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Influence of liming and acidification on the activity of the mycorrhizal communities in a *Picea abies* (L.) Karst. stand

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Abstract

A study of mycorrhizal activity was conducted in a mature Norway spruce (*(Picea abies*) [L.] Karst.) stand subjected to soil treatments of liming and acidification for six years (Höglwald research project). Samples were collected five times during one growing season using a soil corer. All the turgescent, not shriveled mycorrhizal tips were sorted out and identified on the fungal species level as far as yet possible. The proportion of each mycorrhizal type on the plots was calculated. The results revealed a shift in the mycorrhizal communities caused by both acid rain and liming. Data are in agreement with the findings of the more comprehensive study on the mycorrhizal communities carried out by another research group on the same plots (Taylor et al., submitted)

The activity of the predominant types of mycorrhizas, *Piceirhiza gelatinosa, Piceirhiza nigra, Russula ochroleuca-P. abies, Tuber puberulum-P. abies, Tylospora sp.-P. abies, Xerocomus badius-P. abies,* was investigated by staining hand sectioned tips with FDA and their fluorescence. Different FDA-hydrolysing activities of the mycorrihizal types had been found in a previous-year study on the same plots and were confirmed during the second year. The proportion of the different stages of activity of the mycorrhizal tissues was calculated on the type level and in connection to the soil treatments. *X. badius-P. abies* and *R. ochroleuca-P. abies* displayed the most active fungal tissues and proportion increased on the acidic plots while *Tuber puberulum-P. abies* and *Piceirhiza nigra* were the most active types and occurred in higher proportion after liming. Thus, the overall activities of the mycorrhizas were only slightly changed by the treatments. In addition to the mycorrhizal effect acidification reduced while liming enhanced the meristematic activity of the short root tips. The same tendency was found by studying root production on the same plots (Hahn and Marschner, 1998). Although nearly 3000 mycorrhizal tips were studied, the data are still limited, allowing no statistical validation. This is, however, the first investigation connecting overall activity of the mycorrihizal tissues with the proportion of the mycorrhizal types as influenced both by alterations of the forest soil caused by acid rain and liming. The results are interesting and reasonable but further investments are necessary to validate the general conclusions.

Introduction

Increased proportion of dead roots, reduced regeneration ability, and disturbance of the mycorrhizal symbiosis were discussed as symptoms of the 'new type' forest decline ('Waldsterben'; Blaschke, 1980, 1981, 1982; Bosch et al., 1982; Murach, 1983; Schütt et al., 1983). Decline of the fine roots was connected to soil acidification, and was treated by liming of affected forest stands (Gussone, 1983; Wenzel and Ulrich, 1988). The functioning of mycorrhizas in Norway spruce stands was evaluated using FDA active fluorescence as a marker of activity. There was no reduction in mycorrhization, but the life span of the mycorrhizas was lower and the turnover rate was higher in acidified soils when compared to previously limed plots (Kottke et al., 1993).

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No information on short term effects of acidification or liming on the activity of identified mycorrhizal types and communities in the forest stands was, however, available. It was expected that acidification might reduce and liming might enhance activity of mycorrhizas, but the treatments might also influence the ectomycorrhizal fungal species composition. Previous research indicated that mycorrhizal types differed in activity (Ritter, 1990). We, therefore, investigated, the activity of morphologically identified mycorrhizal types on experimentally acidified and limed plots after six years of treatment. The investigations were part of the interdisciplinary research project 'Höglwald'. Soil parameters, soil animal activities, fine root production, fungal and mycorrhizal communities were studied by other research groups.

Material and methods

Sampling

Mycorrhizas were collected in four plots of the experimental station 'Höglwald', an 80-years old pure Norway spruce (*Picea abies* [L.] Karst.) stand near Augsburg, Bavaria. Two plots (B1 and B2) had been watered 15–18 times per year from 1984–1990 by sulphuric acid rain (pH value 2.7–2.8). Two plots (B2 and A2) had been limed in 1984 by 40 dt ha^{-1} dolomite. Untreated plots (A0, A1) served as control. In 1991 when sampling took place watering had ceased. Details of plot design and soil conditions are described in Kreutzer and Weiss (1998). Sampling was carried out in March, April, June, August and October 1991. Five root samples were taken per plot within an area of 12 m^2 at each sampling date. A soil corer of 5.5 cm diameter was used and cores were taken to a depth of 30 cm. The core samples were divided in the horizons OF, 0H, AH and mineral soil in the plots A0 and B1. In the plots A2 and B2 the OF and OH horizons were combined into one OLu-horizon (Kreutzer, 1995). The five root samples of each horizon were pooled in order to obtain sufficient numbers of each mycorrhizal type to compare the influence of the treatments on the plots. No statistical validation was intended because it was known from the previous-year investigation (Qian et al., 1998) that distribution of mycorrhizal types in time and space was such inconsistent that the data basis would not allow statistics.

Identification of mycorrhizal types

The roots were cleaned under tap water. Shriveled, obviously dead mycorrhizas were omitted. The other mycorrhizal root tips were either identified according to the key and personal help of Agerer (1987–1996) or assigned to the 'old' or 'unidentified' groups. The number of the different mycorrhizal types were counted per plot and soil horizon and the proportions calculated.

Evaluation of activity

All the apparently active mycorrhizas were hand sectioned at a thickness of about 100 μm, stained by FDA (fluorescein-diacetate) and estimated visually with respect to UV-fluorescence of the different tissues, outer and inner hyphal sheath, Hartig net and meristem, using a five step scale from bright fluorescence activity to no activity. The analyses were carried out during one week after sampling while the material was kept at 6 °C till analysed. Details of the fluorescence activity evaluation are given in Qian et al. (1998). FDA fluorescence is based on activity of unspecific esterases and proteinases in the cytoplasm of plant and fungal tissues, cleaving fluorescein-diacetate into fluorescein and acetic acid (Rotman and Papermaster, 1966). The fluorescein gives bright yellow-green fluorescence under UV-light. No apparant fluorescene is considered as a signe of cell death. The staining is easy to handle and allows screening of high numbers of mycorrhizal sections within few days after sampling. It is so far the only method to examine activity of the different mycorrhizal tissues, separating fungal activity from root activity, of individual, identified mycorrhizas of the dominant types. All mycorrhizal types observed during this investigation revealed bright fluorescence in at least a few samples indicating that all fungi were infiltrated by the stain.

The meristem of Norway spruce mycorrhizal rootlets becomes surrounded by a metacutin layer during dormancy. The metacutin layer is disrupted by the root tip during each new growth phase. The remnants of the metacutis are an indication of the number of growth-phases of a mycorrhiza (Kottke et al., 1993; Ritter et al., 1989). The metacutin layers were visible in the longitudinal sections because of blue autofluorescence of suberin and lignin. The numbers of the remnants per mycorrhiza were counted in order to obtain further information on growth conditions of rootlets on the differently treated plots.

Table 1. Numbers and proportion of all mycorrhizal types collected in 1991 on the four plots

Mycorrhizal type	Number	Proportion of total observations
Tylospora sp.	436	15.40
Russula ochroleuca	433	15.30
Piceirhiza nigra	416	14.70
Tuber puberulum	197	6.90
Piceirhiza conspicua	190	6.70
Xerocomus badius	169	6.00
Piceirhiza obscura	86	3.00
Piceirhiza gelatinosa	71	2.50
Hygrophorus pustulatus	59	2.10
Amphinema byssoides	49	1.70
Cenoccocum geophilum	36	1.30
Piceirhiza cystidiophora	33	1.20
Piceirhiza glutinosa	23	0.80
Dermocybe cinnamomea	20	0.70
Unidentified	391	13.80
Old mycorrhizas	219	7.70
Non mycorrhizal	11	0.40
Total	2839	100.00

Calculation of the activity of the mycorrhizal communities on the different plots

Proportion of fluorescence activities of the tissue layers was calculated on the level of the mycorrhizal types and on the level of the plots independently of types. Six dominating types were detected more than 100 times during the time of investigation (Table 1) and were used for the calculation. Eight additional types were found less than one hundred times (Table 1) and were put into the category rare types. The tissue fluorescence activities of the rare types, of the old and unidentified mycorrhizas was only regarded for calculating total tissue activities on the different plots. A total number of 2839 sections were considered in the calculation of tissue activity of the different plots.

Despite the large number of sectioned and analysed mycorrhizas no valid differences of the activities of mycorrhizal types between the sampling dates and the soil horizons can be presented. The reason for the difficulties was the inconsistency of mycorrhizal types in time and space (Table 2). Sampling dates were neglected and samples were pooled to compare the activity of the mycorrhizas in the soil horizons.

No appropriate statistical analysis is so far available to handle with the patchy distribution of mycorrhizal types. The multiplication of mycorrhizas is due to different insufficiently studied propagation strategies of the fungi and to the influence on root ramification by the fungi. We therefore withdrew from validating the data by conventional statistics and preferred to interpret results as tendencies.

Results

Influence of soil treatments on the dominant mycorrhizal types

In the fine root systems nearly 100% of the root tips were mycorrhizal. Fourteen mycorrhizal types were identified, but found at very different numbers in total (Table 1) and at the sampling dates (Table 2). Consequently, the proportion of teach type differed greatly among the sampling dates (Table 2). Influence of soil treatments on the proportion of the six dominant types or within the categories 'rare types', 'old' and 'unidentified' are shown in Table 3 calculated on the basis of total numbers of mycorrhizas on each plot. The proportion of the two dominant types in the control plot (A0), *Tylospora* sp.-*P. abies* and *R. ochroleuca-P. abies*, were reduced by acidification and by liming (A2. B1, B2). Acid watering (plot B1) increased the proportion of *Xerocomus badius-P. abies* considerably, but reduced the proportion of *Piceirhiza nigra* and *T. puberulum-P. nigra*. Liming (plots A2 and B2) increased the proportion of *Piceirhiza nigra* and *T. puberulum-P. abies*. The proportion of rare types was enhanced by all of the treatments in comparison to the control. Old and unidentified types were found at more or less the same proportion in all plots.

Influence of soil treatments on the activity of the six dominant mycorrhizal types

Although only turgescent mycorrhizus were sectioned, a surprisingly low level of activity of the hyphal sheath layers was apparent after staining with FDA over all types and treatments (Figures 1 and 2). The outer hyphal sheath was fluorescing at high activity (+++) only in the *X. badius-P. abies* tips from acidified plot B1, (20% of the mycorrhizal tips, Figure 1). The inner hyphal sheaths displayed higher degree of activity in all types, except the *T. puberulum-P. abies* tips (Figure 2) The *X. badius-P. abies* mycorrhizas were promi-

Table 2. Proportion of each dominant mycorrhizal type and the old and unidentified mycorrhizas found at the sampling dates on the four plots. Proportion calculated on the total number of each type displaying the irregular finding of the types

	March	April	June	September	October
Control-plot A0					
Tylospora fibrillosa	35.0	22.7	30.0	–	12.3
Russula ochroleuca	–	20.2	5.5	–	73.4
Piceirhiza nigra	–	–	–	–	–
Tuber puberulum	–	–	–	–	–
Piceirhiza conspicua	–	19.0	–	81.0	–
Xerocomus badius	–	–	–	–	–
Unidentified types	64.3	–	35.7	–	–
Old mycorrhizas	6.0	40.3	–	53.7	–
Limed plot A2					
Tylospora fibrillosa	14.9	56.7	–	–	28.4
Russula ochroleuca	–	41.4	48.3	–	10.3
Piceirhiza nigra	40.9	14.0	9.3	17.2	18.6
Tuber puberulum	–	28.6	27.1	–	44.3
Xerocomus badius	–	–	–	–	–
Unidentified types	–	–	–	28.3	71.7
Old mycorrhizas	–	44.4	8.6	24.7	22.2
Acidified plot B1					
Tylospora fibrillosa	–	14.0	32.6	23.3	30.2
Russula ochroleuca	13.2	–	13.2	33.8	39.7
Piceirhiza nigra	–	–	–	–	–
Tuber puberulum	–	–	–	–	–
Piceirhiza conspicua	–	100.0	–	–	–
Xerocomus badius	23.0	30.0	2.0	31.0	14.0
Unidentified types	–	18.3	–	39.4	42.3
Old mycorrhizas	–	–	100.0	–	–
Acidified and limed plot B2					
Tylospora fibrillosa	–	25.0	–	–	75.0
Russula ochroleuca	–	37.1	11.4	–	51.4
Piceirhiza nigra	26.3	14.6	25.1	10.5	23.4
Tuber puberulum	64.9	–	35.0	–	–
Piceirhiza conspicua	–	49.2	50.8	–	–
Xerocomus badius	–	–	7.5	–	92.5
Unidentified types	18.5	–	31.5	12.0	38.0
Old mycorrhizas	–	75.0	7.1	–	17.9

nently active in plot B1, activity was reduced in plot B2 (liming and acid watering). *R. ochroleuca-P. abies* mycorrhizas revealed an active inner hyphal sheath in all treatments and *Piceirhiza nigra* was the same active on both limed plots.

Influence of treatments was also expressed in the Hartig net layer (Figure 3). Tips of *Tylospora* sp.-*P. abies*, *Xerocomus badius-P. abies* and *Piceirhiza conspicua* showed a high proportion of non-fluorescing Hartig net (60–80%) in plot B1, but up to 15% of the tips showed active Hartig net (+++) in plot B2.

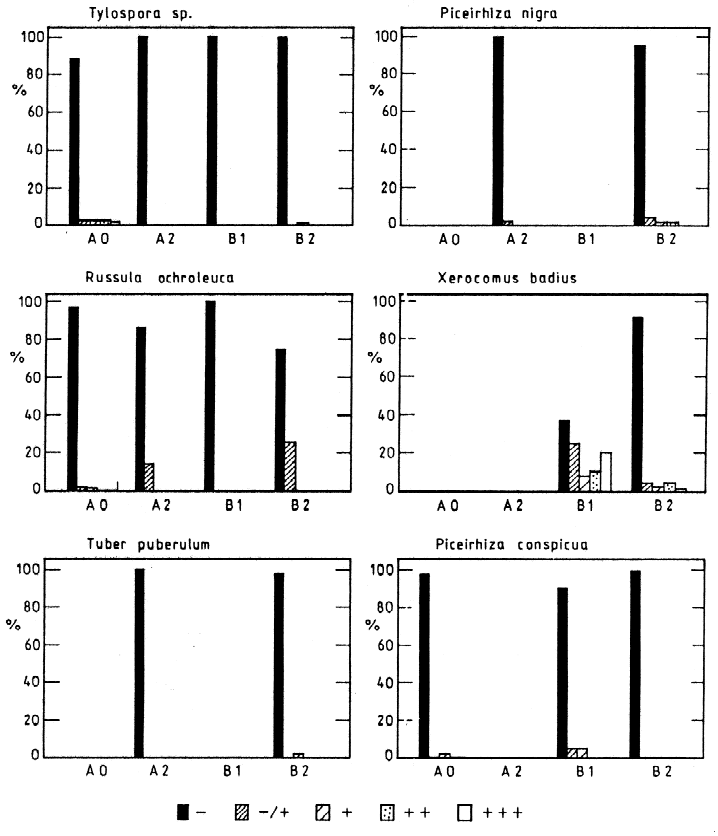

Figure 1. Proportion of mycorrhizas of each type on the four plots displaying different stages of activity in the **outer hyphal sheath**. Legend: – no fluorescence, dead brown tissue; +/- greenish to brownish, dying tissue; + blue green fluorescence. fading tissue: ++ light green fluorescence. less active tissue; +++ Bright green fluorescence activity of tissue.

Table 3. Proportion of dominant, rare, old and unidentified mycorrhizas on the four plots calculated on the basis of pooled numbers of all types irrespective of the sampling date

	Control-plot A0	Limed plot A2	Acidified plot B1	Acidified and limed plot B2
Tylospora fibrillosa	29.4	9	11.5	11.8
Russula ochroleuca	31.6	3.9	20.9	5.1
Piceirhiza nigra	4.4	28.8	0	25.2
Tuber puberulum	0	18.8	0	8.4
Piceirhiza conspicua	12.2	0	5.7	9.6
Xerocomus badius	2.3	0	13.9	7.8
Not identified	2	7.1	19.7	13.5
Old mycorrhizas	9.7	10.9	5.9	5.7
Rare types	8.6	21.6	22.4	12.8

Piceirhiza nigra mycorrhizas displayed 13% of active Hartig net (+++) on plot A2, but only 3.5% on plot B2.

The activity of the meristems reflected differences between the mycorrhizal types and the treatments (Figure 4). *Piceirhiza nigra, R. ochroleuca-P. abies* *X. badius-P. abies* mycorrhizas revealed a prominent higher proportion of active meristems (+++) than the other three types on most of the plots (*X. badius-P. abies* 20.8%, *R. ochroleuca-P. abies* 17% on plot B2). *Piceirhiza nigra* showed 17.2% active meristems on

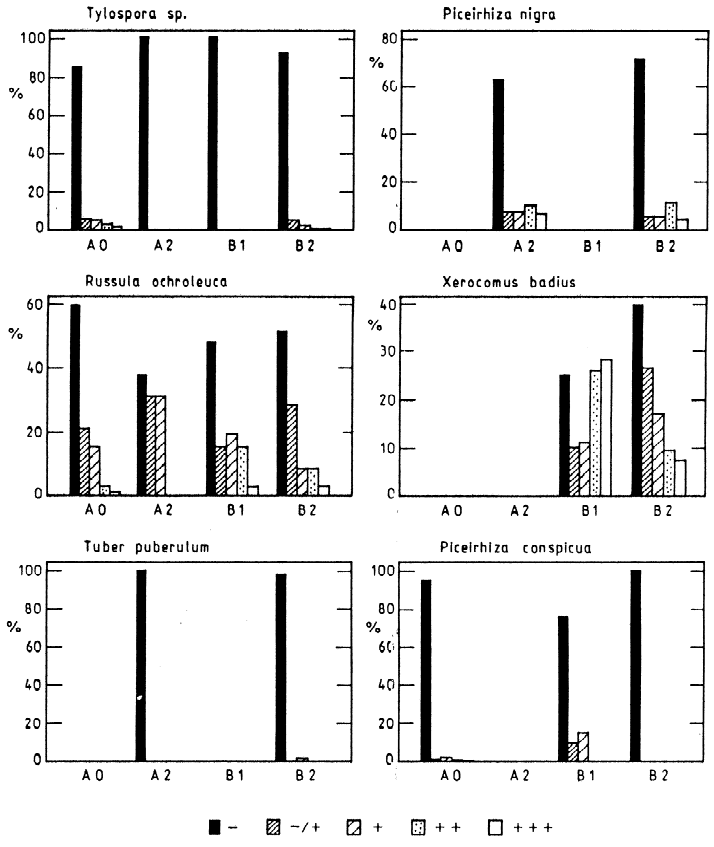

Figure 2. Proportion of mycorrhizas of each type on the four plots displaying different stages of activity in the **inner hyphal sheath**. For explanation of the legend see Figure 1. Note differences in scaling.

plot A2. Activity was lowest in all types on plot B1. On this plot, inactive meristems accounted for 43% of the tips in *Tylospora* sp.-*P. abies*, 39% in *Piceirhiza conspicua*, 31.8% in *R. ochroleuca-P. abies*, and 28% in *X. badius- P. abies.*

Influence of soil treatments on the activity of the mycorrhizal communities

Pooling across mycorrhizal types for every plot showed that a higher proportion of the outer and inner hyphal sheath layers were active in plot B1 compared to the other treatments while the activity of the Hartig net was the lowest in plot B1 (Figure 5). No differences in activity of the Hartig net and hyphal sheath could be detected between plots A0, A2 and B2 (Figure 5).

Influence of soil treatments on the activity and the growth conditions of the root tip meristems

Among soil treatments the proportion of active meristems was highest for plot A2 and lowest for plot B1. The condition of the meristems was similar for plots A0 and B2 (Figure 5). The numbers ot metacutin layers also reflected influence of treatments on growth conditions of rootlets (Figure 6). In the acidified plot B1 more than four layers of metacutin, indicating frequent dormancy and regrowth of the mycorrhizas, were found in 10.8% of the the mycorrhizas while on the plots A2 and B2 70% of all mycorrhizas had only one metacutin-layer. In Figure 7 the state of the meristems is compared. The proportion of growing tips with fully active meristems and without a metacutis was highest on the control plot. Dormant tips with meristems of high fluorescence activity, but surrounded by a metacutis occurred on the limed plots (A2, B2) at higher proportion than on the control plot and the acidified

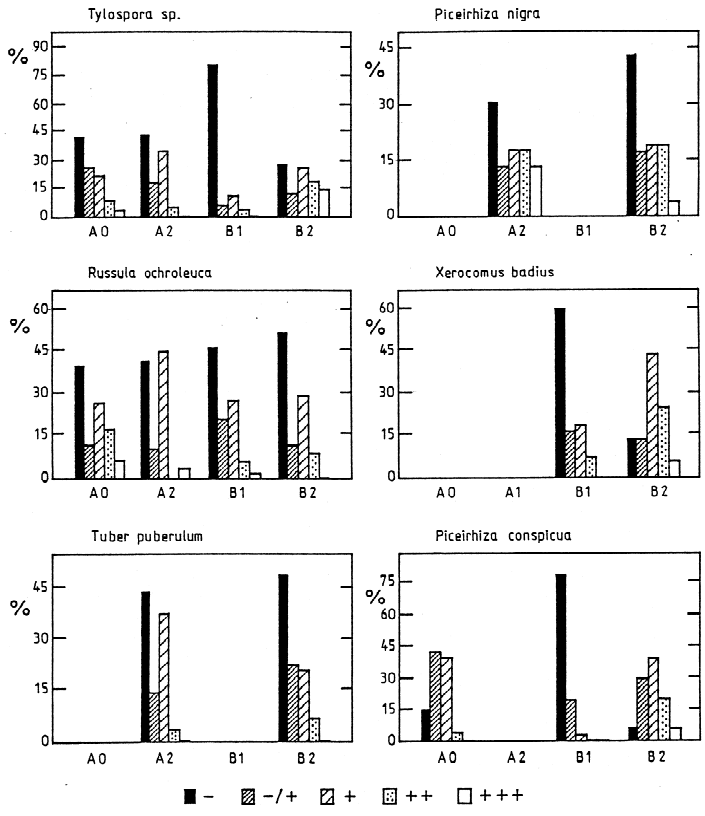

Figure 3. Proportion of mycorrhizas of each type on the four plots displaying different stages of activity in the **Hartig net**. For explanation of the legend see Figure 1. Note differences in scaling.

plot. The highest proportion of dead and the lowest proportion of actively growing mycorrhizas was found on the acidified plot B1. There were only minor differences among the control plot and the limed plots in the proportion of mycorrhizas with low fluorescence activity of the meristem (dying mycorrhizas, Figure 7).

Differences of mycorrhizal activity and growth conditions in the soil horizons

Because of irregular numbers of each type of mycorrhiza in the different horizons (not shown), no calculation of activity at type level or for separate tissue layers is presented. Most distinct vertical differences could be noticed regarding the four categories of mycorrhizal developing stages: growing, dormant, declining and dead (compare Figure 8). The limed plots (A2 and B2) showed only minor differences in the vertical distribution of growing, dormant, declining and dead mycorrhizas. On the acidified plot (B1), a reduction of activity in the OF and OH horizons and an increase in activity of mycorrhizas with depth was observed. On the control plot (A0), the AH-horizon contained the highest proportion of growing mycorrhizas of all treatments, while the proportion of dead mycorrhizas was highest in the OH horizon on plot B1. No differences between treatments could be detected in the mineral soil. Growing mycorrhizas occurred at 36.3% and the proportion of dead and growing mycorrhizas 1:7 in the mineral soil on all plots.

Seasonal fluctuations of mycorrhizal activity

The activity of the pooled mycorrhizas of the four plots represented at the time of sampling shows only slight seasonal dynamic (Figure 9). The lowest fluctuation appeared on the control plot (A0), the highest divergence on the acidic watered plots (B1 and B2). The highest proportion of active mycorrhizas was found in March, June and October with slight differences between the treatments. In plots A0 and A2 a compar-

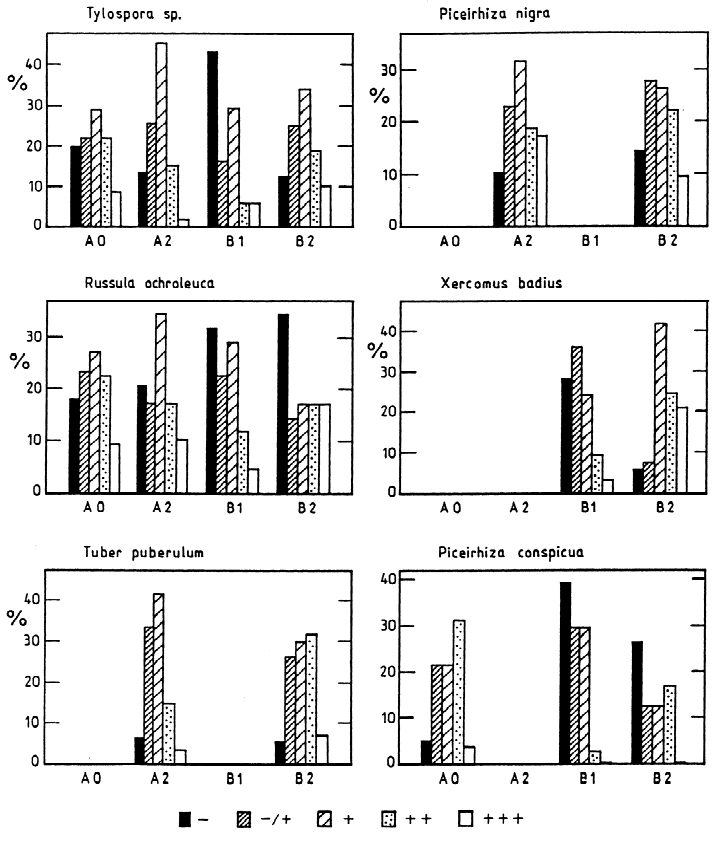

Figure 4. Proportion of mycorrhizas of each type on the four plots displaying different stages of activity in the **meristem**. For explanation of the legend see Figure 1. Note differences in scaling.

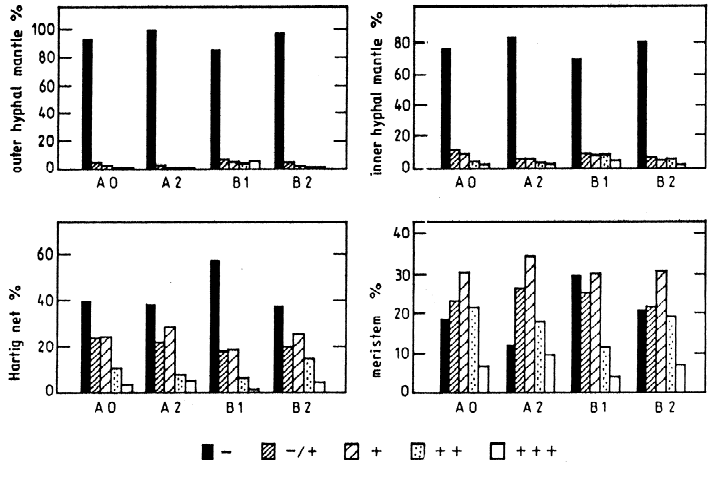

Figure 5. Synopsis respecting all mycorrhizal types on the four plots evaluated on activity of the different mycorrhizal tissue layers. For explanation of the legend see Figure 1. Note differences in scaling.

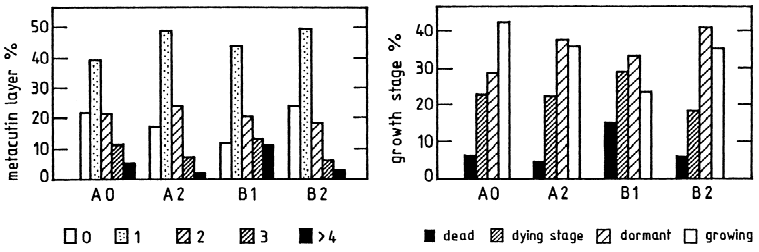

Figure 6. Proportion of mycorrhizas with different numbers of metacutin remnants on the four plots.
Figure 7. Proportion of mycorrhizas on the four plots at a growing, dormant, declining stage or found to be dead. Growing tip means apex with bright fluorescence and without metacutis; dormant mycorrhizas are surrounded by a metacutin layer at the bright fluorescing apex: dying stages show low or no active fluorescence; dead mycorrhizas are without fluorescence.

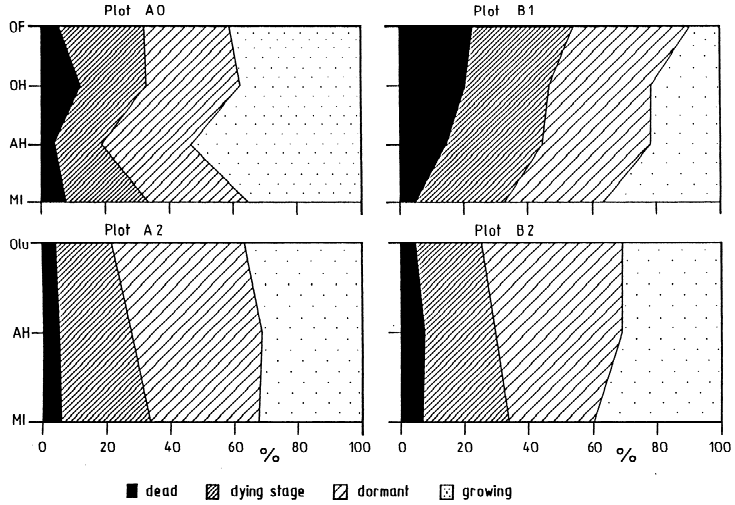

Figure 8. Activity and growth stages of the mycorrhizas in the soil horizons of the four plots. For explanation of the legend see Figure 7.

atively higher activity appeared in March and October. B1 and B2 showed a higher activity in June than in April and August.

Discussion

Visual estimation of the fluorescence activity of ectomycorrhizas showed that liming and acidification of soil influenced fungal tissues and root apical meristems. The activity of the hyphal sheath and Hartig net was connected to the fungal species involved. The higher proportion of active hyphal sheaths in the acidified plots compared to the control and the limed plots (Figure 5) was mainly attributable to the proportion of *X. badius-P. abies* mycorrhizas (Figures 1 and 2) which increased by 10% compared to the control plot. The activity of the inner hyphal sheaths of *X. badius-P. abies.*, *R. ochroleuca P. abies* mycorrhizas and of *Piceirhiza conspicua* was highest on the acidified plot B1 (Figure 2). *Piceirhiza nigra* was the only mycorrhizal type with high hyphal sheath activity on the limed plot (A2) and was most numerous there. *Tylospora* cf. *fibrillosa-P. abies* mycorrhizas displayed the best activity of the hyphal sheaths and highest number of mycorrhizas on the control plot, but became less active and less frequent after acid watering and after liming, respectively. As a result of the change in the proportion of the mycorrhizal types, the overall activity of the hyphal sheaths of the mycorrhizal communities only slightly differed among the treatments. Because of the diversity of mycorrhizal fungi in the forest stand as reflected by the control plot the mycorrhizal communities reacted to the treatments buffer-like, reestablishing functioning mycorrhizas. If one or the other fungal species had been missing, problems in mycor-

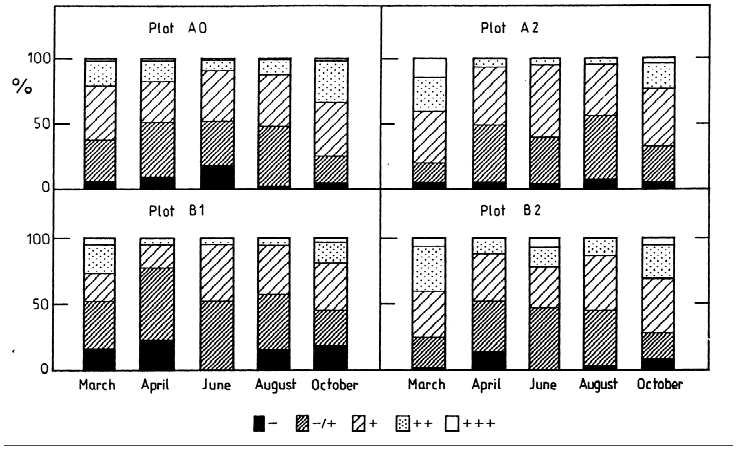

Figure 9. Seasonal fluctuation of the fluorescence activity calculated by pooling the data irrespective of mycorrhizal type and tissue layers. The differences in the fluctuations of tissue activities among the plots may be due to inconsistent finding of types (see Table 2), and root growth dynamics connected to the environment. For explanation of the legend see Figure 1.

rhizal functioning and tree health might have arisen. The observed shift in the mycorrhizal community is validated by the comprehensive study of Taylor et al. (submitted). Physiological studies of the activity of the mycorrhizas could. however, only be performed with few mycorrhizal types on a very restricted enzyme pattern because sufficient amounts of material were not available (Guttenberger et al., 1998). The estimation of the fluorescence resulting from FDA-hydrolysing activity, although only a rough method, yielded first informations on the activities of the mycorrhizal communities.

Liming increased while acidification reduced the meristematic activity of the mycorrhizal rootlets. The findings are in agreement with the data obtained by counting root tips (Hahn and Marschner, 1998, this volume). Increased root production was found on the limed plots and a reduction of root numbers was observed after acidification. In our experiment, the high number of metacutin layers of the mycorrhizas on the acidified plot (B1) indicated frequent dormancy and regrowth of individual root tips. Growth of rootlets was obviously disturbed by the strong acidification of the humus layers. The low activity and frequent interruption of meristematic activity in the acidified humus layer may be due to loss of calcium and magnesium. Damage by toxic aluminium is very unlikely, as the amounts of free aluminium species were very low in the humus layer (Kreutzer et al., 1991). A higher concentration of free aluminium was only measured below 20 cm on plot B1, but mycorrhizal activity was rather high there. Liming increased earthworm activity on the plots (Makeschin, 1991). Consequently the availability of nutrients was enhanced (Schack-Kirchner et al., 1998). Better nourishment in the humus layer may have induced higher meristematic activity.

The results disagree with findings on other acidic Norway spruce plots, where higher root production and turnover rate was found compared to limed plots (Babel, 1981; Kottke et al., 1993; Murach, 1983). Lehto (1994a,b) found detrimental effects on root production short time after liming. The differing effects from acidification and liming are due to the different soil conditions of the investigation sites, to the experimental designs and the time that had passed after treating the soil. It was not within the scope of this publication to present a review on influence of acid rain or liming on mycorrhizas, but to show, for the first time, the different reactions of mycorrhizal types to soil treatments.

Surprisingly small seasonal effects on the proportion of the overall activities of the ectomycorrhizas were observed. The result is in agreement with previous investigations of mycorrhizal activity on several plots in Western Germany (Kottke et al., 1993; Ritter et al., 1989). The increased mycorrhizal production in spring and autumn was only slightly reflected in the proportion of active or dead mycorrhizas when compared with the differences among the treatments. This may mean that the individual life time of the mycorrhizas was more influenced by the treatment than by the season.

The irregular finding of the mycorrhizal types which was due to the patchy distribution of the mycor-

rhizal types in the plots does not allow sound statistical analysis of the data. The results presented, however, point to interesting differences in activity among mycorrhizal types and fungal and root tissues which have not been otherwise recorded.

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