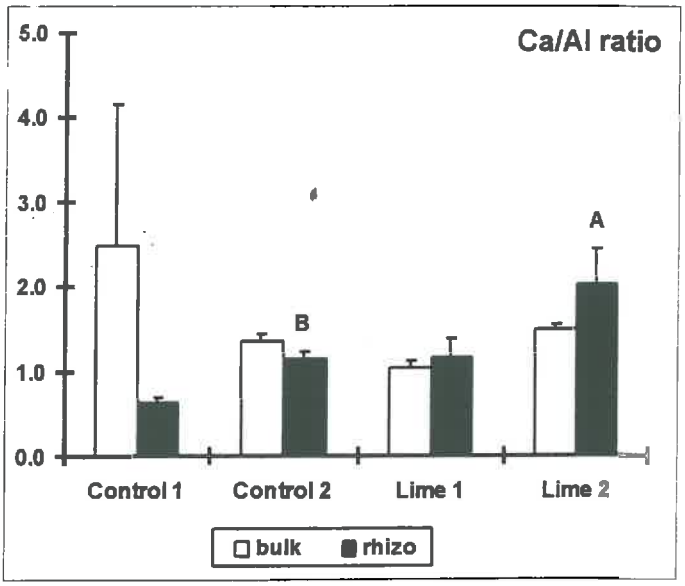

Figure 4 Ca/Al ratio in bulk and rhizosphere soil solution for the different experiments and treatments (no significant differences between bulk and rhizosphere, A and B indicating significant differences at $p<0.05$ between lime and control experiments of experiment 2).

Discussion

The difference in concentrations between the two experiments must be the result of a different irrigation regime (rainwater versus demineralized water), although the age of the seedlings may be an additional explanation. Such a dependency of uptake (activity) on root age or root zone is a well known phenomenon (George and Marschner 1996, Dieffenbach *et al.* 1997). Here, the increase in solute concentrations, indeed, follow the age of seedlings. When ranking from

the 1.5 to 2 months old seedlings (2 separate parts of the second experiment) to the 2 to 4 months old seedlings (first experiment) increase occurred for Mg, Ca, Al and K, mainly in the rhizosphere. On the other hand SO_4^{2-} and Cl^- show a decreasing trend over time. This would mean, that there could be some variation in acitivity of the roots used for the rhizosphere soil solution sampling, affecting the soil solution differently. So, the experimental variation observed, presumably is related to the irrigation regime (and thus overall concentrations) and maybe also the seedling (root) age and activity.

In the control, a significant depletion occurs for many nutrients in the second experiment (Figure 2). Such a depletion of ions like Ca, Mg and K in acidic poor mineral horizons is the most generally observed (Häussling *et al.* 1988; Hinsinger *et al.* 1992, Dieffenbach *et al.* 1997), and reflects a net uptake exceeding transport to the root. In the control of the first experiment, however, significant concentration occurred. When lime was applied, neither depletion nor concentration gradients were observed.

Whether a gradient will form or not, depends on the amounts of ions arriving by mass flow, diffusion, and transport by mycorrhizae to the roots (Yin *et al.* 1991, Marschner *et al.* 1991). The significant concentration gradients in the control of the first experiment suggest that transport to the root was higher, that uptake was lower, or both, as compared to the second experiment. The overall higher solution concentrations in the control of the first experiment suggests that nutrient availability actually was higher than in the second experiment, indicating that the transport to the root explains the depletion or concentration gradients. The lower Ca/Al ratios in the rhizosphere of the control in the first experiment (Figure 4) could suggest less favourable uptake conditions, and may also explain why a concentration gradient of nutrients around the root occurs in response to a disturbed uptake. Ratios of Ca/Al in soil solution < 1.0 can indicate a potential risk for root damage (Cronan and Grigal 1995). In agreement with this, liming increased overall solution levels (both experiments), but did not lead to concentration gradients close to the root, related to the more favourable Ca/Al ratios there. It seems, as a consequence, that the presence or absence of a rhizospheric gradient is related to a deteriorating root function due to the accumulation of Al close to the roots as reflected in low Ca/Al ratios (Fig 4), to the overall solution concentrations (Fig 5), or both.

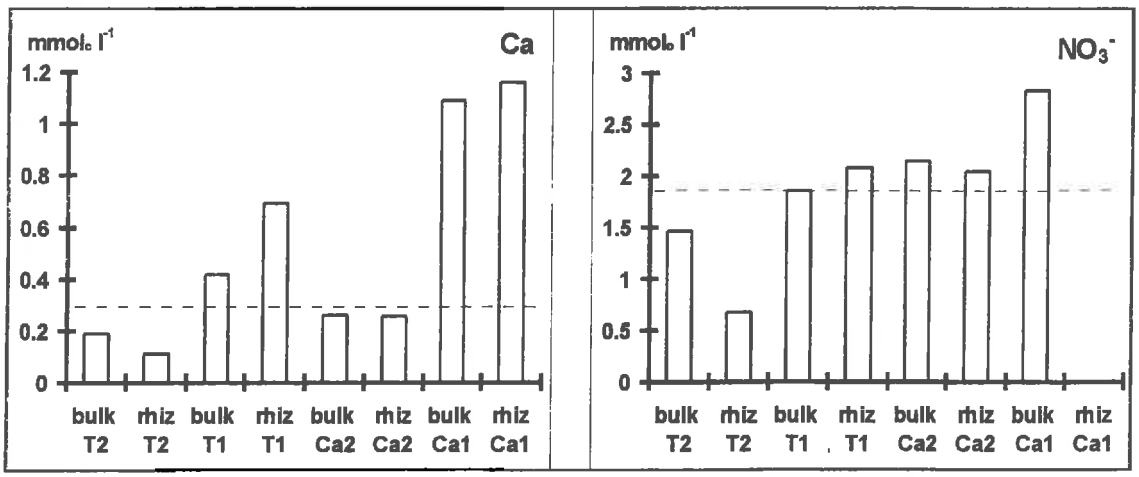

Figure 5 Approximate threshold solution concentrations below which depletion occurs; illustrated for Ca and NO_3^- (based on the mean values of both treatments in both compartments and both experiments).

In Figure 5 hypothetical uptake threshold levels are drawn based on the four experimental comparisons between bulk and rhizosphere of this study for the example of Ca and nitrate. The concept illustrated in that figure, assumes that a mass flow of a solution of about 0.2 $mmol_c\ l^{-1}$ Ca^{2+} and 1.5 $mmol_c\ l^{-1}$ of NO_3^- towards the root, apparently, is not enough to reach the desired uptake level, creating a depletion gradient around the root. Concentrations of around 0.25 and 1.8 $mmol_c\ l^{-1}$ (respectively), were sufficient and no depletion occurred. In agreement with this, solution concentrations were quite low (around 0.06, 0.10 and 0.04 $mmol_c\ l^{-1}$ for Mg, Ca and K, respectively) in the study of Dieffenbach *et al.* (1997), where depletion of these nutrients was observed.

So, the increased overall solution concentrations by liming can explain why the rhizosphere effects observed in the control treatment are levelled. Close to the roots the amount of Ca and N arriving by mass flow do not seem limiting anymore (Fig 5). Another aspect is the cost for uptake of nutritional elements (cations, nitrogen). Gobran and Clegg (1996) suggest that trees growing on nutrient-poor acid soils invest their energy around roots to create a favourable micro-environment for roots and micro-organisms. Thus, the cost could be higher in the control than in the liming treatment. Also, since in the experiment with the youngest seedlings the depletion effects and reversely for the oldest seedlings the concentration effects were most pronounced, the root function seems to deteriorate with age for the control, whereas this is not the case for the limed treatments.

The difference between lime-induced changes in solution concentrations between SO_4^{2-} and the other ions, must be seen in relation to the stimulation of nitrification by lime (Andersson and Persson 1988, Belkacem and Nys 1997), increasing the importance of NO_3^- as a counter ion accompanying cations in downward solute movements. In this study, liming increased both nitrate and ammonium concentrations in bulk and rhizosphere soil as compared to the control treatment (nitrate more than ammonium). Interestingly, nitrate and ammonium rhizosphere gradients were different between the control and the liming treatment in the second experiment. In the control treatment, rhizosphere concentrations of both nitrate and ammonium were lower than in bulk soil (depletion), and this depletion was larger for nitrate than for ammonium, suggesting that nitrate uptake was preferred to ammonium uptake. In the liming treatment no significant differences between bulk and rhizosphere solution occurred. This would mean that both forms are taken up in a rate equal to mass flow, suggesting that more nitrate (higher concentrations) was taken up than ammonium. Ammonium even showed a tendency to increase in the rhizosphere after liming. Thus, although liming stimulated both nitrate and ammonium production, nitrate production was the most stimulated, resulting in a more favourable NO_3^-/NH_4^+ ratio in the soil solution which has been shown to be important for good root function (Callot *et al.* 1982, Gijsman 1990). It has been shown in solution experiments that pedunculate oak (*Quercus robur* L.), in spite of a NH_4^+ preference, can switch easily to NO_3^- as a nitrogen source (Keltjens and Van Loenen 1989). This presumably also holds for sessile oak.

The hypothesis that uptake of nutrients is higher in the liming treatment than in the control, related to better uptake environment (Ca/Al solution ratios) and overall higher solution concentrations, is corroborated by observations of field and rhizotron experiments (in prep.). Indeed, allocation to shoot of biomass and nutrients, is significantly higher in the lime treatment as compared to the control. Possibly, the less favourable Ca/Al ratio in the rhizosphere of the control in the first experiment explains why uptake was less than the potential of nutrients arriving by solution (concentration), whereas uptake levels were much

higher in the liming treatment. Observations on a higher occupation of Ca at the root CEC and a lime-induced stimulation of rhizosphere pH (in prep.) confirm the present observations on the NO_3^-/NH_4^+ uptake ratio. The positive effect of liming on seedling growth must thus be explained in terms of a better root function (volume, efficiency, longevity) due to changes in the rhizosphere.

Conclusions

The application of micro cups to assess the soil solution of the rhizosphere appeared feasible and offers a valuable additional tool for evaluating actual growth conditions. Here, the rhizosphere soil solution in the control treatment was different from the bulk soil solution. Whether this would be a depletion or a concentration close to the roots, depended on overall solution concentrations and possibly seedling (root) age. Liming increased overall solution concentrations and levelled rhizosphere nutrient gradients in the soil solution. As a result, actual uptake potential of nutrients was improved, and NO_3^-/NH_4^+ uptake ratio increased, corroborating observations on root-induced pH increases and higher biomass and nutrient allocation to the shoot.

Acknowledgments

We would like to thank Claude Nys for useful comments on earlier versions of this manuscript. This research was supported by grants of INRA Paris and the Dutch Ministry of Agriculture, Nature Management and Fisheries, Directorate of Science and Knowledge Dissemination.

References

Andersson F and Persson T 1988 Liming as a measure to improve soil and tree condition in areas affected by air pollution. Results and experiences of an ongoing research programme. Naturvårdsverket Report 3518, 131 p.

Bakker M R 1998. The effect of lime and gypsum amendments on a sessile oak (*Quercus* petraea (M.) Liebl.) stand at La Croix-Scaille (French Ardennes) II. Fine root dynamics. submitted to Plant Soil.

Bakker M R, Kerisit R, Verbist K and Nys C 1998. Effects of liming on growth of fine roots and seedlings of Sessile Oak (*Quercus petraea*) in relation to lime-induced changes in rhizosphere chemistry. in prep.

Belkacem S and Nys C 1997 Effects of liming and gypsum regimes on chemical characteristics of an acid forest soil and its leachates. Ann. Sci. For. 54, 169-180.

Callot G, Chamayou H, Maertens C and Salsac L 1982 Mieux comprendre les interactions sol-racine; incidence sur la nutrition minérale. INRA, Paris.

Courchesne F and Gobran G R 1997 Mineralogical variations of bulk and rhizosphere soils from a Norway spruce stand. Soil Sci. Soc. Am. J. 61, 1245-1249.

Cronan C S and Grigal D F 1995 Use of calcium/aluminum ratios as indicators of stress in forest ecosystems. J. Environ. Qual. 24, 209-226.

Dieffenbach A, Göttlein, A and Matzner E 1997. *In-situ* soil solution chemistry in an acid forest soil as influenced by growing roots of Norway spruce (*Picea abies* [L.] Karst.). Plant Soil 192, 57-61.

Gahoonia T S 1993. Influence of root-induced pH on the solubility of soil aluminium in the rhizosphere. Plant Soil 149, 289-291.

George E and Marschner H 1996 Nutrient and water uptake by roots of forest trees. Z. Pflanzenernähr. Bodenk. 159, 11-21.

Gijsman A J 1990. Rhizosphere pH along different root zones of Douglas-fir (*Pseudotsuga menziesii*), as affected by source of nitrogen. Plant Soil 124, 161-167.

Gobran G R and Clegg S 1996 A conceptual model for nutrient availability in the mineral soil-root system. Can. J. Soil Sci. 76, 125-131.

Göttlein, A and Stanjek H 1996. Micro-scale variation of solid-phase properties and soil solution chemistry in a forest podzol and its relation to soil horizons. Eur. J. Soil Sci. 47, 627-636.

Göttlein A, Hell, U and Blasek R 1996. A system for micro-scale tensiometry and lysimetry. Geoderma 69, 147-156.

Grauer U E 1993 Modelling anion amelioration of aluminium phytotoxicity. Plant Soil 157, 319-331.

Häussling M, Jorns C A, Lehmbecker G, Hecht-Buchholz C and Marschner H 1988 Ion and water uptake in relation to root development in Norway spruce (*Picea abies* (L.) Karst.). J. Plant Physiol. 133, 486-491.

Hinsinger P and Gilkes R J 1997 Dissolution of phosphate rock in the rhizosphere of five plant species grown in an acid, P-fixing mineral substrate. Geoderma 75, 231-249.

Hinsinger P, Jaillard B and Dufey J E 1992 Rapid weathering of a Trioctahedral mica by the roots of ryegrass. Soil Sci. Soc. Am. J. 56, 977-982.

Jones D L and Darrah P R 1994. Role of root derived organic acids in the mobilization of nutrients from the rhizosphere. Plant Soil 166, 247-257.

Jongmans A G, Van Breemen N, Lundström U, Van Hees P A W, Finlay R D, Srinivasan M, Unestam T, Giesler R, Melkerud P A and Olsson M 1997 Rock-eating fungi. Nature 389, 682-683.

Keltjens W G and van Loenen E 1989. Effects of aluminium and mineral nutrition on growth and chemical composition of hydroponically grown seedlings of five different forest tree species. Plant and Soil 119, 39-50.

Keltjens W G and van Ulden P S R 1987. Effects of Al on nitrogen (NH_4^+ and NO_3^-) uptake, nitrate reductase activity and proton release in two sorghum cultivars differing in Al tolerance. Plant Soil 104, 227-234.

Marschner H, Häußling M and George E 1991 Ammonium and nitrate uptake rates and rhizosphere pH in non-mycorrhizal roots of Norway spruce [*Picea abies* (L.) Karst.]. Trees 5, 14-21.

Olsthoon A F M, Keltjens W G, van Baren B and Hopman M C G 1991. Influence of ammonium on fine root development and rhizosphere pH of Douglas-fir seedlings in sand. Plant Soil 133, 75-81.

Paris F, Bonnaud P, Ranger J, Robert M and Lapeyrie F 1995 Weathering of ammonium- or calcium-saturated 2:1 phyllosilicates by ectomycorrhizal fungi *in vitro*. Soil Biol. Biochem. 27, 1237-1244.

Unistat Ltd 1995. Unistat version 4 for Windows.

Yin X, Perry J A and Dixon R K 1991 Temporal changes in nutrient concentrations and contents of fine roots in a *Quercus* forest. For. Ecol. Manage. 44, 175-184.

Annexe A (Paper IX) : à soumettre

Effect of liming on the fine root cation exchange sites of Oak (*Quercus petraea* (M.) Liebl.)

M.R. Bakker & C. Nys

Abstract

Nutrient acquisition has been shown to be related to the root exchange capacity of roots (root-CEC). Here, the effects of root-age and liming or gypsum treatments on root-CEC of fine roots of sessile oak (*Quercus petraea*) were studied. In the field, sampling was carried out one to five years, and in rootboxes 3.5 months, after the treatments. Root-CEC was determined by an adapted desorption method based on percolation with 10^{-2} N $CuSO_4$. The results showed that the root-CEC is higher in young whitish roots than in older brownish roots, mainly as a result of higher concentrations of K. Liming or gypsum applications increased relative occupation by Ca of root-CEC and Ca/Al molar ratio, while decreasing relative occupation of Al (all sign. at $P< 0.05$), and this was true for older brownish roots and in the field, but not for young whitish roots. This indicates that the potential of fine roots for uptake of base cations, decreasing with root age in the control, could be maintained or increased after liming or gypsum treatments. Both treatments acted against 'age', so that for a given root-age the roots of the liming or gypsum treatment were in fact 'chemically' younger than those of the control. The results corroborate other results on fine root turnover, fine root mortality, tree growth and foliar nutrition, and suggest that liming and gypsum enhanced root function, perhaps by extending the effective uptake lifetime.

key-words: root exchange sites, liming, gypsum, *Quercus petraea*, fine roots

Introduction

Soil acidification alters the soil chemical environment for tree roots, leading to impaired uptake, increased fine root mortality and a shallower rooting profile (Murach & Schünemann 1985, Hüttl & Zöttl 1993). For uptake, binding of Ca^{2+} and Mg^{2+} at cation exchange sites (mainly carboxylic groups) in the cell wall is of importance (Marschner 1991) and higher concentrations of Ca^{2+} or Mg^{2+} adsorbed to the root exchange sites can stimulate uptake of these cations (Keltjens 1995, Ericsson *et al.*, 1995). With increasing soil acidification, the proportion of Al increases at the exchange complex and competitively reduces the concentration of the basic cations at the root exchange sites and their uptake potential (Rengel 1992). Conversely, additions of Ca or Mg can reduce Al toxicity by competing with Al for external binding sites (Keltjens 1990), increasing the relative proportion of Ca or Mg on the root exchange sites, while decreasing that of Al (Dufey *et al.* 1991). With increasing longevity of fine roots, the concentration of Al in roots increases, indicating a decreasing effectiveness in the uptake of basic cations with age of fine roots (Murach & Schünemann 1985). The present paper focuses on the status of the root exchange capacity (root-CEC) of fine roots of oak as a function of liming treatments, in order to evaluate the effectiveness of these treatments on the fine root function at an acidic site in the French Ardennes. It was hypothesized that liming would increase the basic cation occupation on the root exchange sites and thereby improve root function and longevity. The paper discusses the effect of root-age and liming on the root-CEC.

Materials and methods

Site description and experimental treatments

The French Ardennes site of La Croix-Scaille is situated on a silty clay acidic brown forest soil (FAO Dystric Cambisol; USDA Dystrochrept). Soil pH-H_2O in the top 15 cm layer was on average 3.8, and 4.4 in the 15-45 cm layer. A control (control, C) treatment was compared with doses of $CaCO_3$ (lime, L), $CaSO_4$ (gypsum, G) or a 80/20 mix of the two (Mix) equivalent to 1.4 t ha^{-1} of CaO on a 48 year old (average age) stand of sessile oak (*Quercus petraea* (M.) Liebl.). The liming treatments were applied one (new trial), or four to five years before sampling (old trial). A rootbox experiment was carried out with soil from the La Croix-Scaille site, reconstituting an A and B layer according to field bulk density. Liming and gypsum were applied at the same doses as in La Croix-Scaille and after one month small seedlings of about 4 months old were planted. Sampling was carried out 3.5 months after planting.

Sample preparation

Fine roots were collected with a root corer from field lime trials, or from the rootboxes by opening them from the side. Samples containing soil and fine roots were stored in plastic bags at 1° C, prior to separating the fine roots from the soil. The fine roots were sorted out over a sieve, air-dried and cleaned with help of tweezers and small brushes. Clean roots were stored at - 7°C until further processing. Prior to handling, the samples were re-dried at 30 °C. Then, the roots were cut into fragments of about 5 mm length and weighed. Standard fine root sample weights of 0.15 to 0.25 g were taken.

Pilot studies and the method used

Based on the work of Dufey & Braun (1986) it was decided to follow a $CuSO_4$ - HCl desorption method, which they recommended after comparing three different methods. The principle of this method is to displace the cations adsorbed on to the root exchange sites by a solution of 10^{-2} N $CuSO_4$ (step 1) and to desorb the Cu adsorbed on to these root exchange sites by a 10^{-1} N HCl solution (step 3). The first step would then give the values for every single cation (Ca, Mg etc.), whereas the third step would lead to a single root-CEC value, the sum of all cations adsorbed. Between both steps, the fine root sample should be abundantly washed with a solution of 10^{-4} N $CuSO_4$, in order to make the amount of free Cu ions in the interstitial volume of the roots negligible relative to the fixed Cu ions on the root-CEC (step 2). After using manual percolation and agitation procedures, neither of which appeared satisfactory, an automatic percolation system was developed.

This automatic tubing and rinsing design optimized the doses of percolation and desorption liquids applied in all three steps of the method and thus limited time and effort whilst standardizing the contact time. For step 1 the effluent after desorption with 10^{-2} N $CuSO_4$ was analysed from 20 up to 250 ml. This revealed that desorption reached levels close to 100 % after about 140 ml (Fig. 1a). In step 2, prolonged washing with 100 or 150 ml of the 10^{-4} N $CuSO_4$ solution instead of 50 ml did not lead to significant changes in the amount of Cu desorbed in step three by the HCl solution. Finally, for step 3, the volumes of the desorption solution of 10^{-1} N HCl were varied from 100 up to 500 ml. This revealed that the relative amount of Cu desorbed fell to very low proportions after 200 ml of solution (Fig. 1b) for all treatments and layers.

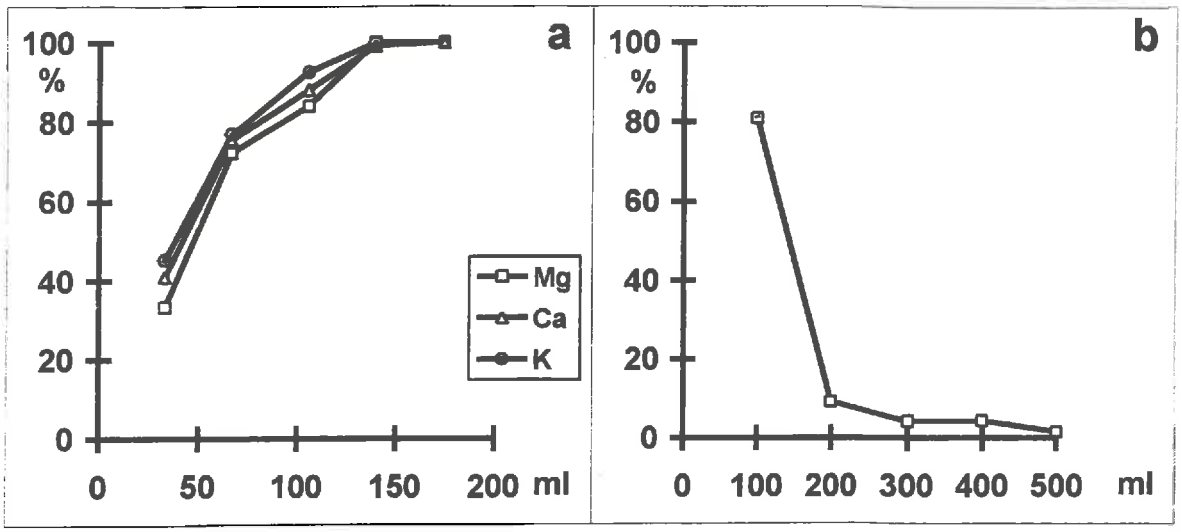

Figure 1 (a) the influence of desorption volume of 10^{-2} N $CuSO_4$ on the amount of cations deplaced using the example of Mg, Ca and K; and (b) percentage desorption of Cu from root-CEC as a function of volume of desorbant HCl (mean of 8 samples).

Two series of fine root samples were analysed by the improved percolation method. Only the first step, desorption of cations by the 10^{-2} N $CuSO_4$ solution, was applied. Fine roots of the rootbox experiment and of the Ardennes field site were treated with about 200 ml of the desorption solution, after which the exact volume of each single sample effluent was determined. pH-H_2O was measured by a glass electrode and selected cations (Mg, Al, Ca, K) were analysed in the effluents by ICP. In the first series, the fine roots of the rootbox experiment (Control = C, Lime = L, Gypsum = G) were separated into white non-lignified roots and brownish lignified roots to obtain more homogeneous samples and find out about the age and functional aspects of root-CEC during the development of the roots. The objective of this series was to assess the influence of root age on root-CEC. In the second series, fine roots from the Ardennes field site for June (C, L-new, G-new and Mix) and September 1995 (C, L-old, L-new, G-new, G-old and Mix), regardless of their colour, were sampled for different soil depths. The objective of this second series was to evaluate the influence of different liming treatments on root-CEC in a field study.

Data analyses

Effects of soil depth, treatment or type of root, were tested by One or Two-Way ANOVAs with the help of Unistat 4.0 for Windows (Unistat Ltd 1995). Depth and treatment effects in the field trial were further interpreted by a comparison of groups means using the Student Newman Keuls test.

Results

Importance of root age

In table 1 the differences between young, whitish roots and older, brownish roots are presented for the control. The only significant difference related to age, in the control, is a lower relative occupation of the root-CEC by K. When lumping both layers, again the relative proportion of K, but also the total amount of K and the sum value, are significantly higher in the younger roots

Table 1 Root-CEC values for rhizotron-grown *Quercus petraea* fine roots in the control treatment for A and B horizon as a function of type of fine roots (young, white roots versus older, brown roots); presented are means and standard errors (in italic) and the letters indicate a significant difference between the two types of roots at $p<0.05$ level.

	Mg	Al	Ca	K	sum	Mg	Al	Ca	K	Ca/Al
type	$mmol_c \cdot 100\ g^{-1}$					%				molar ratio
	A horizon									
young	1.0	1.4	1.2	6.8	10.3	7.8	16.7	8.6	66.8	0.34
	0.6	*0.9*	*0.6*	*2.7*	*4.0*	*3.6*	*6.5*	*3.4*	*5.3*	*0.18*
old	0.5	0.9	0.4	2.2	3.9	12.1	22.7	10.0	55.3	0.44
	0.1	*0.2*	*0.1*	*0.4*	*0.7*	*1.2*	*3.2*	*1.6*	*5.1*	*0.02*
	B horizon									
young	1.1	4.0	0.6	17.1	22.7	3.7	24.1	1.7	70.5a	0.13
	0.5	*0.3*	*0.4*	*6.0*	*7.0*	*1.3*	*8.7*	*1.0*	*6.7*	*0.08*
old	0.8	4.1	0.7	5.4	10.9	7.2	37.7	5.9	49.3b	0.15
	0.1	*0.7*	*0.2*	*1.0*	*1.9*	*0.8*	*1.5*	*2.2*	*3.6*	*0.06*

as compared to the older roots. A similar statistical interpretation for the $CaCO_3$ and $CaSO_4$ treatment separately (data not further presented), shows no significant effects between the roots of the two age classes for the $CaCO_3$ treatment. The effects of the $CaSO_4$ treatment as regards root age were similar those in the control, i.e. higher K and sum values in the young roots, but showed some effect on relative Mg proportion of root-CEC as well (increase with age). So, this individual comparison shows mainly a difference in absolute value of root-CEC, between the young and old roots, related to a higher amount of K adsorbed to the young roots.

Soil depth effects were similar for all treatments: significantly more Ca and / or Mg and significantly less Al was adsorbed the roots of the A horizon as compared to the B horizon.

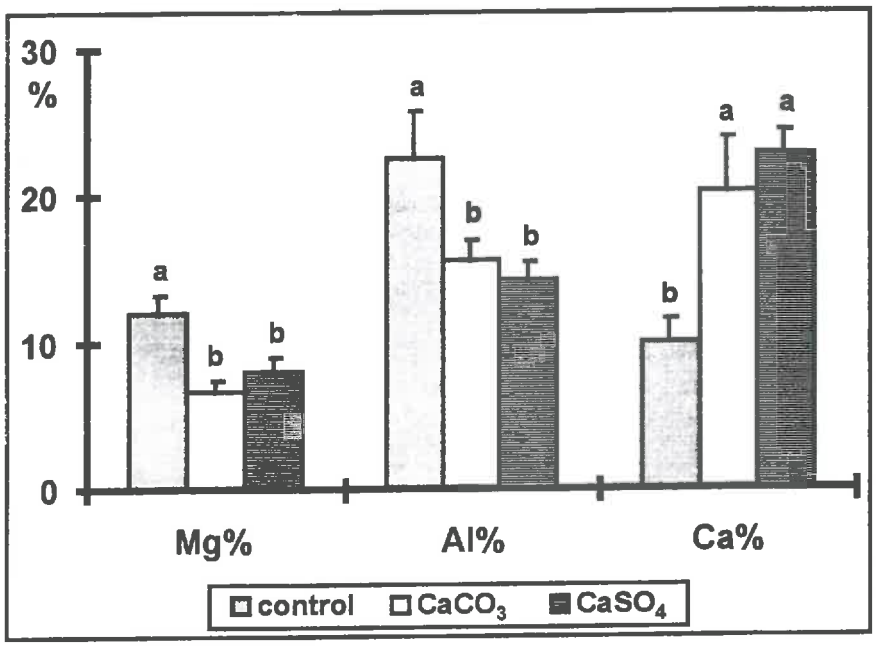

Figure 2 Effects of treatments on relative proportion of Mg, Al and Ca on the root-CEC of the brownish (older, suberized) roots in the A horizon (bars present standard errors and the different letters denote significant treatment effects at $p<0.05$ level).

Effect of liming

Figure 2 illustrates the treatment effects in the rootbox experiment for the older, brownish roots of the A-layer. Effects on the young, whitish roots were not significant due to higher variation, and there were no significant treatment effects at all in the B-layer. Both treatments (G, L) resulted in significantly lower relative amounts of Mg and Al on the root-CEC as compared to the control, while both the relative amounts of Ca and the Ca/Al molar ratio were increased.

Table 2 shows the most important results for the fine roots of the Ardennes site. The data were grouped for June and September and for 0 to 15 cm. This appeared to give better results than each separate period or soil layer. Treatment effects were not significant or not consistent below 15 cm and were limited to significantly lower relative amount of Al and conversely, a higher relative amount of Ca in the top 0 to 5 or 0 to 15 cm as compared to the deeper layers. As can be seen in Table 2, total root-CEC was not significantly affected in the 0 to 15 cm layer, but the relative amounts of Ca and Ca/Al molar ratio on the root-CEC were increased by the treatments, whereas the relative amount of Al decreased. This was significant only in the old treatments (L-old, G-old), five years after their application. Effects on the relative amounts of Mg (about 10 %) and K (about 10 to 15 %) were not significant.

Table 2 Summed root-CEC values (Mg+Al+Ca+K), procentual occupation of root-CEC by Al and Ca, and Ca/Al molar ratio on the root-CEC (data June and September 1995 lumped) for the fine roots of 0-15 cm.

		sum	Al	Ca	Ca/Al
		$mmol_c$	%	%	molar
	n	. 100 g^{-1}			ratio
control	8	3.10 (0.51)	50.0 (7.5) **a**	12.1 (2.6) **b**	0.51 (0.18) **b**
$CaCO_3$-old	4	2.62 (1.0)	15.5 (6.5) **b**	62.2 (12.3) **a**	17.3 (11.3) **a**
$CaSO_4$-old	4	2.68 (1.1)	20.9 (5.4) **b**	36.5 (4.1) **ab**	3.56 (1.29) **b**
$CaCO_3$-new	8	3.26 (0.55)	40.7 (6.8) **ab**	32.9 (7.8) **ab**	2.04 (0.89) **b**
$CaSO_4$-new	8	2.01 (0.29)	48.6 (8.9) **a**	34.6 (8.2) **ab**	1.98 (0.83) **b**
mix	8	2.78 (0.66)	37.8 (7.6) **ab**	36.5 (5.5) **ab**	2.18 (0.53) **b**

Discussion

The influence of soil layers, organic A (or 0-5 cm layer) as compared with the mineral B (or 5-45 cm layers) on root-CEC agrees with the study of Dufey *et al.* (1991). The values of root-CEC in this study are lower than but in the same order of magnitude as those reported for ryegrass and clover (Dufey & Braun 1986) obtained by the original method. Presumably, this can be explained by the fact that these authors worked only with freshly collected young roots.

Root-CEC appeared higher in whitish (non-suberized, young) fine roots than in older brownish (suberized, 'older') fine roots, due to significantly higher absolute levels of K adsorbed on to the root-CEC in the young roots. A higher root-CEC in the younger roots is expected, since with root age root weight increases much more than root-CEC, thus lowering root-CEC g^{-1} of the fine root (Chamuah & Dey 1982, Dufey *et al.* 1985). The relative amount of K, which accounted for 50 to 70 % of the root-CEC in the rootbox experiment for the young roots, decreased significantly with increasing root age. This effect appeared even stronger when compared with the field roots - older on average -, where K accounted for only about 10 % of

root-CEC. Mg, Ca and Al accounted for similar proportions in younger and older roots for all treatments analysed separately.

However, when analysed together, some treatment effects appear on the older, brownish root in the A-layer. The lower proportion of Mg and Al and higher proportion of Ca on the root exchange sites for the $CaCO_3$ and $CaSO_4$ treatments as compared to the control (Fig. 2), compare well with the observations of the field trial (Tab. 2). Together they suggest that with increasing root age – the roots from the field are according to visual characteristics closer to the brownish fraction of the rhizotron experiment – relatively more Ca and less Mg and Al are adsorbed to the exchange sites after both Ca applications. This is in good agreement with the work of Dufey *et al.* (1991) and Ericsson *et al.* (1995).

Consequently, for roots of the same age (planted at the same moment in the rhizotrons), the Ca/Al ratio, and relative proportions of Ca and Al, are theoretically much more favourable for uptake of base cations in both Ca treatments as compared to the control, as higher concentrations of Ca at the root exchange sites can stimulate Ca uptake (Ericsson *et al.* 1995, Keltjens 1995). As this difference between treatments does not occur in the very young roots, but only in the older roots, this means an increase of Al against a decrease of Ca with age for the control, but not in the Ca applications. The treatments react, thus, against 'age' and the roots of both Ca applications are in a way physiologically younger, i.e. contribute differently to uptake. Such an accumulation of Al in fine roots with increasing age leads to a decreased uptake effectiveness and decreased fine root longevity (Murach & Schünemann 1985) and sometimes induces the formation of lateral roots to increase the number of sites for cation uptake (Marschner 1991). Complementary data (Bakker *et al.* 1998) show that the total Ca content in the seedlings is indeed significantly higher in the $CaCO_3$ treatment as compared to the control (and also $CaSO_4$), whereas fine root mortality is lower in the $CaCO_3$ treatment as compared to the control (not assessed for $CaSO_4$).

The practical implication of this is, that the uptake environment for the fine roots after a liming or gypsum treatment, can be characterized by a higher Ca/Al molar ratio and a higher proportion of Ca to the root-CEC (Fig 2), suggesting that root function can be maintained longer in the treated areas than in the control. This build-up of Al on the exchange sites of the roots in the acidic control profile studied could be one of the explanations for the higher fine root mortality and turnover (and thus allocation to fine roots) in the control relative to the limed treatments, in order to maintain a sufficient level of uptake and tree growth as observed in the field trial at La Croix-Scaille (Bakker *in press*).

Conclusion

The root-CEC is higher in young whitish roots than in older brownish roots, mainly as a result of higher concentrations of K. Liming or gypsum applications increased relative occupation by Ca of root-CEC and Ca/Al molar ratio, while decreasing relative occupation of Al (all sign. at $P< 0.05$), and this was true for older brownish roots and in the field, but not for young whitish roots. This indicates that the potential of fine roots for uptake of base cations, decreasing with root age in the control, could be maintained or increased after liming or gypsum treatments. Therefore, it was concluded, that liming and gypsum treatments successfully improved root-CEC composition and perhaps extend the functional lifetime of these roots.

Acknowledgments
We would like to thank Rozenn Kerisit and Kris Verbist for their assistance in performing the greenhouse and laboratory experiments. This research was supported by grants of INRA Paris and the Dutch Ministry of Agriculture, Nature Management and Fisheries, Directorate of Science and Knowledge Dissemination.

References

Bakker, M.R. *in press*. The effect of lime and gypsum applications on a sessile oak (*Quercus petraea* (M.) Liebl.) stand at La Croix-Scaille (French Ardennes) II. Fine root dynamics. Accepted for *Plant and Soil*.

Bakker, M.R., Kerisit, R., Verbist, K. & Nys, C. 1998. Effects of liming on rhizosphere chemistry and growth of fine roots and of shoots of sessile oak (*Quercus petraea*). submitted to *Plant and Soil*.

Chamuah, G.S. & Dey, S.K. 1982. Cation exchange of clonal tea plants and its implications for fertilizer reponses. *J. Sci. Food. Agric.* **33**, 309-317.

Dufey, J.E., Armory, D.E. & Braun, R. 1985. Propriétés électriques et sélectivité d'échange ionique des racines. *Pédologie* **35**, 231-249.

Dufey, J.E. & Braun, R. 1986. Cation exchange capacity of roots: titration, sum of exchangeable cations, copper adsorption. *J. Plant Nutr.* **9**, 1147-1155.

Dufey, J.E., Drimmer, D., Lambert, I. & Dupont, P. 1991. Composition of root exchange sites in acidic soil solutions. In: *Plant roots and their environment*. (eds B.L. McMichael & H. Persson), Elseviers Science Publishers, pp. 31-38.

Ericsson, T., Göransson, A., Van Oene H. & Gobran, G. 1995. Interactions between aluminium, calcium and magnesium - Impacts on nutrition and growth of forest trees. *Ecol. Bull.* **44**, 191-196.

Hüttl, R.F. & Zöttl, H.W. 1993. Liming as a mitigation tool in Germany's declining forests - reviewing results from former and recent trials. *For Ecol. Manage*. **61**, 325-338.

Keltjens, W.G. 1990. Effects of aluminium on growth and nutrient status of Douglas-fir seedlings grown in culture solution. *Tree Physiol.* **6**, 165-175.

Keltjens, W.G. 1995. Magnesium uptake by Al-stressed maize plants with special emphasis on cation interactions at root exchange sites. *Plant Soil* **171**, 141-146.

Marschner, H. 1991. Mechanisms of adaptation of plants to acid soils. *Plant Soil* **134**, 1-20.

Murach, D. & Schünemann, E. 1985. Reaktion der Feinwurzeln von Fichten auf Kalkungsmassnahmen. *Allgemeine Forstzeitschrift* **40**, 1151-1154.

Rengel, Z. 1992. Role of calcium in aluminium toxicity. *New Phytol.* **121**, 499-513.

Unistat Ltd, 1995. Unistat version 4 for Windows.

ANNEXE B : FICHES DE DONNEES

Annexe 3.1 Inventaire des peuplements

La Croix-Scaille (site 1 et 2): Composition par espèce d'arbre (rélevé de mars 1997) avec nombre d'arbres par ha (n ha^{-1}), proportion de la biomasse totale (%),diamètre à 1m30 dbh en cm), surface tarière (G in m^2 ha^{-1}), hauteur moyenne de n arbres dominantes mesurés en mai 1996 (H (n) en m), biomasse totale (W en t ha^{-1}) et la différence de la surface tarière entre juin 1995 et mars 1997 (delta G en m^2 ha^{-1})

	Témoin	$CaCO_3$ ancien	$CaSO_4$ ancien	$CaCO_3$ nouveau	$CaSO_4$ nouveau	Mélange 80/20
chêne						
n ha^{-1}	556	489	1022	1233	667	1100
%	55.9	28.6	74.2	58.2	47.3	61.2
dbh	16.8	15	15.6	13.9	16	14.6
H (n)	15.2 (5)	16.6 (6)	16.5 (8)	15.6 (7)	15.7 (7)	15.3 (8)
W	57.2	46.7	126	104.5	82.4	108
G	11.5	9.3	24.7	20.7	15.8	20.9
DG95-97	-0.05	-0.43	1.02	0.56	1.87	0.08
bouleau						
n ha^{-1}	911	778	533	1200	2000	900
%	42	28.7	22.3	38.8	48.2	33.8
dbh	12.2	12.8	13.2	16.4	12.4	13
H (n)	16.9 (6)	17.7 (6)	16.7 (6)	15.9 (6)	16.5 (6)	15.9 (6)
W	43	46.9	37.9	69.6	83.9	59.7
G	10.5	11.2	8.6	16.8	20.2	13.8
DG95-97	-0.11	0.14	-0.57	0.36	0.03	0.75
sorbier						
n ha^{-1}	44	244	178	467	500	767
%	2.1	3	3.4	1.9	4.5	5
dbh	11.9	8.4	9.5	5.3	6.7	6.3
W	2.1	4.9	5.8	3.3	7.9	8.8
G	0.5	1.4	1.6	1.1	2.3	2.7
DG95-97	0.28	-0.22	-0.71	-0.16	0.18	-0.12
hêtre						
n ha^{-1}	0	133	22	233	0	0
%		39.7	0.02	1.1		
dbh		18.3	3.4	4.9		
W		65	0.04	2		
G		6.8	0.02	0.59		
DG95-97		0.35	-0.04	0.02		

Fontainebleau (site 3) : Rélevé de janvier 1996 avec nombre de chênes par ha (n ha^{-1}), diamètre à 1m30 dbh en cm), surface terrière moyenne (g en cm^2), surface terrière totale (G en m^2 ha^{-1}) et hauteur moyenne de (n) arbres dominantes (nd = non déterminé et les lettres indiquent des différences significatives à $p<0.05$).

	Témoin	CaO	NPKCa
n ha^{-1}	3350	4750	5100
dbh	15.4 **b**	17 **ab**	18.6 **a**
g cm^2	21.4 **b**	27.0 **ab**	32.1 **a**
G m^2 ha^{-1}	7.15 **nd**	12.8 **nd**	16.4 **nd**
H (n)	6.1 (6) **b**	8.4 (6) **a**	9.1 (6) **a**

Bercé (sites 4, 5 et 6) : Rélevé de janvier 1996 avec nombre de chênes mesurés par ha (n ha^{-1}), circonférence à 1m30 (en mm) pour le début de l'expérience et pour 1996, et l'accroissement de la circonférence (en mm) entre ces deux années (les lettres indiquent des différences significatives à $p<0.05$).

	Témoin	NCa
Gaie Mariée (site 4)		
n ha^{-1}	134	134
c130_'69	431	445
c130_'96	771	826
accr. '69-'96	340 **b**	381 **a**
Trembles (site 5)		
n ha^{-1}	140	150
c130_'70	533	537
c130_'96	868	907
accr. '70-'96	335 **b**	370 **a**
Rond du May (site 6)		
n ha^{-1}	45	50
c130_'68	300	302
c130_'96	673	758
accr. '68-'96	373 **b**	456 **a**

Bertranges (site 7) : Rélevé de juin 1995 avec nombre de chênes par ha (n ha^{-1}), la surface terrière moyenne (g en cm^2), et la circonférence à 1m30 (en mm).

	Témoin	CaO
n ha^{-1}	5600	6050
g (cm^2)	34.8	29.8
c_130 (mm)	188	176

Tronçais (site 8) : Rélevé de 1993 avec nombre de chênes mésurés (n) et l'accroissement de la circonférence entre 1984 et 1993 (en mm); les lettres indiquent une différence significative à $p<0.05$.

	Témoin	NPKCa
n	110	110
accr '84_'93	109 **b**	123 **a**

St. Anthonis (sites 9 et 10) : Rélevés du printemps 1988, de l'automne 1991 et l'accroissement entre 1988 et 1991 du diamètre (D en cm) et de l'hauteur (H en m) pour le chêne pédonculé (Quercus robur), après Van den Burg (1994).

	Témoin	Ca
St. Anthonis 35c (site 9)[a]		
D (1988)	21.6	22.3
D (1991)	23.2	24.1
accr. 88-91	1.67	1.81
H (1988)	14.9	15.1
H (1991)	15.8	16.2
accr. 88-91	0.95	1.05
St. Anthonis 46a (site 10)[b]		
D (1988)	3.91	3.74
D (1991)	5.45	5.35
accr. 88-91	1.55	1.60
H (1988)	3.42	3.32
H (1991)	4.26	4.01
accr. 88-91	0.84	0.68

a : basé sur 10 arbres ; b : basé sur 25 arbres ; effet de gel a affecté la croissance en hauteur considérablement sur ce site (pas de statistiques effectuées).

Annexe 3.2 Pré-étude CEC racinaire

Dufey et Braun (1986) ont recommandé la méthode de désorption $CuSO_4$ - HCl, après avoir comparé 3 méthodes différentes. Cette méthode a trois étapes. Dans la première étape, une solution de 10^{-2} *N* $CuSO_4$ est utilisée pour déplacer les cations adsorbés sur la CEC racinaire (CEC_{rac}) de l'échantillon de racine fine étudié. Ensuite, un rinçage avec une solution de 10^{-4} *N* $CuSO_4$ est effectué pour diminuer la quantité d'ions de Cu d'une façon à ce que cette quantité dans le volume interstitiel des racines devienne négligeable par rapport à la quantité d'ions de Cu adsorbés sur la CEC_{rac}. Puis en troisième étape, une solution de 10^{-1} *N* HCl est utilisée pour déplacer les ions de Cu adsorbés sur la CECrac pour obtenir des valeurs singles de la CEC_{rac} pour la capacité totale. Le pH des effluents était déterminé par des électrodes standards.

Dans le cadre de ce travail, trois expériences de test (pré-étude) ont été effectuées :
Expérience 1 était une méthode avec déplacement et rinçage manuel ;
Expérience 2 était un test pour automatiser et optimiser les doses ; et
Expérience 3 était un essai pour déplacer les ions avec une méthode d'agitation.

Expérience 1 : méthode manuelle

Des racines du site 1 de la Croix-Scaille dataient en juin et septembre 1994. Les racines étaient prélevées du sol séché à l'air. Les échantillons de juin étaient nettoyées à sec avec des pincettes et des pinceaux. Ceux de septembre étaient nettoyées à l'eau du robinet. Les racines nettoyées étaient stockées dans une chambre froide (- 7°C) jusqu'à l'expérience (cf stockage de Dufey et Braun 1986). Juste avant les extractions, les racines étaient reséchées à 30°C. Ensuite les racines étaient coupées en petits morceaux d'environ 5 mm de longueur et pesées. Les échantillons étaient placés dans des petites bout s de pipettes en plastique, fermées en bas par des petits bouts de coton verre. Au-dessus de l'échantillon des petits morceaux de membrane de coton étaient placés, afin d'éviter des pertes des particules racinaires. L'ensemble des racines et pipette étaient pesé (poids sec). L'extraction se faisait en trois étapes. D'abord une quantité d'environ 100 ml de 10^{-2} *N* $CuSO_4$ était versée petit à petit (manuellement) sur chaque échantillon. Le temps de contact était de l'ordre de 5 à 10 minutes. Pour la deuxième étape, les échantillons étaient rincés avec 50 ml de 10^{-4} $CuSO_4$ (manuellement). Le poids de l'ensemble (racines + pipettes) était de nouveau déterminé (poids humide) et la différence était la quantité de liquide dans le volume interstitiel des racines dans une concentration de 10^{-4} *N* $CuSO_4$. En troisième étape une quantité de 250 ml (sur quelques échantillons 500 ml pour tester) de 10^{-1} *N* HCl était versée (manuellement). Les effluents des étapes 1 et 3 étaient analysés à la Torche à plasma (ICP) et corrigés pour la quantité de Cu dans le volume interstitiel des racines.

Les résultats sont présentés dans le Tableau 1. Comme on peut voir, il y a une grande différence entre les racines juin et de septembre. Ceci était vrai pour les valeurs singles (après étape 3 ; tableau 1) mais aussi pour les valeurs des cations analysés individuellement (Ca, Mg, Al, K). Pour ces données de cations individuels, la variation était très importante. Il en était conclu qu'il y avait quelques points de considération / amélioration / standardisation possibles :
1) la façon de rincer les racines (de préférence à sec)
2) le temps de contact (à standardiser par méthode automatique)
3) fuites de l'intérieur des racines ? (de préférence garder des bouts de racines plus grands)
4) nécessité des données de pH des effluents pour interpréter les valeurs CEC_{rac} totales
5) hétérogénéité des échantillons (prendre plutôt des racines du même âge).

Table 1 Comparaison des valeurs singles de CEC_{rac} sur des racines fines de *Quercus petraea* à La Croix-Scaille (site 1), nettoyées à sec (juin 1994) ou avec de l'eau du robinet (sept. 1994).

Profondeur	CEC_{rac} en $mmol_c . 100\ g^{-1}$ de racine		
cm	Témoin	$CaCO_3$	$CaSO_4$
	juin 1994		
0-5	13	32	23
5-15	11	12	13
15-30	12	10	12
30-45	8	10	14
	septembre 1994		
0-5	17	16	15
5-15	11	15	12
15-30	17	8	12
30-45	22	14	19

Expérience 2: méthode automatique d'optimisation

Avec l'expérience de la première étude, un dispositif automatique a été developpé. Les racines étaient découpées en bouts plus grands pour éviter des fuits potentielles au maximum. Le calibrage (optimisation des doses d'extraction) se faisait sur toutes les 3 étapes de l'analyse. Un conteneur à 25 places a été utilisé pour faire cette expérience. Douze échantillons provenaient d'un traitement témoin et 12 d'un traitement calcique (échantillons provenant de St. Anthonis, sites 9 et 10). La dernière place était un blanc total. Le poids des échantillons était standardisé à 0.2 - 0.25 g). Les traitements expérimentaux pour les extractions de CEC_{rac} étaient les suivants :

- test de quantité de 10^{-2} *N* $CuSO_4$ jusqu'à 250 ml
- test de rinçage avec des quantités de 50, 100 et 150 ml de 10^{-4} *N* $CuSO_4$
- test de désorption avec des quantités jusqu'à 500 ml de 10^{-1} *N* HCl.

Les résultats pour les étapes 1 et 3 sont présentés dans la figure 1. La figure montre qu'après environ 140 ml de 10^{-2} *N* $CuSO_4$ la désorption est déjà quasi-totale. Puis, en ce qui concerne la désorption avec 10^{-1} *N* HCl, celle-là est atteinte après 200 ml. Après les quantités restantes ne représentaient que 5 à 10 % du total. Pour l'étape 2, le rinçage avec 50, 100 ou 150 ml, les quantités supérieures à 50 ml n'ont pas amélioré le résultat. En conclusion de l'expérience 2, des quantités de 200 ml 10^{-2} *N* $CuSO_4$, 50 ml 10^{-4} *N* $CuSO_4$ et 200 ml de 10^{-1} *N* HCl sont suffisantes pour obtenir des résultats fiables de la CEC_{rac}.

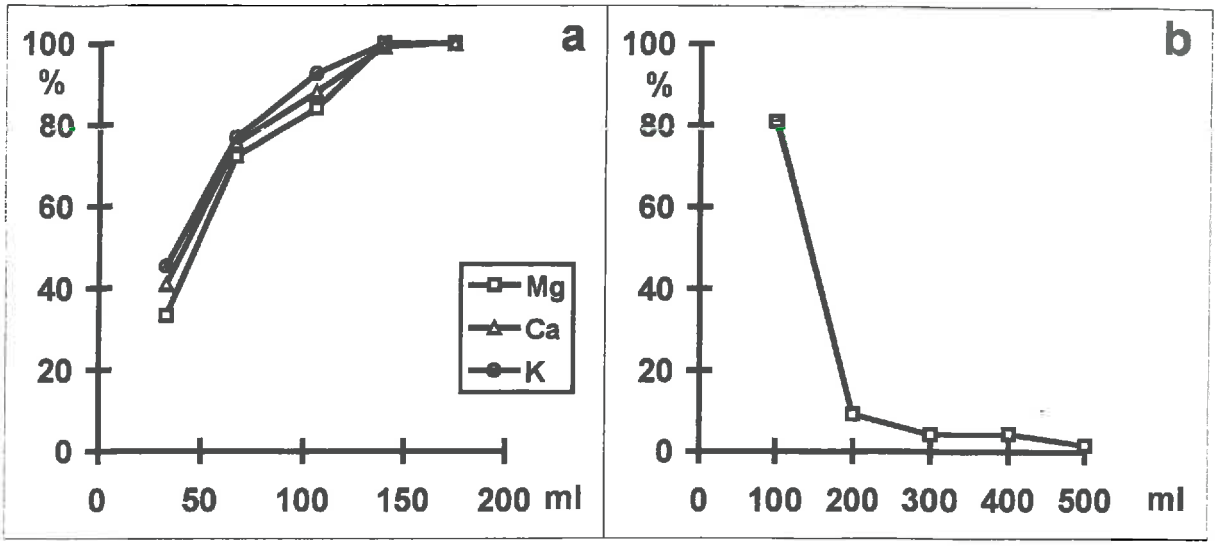

Figure 1 (a) L'influence du volume de desorption de 10^{-2} N $CuSO_4$ sur la quantité de cations déplacés (exemple de Mg, Ca et K) ; et (b) désorption en pourcentage de Cu de la CEC_{rac} en fonction du volume de désorbant HCl (moyenne de 8 échantillons)

Expérience 3 : méthode d'agitation

Des échantillons de St. Anthonis (sites 9 et 10) des témoins étaient mélangés avec 100 ml de 10^{-2} *N* $CuSO_4$, puis mis en agitation avec cette solution. Le temps d'agitation variait de 2 à 60 minutes. A chaque fois 4 échantillons étaient prélevés et analysés à la torche à plasma (ICP) pour de différents éléments. Les durées d'agitation étaient de 2, 5, 10, 20 et 60 minutes. Ceci a montré que les quantités déplacées après un rinçage prolongé, sont quand même sensiblement plus élevées, bien qu'une variation importante existe. Les valeurs de Mg étaient comparables à celles de l'expérience 2, celles de Mn et K plus faibles, mais celles de Ca et Na (surtout de Ca) beaucoup plus élevées après un rinçage prolongé. Il a été conclu que cette méthode donne des résultats trop variables et peu fiables.

Annexe 4.1 Fiches de données pour le sol du terrain

La Croix-Scaille (site 1): Juin 1994 (4 répétitions) ; statistiques par horizon

traitement	couche cm	Mn $cmol_c\ kg^{-1}$	Mg	Al	Ca	Na	K	Al^{3+}	H^+	pH-H_2O	pH-KCl	Ca/Al^{3+}
Témoin	0-5	0.03	0.17	8.26**a**	0.45**b**	0.16	0.25	5.39**a**	1.18	3.99**b**	3.25**b**	0.13**b**
$CaCO_3$-ancien	0-5	0.03	0.22	5.31**b**	5.05**a**	0.17	0.23	2.45**b**	0.72	4.49**a**	3.44**a**	3.09**a**
$CaSO_4$-ancien	0-5	0.05	0.17	6.23**ab**	1.45**b**	0.15	0.25	4.59**a**	0.96	4.09**b**	3.19**b**	0.47**b**
Témoin	5-15	0.02	0.07	6.93	0.15**b**	0.14	0.17**a**	4.97	0.54	4.19	3.48	0.05**b**
$CaCO_3$-ancien	5-15	0.01	0.07	6.18	0.94**a**	0.13	0.11**b**	4.11	0.47	4.47	3.52	0.34**a**
$CaSO_4$-ancien	5-15	0.02	0.08	6.30	0.55**ab**	0.12	0.18**a**	4.66	0.48	4.22	3.38	0.18**ab**
Témoin	15-30	0.01	0.04	3.77	0.09**b**	0.19	0.11	2.80	0.00	4.48	4.03	0.05**b**
$CaCO_3$-ancien	15-30	0.00	0.03	4.05	0.19**a**	0.11	0.09	3.35	0.13	4.46	3.86	0.09**a**
$CaSO_4$-ancien	15-30	0.01	0.05	4.10	0.18**ab**	0.15	0.11	3.62	0.07	4.48	3.85	0.07**a**
Témoin	30-45	0.00	0.03	2.76	0.07**c**	0.12	0.09	2.12	0.00	4.44	4.22	0.05**c**
$CaCO_3$-ancien	30-45	0.00	0.03	2.73	0.13**a**	0.12	0.07	1.86	0.00	4.53	4.19	0.10**a**
$CaSO_4$-ancien	30-45	0.00	0.03	2.65	0.09**b**	0.11	0.09	2.07	0.00	4.44	4.19	0.07**b**

les lettres indiquent des différences entre traitements à $p<0.05$ pour chaque horizon

La Croix-Scaille (Site 1): Septembre 1994 (2 répétitions) ; pas de statistiques

traitement	couche cm	Mn $cmol_c\ kg^{-1}$	Mg	Al	Ca	Na	K	Al^{3+}	H^+	pH-H_2O	pH-KCl	Ca/Al^{3+}
Témoin	0-5	0.07	0.27	7.19	0.58	0.11	0.26	5.36	1.50	3.94	3.19	0.16
	5-15	0.04	0.11	6.79	0.15	0.08	0.16	5.01	0.74	4.10	3.44	0.04
	15-30	0.02	0.06	4.16	0.11	0.08	0.13	3.30	0.20	4.24	3.87	0.05
	30-45	0.01	0.06	3.02	0.10	0.06	0.12	2.29	0.11	4.33	4.12	0.07
$CaCO_3$-ancien	0-5	0.10	0.55	4.20	6.48	0.15	0.32	2.70	1.49	4.02	3.25	3.60
	5-15	0.01	0.19	7.35	1.21	0.08	0.18	5.08	0.91	4.14	3.34	0.36
	15-30	0.01	0.07	4.33	0.21	0.07	0.13	3.29	0.24	4.31	3.90	0.10
	30-45	0.00	0.05	2.78	0.12	0.06	0.12	2.23	0.05	4.41	4.13	0.08
$CaSO_4$-ancien	0-5	0.09	0.34	5.75	2.61	0.11	0.28	4.22	1.55	3.86	3.06	0.93
	5-15	0.04	0.12	6.67	0.73	0.10	0.17	5.07	0.70	4.05	3.44	0.22
	15-30	0.03	0.09	4.44	0.30	0.06	0.11	3.35	0.13	4.34	3.96	0.13
	30-45	0.01	0.05	2.96	0.12	0.06	0.10	2.28	0.10	4.32	4.15	0.08

La Croix-Scaille (site 1): Mars 1995 (2 répétitions) ; pas de statistiques

traitement	couche cm	Mn $cmol_c\ kg^{-1}$	Mg	Al	Ca	Na	K	Al^{3+}	H^+	pH-H_2O	pH-KCl	Ca/Al^{3+}
Témoin	0-5	0.20	0.80	9.07	1.70	0.17	0.72	6.67	2.81	3.57	3.04	0.38
	5-15	0.12	0.15	5.90	0.17	0.08	0.22	4.99	0.86	3.90	3.56	0.05
	15-30	0.06	0.09	3.00	0.20	0.05	0.11	2.79	0.05	4.31	4.14	0.11
	30-45	0.03	0.09	2.82	0.17	0.06	0.12	2.50	0.00	4.40	4.26	0.10
$CaCO_3$-ancien	0-5	0.22	0.87	2.37	8.73	0.23	0.68	1.93	1.42	3.88	3.24	6.78
	5-15	0.08	0.15	6.29	0.86	0.17	0.18	4.96	1.06	3.89	3.50	0.26
	15-30	0.05	0.08	3.78	0.28	0.13	0.10	3.19	0.14	4.28	4.05	0.13
	30-45	0.03	0.06	2.94	0.22	0.11	0.08	2.52	0.05	4.39	4.21	0.13
$CaSO_4$-ancien	0-5	0.24	0.51	4.99	3.18	0.12	0.51	3.65	1.75	3.78	3.22	1.31
	5-15	0.21	0.15	5.78	0.64	0.07	0.22	4.54	0.76	4.05	3.68	0.21
	15-30	0.06	0.07	2.71	0.17	0.04	0.12	2.41	0.00	4.34	4.06	0.11
	30-45	0.05	0.11	2.44	0.36	0.05	0.11	2.09	0.00	4.35	4.27	0.26

La Croix-Scaille (site 1): Septembre 1995 (2 répétitions) ; pas de statistiques

traitement	couche cm	Mn $cmol_c\ kg^{-1}$	Mg	Al	Ca	Na	K	Al^{3+}	H^+	pH-H_2O	pH-KCl	Ca/Al^{3+}
Témoin	0-5	0.07	0.28	7.40	0.61	0.04	0.15	5.43	1.60	3.77	3.13	0.17
	5-15	0.06	0.09	6.56	0.12	0.03	0.16	5.42	0.73	4.06	3.57	0.03
	15-30	0.06	0.04	3.96	0.10	0.03	0.09	3.37	0.18	4.34	3.98	0.04
	30-45	0.04	0.03	3.61	0.08	0.02	0.11	2.91	0.12	4.39	4.11	0.04
$CaCO_3$-ancien	0-5	0.26	0.86	0.57	15.69	0.10	0.36	0.48	0.21	4.78	3.93	49.03
	5-15	0.04	0.16	5.80	2.38	0.05	0.19	4.95	0.65	4.36	3.52	0.72
	15-30	0.01	0.04	4.16	0.18	0.03	0.10	3.57	0.15	4.48	3.97	0.08
	30-45	0.01	0.03	3.09	0.11	0.02	0.08	2.67	0.13	4.47	4.12	0.06
$CaSO_4$-ancien	0-5	0.16	0.45	4.09	3.45	0.07	0.46	3.17	0.92	3.90	3.04	1.63
	5-15	0.02	0.16	6.01	0.91	0.06	0.19	5.04	1.50	3.80	3.07	0.27
	15-30	0.02	0.03	4.14	0.27	0.02	0.10	3.42	0.21	4.30	3.92	0.12
	30-45	0.01	0.02	3.23	0.14	0.03	0.09	2.74	0.14	4.34	4.12	0.08

La Croix-Scaille (site 2): Juin 1994 (4 répétions) ; statistiques par horizon

traitement	couche cm	Mn	Mg	Al	Ca	Na	K	Al^{3+}	H^+	pH-H_2O	pH-KCl	Ca/Al^{3+}
		$cmol_c\ kg^{-1}$										
Témoin	0-5	0.03	0.17	8.26	0.45	0.16	0.25	5.39	1.18	3.99**a**	3.25	0.13
Nouveau bloc	0-5	0.03	0.27	10.12	0.54	0.36	0.28	6.66	1.20	3.78**b**	3.18	0.12
Témoin	5-15	0.02	0.07	6.93	0.15	0.14	0.17	4.97	0.54	4.19	3.48	0.05
Nouveau bloc	5-15	0.01	0.09	8.03	0.17	0.11	0.17	6.63	0.41	3.94	3.44	0.04
Témoin	15-30	0.01	0.04	3.77**b**	0.09	0.19	0.11	2.80	0.00	4.48	4.03	0.05
Nouveau bloc	15-30	0.00	0.04	5.10**a**	0.09	0.13	0.11	3.89	0.12	4.36	3.74	0.03
Témoin	30-45	0.00	0.03	2.76**b**	0.07	0.12	0.09	2.12	0.00	4.44	4.22	0.05
Nouveau bloc	30-45	0.00	0.03	3.93**a**	0.06	0.10	0.09	2.62	0.00	4.45	3.96	0.03

les lettres indiquent des différences entre traitements à $p<0.05$ pour chaque horizon

La Croix-Scaille (site 2): mars 1995 (2 répétitions) ; pas de statistiques

traitement	couche cm	Mn	Mg	Al	Ca	Na	K	Al^{3+}	H^+	pH-H_2O	pH-KCl	Ca/Al^{3+}
		$cmol_c\ kg^{-1}$										
Témoin	0-5	0.20	0.80	9.07	1.70	0.17	0.72	6.67	2.81	3.57	3.04	0.38
	5-15	0.12	0.15	5.90	0.17	0.08	0.22	4.99	0.86	3.90	3.56	0.05
	15-30	0.06	0.09	3.00	0.20	0.05	0.11	2.79	0.05	4.31	4.14	0.11
	30-45	0.03	0.09	2.82	0.17	0.06	0.12	2.50	0.00	4.40	4.26	0.10
$CaCO_3$-nouveau	0-5	0.10	0.93	4.50	8.71	0.17	0.85	3.46	1.56	3.89	3.27	3.78
	5-15	0.08	0.26	7.65	0.39	0.08	0.25	5.93	1.08	3.80	3.38	0.10
	15-30	0.02	0.08	3.95	0.15	0.05	0.12	3.45	0.09	4.34	4.05	0.07
	30-45	0.01	0.14	3.11	0.21	0.04	0.10	2.82	0.07	4.41	4.17	0.11
$CaSO_4$-nouveau	0-5	0.10	0.80	5.70	5.44	0.19	1.26	4.36	2.56	3.69	3.01	1.87
	5-15	0.05	0.13	5.84	0.60	0.07	0.19	5.37	1.10	3.78	3.33	0.17
	15-30	0.03	0.06	3.93	0.17	0.04	0.19	3.23	0.19	4.20	3.90	0.08
	30-45	0.02	0.04	2.42	0.12	0.03	0.06	1.74	0.17	4.31	4.30	0.10
Mélange 80/20	0-5	0.03	0.31	9.42	2.72	0.13	0.28	6.49	1.50	3.93	3.40	0.63
	5-15	0.01	0.16	7.23	0.55	0.07	0.18	5.81	0.97	3.85	3.38	0.14
	15-30	0.01	0.06	4.59	0.28	0.04	0.06	3.84	0.41	4.15	3.70	0.11
	30-45	0.03	0.05	4.94	0.25	0.04	0.13	4.03	0.10	4.32	4.02	0.09

La Croix-Scaille (site 2): Juin 1995 (2 répétitions) ; pas de statistiques

traitement	couche cm	Mn	Mg	Al	Ca	Na	K	Al^{3+}	H^+	pH-H_2O	pH-KCl	Ca/Al^{3+}
		$cmol_c\ kg^{-1}$										
Témoin	0-5	0.05	0.42	8.43	0.98	0.14	0.33	6.71	2.14	3.91	3.15	0.22
	5-15	0.07	0.13	5.04	0.16	0.07	0.21	4.14	0.73	4.26	3.62	0.06
	15-30	0.02	0.08	3.17	0.16	0.05	0.12	2.79	0.21	4.42	3.98	0.09
	30-45	0.02	0.07	2.88	0.12	0.06	0.09	2.49	0.11	4.44	4.12	0.07
$CaCO_3$-nouveau	0-5	0.20	0.86	5.37	12.56	0.19	0.91	4.01	1.61	4.21	3.40	4.70
	5-15	0.28	0.35	5.71	1.12	0.10	0.56	4.40	1.21	4.10	3.50	0.38
	15-30	0.02	0.06	4.32	0.23	0.08	0.09	3.70	0.39	4.32	3.84	0.09
	30-45	0.02	0.04	3.19	0.21	0.06	0.10	2.84	0.08	4.46	4.10	0.11
$CaSO_4$-nouveau	0-5	0.14	0.53	8.30	2.88	0.15	0.84	6.41	2.08	4.02	3.26	0.67
	5-15	0.11	0.12	6.23	0.38	0.07	0.21	5.23	0.76	4.26	3.64	0.11
	15-30	0.08	0.07	3.26	0.23	0.05	0.12	2.94	0.16	4.43	3.94	0.12
	30-45	0.01	0.10	3.45	0.20	0.04	0.07	3.13	0.08	4.45	4.11	0.10
Mélange 80/20	0-5	0.04	0.47	4.69	5.06	0.15	0.81	3.59	2.26	3.77	3.06	2.11
	5-15	0.01	0.09	4.32	0.48	0.08	0.11	3.77	0.89	3.92	3.12	0.19
	15-30	0.00	0.06	3.67	0.22	0.06	0.07	3.35	0.39	4.15	3.50	0.10
	30-45	0.00	0.05	2.85	0.21	0.07	0.06	2.71	0.06	4.41	4.06	0.12

La Croix-Scaille (site 2): Septembre 1995 (2 répétitions) ; pas de statistiques

traitement	couche cm	Mn	Mg	Al	Ca	Na	K	Al^{3+}	H^+	pH-H_2O	pH-KCl	Ca/Al^{3+}
		$cmol_c\ kg^{-1}$										
Témoin	0-5	0.07	0.28	7.40	0.61	0.04	0.15	5.43	1.60	3.77	3.13	0.17
	5-15	0.06	0.09	6.56	0.12	0.03	0.16	5.42	0.73	4.06	3.57	0.03
	15-30	0.06	0.04	3.96	0.10	0.03	0.09	3.37	0.18	4.34	3.98	0.04
	30-45	0.04	0.03	3.61	0.08	0.02	0.11	2.91	0.12	4.39	4.11	0.04
$CaCO_3$-nouveau	0-5	0.08	0.45	10.19	2.74	0.09	0.55	8.67	1.89	3.80	3.23	0.47
	5-15	0.03	0.08	7.49	0.21	0.03	0.17	6.46	0.58	4.02	3.57	0.05
	15-30	0.02	0.03	3.54	0.06	0.02	0.08	3.16	0.14	4.31	3.99	0.03
	30-45	0.01	0.01	2.78	0.03	0.02	0.06	2.32	0.14	4.40	4.19	0.02
$CaSO_4$-nouveau	0-5	0.06	0.47	7.19	4.51	0.10	0.67	5.51	2.12	3.77	3.18	1.23
	5-15	0.07	0.25	7.23	1.73	0.06	0.34	5.70	1.40	3.85	3.28	0.46
	15-30	0.03	0.05	5.46	0.22	0.03	0.12	4.72	0.39	4.16	3.69	0.07
	30-45	0.01	0.04	3.25	0.20	0.02	0.08	2.66	0.13	4.36	4.07	0.11
Mélange 80/20	0-5	0.06	0.25	5.31	3.23	0.05	0.37	4.09	1.26	4.01	3.33	1.18
	5-15	0.06	0.11	6.53	0.68	0.03	0.21	5.34	0.87	4.05	3.40	0.19
	15-30	0.09	0.03	4.05	0.09	0.02	0.12	3.16	0.19	4.43	4.06	0.04
	30-45	0.13	0.02	2.93	0.08	0.02	0.09	2.27	0.12	4.40	4.18	0.05

La Croix-Scaille (site 2): mars 1996 (2 répétitions) ; pas de statistiques

traitement	couche cm	Mn	Mg	Al	Ca	Na	K	Al^{3+}	H^+	pH-H_2O	pH-KCl	Ca/Al^{3+}
		$cmol_c\ kg^{-1}$										
Témoin	0-5	0.10	0.52	5.62	1.35	0.09	0.32	4.86	1.98	4.27	3.07	0.42
	5-15	0.06	0.07	5.81	0.12	0.04	0.14	5.36	0.64	4.21	3.36	0.03
	15-30	0.03	0.03	3.77	0.03	0.02	0.11	3.42	0.24	4.27	3.75	0.01
	30-45	0.01	0.00	2.36	0.00	0.02	0.07	2.04	0.00	4.52	4.18	0.00
$CaCO_3$-nouveau	0-5	0.04	0.28	3.21	6.37	0.06	0.29	2.66	0.87	4.29	3.25	3.59
	5-15	0.04	0.05	7.34	0.31	0.04	0.13	6.19	0.92	4.07	3.28	0.08
	15-30	0.01	0.02	3.69	0.29	0.01	0.07	3.23	0.00	4.45	3.95	0.13
	30-45	0.01	0.00	2.91	0.17	0.01	0.05	2.50	0.00	4.63	4.19	0.10
$CaSO_4$-nouveau	0-5	0.13	0.55	7.72	4.17	0.11	0.35	5.59	2.10	4.16	3.03	1.12
	5-15	0.02	0.16	7.89	0.80	0.06	0.15	6.26	0.84	4.06	3.40	0.19
	15-30	0.01	0.06	4.04	0.21	0.05	0.09	3.58	0.00	4.45	3.86	0.09
	30-45	0.01	0.03	2.98	0.17	0.04	0.09	2.63	0.00	4.70	4.00	0.10
Mélange 80/20	0-5	0.08	0.32	5.72	2.61	0.08	0.24	4.16	0.63	4.42	3.34	0.94
	5-15	0.08	0.07	6.79	0.27	0.02	0.11	5.35	0.24	4.46	3.58	0.08
	15-30	0.03	0.05	3.87	0.23	0.00	0.07	3.33	0.00	4.59	3.98	0.10
	30-45	0.04	0.04	2.97	0.16	0.02	0.06	2.32	0.00	4.68	4.09	0.10

Fontainebleau (site 3): Octobre 1994 (2 répétitions) ; pas de statistiques

traitement	couche cm	Mn	Mg	Al	Ca	Na	K	Al^{3+}	H^+	pH-H_2O	pH-KCl	Ca/Al
		$cmol_c\ kg^{-1}$										
Témoin	0-5	0.12	0.54	0.04	6.79	0.08	0.13	0.00	0.00	6.36	5.42	255
	5-15	0.12	0.31	0.00	3.76	0.08	0.07	0.00	0.00	6.01	4.88	*
	15-25	0.05	0.20	0.12	3.50	0.06	0.04	0.00	0.00	5.98	4.72	43.8
	25-45	0.01	0.22	0.01	10.70	0.08	0.06	0.00	0.00	7.08	5.67	1605
	45-65	0.01	0.11	1.01	8.97	0.05	0.06	0.00	0.00	6.73	5.68	13.3
$CaCO_3$	0-5	0.10	0.36	0.21	3.65	0.04	0.10	0.00	0.06	5.70	5.28	26.1
	5-15	0.03	0.23	0.01	4.23	0.04	0.06	0.00	0.00	6.55	5.33	635
	15-25	0.02	0.18	0.04	3.12	0.01	0.04	0.00	0.00	6.02	5.03	117.0
	25-45	0.01	0.16	0.37	4.26	0.01	0.03	0.00	0.41	6.15	5.17	17.3
	45-65	0.02	0.42	0.06	6.18	0.06	0.08	0.00	0.00	6.15	4.71	155
NPKCa	0-5	0.05	0.51	0.15	8.04	0.06	0.13	0.00	0.00	6.25	5.47	80.4
	5-15	0.03	0.17	0.90	4.44	0.05	0.07	0.15	0.74	5.84	5.13	7.4
	15-25	0.02	0.17	0.70	5.03	0.07	0.05	0.00	0.64	6.47	5.43	10.8
	25-45	0.02	0.32	0.05	6.83	0.12	0.08	0.00	0.00	6.78	5.69	205
	45-65	0.01	0.16	0.00	20.60	0.11	0.07	0.00	0.00	7.63	6.95	*

Les Trembles (site 4): Mars 1995 (3 répétitions) ; pas de statistiques

traitement	couche cm	Mn	Mg	Al	Ca	Na	K	Al^{3+}	H^+	pH-H_2O	pH-KCl	Ca/Al^{3+}
		$cmol_c\ kg^{-1}$										
Témoin	0-5	0.25	0.71	2.58	0.90	0.11	0.41	1.25	1.92	3.73	3.05	1.08
	5-15	0.07	0.10	3.07	0.11	0.05	0.14	0.28	2.39	4.06	3.60	0.59
	15-30	0.05	0.08	2.78	0.07	0.04	0.11	0.27	2.22	4.36	3.93	0.39
	30-45	0.08	0.11	2.73	0.11	0.03	0.12	0.15	2.40	4.40	3.89	1.10
	45-60	0.07	0.52	3.67	0.09	0.10	0.13	0.13	3.18	4.58	3.80	1.04
NCa	0-5	0.30	0.50	2.61	1.29	0.06	0.26	0.95	2.03	3.97	3.30	2.04
	5-15	0.10	0.12	3.34	0.12	0.05	0.11	0.38	2.67	4.25	3.73	0.47
	15-30	0.11	0.10	3.18	0.09	0.03	0.10	0.17	2.78	4.43	3.86	0.79
	30-45	0.07	0.13	3.40	0.08	0.04	0.11	0.12	3.06	4.41	3.83	1.00
	45-60	0.04	0.43	3.95	0.09	0.06	0.13	0.20	3.26	4.47	3.77	0.68

Gaie Mariée (site 5): Mars 1995 (3 répétitions) ; pas de statistiques

traitement	couche cm	Mn	Mg	Al	Ca	Na	K	Al^{3+}	H^+	pH-H_2O	pH-KCl	Ca/Al^{3+}
		$cmol_c\ kg^{-1}$										
Témoin	0-5	0.53	0.75	1.92	1.33	0.10	0.32	0.93	1.49	3.92	3.20	2.15
	5-15	0.05	0.14	2.83	0.16	0.06	0.10	0.29	2.49	4.16	3.56	0.83
	15-30	0.03	0.16	3.12	0.13	0.08	0.08	0.16	2.95	4.35	3.69	1.22
	30-45	0.02	0.59	4.07	0.16	0.10	0.12	0.17	3.75	4.47	3.64	1.41
	45-60	0.04	1.50	3.15	1.39	0.13	0.16	0.08	3.07	4.76	3.64	26.06
NCa	0-5	0.30	0.38	2.49	0.56	0.07	0.18	0.61	2.00	4.06	3.37	1.38
	5-15	0.08	0.11	2.45	0.11	0.06	0.09	0.21	2.05	4.32	3.71	0.79
	15-30	0.07	0.11	2.40	0.13	0.08	0.08	0.10	2.19	4.42	3.85	1.95
	30-45	0.10	0.34	3.16	0.22	0.14	0.10	0.13	2.94	4.53	3.78	2.54
	45-60	0.07	1.44	4.02	0.74	0.11	0.20	0.12	3.79	4.73	3.72	9.25

Rond du May (site 6): Septembre 1995 (2 répétitions) ; pas de statistiques

traitement	couche	Mn	Mg	Al	Ca	Na	K	Al^{3+}	H^+	pH-H_2O	pH-KCl	Ca/Al^{3+}
	cm	$cmol_c\ kg^{-1}$										
Témoin	0-5	0.10	0.41	3.20	0.46	0.11	0.16	1.05	2.74	3.97	3.10	0.66
	5-15	0.00	0.11	3.27	0.08	0.07	0.10	0.26	3.02	4.25	3.65	0.46
	15-30	0.02	0.10	3.10	0.07	0.05	0.08	0.11	2.89	4.44	3.88	0.95
	30-45	0.02	0.11	2.96	0.09	0.05	0.08	0.13	2.73	4.44	3.85	1.04
	45-60	0.02	0.18	3.57	0.08	0.06	0.07	0.21	3.20	4.42	3.82	0.57
NCa	0-5	0.09	0.49	2.36	0.42	0.08	0.18	0.96	2.14	3.99	3.10	0.66
	5-15	0.01	0.11	2.80	0.08	0.09	0.09	0.22	2.49	4.23	3.64	0.55
	15-30	0.01	0.11	2.41	0.07	0.05	0.08	0.10	2.22	4.44	3.90	1.05
	30-45	0.03	0.22	2.76	0.07	0.05	0.06	0.10	2.53	4.48	3.87	1.05
	45-60	0.02	0.49	3.20	0.08	0.06	0.06	0.11	3.12	4.62	3.81	1.09

Bertranges (site 7): Juin 1995 (3 répétitions) ; pas de statistiques

traitement	couche	Mn	Mg	Al	Ca	Na	K	Al^{3+}	H^+	pH-H_2O	pH-KCl	Ca/Al^{3+}
	cm	$cmol_c\ kg^{-1}$										
Témoin	0-5	0.82	0.85	0.99	2.38	0.09	0.51	0.20	0.90	4.97	4.08	17.85
	5-15	0.44	0.39	2.16	0.86	0.09	0.26	0.24	1.98	4.88	4.00	5.38
	15-30	0.33	0.30	2.04	0.67	0.09	0.14	0.22	1.85	4.86	4.05	4.57
CaO	0-5	0.69	0.71	1.09	2.94	0.10	0.40	0.21	0.94	4.87	4.21	21.00
	5-15	0.51	0.35	1.29	1.30	0.07	0.18	0.15	1.16	4.88	4.07	13.00
	15-30	0.22	0.25	1.97	0.52	0.06	0.13	0.13	1.82	4.76	4.03	6.00

Tronçais (site 8): Septembre 1995 (2 répétitions) ; pas de statistiques

traitement	couche	Mn	Mg	Al	Ca	Na	K	Al^{3+}	H^+	pH-H_2O	pH-KCl	Ca/Al^{3+}
	cm	$cmol_c\ kg^{-1}$										
Témoin	0-5	0.09	0.17	1.34	0.29	0.05	0.12	0.11	1.30	4.84	3.95	3.95
	5-15	0.02	0.09	1.35	0.11	0.16	0.20	0.09	1.30	4.63	3.97	1.83
	15-30	0.03	0.14	1.38	0.14	0.33	0.39	0.08	1.29	4.71	3.98	2.63
	30-45	0.07	0.19	1.37	0.18	0.21	0.30	0.09	1.29	4.72	3.97	3.00
	45-60	0.06	0.53	3.03	0.35	0.06	0.08	0.10	2.65	4.81	3.81	5.25
NPKCa	0-5	0.17	0.42	0.79	1.05	0.07	0.21	0.11	0.83	4.60	3.91	14.32
	5-15	0.03	0.15	1.26	0.26	0.05	0.11	0.05	1.20	4.46	4.03	7.80
	15-30	0.05	0.11	1.32	0.13	0.04	0.07	0.09	1.24	4.52	4.09	2.17
	30-45	0.04	0.12	1.37	0.14	0.11	0.16	0.09	1.24	4.63	4.11	2.33
	45-60	0.07	0.14	1.86	0.17	0.05	0.11	0.08	1.70	4.54	4.05	3.19

St.Anthonis 35c (site 9): Octobre 1995 (2 répétitions) ; pas de statistiques

traitement	couche	Mn	Mg	Al	Ca	Na	K	Al^{3+}	H^+	pH-H_2O	pH-KCl	Ca/Al^{3+}
	cm	$cmol_c\ kg^{-1}$										
Témoin	0-5	0.03	0.17	1.19	0.77	0.05	0.07	0.68	1.09	4.07	3.08	1.70
	5-15	0.01	0.05	1.68	0.18	0.05	0.03	0.41	1.47	4.00	3.41	0.66
	15-30	0.01	0.04	1.69	0.13	0.05	0.03	0.26	1.51	4.12	3.71	0.75
	30-45	0.00	0.04	1.68	0.10	0.08	0.02	0.22	1.48	4.14	3.80	0.68
	45-60	0.00	0.03	1.61	0.09	0.05	0.02	0.13	1.41	4.27	3.94	1.04
Ca	0-5	0.10	0.47	0.87	3.33	0.11	0.05	0.35	0.82	4.11	3.47	14.27
	5-15	0.01	0.12	1.79	0.56	0.12	0.10	0.34	1.54	4.13	3.58	2.47
	15-30	0.01	0.12	1.51	0.59	0.09	0.06	0.17	1.30	4.40	3.94	5.21
	30-45	0.01	0.09	1.52	0.37	0.09	0.03	0.13	1.32	4.48	3.97	4.27
	45-60	0.01	0.06	1.23	0.26	0.09	0.04	0.10	1.10	4.68	4.12	3.90

St.Anthonis 46a (site 10): Octobre 1995 (3 répétitions) ; pas de statistiques

traitement	couche	Mn	Mg	Al	Ca	Na	K	Al^{3+}	H^+	pH-H_2O	pH-KCl	Ca/Al^{3+}
	cm	$cmol_c\ kg^{-1}$										
Témoin	0-5	0.01	0.19	1.67	0.98	0.06	0.11	2.25	1.25	3.74	2.59	0.65
	5-15	0.00	0.02	1.55	0.15	0.01	0.04	0.83	1.35	4.01	2.66	0.27
	15-30	0.00	0.01	2.83	0.15	0.01	0.04	1.04	2.46	3.93	3.08	0.22
	30-45	0.00	0.01	2.59	0.07	0.01	0.03	0.70	2.03	4.05	3.50	0.15
	45-60	0.00	0.00	1.18	0.02	0.00	0.03	0.16	1.05	4.37	3.94	0.19
Ca	0-5	0.02	0.58	1.26	3.58	0.08	0.13	1.02	1.06	4.13	3.18	5.26
	5-15	0.00	0.06	2.20	0.34	0.02	0.06	0.86	1.85	4.03	3.14	0.59
	15-30	0.00	0.04	2.62	0.21	0.01	0.04	0.71	2.04	4.04	3.34	0.44
	30-45	0.00	0.01	2.50	0.06	0.02	0.03	0.30	2.06	4.27	3.83	0.30
	45-60	0.00	0.00	1.28	0.03	0.00	0.03	0.10	1.09	4.59	4.14	0.45

Annexe 4.2 Fiches de données pour la solution du sol du terrain

La Croix-Scaille (site 1 et 2): Mars 1995 ; statistiques par horizon

traitement	profondeur	S	Mg	Ca	Al	K	NO_3^-	NH_4^+	pH-H_2O	Ca/Al
	cm	$mmol_c\ l^{-1}$								mole/mole
Témoin	3	0.09	0.06	0.12	0.07	0.06	0.20	0.03	4.68b	2.6
$CaCO_3$-ancien	3	0.18	0.10	0.34	0.07	0.05	0.10	0.02	5.58a	7.3
$CaSO_4$-ancien	3	0.18	0.07	0.20	0.03	0.06	0.03	0.02	4.67b	10
$CaCO_3$-nouveau	3	0.20	0.10	0.24	0.05	0.06	0.19	0.03	5.50a	7.2
$CaSO_4$-nouveau	3	0.15	0.04	0.17	0.06	0.03	0.06	0.05	5.10ab	4.3
Mélange 80/20	3	0.22	0.06	0.29	0.03	0.03	0.04	0.01	5.09ab	15
Témoin	10	0.15b	0.10	0.21	0.06a	0.04	0.17	0	5.29	5.3
$CaCO_3$-ancien	10	0.19b	0.09	0.20	0.04b	0.03	0.09	0	5.75	7.5
$CaSO_4$-ancien	10	0.15b	0.08	0.23	0.06ab	0.03	0.08	0	5.60	5.8
$CaCO_3$-nouveau	10	0.14b	0.05	0.12	0.11ab	0.04	0.19	0.01	5.18	1.6
$CaSO_4$-nouveau	10	0.41a	0.06	0.30	0.04ab	0.02	0.03	0.01	4.98	11
Mélange 80/20	10	0.14b	0.05	0.18	0.04ab	0.03	0.09	0.01	5.26	6.8
Témoin	20	0.16b	0.08	0.19	0.05	0.04	0.18	0.03	5.45ab	5.7
$CaCO_3$-ancien	20	0.14b	0.06	0.18	0.03	0.02	0.08	0	5.79a	9.0
$CaSO_4$-ancien	20	0.27b	0.07	0.30	0.03	0.03	0.10	0	5.52ab	15
$CaCO_3$-nouveau	20	0.17b	0.03	0.16	0.10	0.03	0.22	0.01	5.30ab	2.4
$CaSO_4$-nouveau	20	0.56a	0.07	0.42	0.12	0.04	0.16	0.03	4.79b	5.3
Mélange 80/20	20	0.29b	0.06	0.24	0.08	0.02	0.10	0.01	5.03b	4.5
Témoin	35	0.23	0.08	0.15	0.03	0.02	0.08	0b	5.32	7.5
$CaCO_3$-ancien	35	0.25	0.07	0.20	0.01	0.03	0.05	0b	5.76	30
$CaSO_4$-ancien	35	0.35	0.08	0.29	0.06	0.03	0.06	0b	5.38	7.3
$CaCO_3$-nouveau	35	0.26	0.05	0.18	0.06	0.02	0.15	0.01b	5.44	4.5
$CaSO_4$-nouveau	35	0.37	0.06	0.28	0.07	0.04	0.14	0.02a	5.03	6.0
Mélange 80/20	35	0.31	0.07	0.27	0.04	0.03	0.07	0.03a	4.87	10

les lettres indiquent des différences entre traitements à $p<0.05$ pour chaque horizon

La Croix-Scaille (site 2): Juin 1995 ; statistiques par horizon (sauf NO_3^- et NH_4^+)

traitement	profondeur	S	Mn	Mg	Ca	Al	Na	K	NO_3^-	NH_4^+	pH-H_2O	Ca/Al
	cm	$mmol_c\ l^{-1}$										mole/mole
Témoin	3	0.15b	0.01	0.06	0.09b	0.12	0.12	0.02	*	*	3.90	1.1
$CaCO_3$-nouveau	3	0.12ab	0.01	0.05	0.14b	0.10	0.11	0.03	*	*	4.19	2.1
$CaSO_4$-nouveau	3	0.27ab	0.01	0.03	0.21b	0.12	0.07	0.02	0.05	0	4.10	2.6
Mélange 80/20	3	0.34a	0.01	0.06	0.66a	0.09	0.08	0.03	0.41	0.01	4.09	11
Témoin	10	0.09	0.01	0.04	0.06b	0.12	0.08b	0.02	0.17	0	3.94	0.75b
$CaCO_3$-nouveau	10	0.07	0.01	0.04	0.07ab	0.18	0.14a	0.03	0.36	0	4.15	0.58ab
$CaSO_4$-nouveau	10	0.25	0.01	0.04	0.26a	0.09	0.11ab	0.02	0.34	0	3.95	4.3a
Mélange 80/20	10	0.24	0	0.05	0.28ab	0.14	0.08b	0.02	0.24	0	3.88	3.0ab
Témoin	20	0.08	0.01	0.06	0.05c	0.25	0.10	0.05	0.32	0.02	4.17a	0.30c
$CaCO_3$-nouveau	20	0.18	0.01	0.03	0.08bc	0.10	0.10	0.02	0.09	0	4.40a	1.2b
$CaSO_4$-nouveau	20	0.30	0	0.03	0.21a	0.13	0.11	0.02	0.15	0.01	4.24a	2.4a
Mélange 80/20	20	0.35	0	0.04	0.23abc	0.28	0.11	0.02	0.08	0.01	3.92b	1.2b
Témoin	35	0.10b	0.01	0.04	0.05b	0.21	0.10	0.02	0.26	0	4.31	0.36b
$CaCO_3$-nouveau	35	0.18ab	0.01	0.04	0.12ab	0.15	0.12	0.02	0.21	0	4.33	1.2ab
$CaSO_4$-nouveau	35	0.43a	0.02	0.03	0.24a	0.28	0.07	0.04	0.28	0	4.40	1.29ab
Mélange 80/20	35	0.28a	0	0.04	0.18a	0.17	0.10	0.03	0.14	0.03	4.10	1.6a

les lettres indiquent des différences entre traitements à $p<0.05$ pour chaque horizon

La Croix-Scaille (site 2): Mars 1996 ; pas de statistiques

traitement	profondeur	S	Mn	Mg	Ca	Al	Na	K	NO_3^-	NH_4^+	pH-H_2O	Ca/Al
	cm	$mmol_c\ l^{-1}$										mole/mole
Témoin	3	0.14	0.01	0.05	0.10	0.14	0.15	0.08	>0.23	0.07	4.31	1.1
	10	0.15	0.02	0.06	0.14	0.20	0.08	0.06	0.31	0.01	4.31	1.1
	20	0.16	0.01	0.06	0.07	0.16	0.10	0.06	>0.21	0.08	4.53	0.66
	35	0.17	0.01	0.04	0.05	0.15	0.09	*	0.09	0.01	4.73	0.50
$CaCO_3$-nouveau	3	0.19	0.01	*	*	*	*	*	*	*	*	*
	10	0.13	*	0.02	0.05	0.13	0.09	0.04	0.08	0.01	4.41	0.58
	20	0.16	0.01	0.03	0.09	0.14	0.09	0.01	0.05	0	4.72	0.96
	35	*	*	*	*	*	*	*	*	*	*	*
$CaSO_4$-nouveau	3	*	*	*	*	*	*	*	*	*	*	*
	10	*	*	*	*	*	*	*	*	*	*	*
	20	0.22	0.01	0.04	0.21	0.13	0.05	0.01	0.09	0.01	4.6	2.4
	35	*	*	*	*	*	*	*	*	*	*	*
Mélange 80/20	3	0.01	*	*	*	*	*	*	*	*	*	*
	10	0.12	0	0.04	0.17	0.09	0.06	0.03	0.16	0.04	4.36	2.8
	20	0.29	0	0.03	0.19	0.18	0.08	0.01	0.09	0	4.46	1.6
	35	0.24	0	0.03	0.17	0.12	0.07	0.02	0.07	0.01	4.54	2.1

La Croix-Scaille (sites 1 et 2): Septembre 1995 ; pas de statistiques

traitement	profondeur	S	Mn	Mg	Ca	Al	Na	K	NO_3^-	NH_4^+	pH-H_2O	Ca/Al
	cm	$mmol_c\ l^{-1}$										mole/mole
Témoin	3	*	0.01	*	*	*	*	*	*	*	*	*
	10	0.26	0.01	0.08	*	*	*	*	*	*	*	*
	20	0.11	0.05	0.14	0.12	0.73	0.17	0.14	0.46	0.01	4.11	0.25
	35	0.11	0.04	0.11	0.22	0.95	0.14	0.05	0.27	0.01	4.40	0.35
$CaCO_3$-ancien	3	0.56	0.01	0.16	0.77	0.11	*	*	*	*	4.52	11
	10	0.34	0.01	0.12	0.51	0.15	0.16	0.04	0.36	0	3.92	5.1
	20	0.14	0	0.05	0.18	0.07	0.07	0.03	0.02	0	4.85	3.9
	35	0.14	0.01	0.03	0.21	0.11	0.08	0.03	0.20	0	4.58	2.9
$CaSO_4$-ancien	3	0.63	0.01	*	*	*	*	*	*	*	*	*
	10	*	*	*	*	*	*	*	*	*	*	*
	20	*	*	*	*	*	*	*	*	*	*	*
	35	*	*	*	*	*	*	*	*	*	*	*
$CaCO_3$-nouveau	3	0.06	*	*	*	*	*	*	*	*	*	*
	10	0.23	0	0.03	0.04	0.18	0.09	0.01	0.02	0	4.09	0.33
	20	0.12	0.01	0.04	0.13	0.11	0.10	0.02	0.15	0	4.62	1.8
	35	0.25	0.02	0.03	0.24	0.36	0.08	0.03	0.39	0	4.46	1.0
$CaSO_4$-nouveau	3	0.29	0.02	0.03	0.39	0.11	0.06	0.02	0.11	0	4.21	5.3
	10	0.27	0.01	0.03	0.20	0.08	0.08	0.02	0.01	0	4.31	3.8
	20	0.20	0.01	0.03	0.13	0.10	0.07	0.02	0.01	0	4.44	2.0
	35	0.48	0.02	0.04	0.32	0.44	0.08	0.07	0.33	0	4.48	1.1
Mélange 80/20	3	0.52	0	0.03	0.72	0.11	0.07	0.02	0.01	0.01	4.28	9.8
	10	0.36	0	0.03	0.15	0.17	0.08	0.01	0.04	0	3.85	1.3
	20	0.46	0	0.04	0.20	0.13	0.08	0.02	0.02	0	4.02	2.3
	35	0.38	0	0.04	0.16	0.11	0.09	0.01	0.01	0	4.02	2.2

Les Trembles (site 4): Mars 1995 ; pas de statistiques

traitement	profondeur	S	Mn	Mg	Ca	Al	Na	K	NO_3^-	NH_4^+	pH-H_2O	Ca/Al
	cm	$mmol_c\ l^{-1}$										mole/mole
Témoin	0-5	0.22	0.03	0.13	0.08	0.59	0.25	0.24	0	0.03	3.98	0.20
	5-15	0.12	0.01	0.08	0.08	0.07	0.31	0.13	0.01	0.12	*	1.7
	15-30	0.13	0.01	0.09	0.06	0.05	0.25	0.04	0.01	0.01	3.99	1.8
	30-45	0.15	0.01	0.09	0.05	0.02	0.23	0.03	0.01	0	3.83	3.8
	45-60	0.14	0.01	0.14	0.06	0.01	0.24	0.02	0.01	0.01	4.70	9.0
NCa	0-5	0.29	*	0.15	0.12	0.43	*	0.19	0	0.17	4.27	0.42
	5-15	0.16	*	0.07	0.05	0.07	*	0.03	0.01	0.09	4.08	1.1
	15-30	0.17	*	0.06	0.05	0.11	*	0.01	0.01	0	3.87	0.68
	30-45	0.19	*	0.09	0.06	0.11	*	0.01	0.01	0.01	3.80	0.82
	45-60	*	*	*	*	*	*	*	*	*	*	*

Gaie Mariée (site 5): Mars 1995 ; pas de statistiques

traitement	profondeur	S	Mn	Mg	Ca	Al	Na	K	NO_3^-	NH_4^+	pH-H_2O	Ca/Al
	cm	$mmol_c\ l^{-1}$										mole/mole
Témoin	0-5	0.48	0.02	0.12	0.15	0.11	0.21	0.14	0.02	0.26	4.32	2.0
	5-15	0.16	0.01	0.10	0.09	0.16	0.04	0.05	0.06	0.09	3.64	0.84
	15-30	0.16	0.01	0.08	0.08	0.06	0.20	0.04	0.01	0.04	3.67	2.0
	30-45	0.16	0.01	0.10	0.06	0.04	0.19	0.02	0.01	0.01	3.81	2.3
	45-60	0.26	0	0.15	0.10	0.01	0.25	0.01	0.01	0	4.32	15
NCa	0-5	0.25	0.02	0.16	0.15	1.03	0.23	0.18	0	0.12	4.32	0.22
	5-15	0.10	0.01	0.09	0.07	0.19	0.21	0.06	0	0.03	3.83	0.55
	15-30	0.14	0.01	0.08	0.09	0.12	0.18	0.06	0.01	0.02	3.71	1.1
	30-45	0.23	0.01	0.13	0.09	0.04	0.24	0.03	0.01	0.01	3.78	3.4
	45-60	0.22	0.01	0.14	0.12	0.01	0.24	0.03	0.01	0.01	4.44	18

Bertranges (site 7): Juin 1995 ; pas de statistiques

traitement	profondeur	S	Mn	Mg	Ca	Al	Na	K	NO_3^-	NH_4^+	pH-H_2O	Ca/Al
	cm	$mmol_c\ l^{-1}$										mole/mole
Témoin	0-5	0.21	0.01	0.24	0.38	0.24	0.25	0.13	0.18	0.11	5.38	2.4
	5-15	0.17	0.01	0.13	0.19	0.11	0.21	0.07	0.03	0.07	5.35	2.6
	15-30	0.17	0.02	0.14	0.26	0.04	0.38	0.23	0.03	0.16	5.07	9.8
CaO	0-5	0.27	0.01	0.26	0.39	0.37	0.30	0.13	0.03	0.11	5.41	1.6
	5-15	0.20	0.01	0.14	0.25	0.12	0.23	0.09	0.04	0.11	5.26	3.1
	15-30	0.17	0.02	0.11	0.23	0.03	0.27	0.08	0.02	0.09	5.51	12

Annexe 4.3 Fiches de résultats pour les racines

La Croix-Scaille: juin 1994 Biomasse racines fines (FRB en kg ha^{-1}), densité en longueur des racines fines FRLD (en cm cm^{-3}), longueur racinaire spécifique, pourcentage des racines très fines (< 0.5 mm) sur le total des racines fines (< 2 mm) (% de biomasse et de longueur racinaire), biomasse des racines grosses (CRB en kg ha^{-1}), masse des fines racines mortes (FRN en kg ha^{-1}) et densité en longueur des fines racines mortes (FRNLD en cm cm^{-3}); avec erreur standard en italic pour racines fines et grosses de 2 à 5 mm. Dans le cadre (racines fines; n = 30) tests statistiques par ANOVA et Student-Newman-Keuls interval pour chaque couche, révélant une valeur significativement plus basse pour **a** que pour **b** ($P < 0.05$).

		Racines fines (< 2 mm)					Racines grosses (> 2 mm)			Racines mortes	
	couche	FRB	FRLD	SRL	fraction très fine		CRB	CRB	CRB	FRN	FRNLD
	cm	kg ha^{-1}	cm cm^{-3}	m g^{-1}	%	%	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	cm cm^{-3}
traitement		n = 30			biomasse	longueur	2-5 mm	5-10	>10 mm	< 2 mm	
Témoin	0-5	799 *87*	3,22 *0,28*	23,5 *1,52* **b**	74.4	94.7	94 *42*	101	0	289	0.93
$CaCO_3$-V	0-5	1142 *153*	3,32 *0,31*	18,1 *1,43* **a**	72.8	93.7	143 *61*	82	0	160	0.52
$CaSO_4$-V	0-5	942 *67*	3,68 *0,20*	20,8 *1,03* **ab**	67.4	96.4	59 *22*	74	0	288	0.81
nouveau	0-5	739 *83*	3,30 *0,29*	24,7 *1,98* **b**	53.2	93.5	153 *72*	62	0	302	0,80
Témoin	5-15	1046 *105* **a**	1,67 *0,14* **a**	18,4 *1,63*	63.3	94,0	501 *142*	678	218	434	1.05
$CaCO_3$-V	5-15	975 *102* **ab**	1,34 *0,11* **a**	16,2 *1,24*	70.2	94.3	359 *128*	419	1482	308	0.48
$CaSO_4$-V	5-15	1370 *121* **b**	2,25 *0,15* **b**	18,0 *1,23*	60.7	94.3	447 *131*	71	557	504	0.45
nouveau	5-15	1024 *112* **ab**	1,56 *0,10* **a**	18,0 *1,60*	75.5	97.7	638 *188*	478	0	244	0.35
Témoin	15-30	854 *78*	1,19 *0,07* **ab**	24,0 *1,86*	79.4	98,0	285 *90*	835	1832	627	1.06
$CaCO_3$-V	15-30	1093 *144*	1,28 *0,12* **b**	22,6 *1,62*	98,0	99.4	494 *201*	199	1962	361	0.39
$CaSO_4$-V	15-30	1102 *209*	1,27 *0,09* **b**	22,6 *1,85*	58.7	95.9	412 *153*	776	912	823	0.47
nouveau	15-30	766 *93*	0,90 *0,10* **a**	20,8 *2,44*	62,0	98.8	804 *320*	439	976	113	0.13
Témoin	30-45	487 *55* **a**	0,68 *0,04*	26,1 *2,09* **b**	91.4	98,0	222 *84*	244	0	293	0,30
$CaCO_3$-V	30-45	738 *90* **b**	0,83 *0,07*	19,0 *1,07* **a**	68.8	95.6	299 *70*	261	551	262	0.25
$CaSO_4$-V	30-45	556 *40* **ab**	0,82 *0,04*	24,8 *1,59* **b**	63.6	95.2	171 *64*	97	260	228	0.27
nouveau	30-45	564 *39* **ab**	0,68 *0,05*	18,7 *1,05* **a**	69.5	95.6	168 *64*	271	122	47	0.06
Témoin	45-55	269 *162*	0,72 *0,41*	29,1 *4,16*			0	0	0	97	0,20
$CaCO_3$-V	45-55	251 *84*	0,46 *0,10*	22,0 *3,83*			0	0	0	210	0.22
$CaSO_4$-V	45-55	215 *116*	0,48 *0,19*	39,4 *14,8*			0	0	0	28	0.08
nouveau	45-55	179 *52*	0,53 *0,21*	26,1 *6,21*			0	0	0	29	0.09

Totales:		Racines vivantes < 2 mm		> 2 mm		Tout	Racines mortes < 2 mm			Tout	
		FRB kg	FRL 10^6 m	CRB kg	CRL 10^6 m	RB kg	RL 10^6 m	FRN kg	FRNL 10^6 m	RN kg	RNL 10^6 m
traitement		ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}
Témoin	0-55	3455	68,0	5010	0.5614	8465	68.6	1740	37.5	2310	37.6
$CaCO_3$-V		4199	66.3	6251	0,5330	10450	66.8	1301	19.2	3392	19.9
$CaSO_4$-V		4185	77.1	3836	0.5019	8021	77.6	1871	20.4	5472	21.1
nouveau		3272	61,0	4111	0.6168	7383	61.6	735	11.2	3296	11.6

La Croix-Scaille: sept. 1994 Biomasse racines fines (FRB en kg ha^{-1}), densité en longueur des racines fines (FRLD en cm cm^{-3}), longueur racinaire spécifique, pourcentage des racines très fines (< 0.5 mm) sur le total des racines fines (< 2 mm) (% de biomasse et de longueur racinaire), biomasse des racines grosses (CRB en kg ha^{-1}), masse des fines racines mortes (FRN en kg ha^{-1}) et densité en longueur des fines racines mortes (FRNLD en cm cm^{-3}); avec erreur standard en italic pour racines fines et grosses de 2 à 5 mm. Dans le cadre (racines fines; n = 12) tests statistiques par ANOVA et Student-Newman-Keuls interval pour chaque couche, révélant une valeur significativement plus basse pour **a** que pour **b** ($P < 0.05$).

		Racines fines (< 2 mm)					Racines grosses (> 2 mm)			Racines mortes	
	couche	FRB	FRLD	SRL	fraction très fine		CRB	CRB	CRB	FRN	FRNLD
	cm	kg ha^{-1}	cm cm^{-3}	m g^{-1}	%	%	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	cm cm^{-3}
traitement		n = 12			biomasse	longueur	2-5 mm	5-10	>10 mm	< 2 mm	
Témoin	0-5	687 *116* **a**	2,61 *0,48*	22,2 *2,86*	46.7	87.2	366 *152*	0	0	152	1
$CaCO_3$-V	0-5	1217 *185* **b**	3,46 *0,48*	15,8 *1,64*	55.2	90	539 *210*	389	0	161	0.63
$CaSO_4$-V	0-5	1082 *138* **ab**	3,69 *0,41*	17,8 *1,07*	44.3	89.1	255 *142*	0	0	239	1.49
Témoin	5-15	974 *219*	1,59 *0,28*	18,7 *1,50*	55.7	92.4	404 *177*	484	931	137	0.46
$CaCO_3$-V	5-15	1064 *190*	1,56 *0,23*	16,6 *1,90*	64.6	91.6	308 *182*	383	0	130	0.19
$CaSO_4$-V	5-15	856 *208*	1,56 *0,25*	21,7 *1,74*	54.7	89.6	237 *94*	155	700	358	0.57
Témoin	15-30	835 *105* **a**	1,08 *0,07* **a**	22,4 *2,85*	36.9	87	255 *159*	0	0	164	0.28
$CaCO_3$-V	15-30	931 *101* **a**	1,11 *0,07* **a**	20,3 *2,60*	31	85.6	355 *196*	0	2009	188	0.13
$CaSO_4$-V	15-30	1389 *124* **b**	1,82 *0,15* **b**	20,8 *1,88*	49.6	90.5	455 *230*	0	0	605	0.97
Témoin	30-45	486 *94*	0,71 *0,06*	29,5 *4,17*	100	100	342 *214*	527	0	95	0.18
$CaCO_3$-V	30-45	848 *163*	1,03 *0,10*	23,3 *3,19*	55.2	91	443 *196*	0	0	82	0.18
$CaSO_4$-V	30-45	644 *127*	0,89 *0,12*	27,5 *4,54*	71.2	94.4	320 *216*	0	0	444	0.59
Témoin	45-55	152 *82*	0,42 *0,08*	35,2 *13,9*			0	0	0	80	0.09
$CaCO_3$-V	45-55	165 *53*	0,52 *0,07*	37,0 *16,2*			0	0	0	46	0.09
$CaSO_4$-V	45-55	331 *52*	0,77 *0,44*	21,8 *9,75*			0	0	0	184	0.26

Totales:		Racines vivantes < 2 mm		> 2 mm		Tout	Racines mortes < 2 mm			Tout	
		FRB	FRL	CRB	CRL	RB	RL	FRN	FRNL	RN	RNL
		kg	10^6 m	kg	10^6 m	kg	10^6 m	kg	10^6 m	kg	10^6 m
traitement		ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}
Témoin	0-55	3134	60,0	3309	0.5772	6443	60.6	628	17.5	1838	17.7
$CaCO_3$-V		4225	70.1	4426	0.5996	8651	70.7	607	10.7	1085	11,0
$CaSO_4$-V		4302	82.3	2122	0.4849	6424	82.8	1830	39,0	1965	39.2

La Croix-Scaille: mars 1995 Biomasse racines fines (FRB en kg ha^{-1}), densité en longueur des racines fines (FRLD en cm cm^{-3}), longueur racinaire spécifique, pourcentage des racines très fines (< 0.5 mm) sur le total des racines fines (< 2 mm) (% de biomasse et de longueur racinaire), biomasse des racines grosses (CRB en kg ha^{-1}), masse des fines racines mortes (FRN en kg ha^{-1}) et densité en longueur des fines racines mortes (FRNLD en cm cm^{-3}); avec erreur standard en italic pour racines fines et grosses de 2 à 5 mm. Dans le cadre (racines fines; n = 12) tests statistiques par ANOVA et Student-Newman-Keuls interval pour chaque couche, révélant une valeur significativement plus basse pour **a** que pour **b** ($P < 0.05$).

		Racines fines (< 2 mm)					Racines grosses (> 2 mm)			Racines mortes	
	couche	FRB	FRLD	SRL	fraction très fine		CRB	CRB	CRB	FRN	FRNLD
	cm	kg ha^{-1}	cm cm^{-3}	m g^{-1}	%	%	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	cm cm^{-3}
traitement		n = 12			biomasse	longueur	2-5 mm	5-10	>10 mm	< 2 mm	
Témoin	0-5	1057 *148* **ab**	2,02 *0,30*	11,2 *1,61*	81.5	96.9	486 *149*	0	0	166	1.26
$CaCO_3$-V	0-5	1152 *160* **ab**	2,62 *0,43*	11,5 *1,28*	35.8	77.1	318 *139*	862	0	326	2.13
$CaSO_4$-V	0-5	1140 *267* **ab**	2,17 *0,52*	10,5 *1,11*	62.5	91.5	264 *122*	0	0	280	0.96
$CaCO_3$-N	0-5	1023 *109* **b**	1,96 *0,23*	9,9 *0,87*	49.6	94.6	363 *164*	38	0	193	0.84
$CaSO_4$-N	0-5	597 *104* **a**	1,23 *0,16*	12,4 *1,63*	81.4	94.9	146 *78*	95	0	198	1.19
Mélange	0-5	1213 *190* **b**	1,94 *0,26*	8,4 *1,27*			233 *116*	341	0	268	1.68
Témoin	5-15	741 *135*	0,66 *0,10*	10,2 *1,17*	61.3	88.5	523 *174*	1186	1731	213	0.6
$CaCO_3$-V	5-15	756 *65*	0,66 *0,06*	9,3 *0,88*	65.6	90.5	690 ***222***	731	543	247	0.6
$CaSO_4$-V	5-15	968 *191*	0,83 *0,15*	9,2 *0,83*	61.6	94.1	659 *134*	0	2358	359	0.3
$CaCO_3$-N	5-15	509 *68*	0,51 *0,07*	10,7 *0,95*	24.1	84	585 *167*	307	1356	343	0.52
$CaSO_4$-N	5-15	860 *80*	0,79 *0,17*	9,8 *1,62*	59.9	87.6	260 *127*	533	0	254	0.34
Mélange	5-15	696 *144*	0,51 *0,09*	8,4 *1,06*	48.2	94	1694 *1322*	1008	0	317	0.74
Témoin	15-30	511 *70*	0,37 *0,04*	13,7 *2,33*	48.3	88.3	583 *166*	327	569	390	0.56
$CaCO_3$-V	15-30	591 *80*	0,37 *0,06*	9,5 *1,12*	19.7	82.6	801 *236*	713	1906	432	0.53
$CaSO_4$-V	15-30	632 *122*	0,44 *0,07*	15,3 *3,37*	22.5	75.9	501 *201*	403	0	621	0.53
$CaCO_3$-N	15-30	597 *109*	0,50 *0,08*	14,7 *2,04*	76.7	96.3	544 *115*	1197	1254	539	0.51
$CaSO_4$-N	15-30	415 *62*	0,34 *0,06*	14,3 *1,85*	58.4	92.6	210 *131*	708	385	161	0.22
Mélange	15-30	454 *80*	0,38 *0,06*	19,5 *5,12*	79.4	93.5	358 *107*	201	0	106	0.15
Témoin	30-45	332 *54*	0,26 *0,03*	14,8 *2,42*	92.6	98.7	196 *112*	0	0	396	0.53
$CaCO_3$-V	30-45	384 *72*	0,28 *0,05*	12,4 *1,32*	70.9	95.9	332 *145*	535	1288	363	0.48
$CaSO_4$-V	30-45	614 *174*	0,32 *0,05*	11,0 *1,55*	39.8	90.2	390 *142*	129	1031	322	0.38
$CaCO_3$-N	30-45	323 *58*	0,29 *0,05*	14,0 *0,87*	100	100	282 *129*	0	0	283	0.24
$CaSO_4$-N	30-45	343 *57*	0,31 *0,06*	15,4 *2,35*	56.9	85.3	190 *112*	0	0	262	0.2
Mélange	30-45	465 *79*	0,35 *0,05*	13,5 *2,00*	38.6	88	480 *177*	797	535	197	0.23
Témoin	45-55	189 *158*	0,16 *0,12*	10,8 *2,53*			130 *130*	0	0	149	0.41
$CaCO_3$-V	45-55	394 *251*	0,42 *0,14*	14,1 *5,50*			0	1611	0	168	0.43
$CaSO_4$-V	45-55	46 *27*	0,09 *0,06*	17,2 *2,90*			0	0	0	305	0.35
$CaCO_3$-N	45-55	36 *20*	0,08 *0,05*	22,5 *0,26*			0	0	0	118	0.23
$CaSO_4$-N	45-55	88 *74*	0,05 *0,00*	18,1 *15,2*			0	0	0	62	0.13
Mélange	45-55	192 *81*	0,22 *0,16*	9,9 *4,22*			0	740	0	156	0.27

Totales:		Racines vivantes < 2 mm		> 2 mm		Tout	Racines mortes < 2 mm		Tout	
		FRB	FRL	CRB	CRL	RB	RL	FRN	FRNL	RN	RNL
		kg	10^6 m	kg	10^6 m	kg	10^6 m	kg	10^6 m	kg	10^6 m
traitement		ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}
Témoin	0-55	2830	27.7	5731	0.73	8561	28.4	1314	32.6	1732	32.7
$CaCO_3$-V		3277	33.7	10330	0.88	13607	34.6	1536	36.1	1893	36.3
$CaSO_4$-V		3400	31.4	5735	0.62	9135	32,0	1887	25,0	2448	25.3
$CaCO_3$-N		2488	27.6	5926	0.71	8414	28.3	1476	23,0	3974	23.3
$CaSO_4$-N		2303	24.2	2527	0.45	4830	24.7	937	16.9	937	16.9
Mélange		3020	28.1	6387	0.74	9407	28.8	1044	24.2	1426	24.2

La Croix-Scaille: juin 1995 Biomasse racines fines (FRB en kg ha^{-1}), densité en longueur des racines fines (FRLD en cm cm^{-3}), longueur racinaire spécifique, pourcentage des racines très fines (< 0.5 mm) sur le total des racines fines (< 2 mm) (% de biomasse et de longueur racinaire), biomasse des racines grosses (CRB en kg ha^{-1}), masse des fines racines mortes (FRN en kg ha^{-1}) et densité en longueur des fines racines mortes (FRNLD en cm cm^{-3}); avec erreur standard en italic pour racines fines et grosses de 2 à 5 mm. Dans le cadre (racines fines; n = 12) tests statistiques par ANOVA et Student-Newman-Keuls interval pour chaque couche, révélant une valeur significativement plus basse pour **a** que pour **b** ($P < 0.05$).

		Racines fines (< 2 mm)					Racines grosses (> 2 mm)			Racines mortes	
	couche	FRB	FRLD	SRL	fraction très fine		CRB	CRB	CRB	FRN	FRNLD
	cm	kg ha^{-1}	cm cm^{-3}	m g^{-1}	%	%	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	cm cm^{-3}
traitement		n = 12			biomasse	longueur	2-5 mm	5-10	>10 mm	< 2 mm	
Témoin	0-5	809 *100*	1,76 *0,20*	11,9 *1,22*	38.1	40	222 *106*	219	0	151	0.63
$CaCO_3$-N	0-5	816 *112*	1,63 *0,18*	11,8 *1,65*	55.3	56.2	267 *116*	0	0	241	0.2
$CaSO_4$-N	0-5	800 *137*	1,27 *0,21*	9,28 *1,34*	38.1	37.5	308 *104*	76	0	116	0.29
Mélange	0-5	958 *136*	2,19 *0,35*	12,0 *1,17*	62.7	66.4	573 *128*	0	0	223	0.78
Témoin	5-15	853 *136*	0,68 *0,09*	8,49 *0,86*	62	62.9	627 *218*	446	231	247	0.42
$CaCO_3$-N	5-15	713 *90*	0,60 *0,11*	8,39 *0,91*	62.5	55.1	383 *111*	163	0	190	0.23
$CaSO_4$-N	5-15	747 *61*	0,60 *0,07*	8,41 *0,98*	65.2	60.9	367 *117*	120	553	56	0.21
Mélange	5-15	878 *170*	0,67 *0,15*	8,38 *1,16*	58.6	54.8	618 *228*	927	617	227	0.38
Témoin	15-30	580 *114*	0,35 *0,04*	11,1 *1,54*	60.5	55.9	726 *319*	180	558	252	0.33
$CaCO_3$-N	15-30	648 *99*	0,43 *0,06*	11,2 *1,86*	59.7	65.2	556 *240*	1061	0	579	0.5
$CaSO_4$-N	15-30	711 *156*	0,46 *0,06*	12,8 *1,75*	65.9	70.9	311 *103*	690	0	431	0.4
Mélange	15-30	577 *150*	0,40 *0,10*	13,0 *2,43*	30.8	38.8	256 *100*	1245	522	646	0.53
Témoin	30-45	483 *115* **ab**	0,32 *0,07* **ab**	11,9 *1,48*	31.4	37.5	110 *51*	500	1085	274	0.38
$CaCO_3$-N	30-45	394 *76* **ab**	0,26 *0,07* **ab**	10,8 *1,47*	38.4	32	373 *184*	242	1451	290	0.3
$CaSO_4$-N	30-45	265 *53* **a**	0,19 *0,03* **a**	16,1 *3,21*	20.2	19.3	131 *70*	42	0	407	0.32
Mélange	30-45	636 *114* **b**	0,42 *0,06* **b**	11,0 *0,97*	35	51.5	233 *116*	1285	0	481	0.39
Témoin	45-55	243 *220*	0,69 *0,55*	43,0 *16,2*			0	0	0	135	0.29
$CaCO_3$-N	45-55	65 *18*	0,11 *0,01*	18,9 *6,26*			136 *136*	0	0	37	0.12
$CaSO_4$-N	45-55	97 *7*	0,22 *0,04*	23,5 *6,07*			162 *162*	691	0	94	0.23
Mélange	45-55	98 *61*	0,08 *0,05*	8,54 *0,04*			0	0	0	49	0.15

		Racines vivantes					Racines mortes				
Totales:		< 2 mm		> 2 mm		Tout		< 2 mm		Tout	
		FRB	FRL	CRB	CRL	RB	RL	FRN	FRNL	RN	RNL
		kg	10^6 m	kg	10^6 m	kg	10^6 m	kg	10^6 m	kg	10^6 m
traitement		ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}
Témoin	0-55	2968	32.6	4904	0.66	7872	33.3	1059	20.8	3907	21.1
$CaCO_3$-N		2636	25.6	4632	0.72	7268	26.3	1337	16.5	3246	16.8
$CaSO_4$-N		2620	24.4	3451	0.66	6071	25.1	1104	16.6	1104	16.6
Mélange		3147	30.8	6276	0.77	9423	31.6	1626	22.9	1746	23.0

La Croix-Scaille: sept. 1995 Biomasse racines fines (FRB en kg ha^{-1}), densité en longueur des racines fines (FRLD en cm cm^{-3}), longueur racinaire spécifique, pourcentage des racines très fines (< 0.5 mm) sur le total des racines fines (< 2 mm) (% de biomasse et de longueur racinaire), biomasse des racines grosses (CRB en kg ha^{-1}), masse des fines racines mortes (FRN en kg ha^{-1}) et densité en longueur des fines racines mortes (FRNLD en cm cm^{-3}); avec erreur standard en italic pour racines fines et grosses de 2 à 5 mm. Dans le cadre (racines fines; n = 12) tests statistiques par ANOVA et Student-Newman-Keuls interval pour chaque couche, révélant des différences (les lettres différentes **a**, **b** et **c** indiquent lesquels atteignent un seuil de p<0.05).

		Racines fines (< 2 mm)					Racines grosses (> 2 mm)			Racines mortes	
	couche	FRB	FRLD	SRL	fraction très fine		CRB	CRB	CRB	FRN	FRNLD
	cm	kg ha^{-1}	cm cm^{-3}	m g^{-1}	%	%	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	cm cm^{-3}
traitement		n = 12			biomasse	longueur	2-5 mm	5-10	>10 mm	< 2 mm	
Témoin	0-5	990 *120* **ab**	1,64 *0,21* **ab**	8,66 *0,74*	31.2	72.7	233 *86*	427	977	456	1.43
$CaCO_3$-V	0-5	987 *147* **ab**	2,06 *0,32* **ab**	11,3 *1,24*	47.2	85	89 *62*	273	0	320	1.31
$CaSO_4$-V	0-5	1283 *255* **b**	2,33 *0,32* **b**	11,3 *1,39*	26.5	73.9	415 *170*	0	0	166	0.97
$CaCO_3$-N	0-5	572 *76* **a**	1,13 *0,13* **a**	11,4 *1,74*	52.2	80.6	226 *113*	0	0	252	0.89
$CaSO_4$-N	0-5	653 *140* **ab**	1,38 *0,19* **ab**	12,6 *1,77*	36.7	74.6	176 *106*	0	0	185	0.68
Mélange	0-5	938 *161* **ab**	1,82 *0,22* **ab**	12,6 *1,94*	17.5	66.6	516 *186*	0	0	347	1.45
Témoin	5-15	755 *59*	0,54 *0,06*	7,16 *0,54* **a**	29.7	72.9	396 *154*	95	0	323	0.57
$CaCO_3$-V	5-15	508 *87*	0,46 *0,08*	9,6 *1,19* **ab**	38.3	72.4	269 *128*	191	0	330	0.56
$CaSO_4$-V	5-15	642 *136*	0,58 *0,10*	10,2 *0,90* **b**	15.7	60.3	110 *61*	207	1435	308	0.54
$CaCO_3$-N	5-15	797 *136*	0,52 *0,08*	7,25 *0,99* **ab**	20.4	66.4	772 *222*	526	0	304	0.6
$CaSO_4$-N	5-15	544 *117*	0,68 *0,16*	23,3 *11,9* **ab**	42.6	90.7	273 *125*	676	0	152	0.32
Mélange	5-15	933 *189*	0,58 *0,08*	8,69 *1,46* **ab**	58	82.6	674 *233*	0	437	308	0.38
Témoin	15-30	544 *118*	0,45 *0,07*	15,3 *2,35*	28	75	153 *153*	442	0	267	0.39
$CaCO_3$-V	15-30	572 *107*	0,51 *0,13*	14,4 *1,71*	66	85.2	234 *103*	1293	0	294	0.38
$CaSO_4$-V	15-30	547 *114*	0,45 *0,07*	15,1 *1,91*	28.7	76.9	726 *181*	979	0	582	0.58
$CaCO_3$-N	15-30	675 *165*	0,46 *0,07*	14,9 *2,42*	45.4	83.2	280 *123*	1346	1901	558	0.52
$CaSO_4$-N	15-30	814 *117*	0,53 *0,07*	10,6 *1,00*	19.7	69.1	633 *295*	0	0	281	0.43
Mélange	15-30	794 *183*	0,52 *0,11*	11,0 *1,22*	26.9	65.4	767 *326*	1078	0	244	0.48
Témoin	30-45	224 *62* **c**	0,23 *0,05* **a**	19,2 *2,45* **b**	28.3	78.4	43 *43*	605	788	276	0.36
$CaCO_3$-V	30-45	734 *160* **a**	0,56 *0,10* **b**	13,5 *1,29* **ab**	38.9	75.9	356 *243*	617	0	522	0.54
$CaSO_4$-V	30-45	413 *86* **bc**	0,38 *0,05* **ab**	17,7 *2,10* **ab**	37.2	86	225 *101*	0	560	344	0.47
$CaCO_3$-N	30-45	374 *73* **bc**	0,24 *0,03* **a**	11,7 *1,52* **a**	43.8	75.3	156 *156*	0	0	763	0.58
$CaSO_4$-N	30-45	500 *112* **abc**	0,42 *0,09* **ab**	16,8 *2,81* **ab**	28.3	75.7	431 *238*	0	0	297	0.48
Mélange	30-45	657 *99* **ab**	0,40 *0,07* **ab**	10,4 *1,53* **a**	12.2	67.7	323 *240*	478	1421	415	0.57
Témoin	45-55	228 *101*	0,30 *0,02*	16,8 *8,14*			316 *316*	0	0	243	0.56
$CaCO_3$-V	45-55	528 *380*	0,43 *0,11*	13,9 *8,00*			760 *760*	0	0	209	0.52
$CaSO_4$-V	45-55	242 *51*	0,49 *0,01*	21,3 *4,26*			279 *279*	0	0	213	0.49
$CaCO_3$-N	45-55	377 *217*	0,23 *0,08*	7,51 *2,25*			0	0	0	218	0.37
$CaSO_4$-N	45-55	828 *191*	0,58 *0,09*	7,67 *2,87*			292 *292*	0	0	238	0.34
Mélange	45-55	101 *60*	0,21 *0,06*	26,2 *9,57*			0	0	0	72	0.16

		Racines vivantes					Racines mortes				
Totales:		< 2 mm		> 2 mm		Tout		< 2 mm		Tout	
		FRB	FRL	CRB	CRL	RB	RL	FRN	FRNL	RN	RNL
		kg	10^6 m	kg	10^6 m	kg	10^6 m	kg	10^6 m	kg	10^6 m
traitement		ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}
Témoin	0-55	2741	26.8	4475	0.41	7216	27.2	1565	29.7	2796	30,0
$CaCO_3$-V		3329	35.2	4082	0.62	7411	35.8	1675	21.1	2815	31.4
$CaSO_4$-V		3127	34.9	4936	0.76	8063	35.7	1613	30.9	3183	31.2
$CaCO_3$-N		2795	23.6	5207	0.71	8002	24.3	2095	30.5	2217	30.6
$CaSO_4$-N		3339	33.9	2481	0.69	5820	34.6	1153	23.7	1197	23.7
Mélange		3423	30.7	5694	0.79	9117	31.5	1386	28.2	1983	28.4

La Croix-Scaille: mars 1996 Biomasse racines fines (FRB en kg ha^{-1}), densité en longueur des racines fines (FRLD en cm cm^{-3}), longueur racinaire spécifique, pourcentage des racines très fines (< 0.5 mm) sur le total des racines fines (< 2 mm) (% de biomasse et de longueur racinaire), biomasse des racines grosses (CRB en kg ha^{-1}), masse des fines racines mortes (FRN en kg ha^{-1}) et densité en longueur des fines racines mortes (FRNLD en cm cm^{-3}); avec erreur standard en italic pour racines fines et grosses de 2 à 5 mm. Dans le cadre (racines fines; n = 12) tests statistiques par ANOVA et Student-Newman-Keuls interval pour chaque couche, révélant une valeur significativement plus basse pour **a** que pour **b** ($P < 0.05$).

		Racines fines (< 2 mm)					Racines grosses (> 2 mm)			Racines mortes	
	couche	FRB	FRLD	SRL	fraction très fine		CRB	CRB	CRB	FRN	FRNLD
	cm	kg ha^{-1}	cm cm^{-3}	m g^{-1}	%	%	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	cm cm^{-3}
traitement		n = 12			biomasse	longueur	2-5 mm	5-10	>10 mm	< 2 mm	
témoin	0-5	1026 *129*	2,54 *0,29*	12,7 *0,78*	64.2	89.4	139 *77*	180	0	190	0.81
$CaCO_3$-N	0-5	918 *129*	1,75 *0,21*	10,2 *0,95*	36.2	79.5	477 *232*	773	0	218	0.51
$CaSO_4$-N	0-5	901 *103*	2,14 *0,23*	12,5 *1,22*	40.7	83.3	253 *98*	0	0	125	0.48
Mélange	0-5	1034 *140*	2,35 *0,36*	11,6 *0,83*	51.4	88.8	328 *132*	0	0	187	0.65
Témoin	5-15	1092 *181* **ab**	0,95 *0,13* **b**	9,91 *1,23*	56.4	84.6	765 *233*	1059	1744	427	0.78
$CaCO_3$-N	5-15	678 *65* **a**	0,48 0,03 **a**	7,62 *0,68*	38.1	80.9	421 *146*	782	0	259	0.33
$CaSO_4$-N	5-15	1155 *121* **b**	0,98 *0,08* **b**	9,00 *0,77*	47	81.5	553 *128*	46	767	240	0.4
Mélange	5-15	712 *96* **ab**	0,64 *0,09* **a**	9,42 *0,72*	47.9	84.7	1129 *304*	1396	2880	103	0.17
Témoin	15-30	571 *81*	0,35 *0,04* **a**	10,3 *1,16*	50	88.6	439 *179*	363	0	371	0.39
$CaCO_3$-N	15-30	838 *114*	0,52 *0,06* **b**	10,0 *0,56*	25.3	75.9	462 *172*	729	0	291	0.29
$CaSO_4$-N	15-30	689 *109*	0,46 *0,06* **ab**	10,8 *0,96*	37.6	88.3	133 *70*	228	0	268	0.25
Mélange	15-30	646 *73*	0,36 *0,04* **a**	8,78 *0,78*	21.1	69.2	798 *202*	729	469	139	0.15
Témoin	30-45	340 *71* **a**	0,26 *0,06*	13,8 *1,58*	59.9	88.3	202 *130*	471	0	175	0.19
$CaCO_3$-N	30-45	414 *78* **a**	0,28 *0,04*	13,6 *2,24*	33.9	84.4	372 *184*	810	992	296	0.22
$CaSO_4$-N	30-45	353 *51* **a**	0,26 *0,04*	12,7 *1,65*	29.1	78.6	225 *112*	0	0	145	0.14
Mélange	30-45	639 *105* **b**	0,43 *0,07*	10,7 *1,26*	33.4	79.5	569 *131*	233	531	158	0.16
Témoin	45-55	222 *160*	0,26 *0,16*	13,6 *2,57*			0	0	0	151	0.19
$CaCO_3$-N	45-55	185 *37*	0,23 *0,05*	12,5 *0,05*			0	726	0	97	0.19
$CaSO_4$-N	45-55	277 *240*	0,21 *0,11*	16,4 *10,22*			0	0	0	52	0.11
Mélange	45-55	331 *165*	0,32 *0,22*	8,41 *2,29*			133 *133*	0	0	92	0.17

		Racines vivantes					Racines mortes				
Totales:		< 2 mm		> 2 mm		Tout	< 2 mm			Tout	
		FRB	FRL	CRB	CRL	RB	RL	FRN	FRNL	RN	RNL
		kg	10^6 m	kg	10^6 m	kg	10^6 m	kg	10^6 m	kg	10^6 m
traitement		ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}
Témoin	0-55	3251	34,0	5362	0.61	8613	34.6	1314	22.5	4707	23.1
$CaCO_3$-N		3033	28,0	6544	0.78	9577	28.8	1161	15.4	2622	15.7
$CaSO_4$-N		3375	33.4	2205	0.42	5580	33.8	830	13.4	1592	13.6
Mélange		3362	33.1	9195	1.08	12557	34.2	679	11.4	1128	11.6

Fontainebleau: octobre 1994 Biomasse racines fines (FRB en kg ha^{-1}), densité en longueur des racines fines (FRLD en cm cm^{-3}), longueur racinaire spécifique, pourcentage des racines très fines (< 0.5 mm) sur le total des racines fines (< 2 mm) (% de biomasse et de longueur racinaire), biomasse des racines grosses (CRB en kg ha^{-1}), masse des fines racines mortes (FRN en kg ha^{-1}) et densité en longueur des fines racines mortes (FRNLD en cm cm^{-3}); avec erreur standard en italic pour racines fines et grosses de 2 à 5 mm. Dans le cadre (racines fines; n = 18 pour 0-45 cm et n = 6 pour 45-65 cm) tests statistiques par ANOVA et Student-Newman-Keuls interval pour chaque couche, révélant une valeur significativement plus basse pour **a** par rapport à **b** et pour **b** par rapport à **c** (P < 0.05).

		Racines fines (< 2 mm)			fraction très fine		Racines grosses (> 2 mm)			Racines mortes	
traitement	couche cm	FRB kg ha^{-1} n = 18	FRLD cm cm^{-3}	SRL m g^{-1}	% biomasse	% longueur	CRB kg ha^{-1} 2-5 mm	CRB kg ha^{-1} 5-10	CRB kg ha^{-1} >10 mm	FRN kg ha^{-1} < 2 mm	FRNLD cm cm^{-3}
Témoin	0-5	898 *144* **a**	4.95 *0.81* **a**	30.4 *2.83*	58.5	94.7	40 *28*	0	0	296	2.24
CaO	0-5	984 *94* **a**	5.87 *0.50* **a**	31.5 *2.21*	71.6	94.4	0	0	0	437	3.34
NPKCa	0-5	1420 *135* **b**	8.37 *0.88* **b**	30.6 *1.90*	78.7	96.1	40 *28*	0	0	175	2.27
Témoin	5-15	1079 *166* **a**	2.08 *0.36* **a**	19.0 *1.28* **a**	46.5	94.4	65 *45*	141	0	341	1.07
CaO	5-15	1630 *177* **b**	3.75 *0.33* **b**	24.3 *1.38* **b**	85.7	99.0	625 *180*	374	0	525	0.98
NPKCa	5-15	2508 *220* **c**	6.04 *0.57* **c**	24.3 *1.49* **b**	78.5	98.7	611 *168*	687	0	332	0.68
Témoin	15-25	591 *108* **a**	0.97 *0.18* **a**	18.9 *1.96*	69.5	95.1	263 *183*	425	0	226	0.36
CaO	15-25	881 *135* **a**	1.33 *0.14* **a**	19.9 *2.59*	75.0	97.1	436 *158*	463	0	107	0.30
NPKCa	15-25	1420 *134* **b**	2.42 *0.24* **b**	17.4 *1.26*	62.2	93.4	720 *301*	723	334	503	0.48
Témoin	25-45	481 *123* **a**	0.46 *0.09* **a**	33.2 *4.85* **b**	59.7	93.8	145 *107*	0	0	311	0.26
CaO	25-45	725 *146* **ab**	0.49 *0.11* **a**	16.6 *2.35* **a**	30.9	84.8	453 *247*	0	0	539	0.44
NPKCa	25-45	1137 *171* **b**	0.90 *0.14* **b**	17.0 *1.92* **a**	42.6	84.6	639 *216*	531	0	197	0.18
Témoin	45-65	343 *157*	0.25 *0.07* **a**	35.9 *12.4*			104 *104*	0	0	212	0.17
CaO	45-65	525 *218*	0.33 *0.11* **a**	22.2 *6.55*			0	0	0	777	0.31
NPKCa	45-65	739 *132*	0.69 *0.15* **b**	18.5 *2.22*			0	0	0	910	0.23
Témoin	65-75	195 *189*	0.43 *0.38*	56.4 *35.3*			129 *129*	0	0	106	0.17
CaO	65-75	163 *0.64*	0.14 *0.01*	8.58 *0.53*			384 *384*	0	0	389	0.31
NPKCa	65-75	436 *297*	0.67 *0.58*	11.8 *5.20*			622 *588*	0	0	455	0.23

		Racines vivantes					Racines mortes				
Totales:		< 2 mm FRB kg ha^{-1}	FRL 10^6 m ha^{-1}	> 2 mm CRB kg ha^{-1}	CRL 10^6 m ha^{-1}	Tout RB kg ha^{-1}	< 2 mm RL 10^6 m ha^{-1}	FRN kg ha^{-1}	FRNL 10^6 m ha^{-1}	Tout RN kg ha^{-1}	RNL 10^6 m ha^{-1}
traitement											
Témoin	0-75	3587	74	1312	0.36	4899	74.4	1492	35.7	1492	35.7
CaO		4908	98	2735	0.60	7643	98.6	2774	47.7	7340	49.5
NPKCa		7661	165	4907	0.81	12567	165.8	2572	33.2	2572	33.2

Bertranges: juin 1995 Biomasse racines fines (FRB en kg ha^{-1}), densité en longueur des racines fines (FRLD en cm cm^{-3}), longueur racinaire spécifique, pourcentage des racines très fines (< 0.5 mm) sur le total des racines fines (< 2 mm) (% de biomasse et de longueur racinaire), biomasse des racines grosses (CRB en kg ha^{-1}), masse des fines racines mortes (FRN en kg ha^{-1}) et densité en longueur des fines racines mortes (FRNLD en cm cm^{-3}); avec erreur standard en italic pour racines fines et grosses de 2 à 5 mm. Dans le cadre (racines fines; n = 16) tests statistiques par ANOVA et Student-Newman-Keuls interval pour chaque couche, révélant pas de différences significatives.

		Racines fines (< 2 mm)			fraction très fine		Racines grosses (> 2 mm)			Racines mortes	
traitement	couche cm	FRB kg ha^{-1} n = 16	FRLD cm cm^{-3}	SRL m g^{-1}	% biomasse	% longueur	CRB kg ha^{-1} 2-5 mm	CRB kg ha^{-1} 5-10	CRB kg ha^{-1} >10 mm	FRN kg ha^{-1} < 2 mm	FRNLD cm cm^{-3}
Témoin	0-5	658 *122*	2.37 *0.36*	25.0 *3.98*	65.1	90.3	65 *37*	0	0	202	0.83
CaO	0-5	786 *136*	3.09 *0.55*	20.3 *1.98*	60.4	87.8	14 *14*	0	0	253	1.44
Témoin	5-15	1131 *164*	1.76 *0.29*	16.3 *2.03*	49.3	81.9	261 *101*	589	0	234	0.54
CaO	5-15	1314 *197*	1.97 *0.33*	15.2 *1.29*	53.3	88.1	469 *98*	870	454	560	1.06
Témoin	15-30	854 *127*	0.60 *0.08*	14.1 *1.80*	65.8	88.9	374 *106*	1454	0	241	0.19
CaO	15-30	914 *170*	0.56 *0.09*	14.2 *3.40*	30.0	78.5	781 *194*	527	1348	390	0.35
Témoin	30-45	125 *3.5*	0.28 *0.13*	14 4 *4.61*			77 *77*	0	0	44	0.13
CaO	30-45	404 *215*	0.43 *0.17*	17.5 *3.20*			402 *402*	977	0	123	0.47

		Racines vivantes					Racines mortes				
Totales:		< 2 mm FRB kg ha^{-1}	FRL 10^6 m ha^{-1}	> 2 mm CRB kg ha^{-1}	CRL 10^6 m ha^{-1}	Tout RB kg ha^{-1}	< 2 mm RL 10^6 m ha^{-1}	FRN kg ha^{-1}	FRNL 10^6 m ha^{-1}	Tout RN kg ha^{-1}	RNL 10^6 m ha^{-1}
traitement											
Témoin	0-45	2768	40.3	2820	0.50	5588	40.8	721	13.3	1178	13.4
CaO		3418	50.0	5842	0.70	9260	50.7	1326	29.2	1326	29.2

Les Trembles: mars 1995 Biomasse racines fines (FRB en kg ha^{-1}), densité en longueur des racines fines (FRLD en cm cm^{-3}), longueur racinaire spécifique, pourcentage des racines très fines (< 0.5 mm) sur le total des racines fines (< 2 mm) (% de biomasse et de longueur racinaire), biomasse des racines grosses (CRB en kg ha^{-1}), masse des fines racines mortes (FRN en kg ha^{-1}) et densité en longueur des fines racines mortes (FRNLD en cm cm^{-3}); avec erreur standard en italic pour racines fines et grosses de 2 à 5 mm. Dans le cadre (racines fines; n = 16) tests statistiques par ANOVA et Student-Newman-Keuls interval pour chaque couche, révélant une valeur significativement plus basse pour **a** que pour **b** (P < 0.05).

		Racines fines (< 2 mm)					Racines grosses (> 2 mm)			Racines mortes	
	couche	FRB	FRLD	SRL	fraction très fine		CRB	CRB	CRB	FRN	FRNLD
	cm	kg ha^{-1}	cm cm^{-3}	m g^{-1}	%	%	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	cm cm^{-3}
traitement		n = 16			biomasse	longueur	2-5 mm	5-10	>10 mm	< 2 mm	
Témoin	0-5	1516 *119*	4.69 *0.36*	15.9 *0.94*	66.5	89.5	156 *74*	0	0	552	2.41
NCa	0-5	1439 *102*	4.30 *0.34*	15.1 *0.79*	53.2	89.2	129 *88*	0	0	457	1.13
Témoin	5-15	992 *99*	0.97 *0.11*	10.0 *0.90*	39.5	83.3	516 *177*	917	0	958	0.75
NCa	5-15	1121 *134*	1.08 *0.12*	10.3 *0.87*	27.1	77.8	632 *153*	867	713	563	0.51
Témoin	15-30	700 *116*	0.51 *0.09*	12.2 *1.25*	37.7	85.5	1083 *315*	93	311	734	0.75
NCa	15-30	740 *91*	0.49 *0.05*	11.4 *1.25*	43.1	87.1	467 *170*	311	0	891	0.55
Témoin	30-45	378 *66* **a**	0.27 *0.03* **a**	13.3 *1.77*	31.8	80.0	346 *118*	355	0	266	0.29
NCa	30-45	592 *73* **b**	0.37 *0.03* **b**	11.1 *1.31*	50.9	85.3	513 *220*	493	0	667	0.52
Témoin	45-60	305 *55*	0.21 *0.03*	14.5 *2.48*	64.1	87.3	305 *55*	119	0	34	0.06
NCa	45-60	517 *91*	0.26 *0.04*	9.59 *1.24*	41.0	83.1	134 *56*	0	264	279	0.16
Témoin	60-75	466 *66*	0.22 *0.06*	6.97 *1.14*			466 *66*	0	0	96	0.14
NCa	60-75	104 *66*	0.12 *0.08*	17.2 *4.31*			0	0	0	99	0.11

		Racines vivantes					Racines mortes				
Totales:		< 2 mm		> 2 mm		Tout	< 2 mm			Tout	
		FRB	FRL	CRB	CRL	RB	RL	FRN	FRNL	RN	RNL
		kg	10^{6} m	kg	10^{6} m	kg	10^{6} m	kg	10^{6} m	kg	10^{5} m
traitement		ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}
Témoin	0-75	4357	51.3	4667	0.87	9024	52.2	2640	38.2	4270	38.76
NCa		4513	50.8	4523	0.69	9036	51.5	2956	31.0	3607	31.02

Gaie Mariée: mars 1995 Biomasse racines fines (FRB en kg ha^{-1}), densité en longueur des racines fines (FRLD en cm cm^{-3}), longueur racinaire spécifique, pourcentage des racines très fines (< 0.5 mm) sur le total des racines fines (< 2 mm) (% de biomasse et de longueur racinaire), biomasse des racines grosses (CRB en kg ha^{-1}), masse des fines racines mortes (FRN en kg ha^{-1}) et densité en longueur des fines racines mortes (FRNLD en cm cm^{-3}); avec erreur standard en italic pour racines fines et grosses de 2 à 5 mm. Dans le cadre (racines fines; n = 16) tests statistiques par ANOVA et Student-Newman-Keuls interval pour chaque couche, révélant une valeur significativement plus basse pour **a** que pour **b** (P < 0.05).

		Racines fines (< 2 mm)					Racines grosses (> 2 mm)			Racines mortes	
	couche	FRB	FRLD	SRL	fraction très fine		CRB	CRB	CRB	FRN	FRNLD
	cm	kg ha^{-1}	cm cm^{-3}	m g^{-1}	%	%	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	cm cm^{-3}
traitement		n = 16			biomasse	longueur	2-5 mm	5-10	>10 mm	< 2 mm	
Témoin	0-5	1023 *82* **b**	3.33 *0.30*	16.6 *1.04*	54.0	90.9	187 *76*	0	0	321	0.97
NCa	0-5	813 *73* **a**	2.93 *0.38*	18.9 *1.69*	61.9	93.6	89 *72*	0	0	318	1.06
Témoin	5-15	786 *86*	0.70 *0.09* **a**	9.48 *0.97* **a**	42.7	85.2	551 *122*	350	0	336	0.42
NCa	5-15	977 *167*	1.17 *0.18* **b**	14.9 *2.01* **b**	68.3	92.0	490 *107*	201	0	922	0.81
Témoin	15-30	559 *127*	0.42 *0.08*	12.0 *1.47*	38.6	81.3	550 *224*	100	319	244	0.26
NCa	15-30	751 *96*	0.52 *0.07*	10.5 *1.06*	22.1	91.5	595 *215*	407	0	391	0.55
Témoin	30-45	485 *92*	0.31 *0.06*	13.4 *2.35*	36.4	80.9	229 *116*	299	0	455	0.29
NCa	30-45	389 *50*	0.29 *0.04*	14.8 *2.69*	59.4	84.8	322 *178*	0	0	135	0.13
Témoin	45-60	183 *51*	0.10 *0.02*	14.9 *2.84*	86.0	96.8	89 *64*	483	0	104	0.10
NCa	45-60	208 *64*	0.11 *0.02*	15.7 *5.08*	39.6	73.4	75 *39*	0	697	220	0.11
Témoin	60-75	421 *147*	0.14 *0.03*	6.77 *2.39*			188 *188*	0	0	73	0.15
NCa	60-75	148 *67*	0.10 *0.06*	19.0 *10.8*			472 *472*	0	0	139	0.08

		Racines vivantes					Racines mortes				
Totales:		< 2 mm		> 2 mm		Tout	< 2 mm			Tout	
		FRB	FRL	CRB	CRL	RB	RL	FRN	FRNL	RN	RNL
		kg	10^{5} m	kg	10^{5} m	kg	10^{6} m	kg	10^{6} m	kg	10^{6} m
traitement		ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}
Témoin	0-75	3457	38.3	3345	0.66	6802	39.0	1533	21.0	2706	21.3
NCa		3286	41.8	3348	0.68	6634	42.5	2125	26.2	4795	26.4

Rond du May: sept. 1995 Biomasse racines fines (FRB en kg ha^{-1}), densité en longueur des racines fines (FRLD en cm cm^{-3}), longueur racinaire spécifique, pourcentage des racines très fines (< 0.5 mm) sur le total des racines fines (< 2 mm) (% de biomasse et de longueur racinaire), biomasse des racines grosses (CRB en kg ha^{-1}), masse des fines racines mortes (FRN en kg ha^{-1}) et densité en longueur des fines racines mortes (FRNLD en cm cm^{-3}); avec erreur standard en italic pour racines fines et grosses de 2 à 5 mm. Dans le cadre (racines fines; n = 16) tests statistiques par ANOVA et Student-Newman-Keuls interval pour chaque couche, révélant une valeur significativement plus basse pour **a** que pour **b** ($P < 0.05$).

		Racines fines (< 2 mm)					Racines grosses (> 2 mm)			Racines mortes	
	couche	FRB	FRLD	SRL	fraction très fine		CRB	CRB	CRB	FRN	FRNLD
	cm	kg ha^{-1}	cm cm^{-3}	m g^{-1}	%	%	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	cm cm^{-3}
traitement		n = 16			biomasse	longueur	2-5 mm	5-10	>10 mm	< 2 mm	
Témoin	0-5	2194 *179*	5.11 *0.50*	11.9 *0.91*	28.2	80.1	464 *155*	132	0	95	0.73
NCa	0-5	1716 *223*	4.12 *0.46*	12.8 *0.82*	34.5	77.7	289 *98*	399	0	220	0.99
Témoin	5-15	1043 *119*	0.92 *0.09*	9.65 *0.88*	20.7	63.6	497 *105*	398	0	298	0.58
NCa	5-15	827 *75*	0.81 *0.09*	9.95 *0.69*	28.6	78.6	562 *126*	254	0	494	0.75
Témoin	15-30	1209 *124* **b**	0.63 *0.06*	8.25 *0.68* **a**	22.0	76.3	888 *213*	755	922	844	0.82
NCa	15-30	651 *95* **a**	0.46 *0.06*	12.3 1.43 **b**	48.3	79.7	588 *154*	118	0	316	0.58
Témoin	30-45	1091 *137* **b**	0.61 *0.07*	9.08 *0.98*	26.5	76.5	827 *206*	1437	0	997	0.88
NCa	30-45	598 *81* **a**	0.45 *0.07*	12.7 *1.58*	53.9	83.4	386 *168*	390	0	480	0.60
Témoin	45-60	777 *95*	0.47 *0.06*	9.95 *0.98*	24.6	75.6	367 *120*	527	0	334	0.49
NCa	45-60	563 *86*	0.35 *0.04*	10.7 *1.01*	42.5	78.5	209 *113*	278	0	145	0.28
Témoin	60-75	633 *341*	0.43 *0.18*	11.3 *1.84*			0	0	0	334	0.49
NCa	60-75	554 *420*	0.32 *0.19*	11.4 *3.59*			0	0	0	145	0.28

		Racines vivantes					Racines mortes				
Totales:		< 2 mm		> 2 mm		Tout		< 2 mm		Tout	
		FRB	FRL	CRB	CRL	RB	RL	FRN	FRNL	RN	RNL
		kg	10^6 m	kg	10^6 m	kg	10^6 m	kg	10^6 m	kg	10^6 m
traitement		ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}
Témoin	0-75	6947	66.9	7214	1.05	14161	68	2902	49.6	4254	49.9
NCa		4905	52.3	3473	0.67	8382	53	1800	38.3	4491	38.5

Tronçais: sept. 1995 Biomasse racines fines (FRB en kg ha^{-1}), densité en longueur des racines fines (FRLD en cm cm^{-3}), longueur racinaire spécifique, pourcentage des racines très fines (< 0.5 mm) sur le total des racines fines (< 2 mm) (% de biomasse et de longueur racinaire), biomasse des racines grosses (CRB en kg ha^{-1}), masse des fines racines mortes (FRN en kg ha^{-1}) et densité en longueur des fines racines mortes (FRNLD en cm cm^{-3}); avec erreur standard en italic pour racines fines et grosses de 2 à 5 mm. Dans le cadre (racines fines; n = 16) tests statistiques par ANOVA et Student-Newman-Keuls interval pour chaque couche, révélant pas de différences significatives.

		Racines fines (< 2 mm)					Racines grosses (> 2 mm)			Racines mortes	
	couche	FRB	FRLD	SRL	fraction très fine		CRB	CRB	CRB	FRN	FRNLD
	cm	kg ha^{-1}	cm cm^{-3}	m g^{-1}	%	%	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	cm cm^{-3}
traitement		n = 16			biomasse	longueur	2-5 mm	5-10	>10 mm	< 2 mm	
Témoin	0-5	879 *95*	2.50 *0.19*	14.9 *0.87*	38.6	76.9	104 *65*	0	0	353	1.46
NPKCa	0-5	997 *83*	2.68 *0.24*	14.0 *1.26*	32.0	83.7	164 *81*	0	0	232	1.55
Témoin	5-15	977 *100*	0.82 *0.08*	8.74 *0.59*	29.3	76.2	658 *152*	970	0	421	0.78
NPKCa	5-15	1026 *118*	0.76 *0.09*	7.68 *0.57*	29.8	78.8	896 *159*	331	601	533	0.89
Témoin	15-30	863 *118*	0.41 *0.04*	8.17 *0.65*	21.5	70.8	730 *214*	1189	1609	684	0.63
NPKCa	15-30	810 *124*	0.43 *0.06*	8.86 *0.95*	32.4	77.3	968 *222*	672	2431	746	0.79
Témoin	30-45	577 *91*	0.25 *0.03*	9.57 *2.41*	37.9	78.3	511 *160*	802	424	249	0.33
NPKCa	30-45	513 *105*	0.23 *0.04*	9.51 *2.22*	29.9	73.4	579 *312*	0	0	373	0.39
Témoin	45-60	324 *88*	0.18 *0.04*	14.0 *7.09*	10.3	57.1	171 *171*	0	1234	249	0.33
NPKCa	45-60	526 *173*	0.17 *0.03*	8.41 *1.82*	16.0	51.9	396 *214*	252	802	373	0.39

		Racines vivantes					Racines mortes				
Totales:		< 2 mm		> 2 mm		Tout		< 2 mm		Tout	
		FRB	FRL	CRB	CRL	RB	RL	FRN	FRNL	RN	RNL
		kg	10^6 m	kg	10^6 m	kg	10^6 m	kg	10^6 m	kg	10^6 m
traitement		ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}	ha^{-1}
Témoin	0-60	3620	33.3	8402	0.82	12022	34.1	1956	34.6	2301	34.7
NPKCa		3872	33.5	8092	0.93	11964	34.4	2257	40.1	3409	40.4

St.Anthonis 35c: oct. 1995 Biomasse racines fines (FRB en kg ha^{-1}), densité en longueur des racines fines (FRLD en cm cm^{-3}), longueur racinaire spécifique, pourcentage des racines très fines (< 0.5 mm) sur le total des racines fines (< 2 mm) (% de biomasse et de longueur racinaire), biomasse des racines grosses (CRB en kg ha^{-1}), masse des fines racines mortes (FRN en kg ha^{-1}) et densité en longueur des fines racines mortes (FRNLD en cm cm^{-3}); avec erreur standard en italic pour racines fines et grosses de 2 à 5 mm. Dans le cadre (racines fines; n = 16) tests statistiques par ANOVA et Student-Newman-Keuls interval pour chaque couche, révélant une valeur significativement plus basse pour **a** que pour **b** ($P < 0.05$).

		Racines fines (< 2 mm)					Racines grosses (> 2 mm)			Racines mortes	
traitement	couche cm	FRB kg ha^{-1} n = 16	FRLD cm cm^{-3}	SRL m g^{-1}	fraction très fine % biomasse	% longueur	CRB kg ha^{-1} 2-5 mm	CRB kg ha^{-1} 5-10	CRB kg ha^{-1} >10 mm	FRN kg ha^{-1} < 2 mm	FRNLD cm cm^{-3}
Témoin	0-5	1132 *101* **a**	4.65 *0.34* **a**	21.3 *0.88*	58.6	92.6	61 *30*	0	0	494	1.48
Ca	0-5	1677 *189* **b**	7.76 *0.79* **b**	23.8 *0.91*	66.0	93.2	108 *54*	46	0	628	1.84
Témoin	5-15	1331 *117*	2.04 *0.18*	15.8 *1.02*	44.5	88.5	300 *105*	285	0	910	2.31
Ca	5-15	1068 *101*	1.74 *0.12*	17.3 *1.18*	33.3	82.2	433 *126*	189	0	561	1.53
Témoin	15-30	1831 *161*	1.81 *0.13*	15.3 *0.77*	35.1	84.5	1065 *194*	541	1641	740	1.40
Ca	15-30	1751 *124*	1.63 *0.11*	14.5 *0.85*	33.6	84.4	738 *139*	1915	882	525	1.22
Témoin	30-45	1326 *129*	1.33 *0.13*	15.8 *1.04*	53.6	85.8	813 *158*	1085	2441	349	0.93
Ca	30-45	1278 *125*	1.19 *0.10*	14.8 *0.94*	44.6	87.3	981 *194*	1127	1624	398	0.62
Témoin	45-60	803 *138*	0.87 *0.13* **b**	18.9 *1.40*	65.3	86.7	257 *96*	205	0	552	0.65
Ca	45-60	828 *145*	0.61 *0.06* **a**	14.6 *1.68*	60.0	87.2	219 *107*	82	0	400	0.53
Témoin	60-75	120 *75*	0.07 *0.02*	11.5 *4.73*			0	0	0	238	0.33
Ca	60-75	295 *232*	0.30 *0.25*	13.5 *2.25*			0	0	0	179	0.34

		Racines vivantes					Racines mortes				
Totales:		< 2 mm		> 2 mm		Tout		< 2 mm		Tout	
traitement		FRB kg ha^{-1}	FRL 10^6 m ha^{-1}	CRB kg ha^{-1}	CRL 10^6 m ha^{-1}	RB kg ha^{-1}	RL 10^6 m ha^{-1}	FRN kg ha^{-1}	FRNL 10^6 m ha^{-1}	RN kg ha^{-1}	RNL 10^6 m ha^{-1}
Control	0-75	6543	104.9	8694	1.05	15237	106.0	3283	80.2	3617	80.5
Ca		6897	112.2	8344	1.11	15241	113.3	2691	65.2	2984	65.4

St.Anthonis 46a: oct. 1995 Biomasse racines fines (FRB en kg ha^{-1}), densité en longueur des racines fines (FRLD en cm cm^{-3}), longueur racinaire spécifique, pourcentage des racines très fines (< 0.5 mm) sur le total des racines fines (< 2 mm) (% de biomasse et de longueur racinaire), biomasse des racines grosses (CRB en kg ha^{-1}), masse des fines racines mortes (FRN en kg ha^{-1}) et densité en longueur des fines racines mortes (FRNLD en cm cm^{-3}); avec erreur standard en italic pour racines fines et grosses de 2 à 5 mm. Dans le cadre (racines fines; n = 16) tests statistiques par ANOVA et Student-Newman-Keuls interval pour chaque couche, révélant une valeur significativement plus basse pour **a** que pour **b** ($P < 0.05$).

		Racines fines (< 2 mm)					Racines grosses (> 2 mm)			Racines mortes	
traitement	couche cm	FRB kg ha^{-1} n = 16	FRLD cm cm^{-3}	SRL m g^{-1}	fraction très fine % biomasse	% longueur	CRB kg ha^{-1} 2-5 mm	CRB kg ha^{-1} 5-10	CRB kg ha^{-1} >10 mm	FRN kg ha^{-1} < 2 mm	FRNLD cm cm^{-3}
Témoin	0-5	2093 *332*	6.68 *0.95*	16.2 *0.88* **a**	63.8	90.7	106 *77*	0	0	812	2.67
Ca	0-5	1755 *182*	7.53 *0.69*	22.2 *0.93* **b**	47.0	91.5	86 *51*	88	0	697	3.18
Témoin	5-15	1099 *176*	1.43 *0.27*	13.3 *1.10* **a**	48.8	91.1	289 *99*	697	0	557	0.72
Ca	5-15	1056 *99*	1.89 *0.20*	17.9 *0.87* **b**	48.1	89.8	474 *135*	600	0	288	0.48
Témoin	15-30	1136 *189*	0.80 *0.15*	10.4 *0.76* **a**	36.8	86.4	507 *121*	404	879	438	0.45
Ca	15-30	881 *130*	0.87 *0.09*	16.7 *1.51* **b**	39.1	84.1	426 *130*	763	0	372	0.41
Témoin	30-45	577 *85*	0.34 *0.05*	9.99 *0.91*	26.7	74.0	164 *54*	1111	267	520	0.36
Ca	30-45	730 *91*	0.39 *0.04*	8.61 *0.44*	24.4	78.2	226 *117*	510	0	568	0.38
Témoin	45-60	357 *73*	0.16 *0.03*	12.1 *2.87*	29.2	68.3	156 *78*	0	0	805	0.35
Ca	45-60	435 *114*	0.16 *0.03*	12.1 *4.41*	27.0	67.8	192 *89*	152	0	737	0.30
Témoin	60-75	98 *75*	0.04 *0.01*	20.7 *13.1*			0	0	0	213	0.17
Ca	60-75	189 *163*	0.06 *0.02*	23.0 *16.2*			0	0	0	244	0.14

		Racines vivantes					Racines mortes				
Totales:		< 2 mm		> 2 mm		Tout		< 2 mm		Tout	
traitement		FRB kg ha^{-1}	FRL 10^6 m ha^{-1}	CRB kg ha^{-1}	CRL 10^6 m ha^{-1}	RB kg ha^{-1}	RL 10^6 m ha^{-1}	FRN kg ha^{-1}	FRNL 10^6 m ha^{-1}	RN kg ha^{-1}	RNL 10^6 m ha^{-1}
Control	0-75	5360	67.2	4580	0.56	9940	67.8	3345	40.5	3492	40.6
Ca		5046	78.7	3517	0.59	8563	79.3	2906	39.2	3137	39.3

Annexe 4.4 Fiches de résultats pour les mycorhizes

La Croix-Scaille: mars 1995 Nombre total d'apex avec mycorhizes (M in 10^9 ha^{-1}), longueur des racines fines (L en 10^6 m ha^{-1}), longueur spécifique des racines (SRL en m g^{-1}), nombre d'apex par cm de racine fine (N/l) et pourcentage de mycorhizes par morphotypes principaux (A1-C2) en fonction des traitements calciques 5 années (V) et 1 année (N) après l'application (pour les racines n = 12 pour 0-45 cm et 2 pour 45-55 cm; pour les mycorhizes n = 4 pour 0-45 cm et 2 pour 45-55 cm; les effets significatifs entre traitements à l'intérieur de la même couche indiqués avec des lettres différentes a, b, et c ; @ = non testé pour valeur somme)

Couche		racines				morphotypes mycorhiziens en %					
cm		M	L	SRL	N/l	A1	A2	B	C1	C2tot	Ctot
0-5	Témoin	3.98	10.1	11.2	4.94 **ab**	0	0	2	62	36	98
	$CaCO_3$-V	3.06	13.1	11.5	2.68 **b**	15	4	1	47	34	81
	$CaCO_3$-N	3.55	9.82	9.91	4.35 **ab**	0	2	6	66	26	92
	$CaSO_4$-V	6.46	10.9	10.5	3.46 **ab**	2	14	0	50	34	84
	$CaSO_4$-N	2.67	6.15	12.4	4.67 **ab**	0	8	6	56	29	85
	Mélange	5.58	9.70	8.40	5.46 **a**	1	4	6	65	24	89
5-15	Témoin	3.11	6.55	10.2	3.60	10	1	1	59	29	88
	$CaCO_3$-V	2.02	6.62	9.32	2.99	1	0	2	51	47	98
	$CaCO_3$-N	5.16	5.14	10.7	6.66	2	0	1	40	57	97
	$CaSO_4$-V	4.98	8.25	9.23	4.34	1	1	1	52	45	97
	$CaSO_4$-N	1.86	7.93	9.76	3.09	1	1	1	47	50	97
	Mélange	1.63	5.15	8.41	3.35	1	11	1	43	44	87
15-30	Témoin	1.97	5.58	13.7	3.10	1	1 **b**	0	78 **a**	19 **b**	97
	$CaCO_3$-V	0.52	5.59	9.53	1.65	2	0 **b**	1	53 **b**	44 **ab**	97
	$CaCO_3$-N	1.87	7.50	14.7	2.40	2	0 **b**	1	51 **b**	46 **a**	97
	$CaSO_4$-V	0.70	6.62	15.3	1.60	1	1 **b**	1	68 **ab**	28 **ab**	96
	$CaSO_4$-N	1.24	5.03	14.3	2.42	0	1 **b**	1	58 **ab**	41 **ab**	99
	Mélange	1.24	5.73	19.5	1.85	5	8 **a**	6	48 **b**	32 **ab**	80
30-45	Témoin	0.49	3.84	14.8	1.81	0	1	1	66	32	98
	$CaCO_3$-V	0.37	4.23	12.4	1.02	0	0	0	58	42	100
	$CaCO_3$-N	0.75	4.28	14.0	1.63	1	0	2	47	50	97
	$CaSO_4$-V	0.97	4.81	11.0	2.05	1	1	2	68	28	96
	$CaSO_4$-N	0.77	4.59	15.4	1.29	0	0	0	65	34	99
	Mélange	1.32	5.27	13.5	2.18	0	1	7	60	32	92
45-55	Témoin	0.16	1.64	10.8	1.12	0	0	2	78 **a**	20 **b**	98
	$CaCO_3$-V	0.46	4.17	14.1	1.17	0	0	0	58 **b**	41 **a**	99
	$CaCO_3$-N	0.07	0.82	22.5	0.82	0	0	0	77 **ab**	23 **ab**	100
	$CaSO_4$-V	0.22	0.88	17.2	1.94	0	0	0	76 **ab**	24 **ab**	100
	$CaSO_4$-N	0.17	0.47	18.1	3.82	0	0	0	46 **ab**	54 **ab**	100
	Mélange	0.31	2.23	9.85	1.17	0	0	3	69 **ab**	28 **ab**	97
somme		ns	@	@	ns	ns	ns	*	*	*	ns

La Croix-Scaille: juin 1995 Nombre total d'apex avec mycorhizes (M in 10^9 ha^{-1}), longueur des racines fines (L en 10^6 m ha^{-1}), longueur spécifique des racines (SRL en m g^{-1}), nombre d'apex par cm de racine fine (N/l) et pourcentage de mycorhizes par morphotypes principaux (A1-C2) en fonction des traitements calciques 1 année (N) après l'application (pour les racines n = 12 pour 0-45 cm et 2 pour 45-55 cm; pour les mycorhizes n = 4 pour 0-45 cm et 2 pour 45-55 cm; les effets significatifs entre traitements à l'intérieur de la même couche indiqués avec des lettres différentes a et b ; @ = non testé pour valeur somme)

Couche		racines				morphotypes mycorhiziens en %							
cm		M	L	SRL	N/l	A1	A2	B	C1	C2oth	C2(X)	C2tot	Ctot
0-5	Témoin	3.17	8.78 **ab**	11.9	4.70 **ab**	0	0 **b**	1	71	16	12	28	99
	$CaCO_3$-N	4.49	8.16 **ab**	11.8	4.92 **ab**	0	2 **ab**	2	55	21	21	42	97
	$CaSO_4$-N	2.74	6.33 **b**	9.28	3.59 **b**	0	2 **ab**	1	69	14	15	29	98
	Mélange	6.94	11.0 **a**	12.0	6.04 **a**	0	5 **a**	0	59	20	16	36	95
5-15	Témoin	0.92	6.82	8.49	1.97	0	3	1	55	20	21	41	96
	$CaCO_3$-N	2.18	6.04	8.39	3.38	0	1	6	63	18	13	31	94
	$CaSO_4$-N	1.27	5.97	8.41	2.70	0	1	1	67	21	10	31	98
	Mélange	1.31	6.71	8.38	2.48	1	1	0	61	15	22	37	98
15-30	Témoin	0.45 **b**	5.29	11.1	1.49 **b**	0	0	0	71	15	14	29	100
	$CaCO_3$-N	2.22 **a**	6.47	11.2	2.99 **a**	0	2	0	64	25	8	33	97
	$CaSO_4$-N	2.03 **a**	6.91	12.8	2.66 **ab**	0	1	0	65	26	8	34	99
	Mélange	1.21 **ab**	5.99	13.0	2.38 **ab**	0	2	0	69	17	12	29	98
30-45	Témoin	0.40	4.81 **ab**	11.9	1.33	0	1	0	64	16	19	35	99
	$CaCO_3$-N	0.58	3.86 **ab**	10.8	1.47	0	1	0	64	19	16	35	99
	$CaSO_4$-N	0.78	2.91 **a**	16.1	2.26	0	0	1	77	16	6	22	99
	Mélange	0.82	6.33 **b**	11.0	1.71	0	1	0	63	25	11	36	99
45-55	Témoin	0.87	6.88	43.0	1.38	0	0	0	70	26	4	30	100
	$CaCO_3$-N	0.16	1.11	18.9	1.42	0	0	0	76	20	5	25	101
	$CaSO_4$-N	0.22	2.24	23.5	1.12	0	2	0	74	25	0	25	99
	Mélange	0.13	0.84	8.54	2.44	0	0	0	57	29	14	43	100
somme		ns	@	@	ns	ns	ns	ns	ns	ns	ns	ns	ns

La Croix-Scaille: septembre 1995 Nombre total d'apex avec mycorhizes (M in 10^9 ha^{-1}), longueur des racines fines (L en 10^6 m ha^{-1}), longueur spécifique des racines (SRL en m g^{-1}), nombre d'apex par cm de racine fine (N/l) et pourcentage de mycorhizes par morphotypes principaux (A1-C2) en fonction des traitements calciques 5 années (V) et 1 année (N) après l'application (pour les racines n = 12 pour 0-45 cm et 2 pour 45-55 cm; pour les mycorhizes n = 4 pour 0-45 cm et 2 pour 45-55 cm; les effets significatifs entre traitements à l'intérieur de la même couche indiqués avec des lettres différentes a, b, et c ; @ = non testé pour valeur somme)

Couche		racines				morphotypes mycorhiziens en %							
cm		M	L	SRL	N/l	A1	A2	B	C1	C2oth	C2(X)	C2tot	Ctot
0-5	Témoin	3.97	8.22 **ab**	8.66	5.15	1	1	2	79 **a**	7 **b**	10	17 **b**	96
	$CaCO_3$-V	3.56	10.3 **ab**	11.3	3.77	1	7	3	51 **b**	17 **a**	21	38 **a**	89
	$CaCO_3$-N	4.05	5.65 **c**	11.4	6.76	0	2	0	70 **ab**	16 **ab**	12	28 **ab**	98
	$CaSO_4$-V	5.30	11.7 **a**	11.3	4.43	1	16	2	58 **b**	11 **ab**	14	25 **ab**	83
	$CaSO_4$-N	2.41	6.99 **bc**	12.6	4.01	0	6	0	70 **ab**	12 **ab**	12	24 **ab**	94
	Mélange	4.30	9.12 **ab**	12.6	3.77	0	6	2	78 **a**	6 **b**	8	14 **b**	92
5-15	Témoin	0.91	5.43	7.16 **b**	2.40	0	0	0	69	10	21 **ab**	31 **ab**	100
	$CaCO_3$-V	0.96	4.59	9.6 **ab**	1.61	0	1	0	53	16	30 **a**	46 **a**	99
	$CaCO_3$-N	0.82	5.23	7.25 **ab**	1.61	0	0	0	64	15	20 **ab**	35 **ab**	99
	$CaSO_4$-V	2.24	5.80	10.2 **a**	3.42	1	6	0	71	17	5 **b**	22 **b**	93
	$CaSO_4$-N	0.87	6.77	23.3 **ab**	2.14	0	0	0	71	11	18 **ab**	29 **ab**	100
	Mélange	1.81	5.78	8.69 **ab**	3.30	0	3	0	64	11	22 **a**	33 **ab**	97
15-30	Témoin	2.88	6.72	15.3	3.19	0	1	3	77	7 **b**	12	19	96
	$CaCO_3$-V	1.12	7.66	14.4	1.56	0	0	0	80	13 **ab**	7	20	100
	$CaCO_3$-N	1.24	6.84	14.9	2.51	0	1	0	65	15 **ab**	19	34	99
	$CaSO_4$-V	2.00	6.78	15.1	2.29	0	1	0	75	17 **a**	7	24	99
	$CaSO_4$-N	1.87	8.02	10.6	2.22	0	1	1	72	9 **b**	16	25	97
	Mélange	2.60	7.76	11.0	2.03	0	3	2	76	13 **ab**	7	20	96
30-45	Témoin	0.95	3.39 **b**	19.2 **a**	2.28	0	1	1	78 **a**	8 **b**	12 **a**	20	98
	$CaCO_3$-V	1.38	8.38 **a**	13.5 **ab**	2.39	0	0	0	77 **ab**	17 **a**	6 **ab**	23	100
	$CaCO_3$-N	0.54	3.56 **b**	11.7 **b**	1.70	0	1	0	69 **ab**	16 **ab**	14 **ab**	30	99
	$CaSO_4$-V	2.18	5.68 **ab**	17.7 **ab**	3.17	0	0	0	65 **ab**	15 **a**	19 **ab**	35	100
	$CaSO_4$-N	1.08	6.28 **ab**	16.8 **ab**	1.68	0	1	0	79 **ab**	20 **ab**	1 **b**	21	100
	Mélange	1.10	6.01 **ab**	10.4 **b**	2.19	0	2	1	67 **b**	12 **ab**	18 **ab**	30	97
45-55	Témoin	1.47	3.00 **b**	16.8	5.27	0	0	0	54	32	14	46	100
	$CaCO_3$-V	2.87	4.29 **ab**	13.9	6.30	0	0	0	49	44	7	51	100
	$CaCO_3$-N	0.46	2.35 **ab**	7.51	1.91	0	0	0	64	30	5	35	99
	$CaSO_4$-V	2.65	4.94 **a**	21.3	5.56	0	0	0	53	40	8	48	101
	$CaSO_4$-N	2.15	5.80 **ab**	7.67	3.56	0	0	5	59	35	1	36	95
	Mélange	0.49	2.06 **b**	26.2	2.39	0	4	0	48	22	26	48	96
somme		ns	@	@	ns	ns	ns	ns	ns	*	ns	ns	ns

La Croix-Scaille: mars 1996 Nombre total d'apex avec mycorhizes (M in 10^9 ha^{-1}), longueur des racines fines (L en 10^6 m ha^{-1}), longueur spécifique des racines (SRL en m g^{-1}), nombre d'apex par cm de racine fine (N/l) et pourcentage de mycorhizes par morphotypes principaux (A1-C2) en fonction des traitements calciques 18 mois (N) après l'application (pour les racines n = 12 pour 0-45 cm et 2 pour 45-55 cm; pour les mycorhizes n = 4 pour 0-45 cm et 2 pour 45-55 cm; les effets significatifs entre traitements à l'intérieur de la même couche indiqués avec des lettres différentes a et b ; @ = non testé pour valeur somme)

Couche		racines				morphotypes mycorhiziens en %							
cm		M	L	SRL	N/l	A1	A2	B	C1	C2oth	C2(X)	C2tot	Ctot
0-5	Témoin	9.40	12.7	12.7	6.26	0	1	5	73	7	14	21	94
	$CaCO_3$-N	3.78	8.75	10.2	3.60	0	1	0	77	13	10	23	100
	$CaSO_4$-N	6.22	10.7	12.5	5.38	0	1	1	80	2	16	18	98
	Mélange	6.69	11.7	11.6	5.26	0	5	1	82	6	7	13	95
5-15	Témoin	7.51 **a**	9.50 **a**	9.91	6.04 **a**	0	2	3	79	3	13	16	95
	$CaCO_3$-N	1.73 **b**	4.82 **b**	7.62	2.96 **b**	2	1	2	83	7	6	13	96
	$CaSO_4$-N	5.41 **ab**	9.83 **a**	9.00	5.63 **ab**	0	1	0	69	1	28	29	98
	Mélange	2.38 **b**	6.37 **b**	9.42	3.71 **ab**	0	3	1	80	11	6	17	97
15-30	Témoin	2.92	5.28 **b**	10.3	4.15	0	0	1	79	9	11	20 **a**	99
	$CaCO_3$-N	3.01	7.85 **a**	9.95	3.60	0	0	0	93	2	6	8 **b**	101
	$CaSO_4$-N	2.52	6.87 **ab**	10.8	3.31	0	0	0	79	2	19	21 **ab**	100
	Mélange	1.92	5.33 **b**	8.78	2.97	0	1	1	85	2	10	12 **ab**	97
30-45	Témoin	1.65	3.90 **b**	13.8	3.45 **a**	0	1	5	76	10	8	18	94
	$CaCO_3$-N	0.70	4.22 **b**	13.6	1.52 **b**	0	1	0	80	8	12	20	100
	$CaSO_4$-N	1.31	3.85 **b**	12.7	2.57 **ab**	0	1	0	87	4	8	12	99
	Mélange	2.34	6.45 **a**	10.7	2.89 **ab**	0	1	4	82	5	9	14	96
45-55	Témoin	0.44	2.62	13.6	3.05	0	1	1	77	4	17 **ab**	21 **ab**	98
	$CaCO_3$-N	0.54	2.31	12.5	2.36	0	0	1	90	4	5 **b**	9 **ab**	99
	$CaSO_4$-N	0.63	2.09	16.4	3.34	0	4	1	91	3	1 **b**	4 **b**	95
	Mélange	0.57	3.17	8.41	1.59	0	0	0	72	4	24 **a**	28 **a**	100
somme		*	@	@	ns	ns	ns	*	ns	ns	ns	ns	ns

Fontainebleau: octobre 1994 Nombre total d'apex avec mycorhizes (M in 10^9 ha^{-1}), longueur des racines fines (L en 10^6 m ha^{-1}), longueur spécifique des racines (SRL en m g^{-1}), nombre d'apex par cm de racine fine (N/l) et pourcentage de mycorhizes par morphotypes principaux (A1-C2) en fonction des traitements calciques 25 années après l'application (pour les racines n = 18 pour 0-45 cm et 6 pour 45-65 cm; pour les mycorhizes n = 4; les effets significatifs entre traitements à l'intérieur de la même couche indiqués avec des lettres différentes a, b, et c ; @ = non testé pour valeur somme)

Couche		racines				morphotypes mycorhiziens en %					
cm		M	L	SRL	N/l	A1	A2	B	C1	C2	Ctot
0-5	Témoin	10.7	24.7 **b**	30.4	4.03	0	4	5	36 **a**	55 **b**	91
	$CaCO_3$	9.70	29.3 **b**	31.5	4.85	5	3	6	40 **a**	44 **b**	84
	NPKCa	25.6	41.9 **a**	30.6	5.48	0	6	3	12 **b**	79 **a**	91
5-15	Témoin	7.83 **b**	20.8 **c**	19.0 **b**	4.57	1	7	3	35 **a**	54	89
	$CaCO_3$	12.6 **b**	37.5 **b**	24.3 **a**	3.97	2	10	3	32 **a**	53	85
	NPKCa	38.8 **a**	60.4 **a**	24.3 **a**	5.20	1	14	5	9 **b**	72	81
15-25	Témoin	2.53	9.70 **b**	18.9	3.05	3	5	4	43 **a**	46	89
	$CaCO_3$	4.31	13.3 **b**	19.9	3.46	1	4	5	25 **b**	65	90
	NPKCa	6.17	24.2 **a**	17.4	2.61	1	20	2	9 **b**	69	78
25-45	Témoin	1.36	9.3 **b**	33.2 **a**	1.24	1 **b**	0 **b**	4	48 **a**	47	95 **a**
	$CaCO_3$	1.34	9.8 **b**	16.6 **b**	2.06	0 **b**	5 **b**	4	30 **ab**	61	91 **a**
	NPKCa	3.40	17.9 **a**	17.0 **b**	1.63	3 **a**	18 **a**	5	12 **b**	61	73 **b**
45-65	Témoin	0.65	5.1 **b**	35.9	1.36	1	2	2	44 **a**	51	95
	$CaCO_3$	0.65	6.7 **b**	22.2	1.66	1	1	11	26 **ab**	60	88
	NPKCa	2.46	13.8 **a**	18.5	1.57	9	18	3	14 **b**	56	70
somme		*	@	@	ns	ns	*	ns	*	*	*

Les Trembles: mars 1995 Nombre total d'apex avec mycorhizes (M in 10^9 ha^{-1}), longueur des racines fines (L en 10^6 m ha^{-1}), longueur spécifique des racines (SRL en m g^{-1}), nombre d'apex par cm de racine fine (N/l) et pourcentage de mycorhizes par morphotypes principaux (A1-C2) en fonction des traitements calciques 26 années après l'application (pour les racines n = 16 pour 0-60 cm et 1 pour 60-75 cm; pour les mycorhizes n = 4 pour 0-60 cm et 1 pour 60-75 cm; les effets significatifs entre traitements à l'intérieur de la même couche indiqués avec des lettres différentes a et b ; @ = non testé pour valeur somme)

Couche		racines				morphotypes mycorhiziens en %							
cm		M	L	SRL	N/l	A1	A2	B	C1	C2oth	C2(X)	C2tot	Ctot
0-5	Témoin	22.00	23.5	15.9	8.90	1	2 **b**	4	48	19	27	46	94
	$CaCO_3$	10.95	21.5	15.1	5.59	4	6 **a**	0	43	26	20	46	89
5-15	Témoin	5.88	9.70	10.0	4.89 **a**	2	3	1	33	29	31 **a**	60	93
	$CaCO_3$	2.71	10.7	10.3	2.27 **b**	0	6	0	48	31	15 **b**	46	94
15-30	Témoin	1.39	7.7	12.2	2.77	1	5	0	41	30	23	53	94
	$CaCO_3$	1.15	7.4	11.4	1.92	2	4	2	46	27	18	45	91
30-45	Témoin	0.72	4.0 **b**	13.3	2.11	2	6	0	40	28	24	52	92
	$CaCO_3$	1.80	5.5 **a**	11.1	3.44	1	3	1	44	31	20	51	95
45-60	Témoin	0.75	3.1	14.5	2.1	0	2	1	42	30	25	55	97
	$CaCO_3$	0.48	3.9	9.6	1.7	0	3	1	46	30	20	50	96
60-75	Témoin	0.07	3.3	7.0	0.17	0	13	0	57	30	0	30	87
	$CaCO_3$	0.29	1.8	17.2	6.16	0	0	0	48	36	17	53	101
somme		ns	@	@	ns	ns	ns	ns	ns	ns	ns	ns	ns

Gaie Mariée: mars 1995 Nombre total d'apex avec mycorhizes (M in 10^9 ha^{-1}), longueur des racines fines (L en 10^6 m ha^{-1}), longueur spécifique des racines (SRL en m g^{-1}), nombre d'apex par cm de racine fine (N/l) et pourcentage de mycorhizes par morphotypes principaux (A1-C2) en fonction des traitements calciques 27 années après l'application (pour les racines n = 16 pour 0-60 cm et 3 pour 60-75 cm; pour les mycorhizes n = 4 pour 0-60 cm et 1 pour 60-75 cm; les effets significatifs entre traitements à l'intérieur de la même couche indiqués avec des lettres différentes a et b ; @ = non testé pour valeur somme)

Couche		racines				morphotypes mycorhiziens en %							
cm		M	L	SRL	N/l	A1	A2	B	C1	C2oth	C2(X)	C2tot	Ctot
0-5	Témoin	6.45	16.7	16.6	3.77	1	4	1	43	23	27	50	93
	$CaCO_3$	9.87	14.7	18.9	4.12	1	7	3	48	16	25	41	89
5-15	Témoin	1.15	7.0 **b**	9.5 **b**	2.38	2	10	0	36	33 **a**	19	52 **a**	88
	$CaCO_3$	3.37	11.7 **a**	14.9 **a**	3.70	2	6	3	54	22 **b**	12	34 **b**	88
15-30	Témoin	1.01	6.2	12.0	2.70	3	3	3	36	32	24	56	92
	$CaCO_3$	1.14	7.8	10.5	2.30	2	6	0	41	32	20	52	93
30-45	Témoin	0.50	4.7	13.4	3.27	0	2	0	37	45	16	61	98
	$CaCO_3$	1.44	4.4	14.8	2.10	4	1	0	34	39	23	62	96
45-60	Témoin	0.06	1.5	14.9	0.97	0	0	0	37	46	17	63	100
	$CaCO_3$	0.11	1.7	15.7	1.51	2	0	0	47	41	10	51	98
60-75	Témoin	0.11	2.2	6.8	0.75	0	0	0	34	66	0	66	100
	$CaCO_3$	0.18	1.5	19	3.02	0	1	1	46	33	18	51	97
somme		ns	@	@	ns	ns	ns	ns	ns	ns	ns	*	ns

Rond du May: septembre 1995 Nombre total d'apex avec mycorhizes (M in 10^9 ha^{-1}), longueur des racines fines (L en 10^6 m ha^{-1}), longueur spécifique des racines (SRL en m g^{-1}), nombre d'apex par cm de racine fine (N/l) et pourcentage de mycorhizes par morphotypes principaux (A1-C2) en fonction des traitements calciques 27 années après l'application (pour les racines n = 16 pour 0-60 cm et pour les mycorhizes n = 4 pour 0-60; les effets significatifs entre traitements à l'intérieur de la même couche indiqués avec des lettres différentes a et b ; @ = non testé pour valeur somme)

Couche		racines				morphotypes mycorhiziens en %							
cm		M	L	SRL	N/l	A1	A2	B	C1	C2oth	C2(X)	C2tot	Ctot
0-5	Témoin	13.6	25.5	11.9	6.61	0	2	2	54	10	33	43	97
	$CaCO_3$	8.17	20.6	12.8	4.02	0	2	0	57	15	26	41	98
5-15	Témoin	3.02	9.2	9.70	2.82	0	4	0	44 **b**	19	33	52	96
	$CaCO_3$	1.97	8.1	10.0	2.87	0	2	1	61 **a**	13	24	37	98
15-30	Témoin	3.30	9.4	8.3 **b**	3.30	0	3	0	52	14	30	44	96
	$CaCO_3$	2.45	6.9	12.3 **a**	3.11	0	3	1	48	20	28	48	96
30-45	Témoin	4.37	9.2	9.10	3.94	0	2	0	70	8	20	28	98
	$CaCO_3$	2.22	6.7	12.7	3.31	0	4	2	62	18	14	32	94
45-60	Témoin	5.68	7.1	10.0	4.94	0	2	3	63	7	25	32	95
	$CaCO_3$	1.05	5.2	10.7	1.85	0	0	0	60	22	17	39	99
somme		*	@	@	ns	ns	ns	ns	ns	*	ns	ns	ns

Bertranges: juin 1995 Nombre total d'apex avec mycorhizes (M in 10^9 ha^{-1}), longueur des racines fines (L en 10^6 m ha^{-1}), longueur spécifique des racines (SRL en m g^{-1}), nombre d'apex par cm de racine fine (N/l) et pourcentage de mycorhizes par morphotypes principaux (A1-C2) en fonction des traitements calciques 24 années après l'application (pour les racines n = 16 pour 0-30 cm et 2 pour 30-45 cm; pour les mycorhizes n = 4 pour 0-30 et 2 pour 30-45 cm; les effets significatifs entre traitements à l'intérieur de la même couche indiqués avec des lettres différentes a et b ; @ = non testé pour valeur somme)

Couche		racines				morphotypes mycorhiziens en %							
cm		M	L	SRL	N/l	A1	A2	B	C1	C2oth	C2(X)	C2tot	Ctot
0-5	Témoin	10.8	11.8	25.0	5.33	0	1 **a**	3	50	15	33	48	98
	$CaCO_3$	10.6	15.4	20.3	6.77	0	6 **a**	2	33	23	36	59	92
5-15	Témoin	6.47	17.6	16.3	4.07	0	1	0	44	13 **b**	42	55	99
	$CaCO_3$	17.7	19.7	15.2	6.69	0	1	0	26	23 **a**	49	72	98
15-30	Témoin	10.1	9.1	14.1	17.7	0	2	0	50	20	28	48	98
	$CaCO_3$	1.91	8.5	14.2	2.38	0	1	0	44	19	35	54	98
30-45	Témoin	3.61	1.8	14.4	2.51	0	0	2	54	28	17	45	99
	$CaCO_3$	12.2	6.4	17.5	3.55	0	1	0	45	18	36	54	99
somme		ns	@	@	ns	ns	ns	ns	*	ns	ns	*	ns

Tronçais: septembre 1995 Nombre total d'apex avec mycorhizes (M in 10^9 ha^{-1}), longueur des racines fines (L en 10^6 m ha^{-1}), longueur spécifique des racines (SRL en m g^{-1}), nombre d'apex par cm de racine fine (N/l) et pourcentage de mycorhizes par morphotypes principaux (A1-C2) en fonction des traitements calciques 14 années après l'application (pour les racines n = 16 pour 0-30 cm et entre 4 et 13 pour 30-60 cm; pour les mycorhizes n = 4 pour 0-60; les effets significatifs entre traitements à l'intérieur de la même couche indiqués avec des lettres différentes a et b ; @ = non testé pour valeur somme)

Couche		racines				morphotypes mycorhiziens en %							
cm		M	L	SRL	N/l	A1	A2	B	C1	C2oth	C2(X)	C2tot	Ctot
0-5	Témoin	6.79	12.5	14.9	5.32	0	1	1	48	25 **a**	25	50	98 **a**
	NPKCa	4.68	13.4	14.0	5.30	0	7	8	50	8 **b**	28	36	86 **b**
5-15	Témoin	3.64	8.2	8.74	4.29	0	0	2	52	20	26	46	98 **a**
	NPKCa	3.01	7.6	7.68	4.82	0	12	1	51	17	19	36	87 **b**
15-30	Témoin	1.75	6.2	8.17	3.11	0	1	2	47	25	25	50	97
	NPKCa	1.72	6.5	8.86	3.17	0	5	2	48	13	31	44	92
30-45	Témoin	1.46	3.7	9.57	3.39	0	0	2	45	21	32	53	98
	NPKCa	1.73	3.5	9.51	5.07	0	2	2	37	14	43	57	94
45-60	Témoin	1.20	2.7	14.0	5.37	0	0	0	59	22	19	41	100
	NPKCa	1.56	2.5	8.41	6.50	0	0	0	50	14	36	50	100
somme		ns	@	@	ns	ns	*	ns	ns	*	ns	ns	*

St. Anthonis 35c: octobre 1995 Nombre total d'apex avec mycorhizes (M in 10^9 ha^{-1}), longueur des racines fines (L en 10^6 m ha^{-1}), longueur spécifique des racines (SRL en m g^{-1}), nombre d'apex par cm de racine fine (N/l) et pourcentage de mycorhizes par morphotypes principaux (A1-C2) en fonction des traitements calciques 7 années après l'application (pour les racines n = 16 pour 0-60 cm et 2 pour 60-75 cm; pour les mycorhizes n = 4 pour 0-60 et 2 pour 60-75 cm; les effets significatifs entre traitements à l'intérieur de la même couche indiqués avec des lettres différentes a et b ; @ = non testé pour valeur somme)

Couche		racines				morphotypes mycorhiziens en %							
cm		M	L	SRL	N/l	A1	A2	B	C1	C2oth	C2(X)	C2tot	Ctot
0-5	Témoin	41.2	23.3 **b**	21.3	17.3	0	0	14	60	7	19	26	86
	$CaCO_3$	59.1	38.8 **a**	23.8	11.4	0	8	1	61	10	20	30	91
5-15	Témoin	12.2	20.4	15.8	5.19	0	0	6	64	3	27	30	94
	$CaCO_3$	11.0	17.4	17.3	7.47	0	1	2	82	5	10	15	97
15-30	Témoin	26.9	27.1	15.3	9.80	0	0	12	71	1 **b**	15	16	87
	$CaCO_3$	28.8	24.5	14.5	10.7	0	0	2	82	6 **a**	10	16	98
30-45	Témoin	19.6	20.0	15.8	10.2	0	0	13	72	4	11	15	87
	$CaCO_3$	15.0	17.9	14.8	8.41	0	0	1	93	4	2	6	99
45-60	Témoin	8.76	13.1 **a**	18.9	7.06	0	0	5	82	5	8	13	95
	$CaCO_3$	7.04	9.2 **b**	14.6	7.28	1	2	2	86	8	1	9	95
60-75	Témoin	0.59	1.0	11.5	6.04	0	0	0	83	13	3	16	99
	$CaCO_3$	4.65	4.5	13.5	8.09	0	4	0	61	33	2	35	96
somme		ns	@	@	ns	ns	ns	*	ns	*	ns	ns	ns

St. Anthonis 46a: octobre 1995 Nombre total d'apex avec mycorhizes (M in 10^9 ha^{-1}), longueur des racines fines (L en 10^6 m ha^{-1}), longueur spécifique des racines (SRL en m g^{-1}), nombre d'apex par cm de racine fine (N/l) et pourcentage de mycorhizes par morphotypes principaux (A1-C2) en fonction des traitements calciques 7 années après l'application (pour les racines n = 16 pour 0-60 cm et 3 pour 60-75 cm; pour les mycorhizes n = 4 pour 0-60 et 3 pour 60-75 cm; les effets significatifs entre traitements à l'intérieur de la même couche indiqués avec des lettres différentes a et b ; @ non testé pour valeur somme)

Couche		racines				morphotypes mycorhiziens en %							
cm		M	L	SRL	N/l	A1	A2	B	C1	C2oth	C2(X)	C2tot	Ctot
0-5	Témoin	19.5	33.4	16.2 **b**	5.77	0	8	1	74	8	9	17	91
	$CaCO_3$	35.3	37.6	22.2 **a**	8.03	0	11	1	50	8	30	38	88
5-15	Témoin	3.22 **b**	14.3	13.3 **b**	4.42	1	4	2	84	7	3	10	94
	$CaCO_3$	13.8 **a**	18.9	17.9 **a**	9.65	0	7	2	63	6	21	27	90
15-30	Témoin	1.44	12.1	10.4 **b**	2.56	0	0	0	88	8	4	12	100 **a**
	$CaCO_3$	13.8	13.0	16.7 **a**	11.5	0	6	4	63	9	18	27	90 **b**
30-45	Témoin	0.99	5.1	9.99	3.08	0	1	2	79	10	8	18	97
	$CaCO_3$	5.68	5.9	8.61	6.49	0	3	7	76	9	5	14	90
45-60	Témoin	0.39	2.3	12.1	4.73	0	2	7	73	8	9	14	87
	$CaCO_3$	0.54	2.4	12.1	3.31	0	13	0	69	8	10	18	87
60-75	Témoin	0.23	0.5	20.7	4.87	0	0	0	53	32	15	47	100
	$CaCO_3$	0.36	0.9	23.0	4.25	0	3	1	59	23	14	37	90
somme		ns	@	@	ns	ns	ns	ns	*	ns	*	ns	*

Annexe 4.5 Fiches de données des éléments minéraux dans les racines fines

La Croix-Scaille (site 1) : Juin 1994 ; pas de statistique										
traitement	prof	n	S	P	K	Ca	Mg	Mn	Al	Ca/Al
	cm					g kg^{-1}				mole/mole
Témoin	0-5	2	1.22	0.78	6.46	6.86	1.27	0.17	*	*
	5-15	2	1.75	0.71	5.69	9.60	1.82	0.21	*	*
	15-30	2	1.17	0.45	10.36	7.18	1.45	0.17	*	*
	30-45	2	1.41	0.88	4.08	6.78	1.95	0.17	*	*
	45-55	2	1.51	1.18	11.80	10.10	2.11	0.30	*	*
$CaCO_3$-V	0-5	2	1.01	0.39	4.73	5.06	1.42	0.05	*	*
	5-15	2	0.79	0.46	2.65	5.71	1.64	0.07	*	*
	15-30	2	0.76	0.25	9.70	5.80	1.27	0.08	*	*
	30-45	2	0.71	0.26	5.95	4.40	1.80	0.08	*	*
	45-55	2	0.75	0.11	9.84	5.79	2.58	0.11	*	*
$CaSO_4$-V	0-5	2	1.66	0.83	9.47	8.51	2.31	0.22	*	*
	5-15	2	1.46	0.67	4.07	4.61	1.67	0.20	*	*
	15-30	2	0.99	0.54	3.58	4.95	1.53	0.16	*	*
	30-45	2	1.79	0.59	5.57	6.77	2.03	0.21	*	*
	45-55	2	1.76	0.85	7.97	7.09	1.78	0.21	*	*
Nouveau	0-5	1	2.60	1.43	2.73	13.98	2.05	0.10	*	*
bloc	5-15	1	2.73	1.25	3.30	9.22	1.88	0.15	*	*
	15-30	1	2.65	0.93	0.29	8.54	1.74	0.20	*	*
	30-45	1	1.32	0.68	15.90	4.87	1.55	0.15	*	*
	45-55	1	1.45	2.53	8.02	13.02	2.43	0.52	*	*

La Croix-Scaille (site 1) : Septembre 1994 ; pas de statistique										
traitement	prof	n	S	P	K	Ca	Mg	Mn	Al	Ca/Al
						g kg^{-1}				mole/mole
Témoin	0-5	2	1.29	0.73	4.09	3.47	1.16	0.13	*	*
	5-15	2	1.95	0.80	4.25	3.00	0.94	0.15	*	*
	15-30	2	1.13	0.56	3.51	6.18	0.94	0.24	*	*
	30-45	2	1.12	0.42	3.72	2.66	0.95	0.08	*	*
	45-55	2	1.55	0.89	5.45	2.93	1.43	0.20	*	*
$CaCO_3$-V	0-5	1	0.75	0.54	1.38	6.30	1.32	0.11	*	*
	5-15	2	1.54	0.76	8.33	5.47	0.83	1.06	*	*
	15-30	2	0.74	0.40	2.56	2.28	0.60	0.04	*	*
	30-45	2	0.90	0.52	2.93	1.40	1.15	0.07	*	*
	45-55	2	1.34	0.89	3.29	3.26	0.63	0.07	*	*
$CaSO_4$-V	0-5	2	1.52	0.73	7.65	6.32	1.17	0.17	*	*
	5-15	2	1.09	0.59	6.89	4.98	1.41	0.10	*	*
	15-30	2	0.39	0.51	2.60	3.58	0.96	0.10	*	*
	30-45	2	1.85	1.36	4.06	4.34	0.72	0.07	*	*
	45-55	2	0.88	0.44	3.62	4.40	0.97	0.06	*	*

La Croix-Scaille (sites 1 et 2) : Mars 1995 ; pas de statistique										
traitement	prof	n	S	P	K	Ca	Mg	Mn	Al	Ca/Al
						g kg^{-1}				mole/mole
Témoin	0-5	2	*	0.86	2.04	2.33	0.79	0.35	1.65	0.945
	5-15	2	*	0.59	2.05	1.66	0.73	0.27	2.86	0.39
	15-30	2	*	0.37	2.26	1.44	0.76	0.23	5.87	0.165
	30-45	2	*	0.30	2.57	1.06	0.67	0.27	7.33	0.105
	45-55	1	*	0.24	3.25	1.91	0.84	0.04	5.90	0.225
$CaCO_3$-V	0-5	2	*	0.53	2.33	3.93	0.89	0.10	1.62	1.635
	5-15	2	*	0.34	2.74	2.40	0.90	0.08	3.53	0.465
	15-30	2	*	0.26	2.78	1.53	0.74	0.07	6.48	0.165
	30-45	2	*	0.23	3.05	1.60	0.98	0.07	6.79	0.165
	45-55	1	*	0.21	3.06	1.91	0.95	0.02	7.44	0.165
$CaSO_4$-V	0-5	1	*	0.66	2.40	2.30	1.04	0.28	0.46	3.375
	5-15	2	*	0.59	2.47	2.30	0.65	0.15	6.40	0.24
	15-30	2	*	0.44	3.16	2.24	0.72	0.23	7.99	0.195
	30-45	2	*	0.47	3.57	1.80	0.68	0.15	9.78	0.12
	45-55	1	*	0.26	4.28	2.73	1.19	0.09	10.46	0.18
$CaCO_3$-N	0-5	2	*	0.33	1.39	1.79	0.52	0.06	2.30	0.525
	5-15	2	*	0.49	1.87	1.74	0.50	0.13	4.54	0.255
	15-30	2	*	0.35	2.09	1.78	0.63	0.21	6.32	0.195
	30-45	2	*	0.47	8.37	1.62	0.56	0.20	8.03	0.135
	45-55	2	*	0.26	2.49	2.31	0.62	0.08	8.90	0.18
$CaSO_4$-N	0-5	2	*	1.08	2.72	2.30	0.73	0.19	2.74	0.57
	5-15	2	*	0.60	3.56	1.85	0.69	0.23	4.57	0.27
	15-30	2	*	0.30	2.27	1.82	0.63	0.17	6.58	0.18
	30-45	2	*	0.33	2.57	1.33	0.64	0.10	9.09	0.105
	45-55	1	*	0.31	2.43	1.87	0.54	0.13	7.30	0.18
Mélange	0-5	2	*	0.68	2.41	2.75	0.72	0.11	2.26	0.825
	5-15	2	*	0.62	2.65	1.05	0.72	0.14	2.35	0.30
	15-30	2	*	0.60	2.37	1.43	0.71	0.06	4.92	0.195
	30-45	2	*	0.37	2.50	1.03	0.67	0.05	4.61	0.15
	45-55	1	*	1.36	6.45	8.37	1.41	0.52	2.21	2.55

La Croix-Scaille (site 2) : Juin 1995 ; pas de statistique										
traitement	prof	n	S	P	K	Ca	Mg	Mn	Al	Ca/Al
						g kg^{-1}				mole/mole
Témoin	0-5	2	*	0.57	1.79	2.90	0.87	0.18	1.67	1.17
	5-15	2	*	0.33	1.55	1.34	0.48	0.09	2.30	0.39
	15-30	2	*	0.39	2.48	2.53	1.00	0.13	7.21	0.24
	30-45	2	*	0.33	3.26	1.68	0.97	0.19	8.76	0.135
$CaCO_3$-N	0-5	2	*	0.68	2.25	4.08	0.62	0.17	1.50	1.83
	5-15	2	*	0.35	1.96	1.63	0.52	0.20	3.59	0.30
	15-30	2	*	0.32	3.18	2.05	0.69	0.15	6.92	0.195
	30-45	2	*	0.29	4.38	1.69	0.69	0.16	8.84	0.135
$CaSO_4$-N	0-5	2	*	0.65	2.43	2.84	0.66	0.19	2.53	0.765
	5-15	2	*	0.47	3.27	2.89	0.82	0.15	4.11	0.48
	15-30	2	*	0.50	3.32	3.53	0.73	0.17	6.31	0.375
	30-45	2	*	0.40	3.17	1.60	0.67	0.11	8.53	0.12
Mélange	0-5	2	*	0.79	2.25	3.31	0.77	0.05	2.60	0.855
	5-15	2	*	0.54	1.73	2.10	0.70	0.06	3.10	0.45
	15-30	2	*	0.59	2.75	1.90	0.74	0.04	6.58	0.195
	30-45	2	*	0.41	3.22	1.68	0.71	0.04	9.93	0.12

La Croix-Scaille (sites 1 et 2) : Septembre 1995 ; pas de statistique										
traitement	prof	n	S	P	K	Ca	Mg	Mn	Al	Ca/Al
						g kg^{-1}				mole/mole
Témoin	0-5	2	2.02	1.20	5.25	3.16	1.08	0.26	4.65	0.57
	5-15	2	1.26	0.57	4.43	2.65	1.09	0.28	7.59	0.225
	15-30	2	1.93	0.78	4.36	2.44	1.18	0.32	9.15	0.225
	30-45	2	1.38	0.39	5.86	1.88	1.08	0.57	13.00	0.105
$CaCO_3$-V	0-5	2	1.58	0.84	3.07	8.46	0.99	0.10	2.92	1.86
	5-15	2	1.54	0.67	4.12	4.90	1.01	0.11	7.70	0.405
	15-30	2	0.98	0.45	4.51	5.39	1.15	0.07	6.10	0.585
	30-45	2	1.21	0.50	5.33	1.97	1.02	0.10	15.04	0.09
$CaSO_4$-V	0-5	2	1.26	0.73	3.51	3.78	1.06	0.40	2.69	0.99
	5-15	2	1.20	0.65	4.76	3.12	1.15	0.40	7.33	0.285
	15-30	2	1.25	0.54	6.86	3.29	1.51	0.38	12.61	0.195
	30-45	2	1.61	0.63	6.00	2.28	1.30	0.30	13.54	0.135
$CaCO_3$-N	0-5	2	1.25	0.78	3.28	4.16	1.08	0.13	4.24	0.855
	5-15	2	1.24	0.70	4.30	3.44	0.96	0.18	5.48	0.42
	15-30	2	1.82	0.54	4.25	3.31	1.14	0.21	17.60	0.195
	30-45	2	2.40	0.77	4.47	2.15	1.24	0.24	14.88	0.105
$CaSO_4$-N	0-5	2	1.43	0.81	3.92	3.00	0.91	0.36	4.13	0.495
	5-15	2	1.95	0.98	4.74	3.30	0.97	0.19	9.48	0.24
	15-30	2	1.21	0.48	6.56	4.86	1.05	0.15	10.96	0.345
	30-45	2	1.05	0.48	5.58	2.61	0.95	0.16	12.87	0.135
Mélange	0-5	2	1.25	0.87	3.01	3.78	1.08	0.09	2.66	0.96
	5-15	2	1.24	0.78	3.40	3.89	0.84	0.07	4.30	0.75
	15-30	2	2.08	0.94	4.76	3.28	1.35	0.09	11.13	0.20
	30-45	2	1.94	0.66	6.43	2.29	1.30	0.09	11.31	0.15

Fontainebleau (site 3) : Octobre 1994 ; pas de statistique										
traitement	prof	n	S	P	K	Ca	Mg	Mn	Al	Ca/Al
						g kg^{-1}				mole/mole
Témoin	0-5	1	1.31	0.40	1.88	14.09	1.42	0.21	*	*
	5-15	1	0.96	0.13	1.47	13.42	1.30	0.36	*	*
	15-25	1	0.79	0.02	1.42	12.93	0.82	0.22	*	*
	25-45	1	0.52	0.00	2.56	12.71	1.02	0.08	*	*
	45-65	1	0.87	0.00	3.74	32.89	1.45	0.06	*	*
CaO	0-5	1	1.25	0.38	7.69	20.04	1.21	0.17	*	*
	5-15	1	1.10	0.00	5.44	25.20	1.34	0.12	*	*
	15-25	1	1.13	0.00	4.85	20.27	2.00	0.27	*	*
	25-45	1	1.02	0.00	3.68	14.54	0.96	0.09	*	*
	45-65	1	1.07	0.22	6.43	36.07	1.16	0.09	*	*
NPKCa	0-5	1	1.34	0.51	1.46	7.32	1.81	0.19	*	*
	5-15	1	1.03	0.36	1.64	3.75	1.96	0.20	*	*
	15-25	1	0.78	0.18	1.51	8.06	1.49	0.30	*	*
	25-45	1	0.80	0.00	2.09	7.40	1.81	0.20	*	*
	45-65	1	0.80	0.00	2.12	13.89	1.54	0.10	*	*

Les Trembles (site 4) : Mars 1995 ; pas de statistique										
traitement	prof	n	S	P	K	Ca	Mg	Mn	Al	Ca/Al
						g kg^{-1}				mole/mole
Témoin	0-5	2	*	0.47	2.34	2.04	0.99	0.54	1.08	1.275
	5-15	2	*	0.37	2.44	2.90	0.85	0.47	2.11	0.93
	15-30	2	*	0.22	2.52	1.51	0.86	0.23	4.79	0.21
	30-45	2	*	0.27	3.09	1.31	0.71	0.21	6.72	0.135
	45-60	2	*	0.18	2.69	2.68	1.26	0.14	5.24	0.345
NCa	0-5	2	*	0.50	2.57	3.23	1.08	0.49	1.23	1.77
	5-15	2	*	0.33	1.96	2.25	0.84	0.18	4.38	0.345
	15-30	2	*	1.13	2.50	2.93	0.91	0.24	4.42	0.45
	30-45	2	*	0.28	2.66	1.45	0.77	0.18	4.35	0.225
	45-60	2	*	0.21	2.63	0.86	1.03	0.15	3.33	0.18

Gaie Mariée (site 5) : Mars 1995 ; pas de statistique										
traitement	prof	n	S	P	K	Ca	Mg	Mn	Al	Ca/Al
						g kg^{-1}				mole/mole
Témoin	0-5	2	*	0.40	2.30	2.59	1.33	0.55	0.89	1.965
	5-15	2	*	0.34	2.73	2.57	1.23	0.47	2.79	0.63
	15-30	2	*	0.30	3.04	2.04	1.01	0.20	5.53	0.255
	30-45	2	*	0.24	3.36	4.02	0.95	0.16	4.22	0.645
	45-60	2	*	0.18	2.95	2.14	1.08	0.08	4.69	0.30
NCa	0-5	2	*	0.58	2.59	5.17	1.20	1.18	2.64	1.32
	5-15	2	*	0.37	2.65	4.95	0.99	1.16	2.34	1.425
	15-30	2	*	0.37	2.00	4.51	1.30	0.22	4.39	0.69
	30-45	1	*	0.27	2.98	4.67	1.30	0.23	3.58	0.885
	45-60	1	*	0.19	3.18	4.83	0.92	0.18	2.76	1.185

Rond du May (site 6) : Septembre 1995 ; pas de statistique										
traitement	prof	n	S	P	K	Ca	Mg	Mn	Al	Ca/Al
						g kg^{-1}				mole/mole
Témoin	0-5	2	1.24	0.54	4.03	3.91	1.55	0.70	1.67	1.65
	5-15	2	0.94	0.37	3.79	3.40	1.68	0.47	3.77	0.615
	15-30	2	0.89	0.43	4.01	2.16	1.12	0.46	5.42	0.285
	30-45	2	0.86	0.37	4.88	1.84	1.38	0.37	5.52	0.24
	45-60	1	0.84	0.37	5.89	1.91	1.29	0.30	5.85	0.225
NCa	0-5	2	1.14	0.50	3.59	4.46	1.61	0.58	1.55	2.01
	5-15	2	1.14	0.36	3.95	3.31	1.43	0.35	4.20	0.585
	15-30	2	1.17	0.35	3.93	4.03	1.38	0.39	5.44	0.525
	30-45	2	0.85	0.34	4.64	4.25	1.31	0.23	4.92	0.81
	45-60	2	0.96	0.32	4.51	2.56	1.40	0.28	4.55	0.375

Bertranges (site 7) : Juin 1995 ; pas de statistique										
traitement	prof	n	S	P	K	Ca	Mg	Mn	Al	Ca/Al
						g kg^{-1}				mole/mole
Témoin	0-5	2	*	0.48	3.59	3.10	1.37	0.23	6.27	0.33
	5-15	2	*	0.41	2.61	3.97	1.21	0.39	4.81	0.555
	15-30	2	*	0.33	2.51	4.57	1.10	0.22	4.34	0.705
CaO	0-5	2	*	0.34	2.63	5.65	1.51	0.29	3.76	1.005
	5-15	2	*	0.32	2.14	4.35	1.37	0.35	4.52	0.645
	15-30	2	*	0.29	2.54	6.25	1.47	0.25	4.17	1.005

Tronçais (site 8) : Septembre 1995 ; pas de statistique										
traitement	prof	n	S	P	K	Ca	Mg	Mn	Al	Ca/Al
						g kg^{-1}				mole/mole
Témoin	0-5	2	1.13	0.57	4.98	4.86	1.80	0.88	3.92	0.87
	5-15	2	0.89	0.46	4.77	4.77	1.64	0.71	4.75	0.705
	15-30	2	1.00	0.50	6.19	3.61	1.61	0.75	5.51	0.45
	30-45	1	1.15	0.53	6.31	5.82	1.85	0.47	5.96	0.66
NPKCaMg	0-5	2	1.63	1.13	6.22	4.86	1.66	0.77	3.69	0.885
	5-15	2	1.12	0.91	3.99	4.01	1.57	0.56	4.77	0.57
	15-30	2	1.06	0.75	3.63	4.59	1.39	0.48	5.36	0.585
	30-45	2	1.31	0.86	6.58	2.89	1.39	0.32	8.13	0.24

St.Anthonis 35c (site 9) : Octobre 1995 ; pas de statistique										
traitement	prof	n	S	P	K	Ca	Mg	Mn	Al	Ca/Al
						g kg^{-1}				mole/mole
Témoin	0-5	2	1.449	0.697	1.956	4.889	1.119	0.137	1.089	6.75
	5-15	2	1.467	0.87	1.974	4.618	1.022	0.175	3.477	1.95
	15-30	2	1.659	0.798	2.327	3.33	0.88	0.163	5.05	0.975
	30-45	2	1.4	0.62	2.263	2.575	0.651	0.125	4.916	0.795
	45-60	2	1.687	0.489	2.435	1.762	0.563	0.08	6.548	0.42
Ca	0-5	2	1.777	0.947	1.826	6.031	1.279	0.201	1.458	6.0
	5-15	2	1.343	1.169	1.731	3.637	0.921	0.268	4.387	1.23
	15-30	2	1.334	0.795	2.151	4.718	1.039	0.258	4.964	1.41
	30-45	2	1.404	0.711	1.795	5.628	1.007	0.142	5.525	1.5
	45-60	2	2.131	0.436	1.45	3.964	0.833	0.057	8.514	0.705

St.Anthonis 46a (site 10) : Octobre 1995 ; pas de statistique										
traitement	prof	n	S	P	K	Ca	Mg	Mn	Al	Ca/Al
						g kg^{-1}				mole/mole
Témoin	0-5	3	1.45	0.69	2.25	5.79	1.04	0.06	1.09	7.95
	5-15	3	1.34	0.68	1.70	4.17	0.74	0.02	4.11	1.5
	15-30	3	1.10	0.67	2.92	3.17	0.63	0.02	5.19	0.93
	30-45	3	1.03	0.61	2.12	1.97	0.47	0.01	7.31	0.405
	45-60	3	0.80	0.50	1.80	0.95	0.31	0.01	8.10	0.18
Ca	0-5	3	1.41	0.71	2.13	6.32	1.47	0.04	0.91	10.5
	5-15	3	1.06	0.54	2.22	5.61	1.12	0.03	2.41	3.45
	15-30	3	1.10	0.63	2.07	3.91	0.83	0.02	5.15	1.125
	30-45	3	0.95	0.56	2.40	2.45	0.73	0.01	9.14	0.39
	45-60	3	1.39	0.48	2.12	0.38	0.31	0.00	11.28	0.06