Plant and Soil **199:** 111–116, 1998.

Studies of pathogenic and antagonistic microfungal populations and their potential interactions in the mycorrhizoplane of Norway spruce (*Picea abies* (L.) Karst.) and beech (*Fagus sylvatica* L.) on acidified and limed plots

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Accepted in revised form 8 August 1997

Key words: acidification, antagonism, liming, microfungi, mycorrhizoplane, pathogens

Abstract

Recent tree decline was hypothesized to be connected to root damage caused by soil acidification and increased frequency of pathogenic root colonizing fungi. The rhizoplane is constituted by the mycorrhizal sheath and a high diversity of microfungi, some of which are known to behave antagonistically against pathogens. Disturbance of the balance between pathogens and antagonists by soil acidification may endanger the health of tree roots. Liming may stabilize the interactions. The microfungal populations connected to the mycorrhizoplane of Norway spruce (*Picea abies*) and beech (*Fagus sylvatica*) were, therefore, investigated on experimental Norway spruce plots that had been treated with acidified water or were limed. Beech presented the original forest and was left untreated. Eight microfungal species known as either pathogenic or antagonistic, *Trichoderma viride, T. hamatum, T. polysporum, Cylindrocarpon destructans, Sesquicillium candelabrum, Mycelium radicis atrovirens, Tolyplocladium geodes* and *Oidiodendron maius,* were isolated from the mycorrhizoplanes and their abundance in the five different plots compared. Acidification enhanced the frequency of *Mycelium radicis atrovirens* and *Oidiodendron maius* but reduced *Trichoderma viride*. Liming promoted *Sesquicillium candelabrum* and *Cylindrocarpon destructans*. Detailed analysis of the population patterns indicated that changes in the frequency of a particular fungal species may not only be caused by shift of chemical soil factors but also by antagonistic interactions between the microfungi, thus reducing pathogenic attacks on rootlets.

Introduction

Recent tree decline was hypothesized to be connected to root damage caused by soil acidification (Ulrich, 1990). Apart from direct detrimental effects of soil chemistry, root damage by increasing frequency of pathogenic fungi colonizing roots was discussed. Biotrophic and parasitic microfungi on roots were detected (Courtois, 1983; Molin et al., 1960; Schüler, 1982). Several dominating microfungal species on the mycorrhizoplane are known as potentially weak root pathogens, e.g. *Cylindrocarpon* spp. (Hart, 1965; Kluge, 1966), *Sesquicillium candelabrum* (Bonorden) Gams (Schönhar, 1989) and *Trichoderma polysporum* (Link ex Pers.) Rifai (Schönhar, 1987). *Trichoderma viride* Pers. ex Gray and *T. hamatum* (Bon.) Bain appeared to be involved in root pathogenesis of Norway spruce seedlings (*Picea abies* (L.) Karst. (Forbrig, 1987; Kattner, 1989) or root necrosis of grown up trees (Schönhar, 1984, 1986, 1987). Some are considered to behave as antagonists, e.g. *Oidiodendron griseum* Robak and *Thysanophora penicilloides* Roumegere & Kendrick (Ritter et al., 1989). Lundgren et al. (1978) found *Tolyplocladium* spp. expressing antagonistic effects in culture conditions. *T. viride* is well known as mycoparasitic (Dennis and Webster, 1971a,b,c) and *T. polysporum* was also found to display antifungal potential (Komatsu, 1976). Antagonis-

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tic potential was also hypothesized for *Mycelium radicis atrovirens* (= Mra Melin 1923) by Manka (1970) and Kowalski (1980a, 1982b). The frequently isolated, dark, septate mycelia are, however, a heterogenous group of different species. Some isolates even may form ectendomycorrhizas (Kowalski, 1973). In undisturbed conditions, pathogenecity may be balanced by the antibiotic effectiveness of microfungi and by the mycorrhizal sheath. Increasing soil acidification may disturb the delicate equilibrium. Whether liming could restore the original situation was an open question.

The microfungal populations occurring on the mycorrhizoplane of Norway spruce were, therefore, studied in the experimental plots of the "Höglwald-project" after six years of artificial acid rain and compensative liming. A neighbored, untreated 140 years-old beech (*Fagus sylvatica* L.) plot, presenting the original vegetation, was investigated as an additional control. Special attention was paid to the biodiversity and frequency of the potentially pathogenic or antagonistic microfungi *Trichoderma viride, T. hamatum, T. polysporum, Cylindrocarpon destructans, Sesquicillium candelabrum, Mycelium radicis atrovirens, Tolyplocladium geodes* and *Oidiodendron maius*.

Materials and methods

Investigation plots

The investigations were carried out on four plots of 2500 m^2 in a 75–80-years-old Norway spruce stand and on a neighbored 140 years-old beech stand in the Höglwald, Bavaria. Two plots of Norway spruce were limed in 1984 by 40 dt/ha of dolomit (A2 and B2). One limed plot (B2) and one additional plot (B1) had been watered 15 to 18 times per year by sulfur-acid water of pH 2.7 to 2.8, from 1984 to 1990. The Norway spruce control plot A1 and the beech stand were left untreated. Watering was stopped in the year of sampling. Only rain came down and input of water was the same on all the investigated plots during the time of sampling. For detailed description of the experiment see Kreutzer and Weiss (1998).

Sampling

Samples were collected monthly or two-monthly from July 1990 to November 1991, in spring, summer and autumn. Sampling was carried out by means of a soil corer, 5 cm of diameter, in the humus layer and the Ah horizon. Five samples per plot were taken and unified at each time of sampling.

Isolation of microfungi

All mycorrhizal rootlets were sorted out and identified as far as possible according to Agerer (1987–1993; see Qian et al., 1998 and Taylor et al., submitted). Mycorrhizas were then washed 10 times for 15 minutes each in 20 mL of dest. water in glass vials on a shaker (260 U/min). The aim of this washing procedure was the elimination of fungal spores (Harley and Waid, 1955). Thus, the isolated species came from the mycelia tightly connected to the mycorrhizoplane and not from adhesive spores. The cleaned mycorrhizas were incubated on malt agar (MEA, Gams et al., 1980) or carboxymethyl cellulose agar (CMC). The agar plates were controlled regularly and all species producing spores were isolated and identified (Domsch et al., 1980). The frequencies of the microfungal isolates were calculated per mycorrhizal types, per plots and per horizons (El-Ashker, 1993). 40% of the 4300 isolates obtained from the mycorrhizoplanes belonged to eight species known as weak root pathogens, namely *Trichoderma viride, T. hamatum, T. polysporum, Cylindrocarpon destructans, Sesquicillium candelabrum,* or as fungal antagonists, e.g. *Tolyplocladium geodes, Mycelium radicis atrovirens* Melinor, and *Oidiodendron maius*. Only these isolates are considered here, while the whole microfungal diversity will be treated elsewhere (in preparation).

Statistics

Student t-test was applied to search for significant differences in frequency of the pathogenic or antagonistic microfungi isolated from the plots. Mean and standard deviation were calculated using the numbers of isolates per fungal species at the different sampling dates.

Results

Frequencies and percentages of the eight microfungal species under consideration are presented in Table 1. All the species were found on each plot, except *O. maius*, which was not detected in the Norway spruce control plot (A1). Species abundancies differed statistically significant between the plots (Figure 1, Table 2). *T. viride* was isolated most frequently from the beech and the untreated Norway spruce stand. It was signif-

Table 1. Frequencies and percentage frequencies of isolates of the eight dominating, potentially pathogenic or antagonistic fungi. Percentage frequencies were calculated on the basis of the number of all isolates, including non-dominant species. A1/A2 and B1/B2 *Picea abies* plots, F *Fagus sylvatica* plot

FUNGI PLOTS FREQUEN.	Control A1	Liming A2	Acid B1	Acid+lim. B2	*Fagus silvatica*
Trichoderma viride	67	44	11	11	63
Trichoderma hamatum	22	42	30	22	58
Trichoderma polysporum	108	89	15	26	44
Cyclindrocarpon destructans	10	16	8	49	27
Sesquicillium candelabrum	54	104	53	88	44
Mycelium radicis atrovirens	43	71	100	88	28
Tolyplocladium geodes	19	25	2	15	4
Oidiodendron maius	0	1	61	10	1
total isolates	958	996	817	870	661
FUNGI PERCENT	of dominating species from total isolate				
Trichoderma viride	7.00	4.40	1.40	1.30	9.50
Trichoderma hamatum	2.30	4.20	3.70	2.50	8.80
Trichoderma polysporum	11.30	8.90	1.80	3.00	6.70
Cyclindocarpon destructans	1.04	1.60	1.00	5.60	4.10
Sesquicillium candelabrum	5.60	10.40	6.50	10.10	6.70
Mycelium radicis atrovirens	4.50	7.10	12.20	10.10	4.20
Tolyplocladium geodes	2.00	2.50	0.20	1.70	0.60
Oidiodendron maius	0.00	0.10	7.50	1.10	0,15
percentage of total isolates	33.74	39.20	34.30	35.40	40.80

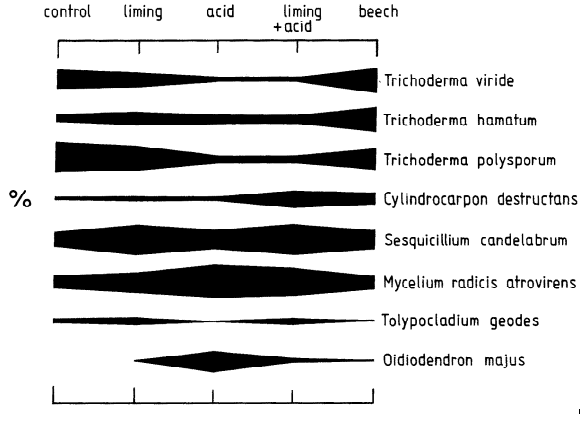

Figure 1. Percentage frequencies of the eight dominating microfungal species known as pathogenic or antagonistic isolated from the mycorrhizoplane from the differently treated Norway spruce plots, namely control, limed, acidic watered, limed and acid watered, and untreated beech stand.

Table 2. Results from statistic evaluation of frequencies of the eight microfungi on the different plots (students t-test, t-0.5). Arabic numbers 1 to 4 indicate how many of the plots were significantly different in frequency of a given species. A1, A2, B1, B2 (all *Picea abies*) and F (*Fagus sylvatica*) indicate the plots were no significant difference in frequency was detected

	Control A1	Limed A2	Acid. B1	Lim. + acid B2	Beech F
T.viride	3^{F}	4	3^{B2}	3^{B1}	3^{A1}
T.hamatum	$2^{B1\ B2}$	3^{B1}	$1^{A1\ A2\ B2}$	$2^{A1\ B1}$	4
T.polysporum	3^{A2}	$2^{A1\ F}$	3^{B2}	3^{B1}	3^{A2}
C.destructans	$2^{A2\ B1}$	$2^{A1\ B1}$	$2^{A1\ A2}$	3^{F}	3^{B2}
S.candelabrum	$2^{B1\ F}$	3^{B2}	$2^{A1\ F}$	3^{A2}	$3^{B1\ A1}$
Mra	3^{F}	4	3^{B2}	3^{B1}	3^{A1}
Toly.geodes	$2^{A2\ B2}$	$2^{A1\ B2}$	3^{F}	$2^{A1\ A2}$	3^{B1}
O.maius	$2^{A2\ F}$	$2^{A1\ F}$	4	4	$2^{A1\ A2}$

icantly less abundant on the two artificially acidified plots (B1 and B2). Liming alone (A2) reduced the relative frequency of *T. viride* significantly in comparison to the control and the beech plot, but the fungus was still significantly more frequent on the limed plot than on the acidified plots. There was no significant difference in the numbers of isolates of *T. viride* between the acidified and the acidified and additionally limed plots (B1 and B2). Acidic treatments similarly reduced the numbers of isolates of *T. polysporum*. However, the fungus

was significantly less frequent on the beech stand than on the control Norway spruce plot and liming did not reduce the population in a statistically significant size. *T. hamatum* was significantly more abundant in the beech stand compared to all Norway spruce plots. The fungal population increased significantly in the mycorrhizoplane of Norway spruce after liming. Differences between the other treatments in the Norway spruce plots were non-significant. *C. destructans* was only isolated at about 1% in all but the limed and additionally acidic watered Norway spruce plot (B2), where it increased to reach about the same level as found in the beech stand. *S. candelabrum* appeared most frequently on the two limed plots (A2 and B2). Liming and additional acid rain resulted in the same frequency as liming alone. Untreated Norway spruce, beech and acidified Norway spruce plots were not significantly different in abundancy of *S. candelabrum. Mycelium radicis atrovirens* became more frequent on the artificially acidified plots (B1, B2) in comparison to the control, but showed the same frequency on beech and untreated spruce plots. Liming and the combination of liming and acidic watering yielded only non significant differences. The frequency of *Tolyplocladium geodes* was not significantly different between beech and acidified Norway spruce (B1), and between the control and the limed treatments, but the two groups were significantly different. The frequency of *O. maius* was not significantly different between beech and untreated spruce, and was not significantly enhanced by liming. Artificial acid rain and the combination of acid watering and liming significantly increased the population. There was also a significant difference between the two acidified treatments.

Discussion

The eight microfungal species isolated from the mycorrhizoplane of *P. abies* and *F. sylvatica* which constituted at least 1% of the total isolates are widespread and frequently occurring fungi in forest stands (Schönhar, 1984, 1986; Söderström and Bååth, 1984). As all the results were obtained by selective isolation techniques, they do not reflect the complete diversity occurring in the field. The frequency of the weak pathogens may be overestimated because of the selective isolation technique favouring some of the fast growing fungi like *T. viride*. Seasonal shifts in population density were neglected as the number of isolates was insufficient. The influence of the treatments on the occurrence of the eight fungal species is, however, well reflected when the whole data set is regarded.

No significant dependence of the microfungal populations on the mycorrhizal type was found (not shown). It is presumed, therefore, that the physical and chemical soil parameters influenced the growth conditions in the mycorrhizoplanes independently from the mycorrhizal fungus forming the sheath. The treatments had considerably changed the soil parameters and the humus formation of the plots under investigation (Kreutzer, 1995). Probably the most important effects came from the changes in the humus formation. Because of an extreme increase in the population of earthworms (Makeschin, 1991), the humus layer in A2 and B2 was transformed into an OLU horizon instead of OF/OH on the other plots. The acid watering had accelerated the effect of liming (Kreutzer, 1989). Thus the plots A2 and B2 were similar in respect to pH, Ca, Mg and Al levels. The similarity of humus conditions in the plots A2 and B2 was reflected in the non significant differences in frequency of the two microfungal species *S. candelabrum* and *Tolyplocladium geodes* (Table 2).

The reduced frequency of *T. viride* after acidification found in this experiment contradicts data from literature. *T. viride* was found more frequently in acidified stands with damaged Norway spruce trees by several investigators (Danielson, 1971; Domsch and Gams, 1970; Schönhar, 1987; Söderström and Bååth, 1978; Taylor and Parkinson, 1964; Warcup, 1951; Weber, 1990). pH-tolerance of *T. viride* is, however, rather large (pH 3.1 to 8.0; Domsch and Gams, 1970). The most alike percentage frequencies of the eight microfungi were noted between the untreated *Picea abies* and the untreated *Fagus sylvatica* plots. This rather unexpected result may indicate a stable equilibrium of the mycorrhizoplane populations in the old, undisturbed stands. Similar, non significant differences in population patterns on Norway spruce and beech have been found by Söderström and Bååth (1978). The significant changes in frequencies of the fungi after treating the soil by acidic water and lime, however, indicate that the balance between the fungal species may be rather delicate. Comparing the percentage frequencies of the fungi (Figure 1), it appears that additional to the soil effects antagonistic interactions between the species may influence abundancy. The presentation reveals that *O. maius* and *Mycelium radicis atrovirens* became dominant on the acidified plots where the *Trichoderma* species, *S. candelabrum* and *T. geodes* decreased in frequency. *S. candelabrum*

dominated all other species on the limed plots where *Mycelium radicis atrovirens* and *O. maius* declined and where *Trichoderma* species appeared in lower frequency. *C. destructans* was less frequent where *Trichoderma* became the dominant species. Microfungi from soil are known for their antibiotic interactions (Cooke and Baker, 1983; Dennis and Webster, 1971a,b,c; Komatsu, 1976; Oliviera and Garbaye, 1989; Varese and Luppi-Mosca, 1992). Own results from dual cultures showed that all tested fungi had antagonistic abilities (in prep.). Improved growth conditions for a species could increase its antibiotic power and thus the fungus may suppress other species. *S. candelabrum* was promoted after liming and may have suppressed *Trichoderma* spp.. Weber (1990) found a relative decrease of *T. viride* and a proportional increase of *O. griseum* and *Thysanophora penicilloides* in a limed *P. abies* stand. It was hypothesized that a direct, antagonistic interaction between the species may be responsible for the change in dominancy (Ritter et al., 1989). This could mean that *O. maius* can only occur in higher frequency when *Trichoderma* is suppressed. Taylor (1964) reported an inhibitory effect of *C. destructans* towards *T. viride*. Growth promotion of *C. destructans* on plot B2 may have enhanced its antagonistic abilities against *Trichoderma* spp. *C. destructans* appeared to be suppressed in the acidified plot (B1) while *Mycelium radicis atrovirens* and *O. maius* occurred more abundantly. It seems likely that *Mycelium radicis atrovirens* could only become more frequent when *C. destructans* and *Trichoderma* spp. were suppressed. MRA increased significantly in the limed plots in comparison to the control and beech plots. The increase of the MRA corresponds to a reduction of the isolation frequency of *Trichoderma* spp., *S. candelabrum* and *C. destructans*. Experiments with *Abies alba* Mill. seedlings showed that occurrence of *C. destructans* and MRA was negatively correlated (Kowalski, 1980; Manka et al., 1968). Manka (1970) considered the death of *Taxus baccata* L. seedlings caused by infection of *C. destructans* due to a lack of biological protection by *Mycelium radicis atrovirens*. Weber (1990) points to similar interactions on rootlets of Norway spruce.

The results show that the populations of the eight dominating microfungal species on the mycorrhizoplane were changed by the soil treatments. Liming was not compensating acidification, but favoured *S. candelabrum* and to some part *C. destructans*. After experimental acidification of the soil growth of MRA and *O. maius* were improved while all other micofungi occurred less frequently. It is concluded from the results that well adapted species became significantly more frequent and probably suppressed less adapted species. The diversity of the microfungal species, all of them with antagonistic properties, may have guaranteed biocontrol of the potentially weak parasites. This may explain why no severe damage of mycorrhizas was observed in the Höglwald plots (Qian et al., 1998).

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Section editor: R F Hüttl