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REGULAR ARTICLE

Response of the fine root system in a Norway spruce stand to 13 years of reduced atmospheric nitrogen and acidity input

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Abstract Atmospheric inputs of acids and nitrogen (N) have altered growth and vitality of forests for decades, but there is a lack of understanding concerning the response of these forests to reduced deposition. We studied fine root parameters of a Norway spruce stand treated with reduced input (clean rain) for 13 years. Fine roots of the clean rain plot had smaller N and Al contents, however, fine roots in the subsoil were still subjected to soil acidity and Al toxicity as indicated by a fine root Ca/Al ratio of less than 0.5. The treatment effect was most pronounced in the organic layer of the clean rain plot where fine root biomass increased by 66% and the live/dead ratio of fine roots increased by more than 100%. The elevated live/dead ratio was attributed to reduced mortality and faster decomposition of fine root litter. The latter was supported by a positive relationship between live/dead ratio and manganese content of fine roots. In contrast to the organic layer, fine root biomass was not different in the mineral soil. However, at 20–40 cm fine root diameter was greater and specific root tip density was smaller than in the topsoil likely because of strong N limitation as indicated by a C/N ratio of >50. Based on these morphological changes we postulate differing functional properties of fine roots in the organic layer and mineral soil below 20 cm depth. Further, our results suggest that *Picea abies* is able to adapt morphology and functional traits of its root system following reduced N availability.

Keywords Solling roof project · Norway spruce · Atmospheric deposition · Fine roots · Re-establishment

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Introduction

In the past decades, emissions of nitric oxides, ammonia and sulfur dioxide originating from traffic, industrial processes and agriculture have affected nutrient cycling in forest ecosystems (Matzner 2004). Although great efforts have been made to reduce these emissions, atmospheric input of reactive nitrogen (N) is still high and affects the N cycle of forest ecosystems in Germany (Borken and Matzner 2004). An excess of ammonium and nitrate in soils results in acidification, depletion of nutrient cations, eutrophication and therefore influences organisms and ecosystem processes (Boxman et al. 1995; Aber et al. 1998).

As fine roots react to altered soil conditions such as changing water or nutrient availability, they can serve as indicators of the plant's nutritional status (Münzenberger et al. 1995; Persson and Ahlström 2002). Furthermore, parameters governing fine root stocks and dynamics are of major importance for our understanding of belowground carbon (C) allocation and C sequestration in soils (Helmisaari et al. 2007). The consequences of atmospheric deposition for fine root systems are (1) increased N availability and nutrient imbalances in nutrient-poor systems, (2) root damages by Al toxicity induced by soil acidification, and (3) secondary implications for mycorrhiza and other root-associated soil organisms (Boxman et al. 1998; Nadelhoffer 2000).

In relation to its environment, the plant has to meet a trade-off between sufficient nutrient uptake together with a minimum of C investment for production and maintenance of roots (Eissenstat et al. 2000; Bakker et al. 2009). Dynamic adaption to changing soil conditions includes shedding or maintaining of present roots as well as morphological modifications of fine root systems (Leuschner et al. 2004). So, an altered cost-benefit ratio is an important driver for the adaption of fine root parameters.

Many studies have shown that belowground C allocation and/or fine root biomass decreases with increasing nutrient availability which can be explained by the fact that less active root area is needed to meet the plant's nutrient demand (Persson 1983; Boxman et al. 1995; King et al. 2002; Helmisaari et al. 2007). In the opposite case, i.e. decreased nutrient availability, increasing specific root length is a strategy to reduce the C costs for nutrient uptake (Leuschner et al. 2004).

The live/dead ratio has been used as a vitality criterion of fine roots reflecting stress conditions, root damage and fine root mortality (Godbold et al. 2003; Leuschner et al. 2004; Persson and Stadenberg 2009) although it is influenced by the decomposition of fine root litter. As high N concentrations are known to decelerate the decomposition of litter in later stages (Sollins et al. 1996; Nave et al. 2009), it is questionable whether live/dead ratio can be used as an indicator of fine root vitality when sites with different N availability are compared (Nadelhoffer 2000).

According to Persson and Ahlström (2002), there is a close relationship between N availability and fine root distribution, fine root nutrient concentrations and live/dead ratio. Root damages or structural changes due to N deposition are therefore likely but not always observed. Borken et al. (2007) found no significant influence of site N availability on fine root morphology, biomass and N contents of fine roots in Norway spruce stands with relatively high N input. In particular, there is a lack of knowledge concerning dynamics and time scales of the regeneration process on the transition from N saturated to N limited forests. Prior to this study, Lamersdorf and Borken (2004) postulated increased fine root biomass in the mineral soil of a Norway spruce stand following reduction of N and acidity input. However, they used in-growth cores filled with quartz sand and did not assess fine root parameters of the undisturbed organic layer and mineral soil. Aim of the present study was to investigate the response of the fine root system of the same Norway spruce stand subjected to manipulation of throughfall in a 'clean rain' experiment over a period of 13 years. Data were acquired at the Solling roof experiment in Central Germany where a clean rain treatment is conducted since 1991.

We hypothesize (1) that reduced atmospheric input of N and acids results in an improved nutritional status of the fine roots in terms of higher nutrient contents and Ca/Al ratios, (2) increased fine root biomass, and (3) increased live/dead ratios by enhanced fine root litter decomposition. We further hypothesize (4) a more efficient soil exploitation by means of a changed fine root morphology and (5) a re-establishment of the fine root parameters named above in the mineral soil.

Materials and methods

Study site and experimental design

The study site was a 71-year old (2004) Norway spruce (*Picea abies* (L.) Karst.) plantation at the Solling plateau in Lower Saxony (Solling roof project), Central Germany (51° 31′N, 9° 34′E, 500 m a.s.l.). The climate is semi-continental, montane with a mean annual temperature of 6.4°C and a mean precipitation of 1090 mm a^{-1}. Soils have evolved on periglacial loesses over Triassic sandstone bedrock and are classified as strongly acidified Dystric Cambisols. The organic layer has a thickness of 5–10 cm and corresponds to a moder humus form.

In 1991, transparent roofs covering an area of 300 m^2 each were installed below the canopy about 3–4 m above the forest floor. Throughfall is collected, filtered (350 µm) and subsequently sprinkled on the soil surface underneath the roof. Rainwater for the clean rain treatment is partly deionized and thereby depleted in H^+ (−78% in relation to ambient rain), sulfate (−53%), ammonium (−86%), nitrate (−49%), sodium (−76%), potassium (−26%), calcium (−20%) and magnesium (−7%) (Bredemeier et al. 1998; Lamersdorf and Borken 2004). The roof control plot obtains unmodified water ('roof control'). Ambient N throughfall flux is 33 kg N ha^{-1} a^{-1}, input to the clean rain plot accounts for 11.5 kg N ha^{-1} a^{-1} (Corre and Lamersdorf 2004). Detailed information on the site and the experimental design are given by Bredemeier et al. (1995, 1998) and Corre and Lamersdorf (2004).

Sampling design and sample preparation

Sampling of fine roots (<2 mm) was carried out in October 2004 before the first soil frost event. Seven soil cores were taken on the clean rain plot and the roof control plot using a soil corer with an inner diameter of 8 cm. The sampling spots were randomly chosen and had a maximum distance of 1.5 m to the stems. We sampled the organic layer and the mineral soil layers of 0–5 cm, 5–10 cm, 10–20 cm and 20–40 cm. Soil samples were packed in plastic bags and stored at a maximum temperature of 4°C until further analyses. Fine roots were extracted from the soil samples by washing with tap water using a 2 mm-sieve. Because of adhering humus material, roots from the organic layer were additionally sonicated in a water bath for 30 min. For each individual soil layer, the effective soil volume was calculated considering the coarse soil fraction (>2 mm). After cleaning, dead fine roots were separated by visual examination using a binocular with respect to root colour, elasticity and root tip turgescence.

Biometric fine root parameters

Morphological parameters of live fine roots were assessed using an evaluation software (WinRhizo 2003b, Regent Instruments Inc., 2003) after scanning the fine roots with a resolution of 400 dpi. After morphological analyses, respective fractions of live and dead fine roots were oven-dried at 40°C until constant weight was achieved.

We calculated fine root stock [g m^{-2}], density-related parameters considering effective soil volume (fine root density [g l^{-1} soil], fine root length density [m l^{-1} soil] and root tip density [number of tips l^{-1} soil]), as well as root intrinsic parameters (average fine root diameter [mm] and specific root tip density [tips g^{-1} root]). Live/dead ratio for each sample and soil layer was calculated by dividing fine root biomass by necromass.

Chemical analyses

For chemical analyses, total fine root biomass from 0–5 and 0–10 cm mineral soil depth as well as from 10–20 and 20–40 cm mineral soil depth were pooled to two samples per mineral soil core. Prior to analyses, the dried roots were milled. C and N content were measured with a C/N analyzer (varioEL, elementar Analysensysteme GmbH, Hanau, Germany), P, S, K, Na, Ca, Mg, Mn, Fe and Al were analyzed using ICP-OES (Spectro Analytical Instruments, Kleve, Germany) after digestion with HNO_3. The non-digested residual fraction (silicates) was neglected.

Incubation experiment

An incubation experiment was conducted in order to assess the degradability of the fine root biomass from the clean rain and the control plot, both for fine roots from the organic layer and the mineral soil (0–40 cm). After homogenizing, 0.4 g of dried fine root biomass was placed in a litter bag (polyester, mesh width= 0.1 mm). The maximum length of the root fragments was 5 mm, the number of replications was 5 for each soil compartment and treatment. Before incubation, the roots were stored in deionized water for 48 h until the maximum water content of 3.25 g g^{-1} was achieved. Homogenized and sieved soil (2 mm) from the Bv horizon of the study site was used as incubation medium. The soil was adjusted to a volumetric water content of 25% which corresponds to about 60% of the maximum water holding capacity. Incubation vessels (250 ml) were filled first with 15 g of moist soil. Then, litter bags were placed in the vessel and covered with further 20 g of moist soil. In order to provide sufficient contact between soil and substrate, a slight compaction was performed with a pestle. Total incubation time was 406 days, temperature was constantly held at 20°C. After incubation, the litter bags were recovered from the soil. Mass loss by decomposition was calculated after determination of the dry mass of the washed fine roots.

Statistical analysis

Statistical analysis of the data set was performed using R 2.8.0 (R Development Core Team, 2007). For every soil layer, differences between control and clean rain plot were tested using student's t-test with a significance level of $p=0.05$. We assumed normality when data passed the Shapiro-test ($p>0.1$). Presented values are mean values and standard errors of the mean.

Results

Chemical parameters of fine roots

Decreased throughfall input of N reduced the N content of fine roots by 6–20% in the clean rain plot, though the difference was only significant in the organic layer and in 10–40 cm soil depth (Table 1). Fine root C/N ratio increased to up to more than 50 in the deeper mineral soil (Fig. 1a). Despite lower N contents, N stocks in fine root biomass were similar in the clean rain plot (6.1±1.7 g N m^{-2}) and in the control plot (5.7±2.1 g N m^{-2}) (not shown).

Fe and Al contents of fine roots from the organic layer were significantly decreased in the clean rain plot, while Mn content was higher. At 10–40 cm depth, contents of S, Na, Mg and Al significantly decreased (Table 1). Molar Ca/Al ratios of the fine roots considerably increased during the clean rain treatment (Fig. 1b) and showed the greatest increase in the organic layer from less than 5 to more than 8. In both plots, the Ca/Al ratios strongly decreased from top down within the soil profiles.

Fine root biomass and necromass

Total stock of live fine roots of the clean rain plot was 23% greater than that of the control (Fig. 2a) but the difference was not significant. Solely in the organic layer, the increase of fine root biomass (66%) was significant. With increasing soil depth, a steep decline

Table 1 Element contents [mg g^{-1}] of live fine roots originating from the roof control and the clean rain plot ($n=7$). Standard errors are given in parentheses and asterisks indicate a significant difference with $p<0.05$

Soil layer	Treatment	N	P	S	Na	K	Ca	Mg	Mn	Fe	Al
Organic layer	Roof control	13.2 (0.4)	0.83 (0.04)	0.96 (0.03)	0.08 (0.02)	1.60 (0.15)	5.31 (0.37)	0.65 (0.05)	0.27 (0.02)	1.22 (0.21)	1.46 (0.23)
	Clean rain	11.2 (0.3)*	0.76 (0.02)	0.91 (0.04)	0.11 (0.01)	1.52 (0.07)	5.79 (0.32)	0.72 (0.03)	0.38 (0.03)*	0.71 (0.09)*	0.74 (0.07)*
0–10 cm	Roof control	11.6 (0.5)	0.79 (0.04)	0.85 (0.04)	0.19 (0.03)	2.75 (0.35)	4.29 (0.32)	0.74 (0.07)	0.26 (0.03)	5.94 (0.62)	8.21 (1.11)
	Clean rain	10.9 (0.4)	0.86 (0.05)	0.83 (0.04)	0.21 (0.04)	3.22 (0.39)	4.77 (0.22)	0.76 (0.07)	0.26 (0.04)	7.61 (0.59)	7.36 (1.15)
10–40 cm	Roof control	10.8 (0.4)	0.73 (0.02)	0.89 (0.02)	0.44 (0.04)	3.15 (0.26)	2.68 (0.12)	0.68 (0.06)	0.66 (0.05)	3.20 (0.53)	13.6 (1.13)
	Clean rain	8.6 (0.3)	0.68 (0.04)	0.62 (0.03)*	0.12 (0.01)*	2.57 (0.17)	3.18 (0.16)*	0.52 (0.03)*	0.68 (0.1)	2.73 (0.5)	9.55 (0.35)*

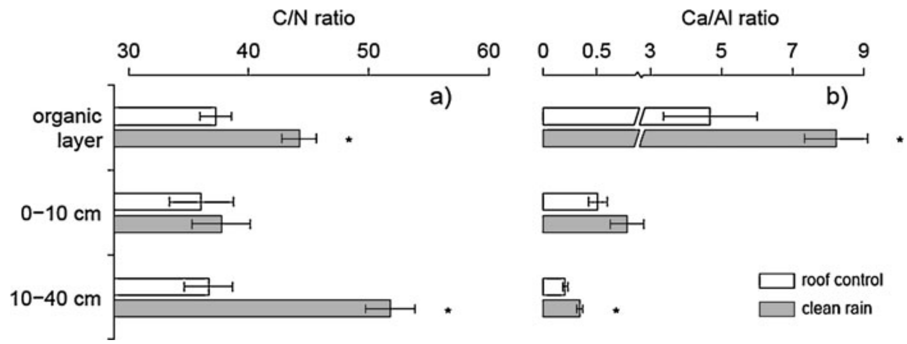


Fig. 1 **a** Mean C/N ratio and **b** mean Ca/Al ratio of fine root tissue for different soil depths in the roof control and clean rain plot (n=7). Bars indicate standard error of the mean, asterisks indicate a significant difference between the treatments with p<0.05

in fine root biomass was observed. Fine root densities followed the same trend and were decreasing within the soil profile from top down (Fig. 2b).

A root inventory in the pre-treatment year 1990 revealed a 30% lower total fine root biomass in the plot designated for the clean rain treatment than in the control plot (Fig. 3). In 1993–1995, fine root biomass was almost equal in both plots which corresponds to a 31% increase in the clean rain plot. Over the whole duration of the experimental manipulation the increase of total fine root biomass in the clean rain plot accounts for 76% (331 g m^{-2} in 1990 to 584 g m^{-2} in 2004). In contrast, total fine root biomass remained unchanged in the control plot. Changes in fine root biomass were most prominent in the organic layer with 121 g m^{-2} in 1990 to 301 g m^{-2} in 2004 (+148%) in the clean rain plot (control plot: 115 g m^{-2} to 181 g m^{-2} (+57%)). In 2004, the organic layer of the clean rain plot represented the greatest fine root pool comprising 52% of total fine root biomass. In the control plot, the organic layer comprised only 38% of the total fine root biomass.

Fine root necromass was not significantly higher in the control plot (314±14 g m^{-2}) than in the clean rain plot (286±19 g m^{-2}) (not shown), but a significantly higher live/dead-ratio of 4.5 (factor 2.5) for the clean rain treatment was observed in the organic layer. The differences in the subsoil were smaller and the values decreased for the clean rain treatment with increasing soil depth, whereas the live/dead ratios in the control plot ranged between 1.5 and 2.0 in all soil layers (Fig. 4).

A positive correlation (r^2=0.74, p<0.0001) was found between Mn content of the live root tissue ranging between 0.2 and 0.5 mg g^{-1} and live/dead

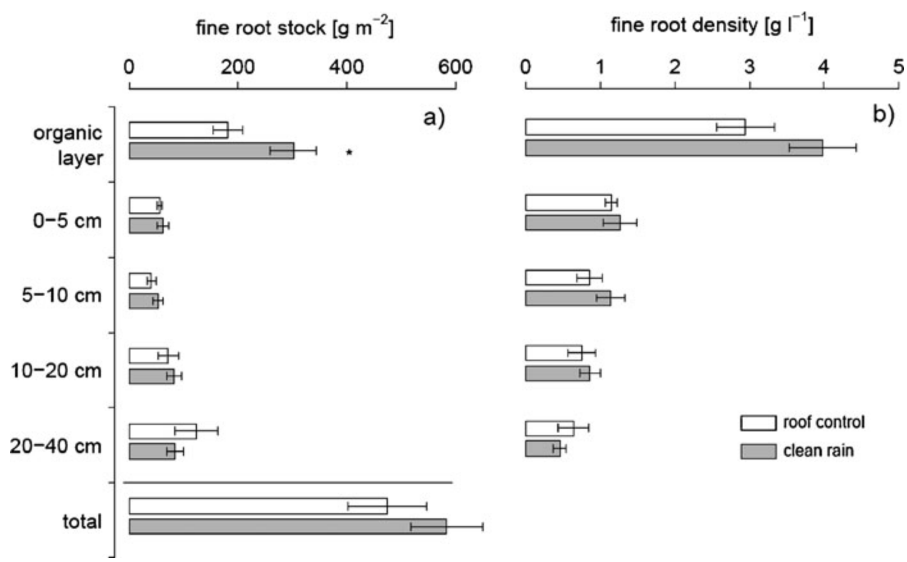


Fig. 2 **a** Mean fine root stock (fine root biomass) and **b** mean fine root density for different soil depths in the roof control and clean rain plot (n=7). Bars indicate standard error of the mean, asterisks indicate a significant difference between the treatments with p<0.05

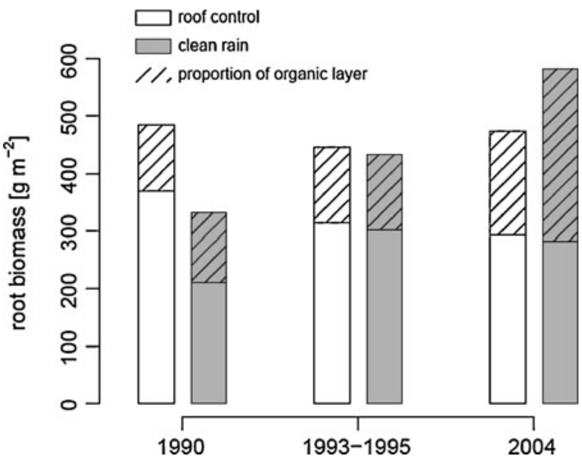


Fig. 3 Development of the mean fine root biomass in organic layer and mineral soil during the experimental manipulation. Data from root inventories earlier than 2004 were obtained from Bredemeier et al. (1998) (n=10, standard deviations not available)

ratio (Fig. 5) of fine roots originating from the organic layer. No such relationship was found for fine roots from the mineral soil (not shown).

Morphological fine root parameters

Fine root length density and fine root tip density followed similar trends between the treatments and along the vertical gradient within the soil profile (Fig. 6). With the exception of the greatest soil depth, fine root length densities were greater in the clean rain

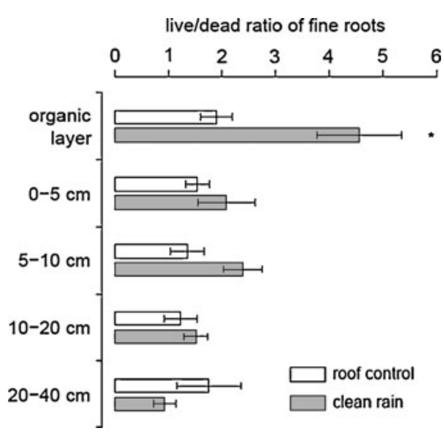


Fig. 4 Mean live/dead ratio for different soil depths in the roof control and clean rain plot (n=7). Bars indicate standard error of the mean, asterisks indicate a significant difference between the treatments with p<0.05

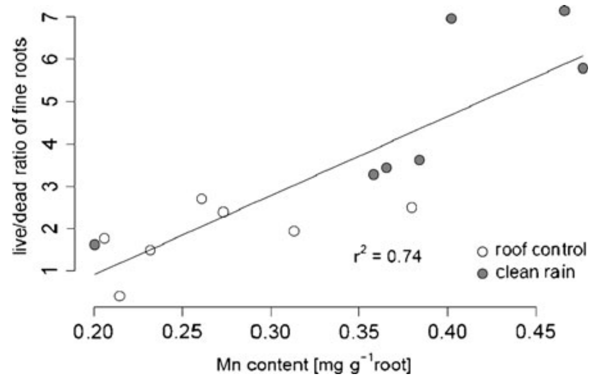


Fig. 5 Relationship between Mn content and live/dead ratio of fine roots originating from the organic horizon of the roof control and the clean rain plot

plot and a similar pattern was observed for root tip densities.

Down to a depth of 20 cm, average fine root diameters ranged between 0.45 and 0.65 mm and were not affected by the experimental manipulation (Fig. 7a). A significantly greater mean fine root diameter was measured at 20–40 cm soil depth in the clean rain plot (0.92 mm vs. 0.75 mm). Specific root tip density decreased significantly by about 50% in the same depth, whereas no response appeared in the uppermost soil layers (Fig. 7b).

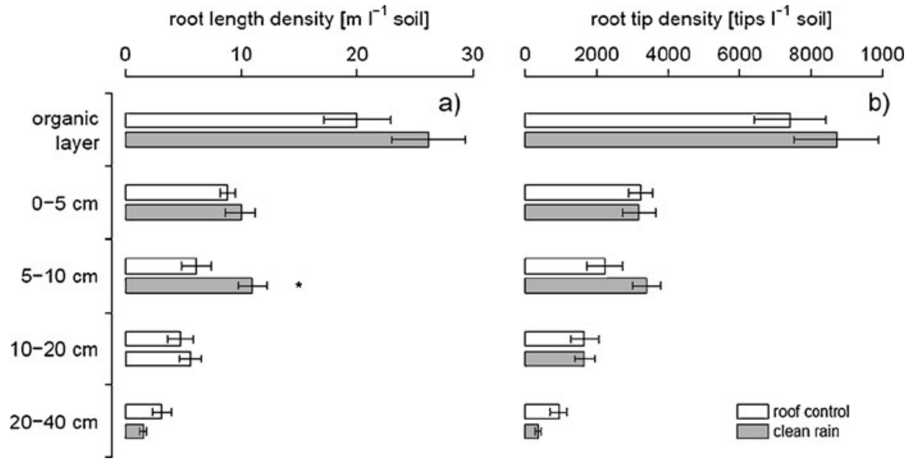
Fine root decomposition

The incubation experiment did not reveal significant differences in fine root decomposition, neither for fine roots from the organic layer nor for those from the mineral soil. For the organic layer fine roots originating from the clean rain plot, although not significant, mean cumulative decomposition was 23% higher and accounted for 25.5±1.3% mass loss within 406 days (control plot: 20.8±1.6%). Decomposition of the fine roots from the mineral soil showed an inverse trend with a smaller difference between the treatments (clean rain plot: 21.7±0.7%, control plot: 23.1±0.7%).

Discussion

The clean rain treatment reduced Al, S and N concentrations of soil solution and N leaching immediately after the beginning of the experimental manipulation (Bredemeier et al. 1995; Lamersdorf

Fig. 6 **a** Mean root length density and **b** mean root tip density for different soil depths in the roof control and clean rain plot (n=7). Bars indicate standard error of the mean, asterisks indicate a significant difference between the treatments with p<0.05



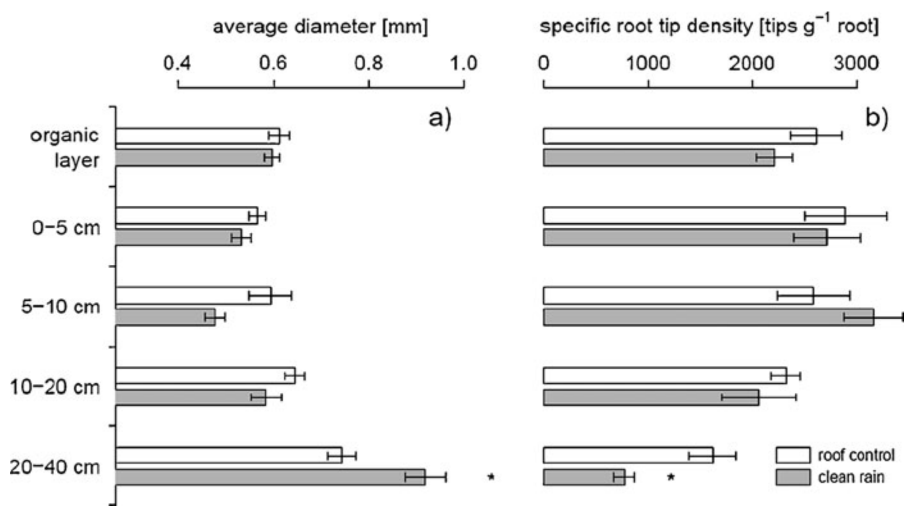
and Borken 2004). In the deeper mineral soil, solute concentrations of Al and S were less reduced than N which equalled the throughfall concentration after about one year of clean rain treatment (Bredemeier et al. 1998). Soil solution pH, however, only increased slightly within the Al buffer range so that the recovery from soil acidification will take some decades even under this reduced deposition scenario (Martinson et al. 2005).

Fine root chemistry

The decrease of N contents of fine roots from the clean rain plot supports the findings of earlier studies observing a strong positive correlation between root N content and N availability in soil solution (Burton et al. 2000; Hendricks et al. 2000; Helmisaari et al. 2007). According to Persson and Ahlström (2002), an increase of fine root C/N ratio indicates a proceeding N limitation and ongoing recovery of the soil and root system. The depth- dependent pattern of the C/N ratio reflects an uneven distribution and availability of N in the soil. The C/N ratio of more than 50 for fine roots in the 10–40 cm depth points to a relative N limitation and, together with greater fine root diameters, might indicate increasing lignification of the fine root tissue.

Interestingly, total N stock of fine roots did not significantly differ between the treatments implying that the same amount of N was allocated in fine roots. It seems that the competitiveness of fine roots relative to other soil organisms was not diminished at reduced N availability. In a N fertilization experiment, fine root N stock was twice as much as in the unfertilized control of a red pine stand (Magill et al. 2004).

Fig. 7 **a** Average fine root diameter and **b** mean specific root tip density for different soil depths in the roof control and clean rain plot (n=7). Bars indicate standard error of the mean, asterisks indicate a significant difference between the treatments with p<0.05



However, this unfertilized stand received only 8 kg N ha^{-1} a^{-1}, suggesting that both fine root biomass and fine root N content can be small when N is strongly limited.

Besides changes in fine root N status, there was also a response of the Ca/Al ratio following clean rain treatment. Fine root Ca/Al ratio is positively correlated to the Ca/Al ratio of soil solution (Vanguelova et al. 2005) and thus a good indicator for the risk of Al toxicity and root vitality. Furthermore, it affects growth and morphology of fine roots (Cronan and Grigal 1995; Jentschke et al. 2001; Vanguelova et al. 2007). The elevated Ca/Al ratios indicate a recovery from soil acidification and diminished risk of Al toxicity. Nevertheless, Ca/Al ratios below 1 in the mineral soil of the clean rain plot suggest an ongoing risk of Al toxicity.

Fine root biomass

Although total fine root biomass by means of stock and density was not significantly different in the clean rain plot after 13 years of experimental manipulation, the significant increase in the organic layer of 66% indicates a treatment effect. The dynamics of fine root biomass during the treatment period as well as the total increase on the clean rain plot since the pre-treatment year of 76% further evidence a response of the fine root system.

We mainly attribute the difference in fine root biomass to the decrease in N input by throughfall. This is in agreement with other studies reporting a negative relationship between N availability and root growth, fine root biomass and/or belowground carbon allocation (Haynes and Gower 1995; Vanguelova et al. 2005; Helmisaari et al. 2007; Bakker et al. 2009). N availability also is a main parameter governing vertical fine root distribution. Under N limitation, the fine roots are forced to preferentially exploit the N richer soil environment, mainly the organic layer, where N replenishment is given by litter input. The deterioration of fine roots in the 20–40 cm depth could be a result of a root architectural trade-off due to inhomogeneous nutrient supply (Drew 1975; Hodge 2004; Ho et al. 2005).

In acidic forest soils, vertical rooting pattern of Norway spruce has been shown to be additionally influenced by Al as roots avoid high Al concentrations in the soil solution (Matzner and Murach 1995). Acidification can therefore lead to a concentration of fine roots in the uppermost soil layers (Persson et al. 1995; Braun et al. 2005). The fact that no increase of rooting depth was found suggests that, except for N availability, chemical properties of the subsoil did not sufficiently respond under clean rain treatment. Given the critical molar Ca/Al ratios of <0.5 (Jentschke et al. 2001) and only marginal changes in soil solution pH, we conclude that Al stress is still present in the subsoil.

In summary, optimized N uptake by increased exploitation in the organic layer together with avoidance of high Al concentrations in the subsoil explain the contrasting development of fine root biomass in the soil profile. A similar depth distribution of microbial biomass and enzyme activity was reported by Enowashu et al. (2009) indicating a vertical adaptation of biological activity to chemical parameters in this soil. Using ingrowth cores filled with quartz sand, Lamersdorf and Borken (2004) observed a greater total fine root biomass in the cores of the clean rain plot. In contrast to our findings, the greatest increase of biomass was detected in a depth assigned to the upper mineral soil which might be explained by artificial growing conditions in the quartz sand.

Fine root necromass and live/dead ratio

The live/dead ratio is controlled by the production and mortality of live fine roots as well as the decomposition of fine root necromass. We explain the greater live/dead ratios in the organic layer and the upper mineral soil of the clean rain plot by an increase of fine root production and/or a reduction of fine root mortality due to improved chemical soil conditions. The smaller live/dead ratio at 20–40 cm soil depth coincides with still low Ca/Al ratios. Additionally, the extremely small N availability at 20–40 cm likely constrains fine root production at this depth whereas relatively higher N availability promotes fine root production in the organic layer.

We found some evidence for accelerated decomposition of fine root litter from the organic layer of the clean rain plot. The observed positive relationship between Mn content and live/dead ratio of fine roots from the organic layer may be attributed to faster decomposition of fine root necromass in the clean rain plot since Mn is an essential element for the synthesis of peroxidases, exo-enzymes produced by white-rot fungi for the degradation of lignin (Berg and McClaugherty 2003). Mn availability affects leaf litter decomposition (Davey et al. 2007) and possibly also influences the decay of fine root litter (Borken et al. 2007). However, we cannot explain the greater Mn contents in the clean rain plot and why no relationship was found for the mineral soil.

Our incubation study suggests faster decomposition of fine root necromass from the organic layer of the clean rain plot. As the conditions for decomposition were different in the incubation experiment using mineral soil from the Bv horizon compared to the *in-situ* condition in the organic layer, we can only characterize the potential degradability of fine root litter. Furthermore, the fact that the roots have been dried and remoistened before incubation could have had an influence on microbial community and the absolute decomposition rate. Lemke (2006) reported an increase of soil organic matter decomposition in the Of and Oh horizon of the same stand and explained the finding by smaller N contents and a subsequently hampered formation of recalcitrant compounds which corroborates our hypothesis of enhanced fine root decomposition in the clean rain plot.

It has to be clarified whether fine root turnover and herewith longevity have changed during the clean rain treatment. Provided that fine root turnover decreases with reduced N availability (Vogt et al. 1993; Nadelhoffer 2000; Majdi and Andersson 2005), we postulate that the increase of soil respiration (Lamersdorf and Borken 2004) resulted from enhanced litter decomposition and transfer of carbohydrates to ectomycorrhiza rather than from increased fine root turnover.

Fine root morphology

Greater root length density and root tip density suggest a more efficient exploitation of the uppermost soil in the clean rain plot. These morphological adaptations allow rising absorptive capacity of the fine root system (Clemensson-Lindell and Persson 1995). In reference to optimality theory in plant ecology (Eissenstat et al. 2000), we interpret these results as a reaction of the plant to reduced N availability, even though the spatial variability of the parameters is very high.

At 20–40 cm, fine roots were thicker and less forked in the clean rain plot. In comparison to the 10–20 cm layer, the changes in diameter and specific root tip density were remarkable and abrupt. Again, as the availability of Al did not fundamentally decrease, we attribute the shift in fine root diameter distribution towards thicker fine roots in the subsoil to the deficiency of N. Consequently, the production of thin fine roots for N uptake is reduced at this depth and promoted in the upper soil for maintenance of plant N supply.

We postulate that changes of morphological traits reflect a shift of root functions within the soil profile of the clean rain plot. We assume that the fine roots in the organic layer and top mineral soil preferentially take up N and other nutrients whereas, below 20 cm soil depth, fine roots may rather accomplish a different function—maybe water uptake or storage. There are indications that fine root systems do not react as a whole plant organ because different root parts have different functions (Ho et al. 2005).

Conclusion

We identified recovery of the fine root system at the Solling site after application of clean rain both by a greater biomass and an improved nutritional status of fine roots. Decreasing N/cation ratios indicated a re-establishment towards natural conditions, i.e. N limitation in the clean rain plot. *Picea abies* responds to altered soil chemical conditions so that the organic layer is increasingly characterized by a spacious and widely forked fine root system with relatively thin fine roots. In the mineral soil below 20 cm, however, fine root properties point to a deterioration of thinner fine roots due to N limitation and ongoing acidification. The chemical composition of the root tissue itself hereby reflects the changed soil solution chemistry and provides an explanation for the shifts in fine root biomass, necromass and morphological traits. Increases in live/dead ratio were attributed to a reduction of fine root mortality as well as to enhanced fine root litter decomposition under clean rain conditions. As the deacidification in terms of increasing Ca/Al ratios in the soil solution is very slow in the mineral soil, we do not expect further increases in total fine root biomass in the next decades. A proceeding decrease in N availability may even fortify the contrasting fine root properties in the topsoil and subsoil.

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