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REGULAR ARTICLE

Does low soil base saturation affect fine root properties of European beech (*Fagus sylvatica* L.)?

Anika K. Richter · Lorenz Walthert · Emmanuel Frossard · Ivano Brunner

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Abstract It is generally believed that high soil solution Al^{3+} in acidic soils with low base saturation (BS), negatively influences the properties of fine roots. Fine roots from European beech (*Fagus sylvatica* L.) trees growing in highly acidic soils with very low BS and potentially high Al^{3+} concentration in the soil solution were analysed and the dependency of fine root properties on soil BS was measured. The fine roots were sampled down to 1 m depth at seven forest sites located on the Swiss Plateau. These sites varied in their BS from 1.4 to 11.4% in the mineral layers. We evaluated relationships between the BS of these mineral layers and fine root properties, such as ratio between bio- and necromass (live/dead ratio), specific root length (SRL), root tip abundance (RTA), root branching abundance (RBA), O_2-consumption, and the Ca/Al molar ratio in the fine root tissue. The fine root properties were compared not only with the BS of the soil, but also with the Ca/Al molar ratio in the fine root tissues. Significant relations of fine root properties occurred when the soils of the seven sites were grouped into two BS groups (<5 and 5–10%). The live/dead ratio, the RTA, the RBA, the O_2-consumption, and Ca/Al molar ratio were lower in the group of BS <5% than in the group 5–10%. Decreases in the morphological properties and in the O_2-consumption were related to decrease in the Ca/Al molar ratio of the fine root tissues. There is evidence that the fine root properties are negatively influenced, nevertheless, fine root systems of mature European beech in their natural ecological environment seem to be able to compensate adverse effects of low BS.

Keywords Aluminium toxicity · Ca/Al molar ratio · *Fagus sylvatica* · Fine root morphology

Abbreviations

BS	base saturation (%)
RTA	root tip abundance (n g^{-1})
RBA	root branching abundance (n g^{-1})
SRL	specific root length (cm g^{-1})
CEC	cation exchange capacity ($mmol_c$ kg^{-1})

Introduction

Since high depositions of acidifying pollutants over the last decades have accelerated soil acidification (Blaser et al. 1999; Graf Pannatier et al. 2004), this may have ecological consequences for forest ecosystems. For example uprooting of forest trees in storms

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has been found to be more frequent on acidic soils (Mayer et al. 2005) and on soils with a low base saturation (BS; Braun et al. 2003). Soil acidification beyond a pH of 5 is accompanied by an increase in free aluminium (Al) species content in the soil solution and contributes to a further decrease in BS (Walthert et al. 2004). Free Al^{3+} is the most important rhizotoxic Al species in the soil solution (Kochian et al. 2005).

Al^{3+} has toxic effects on plants as it hampers fine root growth by inhibiting root-cell elongation and cell division (Matsumoto 2000; Kochian et al. 2005). This results in a change in fine root morphology with the formation of short and stubby roots, dieback of root tips, decline in root elongation, and cessation of the formation of lateral roots (Göransson and Eldhuset 1991; Hirano and Hijii 2000). As a consequence tree fine root systems become degraded and their water and mineral nutrient uptake is, therefore, limited (Matsumoto 2000). Additionally, Al^{3+} competes with essential basic cations such as Mg^{2+} and Ca^{2+} on the soil exchanger and inhibits nutrient absorption to cell walls of fine roots (Göransson and Eldhuset 1995). This can lead to deficiencies in these elements and elevates the Al content in the fine root tissues (Zysset et al. 1996). One indicator for Al^{3+} toxicity is when the Ca to Al molar ratio in the fine root tissues decreases below 0.2 (Cronan and Grigal 1995). Both low basic cation availability (expressed in BS) and high concentrations of Al^{3+} in the soil solution could potentially affect the 'vitality' of the fine roots.

Several methods exist to measure the fine root properties to assess the 'vitality' of the fine roots. One first approach is to analyse the occurrence of fine roots. In acidified soils the mass of living fine roots is decreased and that of dead fine roots is increased, and, thus, the turnover rates are influenced (Jentschke et al. 2001; Godbold et al. 2003; Leuschner et al. 2004; Vanguelova et al. 2005). A second approach is to study fine root morphology (Clemensson-Lindell and Persson 1995; Godbold et al. 2003). Some morphological features, e.g. specific root length $\left(\mathrm{cm\,g_{DW}^{-1}}\right)$ and root tip abundance $\left(\mathrm{tips\,g_{DW}^{-1}}\right)$, are used to evaluate the reactions of fine roots to different soil conditions and different nutrient supplies (Ostonen et al. 1999; Hodge 2004). A third approach assesses fine roots' physiological and chemical responses by determining the respiration activity (Comas et al. 2000; Richter et al. 2007) and the Ca/Al molar ratio of fine roots (Cronan and Grigal 1995). Ca is known to ameliorate Al-induced rhizotoxicity and mitigate other adverse effects of Al (Cronan and Grigal 1995; Rengel and Zhang 2003).

However, little is known about the changeability of fine root properties in relation to soil parameters in situ. One threshold parameter often used to estimate potential fine root damage due to Al^{3+} toxicity is a BS <15% (Cronan and Grigal 1995). According to Leuschner et al. (2006), the growth of European beech (*Fagus sylvatica* L.) can be limited at BS below 3.3%. Hence, in the present study, the main objective was to evaluate whether BS can be used to predict fine root 'vitality' of European beech in soils where Al^{3+} toxicity potentially occurs. We, therefore, hypothesise that (1) fine root properties such as fine root mass, morphology, physiology, and chemistry are related to low soil BS at different depths of forest soils, (2) morphological and physiological properties are related to the Ca/Al molar ratio in the fine root tissue, and (3) fine root properties have the potential to be used to assess plant root stress in soils with a very low BS.

Materials and methods

Forest sites

Fine roots of European beech (*Fagus sylvatica* L.) were sampled in seven forest sites on the Swiss Plateau (Table 1). The forest sites were chosen from the WSL soil data-base (Swiss Federal Institute for Forest, Snow and Landscape Research; for methodical details, see Walthert et al. 2004 and Graf Pannatier et al. 2004). Deeply decalcified soils with a BS<15% in the mineral soil matrix and a lime threshold deeper than 1.50 m depth were selected. The soil types of all sites could be classified as acidic brown soils (Distric Gleysol, Gleyic Cambisol, distric, and Luvisol), with a BS from 1.6 to 24.2% in the Ah-layers and 1.4 to 11.4% in the B-layers (Table 2). The pH ($CaCl_2$) varies between 2.3 and 3.6 in the Ah-layers and 3.4 and 4.2 in the mineral layers (Table 2). All soils have only weak compaction in the deeper mineral layers. Some profiles show a few characteristics of water logging in the lower profile, but none were classified as extremely water logged. Five forest sites belong mainly to the alliance *Luzulo–Fagion,* whereas the other two sites belong to the alliance *Abietion*, where the European beech is secondary (Ellenberg and Klötzli 1972).

Table 1 Description of the seven study sites (in order of increasing mean base saturation)

		Entlebuch (En)	Walterswil (Wa)	Vordemwald (Vw)	Zofingen (Zo)	Niedererlins-bach (Ni)	Triengen (Tr)	Krauchtal (Kr)
Coordinates		8°04′N 46°58′E	7°47′N 47°06′E	7°53′N 47°16′E	7°59′N 47°18′E	8°00′N 47°23′E	8°06′N 47°15′E	7°34′N 47°02′E
Elev. (m a.s.l.)		900	750	480	571	473	840	600
Prec. (mm year^{-1})		1,603	1,324	1,100	1,186	1,036	1,409	1,095
Temp. (°C year^{-1})		6.7	7.4	8.8	8.2	8.7	6.9	8.2
Vegetation type[a]		*Abietum*	*Fagetum* a	*Abietum*	*Fagetum* b	*Fagetum* b	*Fagetum* a	*Fagetum* c
Soil type[b]		Gleysol	Cambisol	Cambisol	Cambisol	Luvisol	Cambisol	Cambisol
BS[c] (%)		3.2	3.9	4.6	7.1	9.3	12.9	18.2
PH[d]		3.6	3.6	3.8	3.7	3.5	3.7	3.7
CEC[e] (mmol$_c$ kg^{-1})		83	84	103	67	125	62	142
Layer[f] (cm)	Ah1	0–7	0–5	0–6	0–5	0–4	0–4	0–6
	Ah2	7–15	5–12	6–15	5–10	4–9	4–8	6–11
	B	15–100	12–100	15–100	10–100	9–100	8–100	11–100

[a] According to Ellenberg and Klötzli (1972); *Abietum*, *Bazzanio–Abietum*; *Fagetum* a *Millio–Fagetum*; *Fagetum* b *Galio odorati Fagetum*; *Fagetum* c *Galio odorati Fagetum luzuletosum*

[b] Classification after FAO: *Gleysol*, Distric Gleysol; *Cambisol*, Gleyic Cambisol, distric

[c] Mean base saturation (not weighted between the horizons; based on element content in milliequivalents per kg fine earth)

[d] Mean pH ($CaCl_2$; not weighted between the horizons)

[e] Mean cation exchange capacity (not weighted between the horizons; based on element content in milliequivalents per kg fine earth)

[f] According to Walthert et al. (2004)

Fine root sampling

At each forest site four individual European beech trees, belonging to the dominant individuals in the stands, were chosen in the vicinity of the soil profile. Each tree was sampled twice with soil cores 1 m away from the stem, once North and once South of the tree. Soil cores containing the fine roots were taken with a HUMAX soil corer (∅ 10 cm) down to 1 m depth consisting of four segments. Each core segment consisted of a plastic tube 25 cm long with the soil left undisturbed during sampling and storage. The

Table 2 Base saturation (BS) and pH ($CaCl_2$) of the soil matrix of each layer of the seven forest sites (abbreviations according to Table 1)

	Layer	En	Wa	Vw	Zo	Ni	Tr	Kr
BS	Ah1	2.2	8.7	6.5	12.1	21.7	8.3	24.2
	Ah2	1.6	3.3	3.4	12.1	11.3	4.1	4.7
	B, −25 cm	1.6	1.4	3.1	3.9	5.8	5.1	3.2
	B, 25–50 cm	2.7	3.3	3.8	4.3	5.8	5.3	3.9
	B, 50–75 cm	4.9	3.7	5.3	4.3	4.8	8.2	11.4
	B, 75–100 cm	6.0	3.7	5.3	5.2	6.4	47.5[a]	61.9[a]
pH	Ah1	3.3	2.8	3.3	3.1	3.1	3.2	2.9
	Ah2	3.4	3.0	3.6	3.1	3.2	3.6	2.3
	B, −25 cm	3.4	3.4	3.9	3.8	3.8	3.8	4.1
	B, 25–50 cm	3.8	4.0	4.0	4.0	3.8	3.9	4.2
	B, 50–75 cm	3.9	4.1	4.0	4.0	3.9	3.8	4.0
	B, 75–100 cm	3.9	4.1	4.0	4.0	3.7	3.9	4.1

[a] Values were excluded from the calculation of the base saturation groups.

core segments were stored in a fridge at 1°C in the laboratory for no longer than 1 week. All forest sites were sampled within 5 weeks.

The first, uppermost soil core segments, containing the Ah- and the upper B-layers, were separated into two Ah-layers, Ah1 and Ah2, and one mineral B-layer. There was more organic matter content in the Ah1-layer than in the Ah2-layer, so, these two layers were separated (according to Walthert et al. 2004). The other three soil core segments of the mineral B-layer were left undivided.

For the fine root (∅<2 mm) measurements, the soil samples were sieved and the fine roots gently washed in a 1 mm sieve with tap water. All the fine root fragments down to 0.5 cm length were collected and stored in iced water. The roots were examined under a microscope to separate living from dead roots (bio- and necromass). Roots with turgescent cells and flexible cell walls, a white stele, and turgescent unbroken root tips were classified as living roots. Brownish, inflexible and air-filled roots were classified as dead (Hertel and Leuschner 2002). The dead roots were dried for 48 h at 60°C and then weighed. Two aliquots of the living fine roots were separated. The first one of an average of five living fine root fragments of 10 cm length was stored in iced water until further morphological measurements (see below). The second aliquot of approximately 0.5 g fresh weight was left in iced water for no longer than 1 h for further physiological measurements (see below). The remaining living fine roots were dried for 48 h at 60°C. Bio- and necromass in each soil layer were expressed in g (dry weight) per volume soil and the ratio between bio- and necromass (live/dead ratio) was measured. For the biomass the dry weight of the two aliquots (morphological measurements and O_2-consumption measurements) and the remaining rest of the whole sample were summarised.

Morphological measurements

For the morphological measurements, the representative aliquots of each sample, were analysed with WinRhizo (V4.1c; Regent Instruments Inc., Quebec, Canada), dried for 48 h at 60°C, and weighed. Length (cm), surface area (cm^2), diameter (cm), number of tips (n) and branches (n) were analysed. The recorded properties were root tip abundance (RTA [n g^{-1}]), root branching abundance (RBA [n g^{-1}]), and specific root length (SRL [cm g^{-1}]), which were expressed on a fine root dry weight basis.

Respiration measurements and element concentrations

For respiration measurements, the aliquots of approximately 0.5 g of living European beech fine roots of each mineral layer were tested to assess the roots' O_2-consumption. Because all roots were washed and freed from the attached soil particles, it is assumed, that the microorganisms, which live on the root surface and within the roots, contribute to the O_2-consumption more or less equally per root. The consumption of O_2 was measured for 20 min with a Clark-type O_2-electrode (Hansatech, King's Lynn, UK). For this measurement, the roots were submersed in 2.5 ml of stirred 1 mmol $CaSO_4$ + 5 mmol MES buffer (adjusted with KOH to pH (H_2O) 5.5; Comas and Eissenstat 2004; Richter et al. 2007). The whole system was kept at a constant temperature of 25°C. After the measurements, roots were dried for 48 h at 60°C and weighed. Respiration was expressed as O_2-consumption per g dry weight and time (nmol O_2 $g^{-1}s^{-1}$). In addition, the O_2-consumption of dead fine roots was also measured in order to compare the two different root conditions. It can be assumed, that the microorganisms which colonise these dead root tissues, account for a major part of the O_2-consumption. In comparison to living roots, however, the O_2-consumption of dead roots was very small (see "Results").

For element analyses, the fine roots previously used for the O_2-consumption measurements were ground for 1 min at 70% speed in a swing mill MM 2000 (Retsch, Haan, Germany). Elements were measured after digestion of the ground material in a high-pressure microwave (Milestone MLS Ultraclave) with an inductively coupled plasma atomic-emission spectrometer (ICP–AES Optima 3000, Perkin Elmer; see Brunner et al. 1999). The fine root element concentrations were expressed as $\left[\text{mol}\,kg_{DM}^{-1}\right]$ and the molar ratio between Ca/Al was calculated. In a few cases, also the element concentration of dead fine roots was analysed.

Statistical analyses

The fine root measurements were averaged per North and South soil core of the tree and soil layers. Per

forest site, the tree data of the four sampled trees were averaged per soil layers and compared with the soil chemical parameters. Soil chemical data were taken from a single soil profile per forest site. The data were subjected to one- and two-way analysis of variance (ANOVA). The significance level was $P<0.05$ by Fisher's PLSD test throughout the text unless stated otherwise. All tests were conducted with StatView 5.0 (SAS Institute, Cary, NY, USA). PCA was conducted with Canoco 4.5 (Biometris–Plant Research International, Wageningen, The Netherlands) and cluster analyses with Systat 10 (Systat Software Inc., California, USA).

Results

Relation of the fine root properties to the soil chemical parameters

Our analyses revealed few relations between fine root properties and soil parameters, which occurred especially in the B-layer (Table 3). In particular, the live/dead ratio and the Ca/Al molar ratio were related with BS or pH within the B-layers (Table 3). No relation between the fine root properties and the water regime in the soil profiles could be found (data not shown). The principal component analyses (PCA; Fig. 1) applied in the B-layers showed negative correlations between soil parameters and RTA, SRL, and O_2-consumption. The fine root properties (except live/dead ratio) appeared to be all strongly related to each other. No PCA for the Ah-layers were made because this study focuses on differences in the fine root properties in the B-layers, where free Al^{3+} in the soil solution can be expected in higher concentrations (Graf Pannatier et al. 2004; Parker 2005).

Two groups of BS

To analyse the trends apparent from the PCA of the B-layers, the seven forest sites were subjected to a cluster analysis with the BS from the soils of the B-layers (Table 2) as the dependent variable (Fig. 2). The deepest layers from the sites at Triengen and Krauchtal were excluded because the BS there was extremely high due to the influence of the high lime content in layers deeper than 1.50 m. The analysis resulted in two clear clusters of sites in two BS-groups. The first group had a very low BS<5% (En, Wa, Vw, Zo), and the second group had BS 5–10% (Ni, Tr, Kr; Fig. 2). The variability of the pH between the forest sites and soil layers was too small to show a natural clustering between the forest sites.

Standing mass and morphological fine root properties

The fine root standing bio- and necromass did not differ between the two BS-groups (data not shown). The live/dead ratio, however, showed slight, but significantly smaller values in the BS-group<5%, in particular in the deepest layers (Fig. 3). The live/dead ratio increased with increasing depth of the soil profile. The increase in the ratio with depth within the BS-group<5% was about 5 times elevated and that of the group 5–10% about 10 times elevated.

The morphological properties of the fine roots also differed between the two BS-groups. The RTA was significantly (10–60% according to soil layer) lower in the BS-group<5% than in the group 5–10% (Fig. 4a). The most distinct differences occurred in the deeper layers (50–100 cm depth). The RBA was significantly (10–40% according to soil layer) lower in the BS-group<5% than in the group 5–10% (Fig. 4b). The soil depth did not appear to affect the

Table 3 *P* values of one-way ANOVA for the mean values of biomass, necromass, live/dead ratio, root tip abundance (RTA), root branching abundance (RBA), specific root length (SRL), O_2-consumption, and Ca/Al molar ratio in the fine root tissues versus base saturation (BS) and pH (*n.s.* not significant; $P<0.05$)

Layer		Bio-mass ($g\ l^{-1}$)	Necromass ($g\ l^{-1}$)	Live/dead ratio	RTA ($n\ g^{-1}$)	RBA ($n\ g^{-1}$)	SRL ($cm\ g^{-1}$)	O_2-consumption (nmol $O_2\ g^{-1}\ s^{-1}$)	Ca/Al
Ah	BS	n.s.	n.s.	0.006	n.s.	n.s.	n.s.	–[a]	–
	pH	n.s.	n.s.	n.s.	0.04	n.s.	n.s.	–	–
B	BS	n.s.	n.s.	0.03	n.s.	n.s.	n.s.	n.s.	n.s.
	pH	0.03	0.04	n.s.	n.s.	n.s.	n.s.	n.s.	<0.001

[a] Not determined

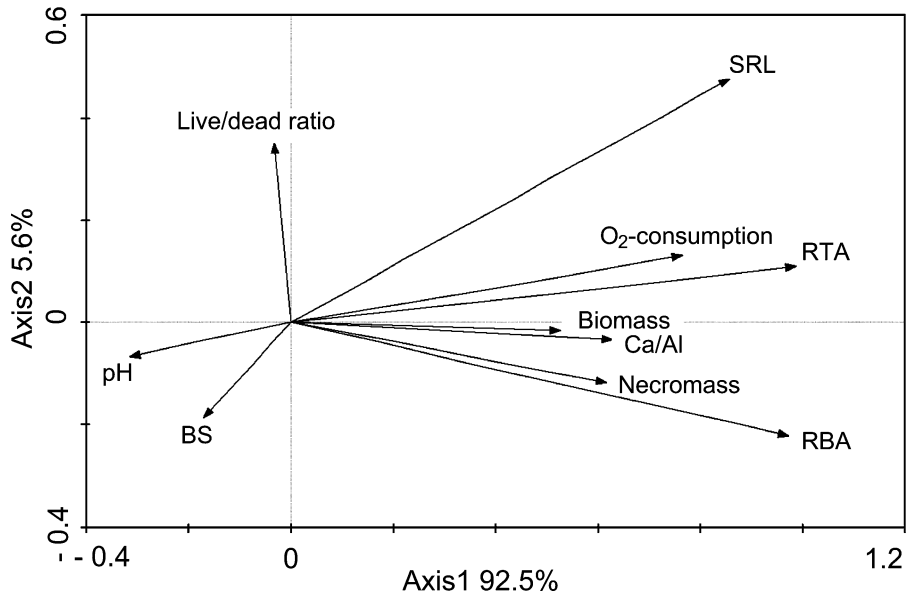

Fig. 1 Principal component analysis (PCA) of the soil chemical parameters and the mean fine root properties in all B-layers: base saturation (BS, %), pH, biomass (g l^{-1}), necromass (g l^{-1}), live/dead ratio, root tip abundance (RTA, n g^{-1}), root branching abundance (RBA, n g^{-1}), specific root length (SRL, cm g^{-1}), O_2-consumption (nmol O_2 $g^{-1}s^{-1}$), and Ca/Al molar ratio. Total explained variance by the 1, 2, and 3 principal axes: 99.8%

RTA and RBA. The SRL, however, was not affected by the BS-groups (Fig. 4c), as the trend towards the lower SRL values (by 5–20%) in lower BS-group as compared to the higher BS-group was not significant.

The other morphological properties, such as length, surface area, and average diameter, did not vary with the BS-groups nor with soil depth (data not shown).

Physiological and chemical fine root properties

There were significant differences between the two BS-groups in the O_2-consumption of the fine roots in the B-layers (Fig. 5a). The O_2-consumption in the BS-group<5% was decreased by about 25% in the uppermost B-mineral layer and by about 5% in the deeper layers. With increasing depth, there was a distinct and significant decrease in both BS-groups from the uppermost layer to the deeper layers. Dead

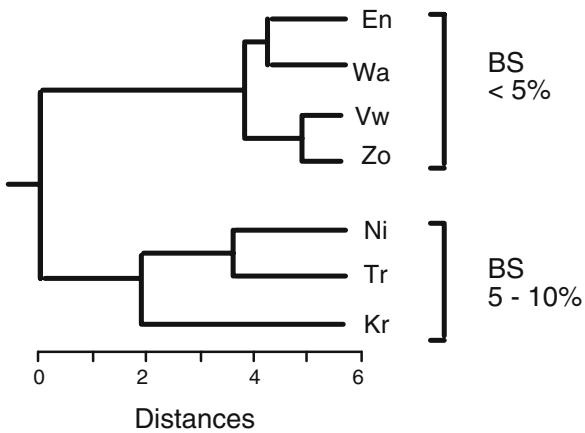

Fig. 2 Cluster analysis of the mean soil base saturation (BS, %) in the B-layers of the seven forest sites (abbreviations according to Table 1)

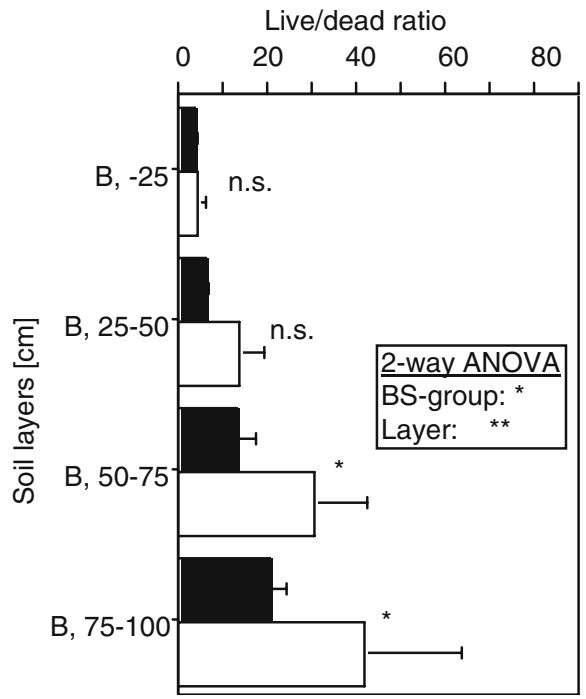

Fig. 3 Live/dead ratio of the fine roots of European beech in the two mean base saturation groups (BS; *black column* <5%, *white column* 5–10%) in the B-layers. Probability levels for the one- and two-way analyses of variance (ANOVA): *P<0.05, **P<0.01; *bars* indicate standard error; *n.s.* not significant

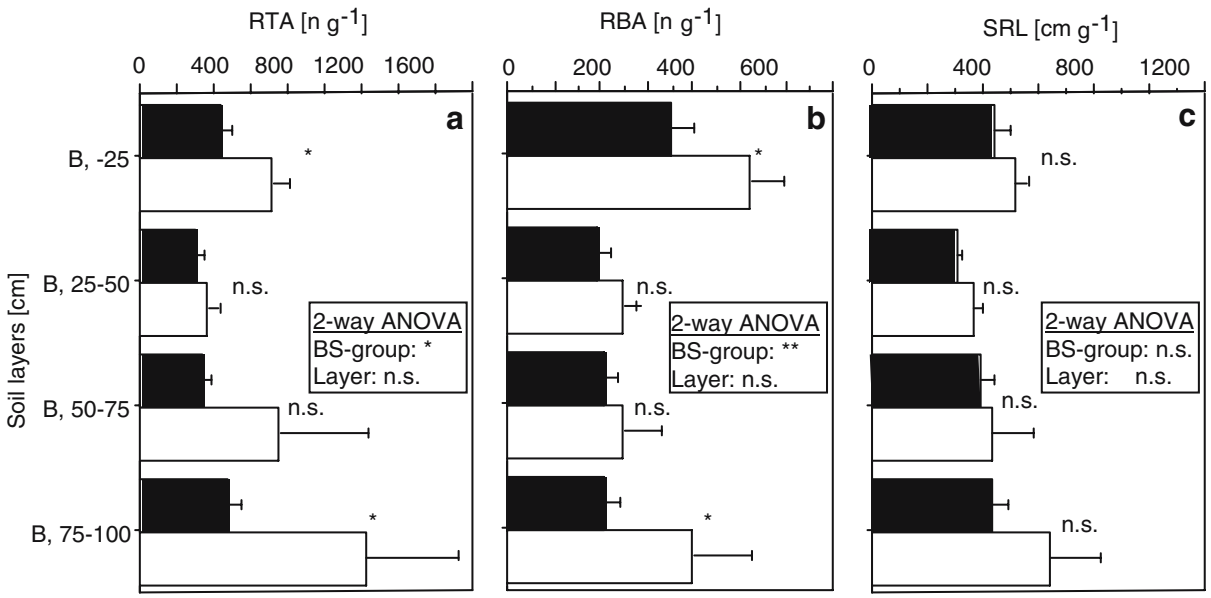

Fig. 4 Root tip abundance (RTA; **a**), root branching abundance (RBA; **b**), and specific root length (SRL; **c**) of the European beech fine roots in the two mean base saturation groups (BS; *black column* <5%, *white column* 5–10%) in the B-layers. Probability levels for the one- and two-way analyses of variance (ANOVA): **P*<0.05, ***P*<0.01; *bars* indicate standard error; *n.s.* not significant

fine roots had a very low O_2-consumption of 0.2± 0.03 nmol O_2 $g^{-1}s^{-1}$.

The Ca/Al molar ratio in the fine roots was significantly smaller in the BS-group<5% throughout the whole soil profile (Fig. 5b). In both BS-groups, there was a distinct decrease from the uppermost layer to the deeper layers. Within the group<5% this decrease continued constantly through the profile until it was by about 50% decreased. In the BS-group 5–10% the decrease occurred mainly between the uppermost B-layer and the subsequent layer, after which almost no further decrease occurred with depth (25–100 cm). The dead fine roots had a very low Ca/Al molar ratio of 0.5±0.1.

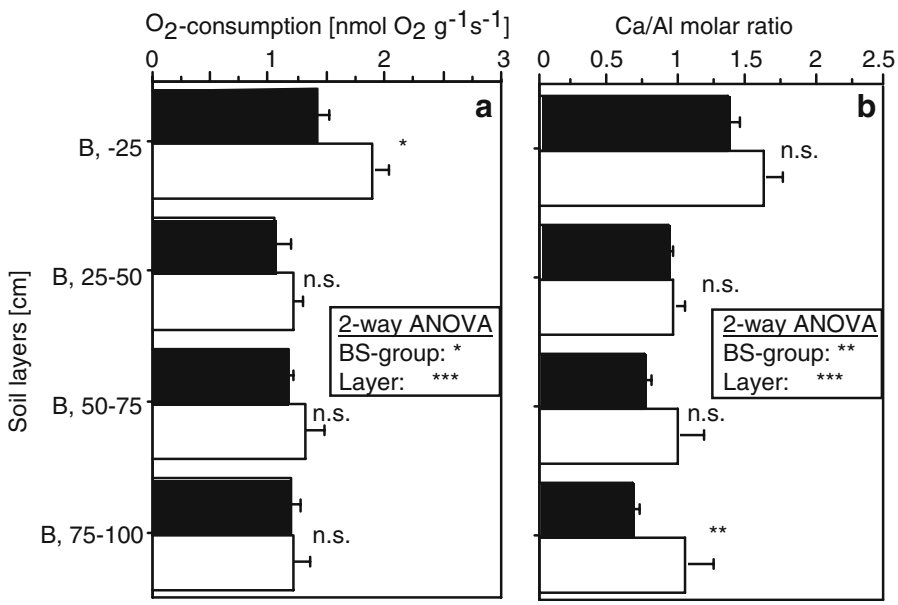

Fig. 5 O_2-consumption (**a**) and Ca/Al molar ratio (**b**) of the European beech fine roots in the two mean base saturation groups (BS; *black column* <5%, *white column* 5–10%) in the B-layers. Probability levels for the one and two-way analyses of variance (ANOVA): **P*< 0.05, ***P*<0.01, ****P*< 0.001; *bars* indicate standard error; *n.s.* not significant

The Ca/Al molar ratio of the fine root tissue was very positively correlated to RTA, RBA, and SRL (Fig. 6), and to the O_2-consumption (Fig. 7).

Discussion

In greenhouse experiments under controlled conditions in hydroponics, fine roots showed a strong response to elevated Al^{3+} concentrations in the nutrient solutions (Godbold and Jentschke 1998; van Schöll et al. 2004). The fine root growth was always heavily impaired immediately after applying Al^{3+} rich solutions. Fine root cell elongation was inhibited and after prolonged exposure to high Al^{3+} concentrations, roots showed an impaired development due to inhibited cell division (Matsumoto 2000; Kochian et al. 2005). However, in in situ measurements, most studies found no inhibition of fine root growth and development. Leuschner et al. (2004) could not find any marked differences in the fine root morphology of European beech stands with variations in soil acidity (pH 2.9–6.7) and fertility (BS, 3.9–98.9%). Ostonen et al. (1999) identified several morphological relationships between the short roots of Norway spruce and soil conditions (humus content, field capacity, and specific soil surface area), but not with the Ca/Al ratio in the soil. Wargo et al. (2003) also found no changes in red spruce root parameters, such as the living root tips per branch and the percentage of dead roots, along a gradient of exchangeable Al/Ca ratios in the forest floor. Nygaard and de Wit (2004) failed to detect any changes in fine root properties, such as decreased biomass or elevated necromass, after applying Al^{3+} in situ during a 3-year experiment in a Norway spruce stand with BS 6% and pH 4.3 in the soil matrix. Eldhuset et al. (2006) also found no prominent changes in the same fine root properties after a further 4 years in the same experiment.

We were, nevertheless, in our study able to identify a series of changes in the characteristic root properties

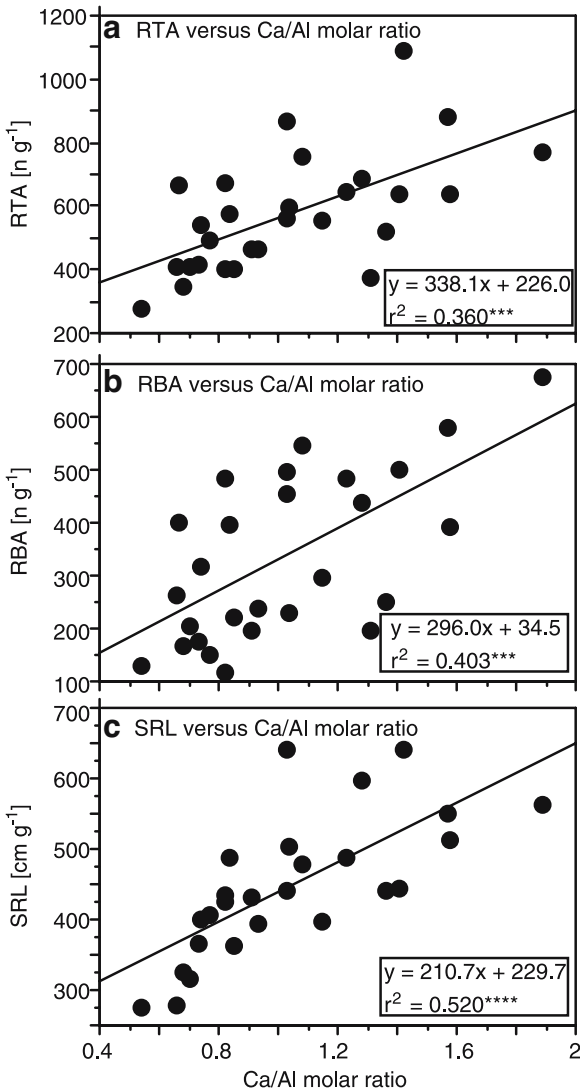

Fig. 6 Relationships between **a** root tip abundance (RTA), **b** root branching abundance (RBA), and **c** specific root length (SRL) of the European beech fine roots and the Ca/Al molar ratios in European beech fine root tissues. Fine roots from the B-layers were analysed. Probability levels for the analyses of variance (ANOVA): ***$P<0.001$, ****$P<0.0001$

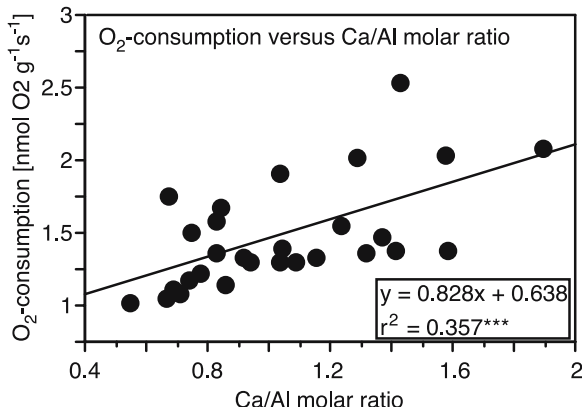

Fig. 7 Relationship between the O_2-consumption of the European beech fine roots and the Ca/Al molar ratio in the European beech fine root tissues. Fine roots from the B-layers were analysed. Probability level for the analyses of variance (ANOVA): ***$P<0.001$

due to the extreme low BS in the soil, e.g. a decreased live/dead ratio and decreased root-tip and root-branching abundance. The fine root properties differed according to the forest site group: the group with low BS (5–10%) or the group with very low BS (<5%). According to Graf Pannatier et al. (2004), there is a trend for Al^{3+} content, beside of the pH dependency, to increase in mineral soils with decreasing BS; therefore, higher Al^{3+} concentrations can be expected at BS<5% than at BS 5–10%. At the forest site Vordemwald, the mean values of Al_{tot} decreased from 23.6 μmol l^{-1} at a depth of 10–20 cm, 18.9 μmol l^{-1} at 40–60 cm, and 3.8 μmol l^{-1} at 60–80 cm as the BS increased from 3.1, 3.8, to 5.3%, respectively (Graf Pannatier et al. 2004). About one third of Al_{tot} is phytotoxic Al^{3+} (Graf Pannatier et al. 2004).

Commonly used fine root properties to assess the 'vitality' of the fine roots are the amount of biomass, necromass, and live/dead ratio, as well as the productivity and mortality of the fine roots. It has often been reported that forests growing on acidic sites have a higher fine root density and fine root mass of both bio- and necromass than forests growing on less acidic sites (Godbold et al. 2003; Jentschke et al. 2001; Vanguelova et al. 2005). In particular, a higher necromass is attributed to the fact that fine root systems on acidic and poor sites have a higher mortality rate (Leuschner et al. 2004). In addition, fine roots from soils with a low BS may have a decreased longevity due to nutrient deficiencies (low BS) and/or Al^{3+} toxicity, as observed by Vanguelova et al. (2005) in a Scots pine stand. Nevertheless, Gaudinski et al. (2001) showed an increase in the age of fine roots measured by radiocarbon with increasing depth (4–6 years at 0–15 cm depth and 15–18 years at 15–30 cm depth), which may also explain the increased live/dead ratio with increasing depth.

Some morphological properties of fine roots appeared to be influenced by very low BS. One significant change was that fine roots had fewer root tips. This may be due to the inhibition of development and growth or to death caused by Al^{3+} toxicity or nutrient deficiencies, as reported in the study of Göransson and Eldhuset (1991). This finding is supported by the study of Leuschner et al. (2004), were the RTA was lower in the first 5 cm of the mineral layer of forest sites with a low BS (9.4 and 3.9%; RTA 390 and 560 n g^{-1}) and higher at sites with a high BS (98.9 and 45.9%; RTA 620 and 640 n g^{-1}). Not only the dieback of root tips but also a cessation of formation of lateral roots were observed in several studies in hydroponics (Göransson and Eldhuset 1991; Hirano and Hijii 2000). This characteristic development could also be seen in our study as the branching abundance was decreased at lower BS. This change in morphology most likely originates from the ability of the trees to use less energy and nutrients for fine root growth when the BS is very low. SRL reflects, for example, the benefits in resource acquisition relative to the cost of resources used for the construction and maintenance of root tissue (Fitter 1991; Espeleta and Donovan 2002). Nevertheless, SRL was only slightly, but not significantly, decreased in sites with very low BS. Morphological plasticity can be considered as a root functional status to provide rapid acquisition of nutrients and water (Ostonen et al. 1999; Paulitz 2002). As a result, we hypothesize that roots with fewer tips and lateral roots (branches) could be less effective in fulfilling these functions.

Very low BS in the soil affects not only the morphology, but also the physiology. The O_2-consumption was also lower at very low BS, as was the Ca/Al molar ratio of the fine root tissue. This ratio shows not only a direct interference of Al with nutrient accumulation in fine roots (Nygaard and de Wit 2004; Vanguelova et al. 2005), but it may also be the result of the fine root system being reduced as the organ for nutrient uptake (see decreased RTA, RBA and SRL; Rengel 1992). In the study of Yamamoto et al. (2002) the O_2-consumption of cultured tobacco cells was also decreased with increasing Al^{3+} in the cultivation medium. This decrease was correlated with a decrease of ATP production and cell growth. Therefore, it can be hypothesized that fine roots growing under very low BS conditions will have a decreased energy potential for their functions, as they have a lower O_2-consumption and an adverse Ca/Al molar ratio in the tissues. However, the fact that O_2-consumption is comparatively high in the first mineral layers may go against this interpretation. The higher O_2-consumption might be due to better soil conditions, e.g. temperature, aeration, or compaction.

All the three morphological properties RTA, RBA, and SRL, as well as the O_2-consumption are strongly related to the Ca/Al molar ratio in the fine root tissues. As this ratio reflects the nutrient status and Al content in the fine roots based on the BS in the soil (Nygaard and de Wit 2004; Vanguelova et al. 2005), this suggests

that these properties could be potentially useful in assessing stress to the plants in soils with a very low BS.

Conclusions

This work provided evidence that the fine root properties in the B-layers are negatively influenced in stands with a BS<5% relative to those with a higher BS. Fine roots in such layers have fewer root tips and laterals, a lower live/dead ratio, a slightly decreased SRL and a decreased respiratory activity. Furthermore, the morphological and physiological properties are also related to the Ca/Al molar ratio in the root tissue. However, according to our data, the most suitable parameter for 'vitality' measurements is probably the measurement of the O_2-consumption. As a physiological parameter, the measurement of the O_2-consumption is a more direct way to analyse the 'vitality' of the fine roots than the standing mass or the morphological and chemical parameters. Additionally, the measurement of the O_2-consumption is an easy and fast method to analyse a physiological feature of fine roots.

Nevertheless, the differences were not that distinct, and significances between the BS-groups did not occur in every soil layer. Nygaard and de Wit (2004) suggested that fine roots seem to be able to compensate adverse soil chemical effects much better under natural conditions than under artificial conditions. They hypothesized that the fine roots are more resistant when they grow within their natural ecological balance with normal soil heterogeneity and microbial community structure. Therefore, we also conclude that fine roots of European beech might have mechanisms (e.g. growth of roots in chemically more suitable parts of the heterogeneous soil) to compensate adverse effects.

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