Oecologia (1988) 77:7–13

Oecologia

Performance of two *Picea abies* (L.) Karst. stands at different stages of decline

V. Root tip and ectomycorrhiza development and their relations to above ground and soil nutrients

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Summary. The development of root tips and apparent ectomycorrhizas was compared in the Fichtelgebirge (FRG) over one growing season in two 30-year-old *Picea abies* stands, both on soils derived from phyllite but showing varying symptoms of decline. Visual symptoms of tree decline reflected a lower relative and absolute mycorrhizal frequency, a lower number of ectomycorrhizas per m^2 leaf area and an uneven vertical distribution of root tips and ectomycorrhizas. The number of apparent ectomycorrhizas per ground area was correlated with the amount of magnesium, calcium, and ammonium, and the pH in the free-drainage soil solution, and with the molar calcium to aluminium ratio in mineral soil extracts. The foliage concentrations of magnesium and calcium were correlated with the numbers of apparent ectomycorrhizas per m^2 leaf or ground area. These observations were used to formulate testable hypotheses concerning the role of the root system and the soil environment in forest decline.

Key words: Forest decline – Ectomycorrhizas – Fine roots – *Picea abies*

As part of a large ecological study on tree decline in northeast Bavaria, the development of ectomycorrhizas was studied over one growing season on 30-year-old spruce (*Picea abies* Karst.). The studies were conducted on two sites, Oberwarmensteinach and Wülfersreuth, which were chosen because of their similar stand age and soil type but obvious differences in decline symptoms (Oren et al. 1988a). Symptoms of tree decline, in particular chlorosis of older needles and needle fall, have been observed on 30-year-old trees at the Oberwarmensteinach site. No symptoms have yet been observed at Wülfersreuth. In addition to the visual difference between the stands at the two sites, the soil profile at the Oberwarmensteinach site shows a higher degree of podsolization (Kaupenjohann et al. 1985). Podsolized forest soil has been associated with an increased proportion of roots in the upper organic horizons (Meyer and Göttsche 1971).

The formation of ectomycorrhizas, the symbiotic relationship between forest tree roots and fungi, is known to be a normal process in healthy root development in temperate forest trees (Meyer 1973) and it is influenced by both the soil environment and the physiological state of the tree host (Kottke and Oberwinkler 1986). We investigated whether the differences in the two study stands were also reflected in the distribution of root tips and in the mycorrhizal status of the trees. Soil water potential, elements in free-drainage soil water, nutrient content, and carbohydrate status in *P. abies* foliage and roots (Oren et al. 1988a, b) were measured in order to gain an insight into which plant, soil, or environmental parameters were related to the mycorrhizal status and the root tip distribution of the two stands.

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Materials and methods

The two sites (Table 1) are 15 km apart, near the villages of Oberwarmensteinach and Wülfersreuth in the Fichtelgebirge, NE Bavaria, FRG (50° N 12° E). Further site characteristics are listed in Oren et al. (1988a). Ten 80-m^2 circular plots were established randomly (5 at each site) in March 1985. Three throughfall rain collectors (100 cm^2 area) were set out and three soil lysimeters were installed just below the Oh horizon (directly above the mineral soil) in each of the ten plots. The solutions were collected weekly from each plot, weighed, and frozen until analysis. The concentrations of magnesium, calcium, sodium, and potassium were measured with an atomic absorption spectrophotometer (AAS) (Perkin Elmer 420), ammonium nitrogen, nitrate-nitrogen, and phosphate with a flow injection analyzer (Tecator Fiastar 5022), and pH determined with a glass electrode. A plot mean of these weekly values was calculated for the time periods between root samples and for the 3-week period before the July root sample. Mineral soil samples were taken in July 1986 for exchangable aluminium and calcium analyses. Three samples of mineral soil per plot were taken to a depth of 20 cm below the organic horizons, mixed, and allowed to air-dry. Soil extracts were prepared by a modified method of König et al. (1986) by mixing 10 g dry soil with 20 ml distilled water, shaking for 24 h, centrifuging at 6000 rev min^{-1} for 10 min, and decanting. The concentrations of calcium and aluminium were measured with AAS. Soil water potential was measured in each plot using soil tensiometers at 10 cm and 20 cm depth. Soil temperature in the Oh horizon and at 5 cm and 10 cm depth in the mineral soil was monitored with thermocouples and recorded weekly.

Root and needle samples were taken on 10 April, 20 May, 22 July, and 25 October (needles) and 6 November (roots), 1985. These sampling times were chosen because

Table 1. Site characteristics of the two study stands. The Oberwarmensteinach stand shows visual symptoms of decline; no visual symptoms have yet been observed in the Wülfersreuth stand

Site description	Declining Ober-warmensteinach	Healthy Wülfersreuth
Elevation (m)	755	675
Stand age (yr)	30±2	30±1
Mean stand density (trees m^{-2})	0.44±0.14	0.31±0.02
Mean leaf area index (m^2 m^{-2} ground area)	11.9±1.1	10.6±0.6
Soil type	podsol	podsolized cambisol
Soil pH range[a]	2.9–4.4	2.8–4.4
Parent rock	phyllite	phyllite
Throughfall (mm) (from 7.84 to 6.85)	1424	1106
Throughfall (mm) (from 5.85 to 11.85)	532±54	434±15
Soil water tension (from 4.85 to 11.85)		
Range (mbar)	0–700	0–700
Median (mbar)	100	100
Soil temperature (from 5.85 to 11.85)		
Range (°C)	3–15	3–15
Humus	10.7±0.9	11.3±1.0
10 cm depth	10.8±0.9	10.8±1.0

[a] Kaupenjohann et al. (1985)

they coincided with specific seasonal phenological states in the tree: in April when the soil was still frozen and photosynthesis and transpiration was still very low, at bud-break in May, after full leaf expansion in July, and in October at the end of the growth period. Tree biomass measurements (height, diameter at breast height, sapwood area and number of trees) were recorded in April and in October, 1985. Leaf area index (m^2 leaf area per m^2 ground area) (LAI) was calculated for each plot using a correlation between sapwood area and leaf area which was established by felling 5 trees at each site in May and again in August (Oren et al. 1986).

Five soil cores were taken in each plot with a 10-cm diameter heavy steel soil corer to a depth of ca. 30 cm at the four harvest dates. The soil cores were taken at random in the plot with the limitation that each point was at least 1.2 m away from any tree. Topographic pecularities which could affect root development, such as low areas, were also avoided. The soil cores were sliced into four sections, between the two organic horizons (Olf and Oh) and at two mineral soil depths (0–5 cm and 5–20 cm mineral soil). The cores were stored immediately in separate plastic containers which were filled with deionized water as soon as they arrived in the laboratory and were left to soak overnight. The roots were then washed gently over 1.0 mm screens and stored in deionized water at 3° C (Murach 1984).

Large roots (greater than 2 mm) were separated from fine roots (less than 2 mm) and the living fine root fragments were further sorted from dead root fragments under the dissecting microscope (Murach 1984). Criteria of viability weren resilieny, turgidity, and color. Brittle, wrinkled, and/or dark brown root fragments were considered dead.

The numbers of root tips and ectomycorrhizal root tips were counted separately on the living fine root material. Apparent ectomycorrhizas (ECM) were distinguished from nonmycorrhizal root tips by turgidity, color, and presence of a hyphal mantle, external mycelium, or rhizomorphs. Living ECM were recognized by their swollen look and light-colored root apex compared to a nonmycorrhizal root tip. Not all ECM types had a distinct hyphal mantle however. Microscopic examinations of some of these types revealed a very thin hyphal mantle, only a few cells thick. In these cases, turgidity (swollenness) and color were the main criteria used. Since Hartig net formations have been observed also in nonswollen root tips without a hyphal mantle (Meyer 1984), the ECM counts made in this study are probably underestimates of the actual number, because they do not include nonswollen mycorrhizas without a hyphal mantle (Kottke and Oberwinkler 1986). They are therefore refered to as "apparent" mycorrhizas. After root tip and ECM counts were made, the root samples were dried for 48 h at 70° C and weighed.

Numbers of root tips and ECM and root biomass were calculated on a soil volume, a m^2 ground area and a m^2 leaf area basis. A plot mean was calculated from the 5 sample cores per plot and the resulting 10 mean plot values were used in statistical analyses to test for differences between the sites, for differences in vertical root distribution, and for correlation analyses between the root, plant, and soil variables measured (Sokal and Rohlf 1975).

Materials and methods used in needle sampling and analyses are described in Oren et al. (1988a, b). Because our aim was to identify indications of decline before visual symptoms were apparent, only healthy-looking trees in each plot at both healthy and declining sites were chosen for above-ground analyses. However, plots were randomly located at each site and roots and soil were randomly sampled within each plot.

Results

No significant differences in soil water tension or in soil temperature were found between sites (Table 1) and neither soil water nor soil temperature correlated with numbers of root tips or ECM in any soil horizon.

The soil was still frozen at the first sample in April and therefore the data from this first harvest represents a good zero-point measurement before any new root growth occurred that year (Table 2). The numbers of living root tips and apparent ectomycorrhizas (ECM) did not change between the April and May samples, but did increase by late July and decreased between the July and early November samples (Table 2). The number of root tips per m^2 of ground area or leaf area was similar at both sites throughout the season. However, more ECM per m^2 leaf area were frequently observed at the visually healthy site. The number of apparent ectomycorrhizas correlated with the total number of root tips in both the organic and mineral horizons (Fig. 1) and the number of root tips was correlated with fine root biomass at all sample times (Fig. 2).

The mycorrhizal frequency (percentage of total root tips which are apparently mycorrhizal) was higher on roots in the Wülfersreuth site compared to those in the visually de-

Table 2. Numbers of root tips and ectomycorrhizal root tips expressed per unit leaf area or ground area in the humus and 0–20 cm mineral soil at the 2 study sites at 4 sampling times

		Ectomycorrhizas m^{-2} leaf area ($\times 10^3$)				Root tips m^{-2} leaf area ($\times 10^3$)			
Horizon	Site	April	May	July	November	April	May	July	November
Humus	D	5.2	4.3	17.0	5.1	12.7	15.2	32.3*	10.7
	H	7.5*	7.4*	15.7	6.7	14.5	17.1	23.3	10.0
Mineral soil	D	1.3	1.3	2.1	1.2	4.3	9.0	5.7	2.7
	H	2.5**	2.8	6.9**	1.8	5.0	7.5	11.9	2.5
Total	D	6.5	5.6	19.1	6.3	17.0	24.2	37.9	13.3
	H	10.0*	10.2*	22.6	8.5	19.6	24.7	35.1	12.7

		Ectomycorrhizas m^{-2} ground area ($\times 10^4$)				Root tips m^{-2} ground area ($\times 10^4$)			
Horizon	Site	April	May	July	November	April	May	July	November
Humus	D	6.1^{a}	5.1^{a}	20.1^{b}	5.4^{a}	15.0^{a}	18.7^{b}	38.5^{c}	11.7^{d}
	H	8.0^{a}	7.6^{a}	16.3^{b}	6.9^{a}	15.5^{a}	17.8^{a}	24.2^{b}	10.4^{c}
Mineral soil	D	1.5^{a}	1.6^{a}	2.5^{a}	1.4^{a}	5.0^{a}	9.5^{a}	6.8^{a}	3.3^{a}
	H	2.6^{a}	3.2^{a}	7.6^{*b}	2.0^{a}	5.4^{a}	8.5^{a}	13.1^{b}	2.8^{a}
Total	D	7.6^{a}	6.7^{a}	22.6^{b}	6.8^{a}	20.0^{a}	28.2^{b}	45.3^{c}	14.7^{d}
	H	10.6^{a}	10.8^{a}	23.9^{b}	8.8^{a}	21.0^{a}	26.4^{a}	37.3^{b}	13.2^{c}

D = declining (Oberwarmensteinach), H = healthy (Wülfersreuth)

Values followed by * and ** indicate significant differences between the sites within each month at $P \leq 0.05$ and $P \leq 0.01$ respectively, otherwise differences are not significant (*T*-test)

Different superscripts denote differences ($P \leq 0.05$) between harvests within each site

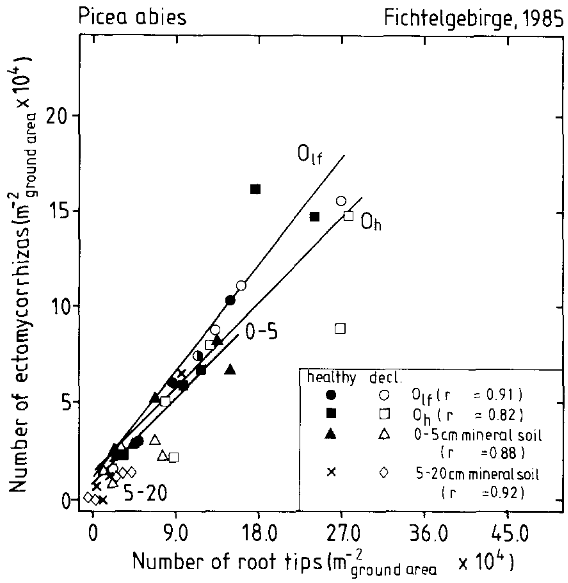

Fig. 1. Relationship between ectomycorrhizal root tips and total root tips in 2 humus horizons (Olf, Oh), in 0–5 cm mineral soil and 5–20 cm mineral soil at two sites

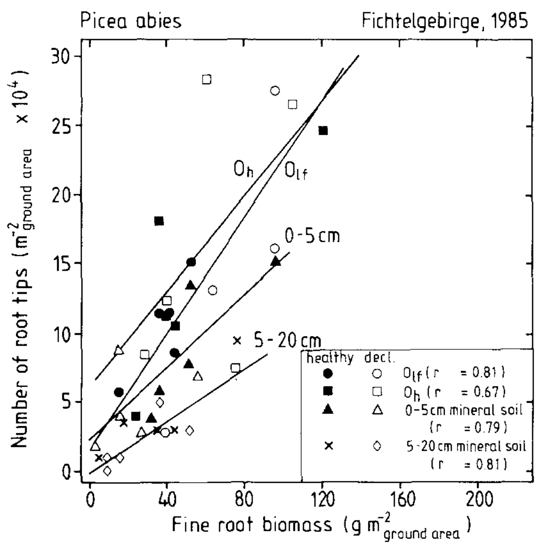

Fig. 2. Relationship between root tips and living fine root biomass in 4 soil horizons at two sites ($n = 10$) (July)

clining site in Oberwarmensteinach, except in May (Table 3). The relative mycorrhizal frequency (number of ectomycorrhizas per gram living fine root biomass) (Kottke and Agerer 1983) was similar between sites in all horizons and sampling times except at mid-season in July when significantly ($P = 0.01$) more ECM per g fine roots were measured on roots in 5–20 cm mineral soil of the Wülfersreuth stand (703 ± 108) (mean ± SE) compared to the Oberwarmensteinach site (258 ± 51).

The vertical distribution (amount per m^2 ground area) of root tips and ECM was significantly different between the two sites in April and July (Fig. 3a, b). A higher proportion of the root tips and ECM was concentrated in the Olf horizon in Oberwarmensteinach compared to a more even distribution in Wülfersreuth, where the highest proportion were found in the Oh horizon (Fig. 3a, b).

Less magnesium and calcium and more ammonium-nitrogen and H^+ were measured in the lysimeter soil solution

Table 3. Ectomycorrhizal frequency (percent of root tips which have formed ectomycorrhizas) in the humus and 0–20 cm mineral soil at 2 sites at 4 sampling times

Horizon		April	May	July	November
Humus (Olf, Oh)	D	41	28	53	49
	H	52*	37	65*	71*
0–20 cm mineral soil	D	32	27	36	45
	H	51*	35	58*	68**
Total	D	36	27	41	46
	H	51*	36	61**	68**

D = declining (Oberwarmensteinach), H = healthy (Wülfersreuth)
Values followed by * and ** indicate significant difference between the sites at $P \leq 0.05$ and $P \leq 0.01$ respectively, otherwise differences are not significant (*T*-test)

Table 4. Element concentration (μmol l^{-1}) in free-drainage soil solution collected just above the mineral soil horizon (mean of the 8-week period between bud-break in May and full leaf expansion in July)

Site	Declining Oberwarmensteinach	Healthy Wülfersreuth
NO_3^--nitrogen	79.4	176.9
NH_4^+-nitrogen	253.7*	129.0
Total *N*	333.1	305.9
HPO_4^--phosphorus	5.0	3.6
K	87.8	57.2
Ca	46.8	157.1*
Mg	8.5	20.1*
Na	7.4	29.1*
H^+	108*	48
Ca[b]	47	129*
Al[b]	643	543

[a] Values obtained from mineral soil extracts

* Values followed by indicated significant differences between the sites at $P \leq 0.05$, otherwise differences are not significant (*T*-test)

at Oberwarmensteinach compared to Wülfersreuth (Table 4). Total soil nitrogen (ammonium + nitrate) was not different between the sites.

The number of apparent ectomycorrhizal root tips in the mineral soil in July was correlated with the pH and with concentrations of calcium and magnesium (Fig. 4a–c) of the free-drainage soil solution collected just above the mineral soil. A negative correlation was found between the numbers of ECM and the concentration of ammonium-nitrogen in the soil solution (Fig. 4d). The total number of living root tips in the first 20 cm of the mineral soil was also correlated with the calcium and magnesium con-

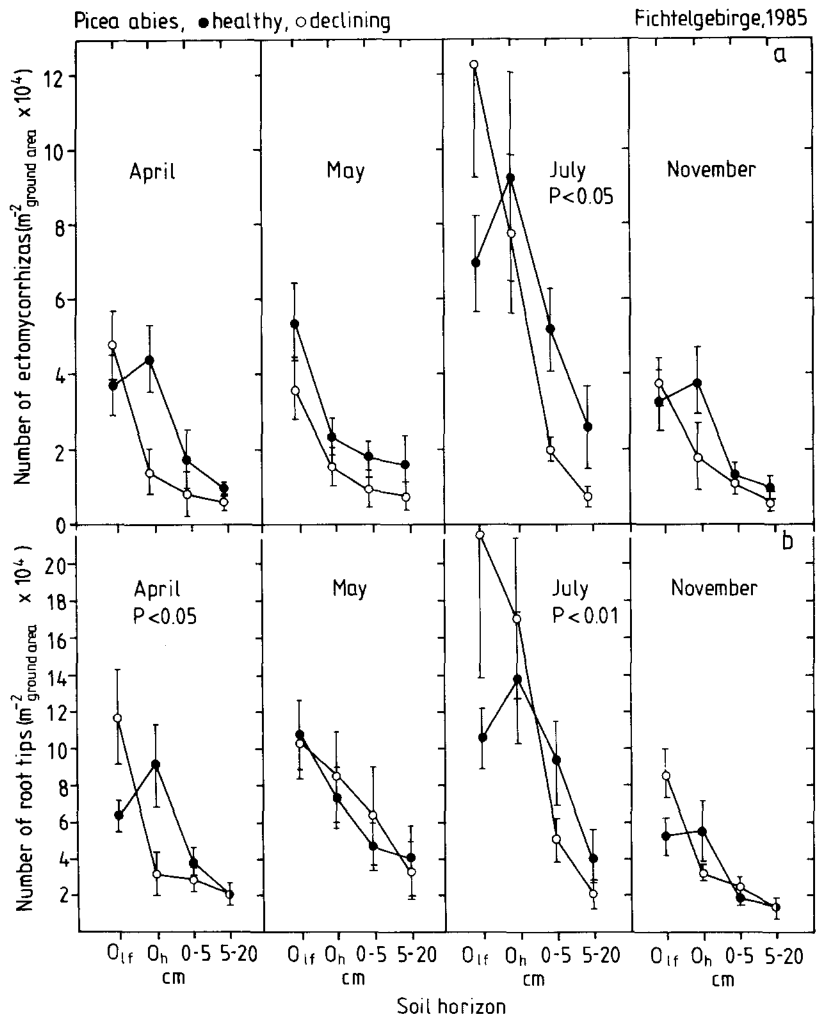

Fig. 3. Vertical distributions of **a** ectomycorrhizal root tips and **b** root tips (number per m^2 ground area) in 4 soil horizons at 2 sites at 4 sample times. **a)** A significant difference between sites (chi-square test) was observed in the July sample (Chi-square = 7.8, $P \leq 0.05$, $n = 5$).
b) Significant differences between sites were observed in April (chi-square = 8.6, $P \leq 0.05$) and in the July sample (chi-square = 7.8, $P \leq 0.05$, $n = 5$)

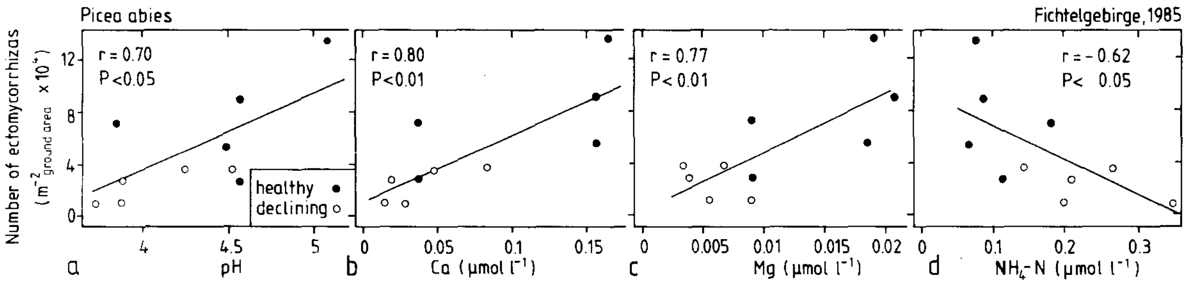

Fig. 4. Correlation between the number of ectomycorrhizas per m^2 ground area in the first 20 cm of mineral soil of both sites and **a** the pH value, **b** Ca concentration, **c** Mg concentration and **d** NH_4 concentration of the free-drainage soil solution (mean of 3 weekly collections before July root sample)

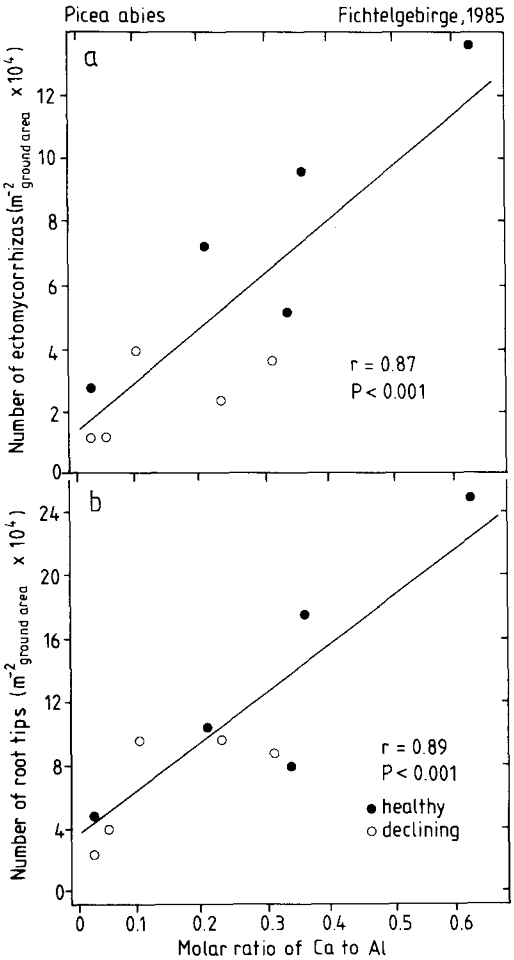

Fig. 5. Correlation between **a** the number of ectomycorrhizas or **b** root tips in the first 20 cm mineral soil of both sites and the molar ratio of Ca to Al in mineral soil extracts ($n = 10$)

tent and pH value of the soil solution ($r = 0.74$, 0.65, 0.69, $P = 0.05$). A correlation was obtained between the number of ECM in the mineral soil and the molar ratio of exchangeable calcium to aluminium in mineral soil extracts (Fig. 5a). No correlation was observed between the numbers of ECM and the amount of exchangeable aluminium alone. The total number of root tips was also correlated with the molar ratio of calcium to aluminium (Fig. 5b), in this case a correlation was also observed with aluminium alone ($r = -0.65$).

The mean foliage magnesium concentration at all harvests throughout the season was correlated to the numbers of ECM per m^2 ground area or leaf area which formed in the mineral horizons (Fig. 6a). A similar positive relationship was found between the calcium content of needles and ECM (Fig. 6b) and a negative correlation was observed between the mean aluminium content of the foliage and numbers of ectomycorrhizas (Fig. 6c), expressed either per m^2 ground area or m^2 leaf area.

Discussion

The visual symptoms of tree decline reflect a low foliar magnesium status in the stand (Oren et al. 1988b). Large differences in foliar calcium were also measured. The differences in the nutrient status of the two stands are probably due to differences in nutrient availability and uptake. The uptake rate of calcium and magnesium at the declining Oberwarmensteinach site was shown to be lower than that at Wülfersreuth as evident from their concentration in the xylem (Osonubi et al. 1988) which is in agreement with their availability from the soil solution. Our data also suggest that the soil chemical characteristics affect the vertical distribution of root tips and their mycorrhizal status.

An extensive mycorrhizal development on mature forest trees is an indicator of a healthy and efficient root system. Highly mycorrhizal root systems function better in nutrient uptake (Bowen 1973). The opportunity for ECM to form depends mainly on the availability of root tips to be "converted" (Chilvers and Gust 1981; Kottke and Oberwinkler 1986). However, this was not the limiting factor at the visually-declining Oberwarmensteinach site since total numbers of root tips was similar to those at the visually healthy site (Table 2). Therefore it seems that differences in the apparent mycorrhizal frequency between the sites are due to differences in the ECM formation process, not the amount of host tissue available to infect. Although the relationship between ECM and root tips was similar at both sites (Fig. 1), the intercept of the regression lines was not at zero which means that the plots falling at the lower part of the line will have lower ECM to root tip ratios than those falling further from the intercept.

ECM formation is dependent on the interactions between plant, soil, and fungus. Differences in foliar carbohydrate contents between the sites were detected in the April samples (Oren et al. 1988a) but no correlations were found between ECM and plant carbohydrate levels. Correlations were found, however, between the numbers of apparent ECM in the mineral soil and the calcium, magnesium, and ammonium content and pH of the soil solution (Fig. 4a–c) and with the molar calcium-to-aluminium ratio in mineral soil extracts (Fig. 5a). These correlations were detected mainly because of differences between the sites. However,

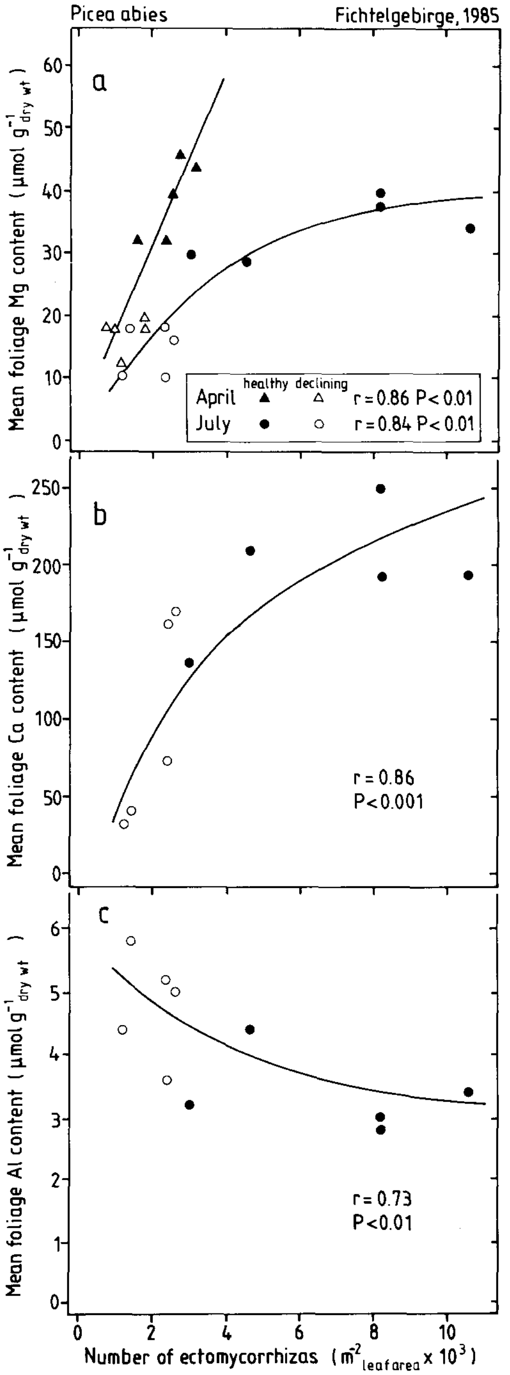

Fig. 6. Correlation between **a** the amount of foliage Mg, **b** Ca or **c** 1 before bud break in April (Mg only) and at full leaf expansion in July and the number of ectomycorrhizal root tips per m^{-2} leaf area in the first 20 cm of mineral soil ($n=10$) of two sites

except where the range is too small, the relationships are also found within the sites. These data suggest that the soil chemical factors which reflect the degree of podsolization or soil acidification (decreasing concentration of calcium and magnesium, increasing ammonium, the molar ratio of calcium to aluminium, decreasing pH) can affect the formation of ECM below the organic horizons or their ability to thrive. Field experiments are now in progress to test this hypothesis. The molar ratio of calcium to aluminium, thought to be a more biologically important indicator of soil conditions than either element alone (Rost-Siebert 1983) was found in most plots to be in the range where root growth and elongation could be affected, particularly below pH 4.2 (Matzner and Ulrich 1985; Rost-Siebert 1983). Very few data are available on the influence of soil chemistry on ECM and it is not known whether ECM are directly affected by aluminium, although some fungi are sensitive to heavy metals in artificial media (Thompson and Medve 1984). Similarly, although ectomycorrhizas are known from laboratory studies to tolerate a rather wide soil pH range (Huang and Trappe 1983), our field studies revealed a correlation between the numbers of apparent ECM and soil pH (Fig. 4a) which could indicate a direct or specific effect on certain ECM species (Huang and Trappe 1983), or it could be interpreted as an indication of the sensitivity of apparent ECM to pH-associated soil processes.

Soil chemical factors may explain the significantly higher proportion of root tips and apparent ECM at the raw humus at the visually declining site since this observation could not be due to either a larger Olf soil volume to exploit (2.6 cm ± 1.0 compared to 1.8 cm ± 1.0 in Wülfersreuth) or that fewer total roots were produced and therefore did not penetrate deeper. Because the water availability in the mineral soil was high (Werk et al. 1988), it is also unlikely that water availability affected the distribution of root tips and ECM. The very high proportion of the root system found in the Olf horizon in the declining site makes it more likely that the root systems of these trees are susceptible to even short-term drought periods, during which water and nutrient uptake will be impaired (Osonubi et al. 1988).

We deliberately investigated healthy-looking trees at both the healthy and declining sites in our above-ground analyses (Oren et al. 1988a) because we were interested in identifying indications of decline before visual symptoms are apparent. It is worthwhile to note, therefore, that even at this stage a lower concentration of foliage magnesium and calcium is associated with fewer ectomycorrhizal root tips supplying a unit of leaf area. We interpret this as an imbalance between the nutrient uptake organs and the nutrient-demanding organs created by an imbalanced soil environment, which still provides enough nutrients for needle growth in some trees but is becoming increasingly unfavorable for adequate vertical distribution and mycorrhization of the root system. This hypothesis is now being tested in field experiments.

The nutrient status of the tree is mainly determined by the nutrient availability in the soil solution, the efficiency of the root system, and plant growth. The correlations we find at our sites between foliar magnesium and calcium content and the number of apparent ECM formed suggests that either the amount of ECM formed determines in part the quantity of nutrients taken up by the plant, or that the magnesium and calcium status of the trees and the amount of ECM able to form in these stands are all related to the same soil environmental factors. If forest stands are receiving increased proton loads from acid rain, this will accelerate soil acidification and cation leaching and depletion (Nömmik et al. 1984), which could lead to imbalances in the soil-plant system as observed in this study.

Acknowledgements. The authors wish to thank Martin Kaupenjohann and Barbara Scheitler for their help in the chemical analyses and Dr. Ralph Hantschel and Martin Kaupenjohann for their cooperation during the course of this project. We thank Dr. Kottke for her advice in identifying ECM.

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Received December 14, 1987