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Mycorrhizal functioning of *Phialocephala fortinii* with *Pinus contorta* on glacier forefront soil: interactions with soil nitrogen and organic matter

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Abstract Plants growing on an environmentally stressed glacier forefront on soil low in N and organic matter have abundant root colonizations by dark-septate fungi. As the plants appeared fit for this severe habitat, it was hypothesized that the dark-septate endophytes were neutral or beneficial rather than detrimental to the plants. To test this hypothesis, we designed a growth-room experiment with *Pinus contorta* grown on forefront soil inoculated with the dark-septate fungus *Phialocephala fortinii* in the absence of climatic stress. N and organic matter treatments were included to explore their interaction with the fungal inoculation. *P. fortinii* colonized roots inter- and intracellularly and occasionally formed microsclerotia. Inoculated plants absorbed significantly more P than noninoculated plants in all combinations of N and organic matter. Without added N, neither inoculation nor organic matter addition improved plant growth or N uptake, showing that N indeed limits plant growth in this substrate. With added N, however, both organic matter addition and inoculation significantly increased total pine biomass and N uptake. The enhanced P uptake by the *P. fortinii*-inoculated pine as well as the increased pine growth and N uptake in the treatment combining *P. fortinii* and N appear as typical mycorrhizal responses.

Key words Deuteromycetes · Fungi · Fungus-host interactions · Symbiosis

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Introduction

N and organic matter buildup play important roles in young ecosystems such as glacier forefronts (Chapin et al. 1994; Matthews 1992; Vitousek and Walker 1989). The introduction of mycorrhizal propagules is essential for establishment of mycorrhiza-dependent plants (Trappe and Luoma 1992). Once mycorrhizal plants and their symbiotic fungi establish on poorly developed substrates, nutrient capture and cycling is greatly enhanced.

Dark-septate, root-endophytic fungi are common in arctic-alpine habitats (Cázares 1992; Haselwandter and Read 1982; Jumpponen and Trappe 1996; Väre et al. 1992). The interactions of dark-septate endophytes and their hosts are controversial, having been suggested to be pathogenic, neutral or beneficial (Fernando and Currah 1996; Haselwandter and Read 1982; O'Dell et al. 1993; Stoyke and Currah 1993; Wang and Wilcox 1985; Wilcox and Wang 1987). Some may function in different ways along the mutualism-parasitism continuum, depending on conditions (Johnson et al. 1997).

Cázares (1992) reported dark-septate endophytes to be common on many plant species on the forefront of Lyman Glacier in the North Cascade Range of Washington State. The plants showed no symptoms of disease and were established in a habitat notable for its poor soil, short growing season and climatic stress. As these plants had to contend with a severely stressful habitat, we hypothesized that the dark-septate colonizations did not adversely affect the plants; imposition of disease in addition to the environmental stresses would not likely lead to successful establishment. To test this hypothesis, we explored effects of a dark-septate endophyte on *Pinus contorta* Dougl. grown on forefront soil without climatic stress; *P. contorta* is an early colonizer at the Lyman Glacier forefront. *Phialocephala fortinii* Wang and Wilcox was selected as the endophyte, because it is frequent at the site (Jumpponen and Trappe 1996) and colonizes roots of *P. contorta* (O'Dell et al.

1993). N and organic matter supplements were included to examine their interactions with the fungus; nitrogen and organic matter are very low away from established plants on the forefront (Jumpponen et al. 1998).

Materials and methods

A composite soil sample was collected at the Lyman Glacier forefront (48° 10′ 14″ N, 120° 53′ 44″ W; elevation ca. 1800 m) within an area that had been deglaciated for less than 20 years and was devoid of plants [see Cázares (1992) and Jumpponen et al. (1998) for site details]. The sample was sieved through a 5-mm screen, air dried, and stored at 4 °C. The organic matter and N contents of the soil were low and likely to limit plant growth (ca. 0.4% organic matter and 0.001% N by soil dry weight; Jumpponen et al. 1998). The soil was pasteurized before use.

Seeds of *P. contorta* were soaked 24 h in deionized water at 4 °C, stratified 14 days at 4 °C, then surface sterilized 55 min in 30% hydrogen peroxide under agitation. Five stratified seeds were sown on 80 g of air-dried soil in 115 ml plastic Cone-tainers (Ray Leach Inc., Corvallis, Ore.). N, organic matter, and *P. fortinii* were applied to each container in a fully factorial design, each treatment at two levels: present or absent. To account for effects of inoculation, an additional control with killed inoculum was included. The result was a 2 × 2 × 2 factorial with an additional inoculum control, nine treatment combinations in total. Ten replicates of each treatment were randomly arranged in the growth room.

An equivalent of 100 kg N/ha of sulfur-coated urea was added to the top of soil in half of all containers; the other half were untreated. The application is approximately 35% of the total N in the nonvegetated forefront soil and less than 5% of total N underneath shrub canopies in the area deglaciated approximately 60 years ago. The sulfur-coated pellets were selected because they dissolve over a 6-month period. Hence, N pulses were avoided during the experiment.

Approximately 1.5% peat by dry weight of soil was added and thoroughly mixed to half of all treatments as the organic matter treatment; the other half were left untreated. The additions resulted in organic matter contents similar to those of naturally occurring soil at the terminal moraine of the Lyman Glacier forefront (Jumpponen et al. 1998). To minimize nutrient additions, the peat was leached with 0.2 N HCl and then thoroughly washed with distilled H_2O. Thus, the focus in this treatment was on effects of organic matter on physical and chemical soil characteristics rather than on nutrient input.

The inoculum of *P. fortinii* [SE24, strain isolated by O'Dell et al. (1993) and maintained at the USDA-PNW Research Station, Corvallis, Ore.] was mixed with vermiculite and Modified Melin Norkrans medium (Marx and Zak 1965) and then incubated for 8 weeks. The control inoculum was separated from the same batch and autoclaved for 25 min. Ten ml of live or killed inoculum was applied to the top of the soil mixture in inoculated treatments and controls, respectively.

Conditions in the growth room were 25 °C, a 16/8-h day/night cycle, and light with an irradiance intensity of ca. 300 μE within the photosynthetically active range. After emergence of the first seedling, subsequent germinants were removed to maintain only one per container. After 12 weeks of growth (the approximate growing season at Lyman Glacier forefront), soil was washed from the roots and the colonized root length estimated by the gridline intersection method (Giovannetti and Mosse 1980). Dark and septate, superficial, inter-, and intracellular mycelium was observed. After examination, seedlings were dried at 80 °C for 48 h and the dry weights of shoot and root recorded.

Due to the low accumulation of foliar biomass in some treatments, foliage from three seedlings within a treatment were pooled for foliar nutrient analyses. Foliar tissue N and P were analyzed by the Kjeldahl method (Thomas et al. 1967) with an Alpkem Rapid Flow Analyzer, Model 300.

A one-way analysis of variance was first used to compare the killed-inoculum control against the no-inoculum control. Analysis of variance showed no significant differences in growth ($P = 0.322$, 0.931, and 0.481 for shoot, root and total biomass, respectively) or nutrient concentrations ($P = 0.460$ and 0.141 for total N and P, respectively). Because of the strong N effect on growth (ca. 50% increase, $P > 0.001$, in shoot, root and total biomass) and foliar N concentration (ca. 100% increase, $P > 0.001$) and absence of three-way interactions ($P = 0.492$, 0.297, 0.357, $P = 0.832$, and 0.199 for shoot, root, total biomass, total N, and total P, respectively), effects of organic matter and fungal inoculation were analyzed separately for the two nitrogen regimes as a 2 × 2 factorial design: two treatments (organic matter and fungal inoculation) at two levels (present or absent).

All response variables, except the root/shoot ratios and the nutrient concentrations, were log-transformed prior to analysis to obtain homogeneity of variances between the treatments. Data were subjected to analysis of variance by the General Linear Models procedure in SYSTAT (SYSTAT 1992) to test for main and interactive effects. Means between the different treatment combinations were compared by Fisher's least significant difference (LSD) test at an alpha level of 0.05.

Results

Root colonization by *Phialocephala fortinii*

Root systems of all inoculated seedlings were colonized by the dark-septate mycelium. Intracellular monilioid chains and microsclerotia as well as superficial or inter- and intracellular, papillate mycelium were observed. No root-associated fungi (mycorrhizal or endophytic) were observed in noninoculated treatments. The degree of root colonization by *P. fortinii* was not significantly affected by application of N or organic matter. Colonized root length ranged from 4 to 20%.

Growth response

Addition of N increased both shoot and total biomass > 50% and root biomass > 40% compared to controls. Analyzed separately for the two N levels, organic matter without added N did not significantly affect shoot biomass, but root biomass decreased by 35% compared to the control (Table 1). Due to the large reduction in root biomass, total biomass and root/shoot ratio also decreased. With added N, the organic matter amendment resulted in an increase of > 40% in shoot biomass compared with the treatment with N alone. The strong positive effect of N amendment was thus further enhanced in presence of organic matter.

Inoculation with *P. fortinii* did not significantly affect shoot, root and total biomass when no N was added (Table 1). With added N, fungal inoculation resulted in a 50% biomass increase over the N treatment alone. The root endophyte hence enhanced growth of the seedling when adequate levels of N were available.

Table 1 Shoot, root and total dry weights (mg) and root/shoot ratios (mean ± standard deviation) of *Pinus contorta* seedlings grown in soil from Lyman Glacier forefront. Shown are the results of four treatment combinations applied under two levels of N (no added N and amendment equal to 100 kg N/ha): Presence (+) or absence (−) of organic matter amendment equal to 1.5% soil dry weight (*OM*) inoculation with *Phialocephala fortinii* (*PF*). Numbers in parentheses indicate number of replicates in each treatment. Same letters in a column indicate nonsignificant differences at $\alpha = 0.05$ based on Fisher's LSD. Source of variation indicates which factors contribute to the observed differences

Treatment	Shoot dry wt.	Root dry wt.	Total dry wt.	Root/shoot
No added N				
OM − PF − (10)	31.30 ± 13.39 a	21.60 ± 7.29 b	52.90 ± 18.67 b	0.72 ± 0.21 b
OM + PF − (9)	26.33 ± 5.29 a	14.00 ± 2.45 a	40.33 ± 7.84 a	0.55 ± 0.10 a
OM − PF + (10)	29.30 ± 6.22 a	19.30 ± 4.27 ab	48.80 ± 8.94 ab	0.67 ± 0.16 ab
OM + PF + (10)	27.60 ± 7.58 a	15.50 ± 4.09 a	43.10 ± 9.62 ab	0.59 ± 0.19 ab
Source of variation				
OM	NS	***	*	*
PF	NS	NS	NS	NS
OM × PF	NS	NS	NS	NS
100 kg N/ha				
OM − PF − (9)	51.00 ± 14.36 a	30.78 ± 10.08 a	81.78 ± 21.22 a	0.63 ± 0.18 b
OM + PF − (10)	72.10 ± 21.04 b	32.00 ± 9.14 ab	104.10 ± 29.10 ab	0.46 ± 0.11 a
OM − PF + (10)	82.50 ± 19.80 bc	47.40 ± 18.07 c	129.90 ± 33.63 b	0.57 ± 0.19 ab
OM + PF + (10)	103.20 ± 29.81 c	43.40 ± 19.79 bc	146.20 ± 42.98 b	0.43 ± 0.16 a
Source of variation				
OM	***	NS[a]	NS	**
PF	**	***	***	NS
OM × PF	NS	NS	NS	NS

[a] NS $P > 0.05$
* $0.05 \geq P > 0.01$, ** $0.01 \geq P > 0.001$, *** $0.001 \geq P$

Nutrient accumulation

The N amendment increased foliar N concentration by 100% relative to the control. Organic matter and fungal inoculum did not affect foliar N concentration when no N was added (Table 2). With added N, organic matter and fungal inoculation increased the foliar N concentration by 25% and 20%, respectively, compared with the N amendment alone. Foliar P concentration significantly increased as a result of inoculation with *P. fortinii* regardless of N or organic matter treatment (Table 2).

Table 2 N and P concentrations (mean ± standard deviation) in *Pinus contorta* foliage following four treatment combinations applied under two levels of added N. For legends and symbols see Table 1

Treatment	Total N (% dry wt.)	Total P (% dry wt.)
Low N		
OM − PF − (3)	0.690 ± 0.057 a	0.074 ± 0.006 a
OM + PF − (3)	0.639 ± 0.031 a	0.076 ± 0.012 a
OM − PF + (3)	0.608 ± 0.114 a	0.087 ± 0.007 b
OM + PF + (3)	0.623 ± 0.039 a	0.100 ± 0.012 b
Source of variation		
OM	NS	NS
PF	NS	**
OM × PF	NS	NS
100 kg N/ha		
OM − PF − (3)	1.414 ± 0.067 a	0.072 ± 0.013 a
OM + PF − (3)	1.780 ± 0.149 c	0.066 ± 0.012 a
OM − PF + (3)	1.642 ± 0.024 b	0.092 ± 0.011 b
OM + PF + (3)	2.110 ± 0.18 d	0.128 ± 0.012 b
Source of variation		
OM	***	NS
PF	**	**
OM × PF	NS	NS

Discussion

The experiment reaffirmed earlier conclusions that N limits plant growth on Lyman glacier as on other glacier forefronts (Chambers et al. 1987, 1988, 1990; Jumpponen et al. 1998). Addition of N together with organic matter in the absence of *P. fortinii* enhanced N uptake by the seedlings, presumably because the organic matter reduced leaching losses of N. With added N, organic matter further increased shoot and total biomass and foliar N concentration. These responses likely resulted from altered ion exchange capacity, increased aeration, or decreased bulk density (Cheng 1977). Addition of organic matter alone in the low-N treatment reduced

root and total biomass. The reduction was possibly due to immobilization of the already low soil N by soil microorganisms (Paul and Clark 1989).

Phialocephala fortinii enhanced P uptake by the pine regardless of N or organic matter treatments. Enhanced P uptake is, of course, among the better-known mycorrhizal functions (Harley and Smith 1983; Smith and Read 1997). When the N limitation was overcome by added N, *P. fortinii* produced two responses classically regarded as mycorrhizal: enhancement of growth and P uptake (Harley and Smith 1983; Smith and Read 1997). Haselwandter and Read (1982) reported analogous increases in growth and P uptake by a *Carex* sp. inoculated with a dark-septate endophyte. Their sterile isolate was similar to *P. fortinii* as shown by preliminary analyses of partial sequences of the small subunit of the nuclear ribosomal DNA (A. Jumpponen, unpublished data).

Because *P. fortinii* seems to behave as a parasite or pathogen under some experimental conditions (Currah et al. 1993; Fernando and Currah 1996; Stoyke and Currah 1993; Wang and Wilcox 1985; Wilcox and Wang 1987), its status as a mycorrhizal fungus under our experimental conditions might be questioned. This depends upon how "mycorrhiza" is defined. The definition of Gerdemann (1970), as modified by Harley (1992) and then Trappe (1996), can be applied: "Dual organs of absorption formed when symbiotic fungi inhabit healthy absorbing organs (roots, rhizomes or thalli) of most terrestrial plants and many aquatics and epiphytes." In our experiment, the roots and fungus formed a dual organ of absorption with no symptoms of disease, hence a symbiosis (Lewis 1973). As Johnson et al. (1997) pointed out, the accuracy of this definition is "not compromised if the dynamic nature of plant responses to mycorrhizal associations is accepted and they are considered to be generally mutualistic, with occasional commensal and parasitic excursions from this norm." Most established plants in the Lyman Glacier forefront seem fit for that stressful habitat, lack symptoms of disease, and are colonized by dark-septate endophytes such as *P. fortinii* (Cázares 1992; Jumpponen and Trappe 1996). The occasions when this fungus was pathogenic may have been "excursions" from the norm or may reflect differences between strains of this anamorphic taxon (Currah et al. 1993; Fernando and Currah 1996).

From our results and those of Haselwandter and Read (1982), we cannot say unequivocally that the symbiosis was mutualistic: although the pine and sedge benefited, we have no direct evidence of benefit to the fungus. However, as *P. fortinii* produced intracellular structures possibly analogous to arbuscules or the hyphal coils of ericoid mycorrhizae, it is reasonable to assume that the fungus obtained photosynthates from the host.

A major difference in the pine reaction to *P. fortinii* from a reaction to any casual soil or rhizosphere fungus is that *P. fortinii* formed intracellular colonizations within the root cortical tissue. As with arbuscular and ericoid mycorrhizae, it had direct contact with the root cells. Some soil fungi such as *Penicillium bilaji* solubilize P from rock phosphate without colonizing root tissue, but the solubilized P is not available to mycorrhiza-dependent host plants in the absence of the mycorrhizal fungus (Kucey 1987). Accordingly, the enhancement of P uptake by hosts colonized by *P. fortinii* strongly supports the mycorrhizal functioning of that system. The increased N and P uptake in the high N–*P. fortinii* combination also indicates enhanced absorbing capacity for the host when its roots are colonized, probably because the architecture of the extramatrical hyphae is more efficient at nutrient capture than that of the roots, and the hyphae serve as a pathway for nutrient transport (Newman 1988; Read et al. 1985). Various combinations of nonmycorrhizal soil organisms may enhance plant growth (Linderman 1988) by mobilizing soil nutrients or producing growth regulators (Shivanna et al. 1994). Suggested mechanisms for such growth promotion are similar to those demonstrated for mycorrhizal fungi and, indeed, have often been deduced with no consideration of whether or not mycorrhizal fungi were functioning in the experimental systems (Linderman 1988).

Results from our study indicate that plant growth is limited by the low levels of N in the soil in the primary successional ecosystem at Lyman Glacier forefront. The function and importance of the root endophytes require further examination; they may function as beneficial root symbionts under some circumstances. Further studies, e.g., with radioisotopes or stable heavy isotopes, are needed to determine the directions of net nutrient fluxes as well as to define the nature of the association between dark-septate root endophytes and their host plants.

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