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ORIGINAL PAPER

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Saprobic characteristics of three fungal taxa from ericalean roots and their association with the roots of *Rhododendron groenlandicum* and *Picea mariana* in culture

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Abstract Simultaneous associations among ectotrophic and ericoid mycorrhizal hosts and their mycorrhizal fungi are expected in boreal bogs where ericaceous shrubs and conifers coexist rooted in an organic matrix dominated by *Sphagnum* mosses. We were thus prompted to examine, in vitro, the abilities of three ericoid mycorrhizal fungi [*Hymenoscyphus ericae*, *Oidiodendron maius*, and Variable White Taxon (VWT)] to associate with *Picea mariana* (Pinaceae), with both *P. mariana* and *Rhododendron groenlandicum* (Ericaceae) simultaneously, and to decompose *Sphagnum fuscum*. *Hymenoscyphus ericae* and VWT developed an intracellular association with roots of *P. mariana* and with roots of *R. groenlandicum*. Two strains of *O. maius* did not form typical infection units in *R. groenlandicum*, nor did they colonize the root cells of *P. mariana*. Mass losses incurred by sterilized *S. fuscum* plants inoculated with these three taxa indicated that *O. maius* could be more efficient as a free-living saprophyte on this material than either *H. ericae* or VWT and may in part explain why atypical associations with the roots of ericaceous hosts were formed.

Keywords Ericoid mycorrhiza · Ectomycorrhiza · *Oidiodendron maius* · *Hymenoscyphus ericae* · Variable White Taxon

Introduction

The best-known ericoid mycorrhizal associate of members of the Ericales is the ascomycete *Hymenoscyphus ericae* (Read) Korf and Kernan with its distinctive arthroconidial anamorph *Scytalidium vaccinii* Dalpé, Litten and Sigler (Hambleton et al. 1999). A second common ericoid mycorrhizal associate is the hyphomycete *Oidiodendron maius* Barron, a species that also forms arthroconidia. A third ericoid mycorrhizal endophyte, "Variable White Taxon" (VWT), has been described, but all isolates are sterile in culture and it remains unnamed (Hambleton and Currah 1997). Other fungi have been implicated in these relationships but their characteristics are less well defined (e.g., Dalpé 1986; Stoyke et al. 1992; Liu et al. 1998; Monreal et al. 1999; Bergero et al. 2000). Molecular data has shown that *O. maius* is allied with species in the teleomorphic genus *Myxotrichum* (Hambleton et al. 1999), and the taxonomic disposition of *H. ericae*, *O. maius*, and VWT is among the inoperculate discomycetes (Hambleton 1998).

Until recently, inoperculate discomycetes were considered unusual as ectotrophic associates. Bergero et al. (2000) showed that some species of *Oidiodendron* and two other unidentified and non-sporulating dematiaceous isolates from *Erica arborea* L. and *Quercus ilex* L. growing in close proximity in a Mediterranean woodland in Italy could form mycorrhiza-like structures in the roots of both species. Their findings, plus reports of *H. ericae*-like fungi from ectomycorrhizal conifer roots (Vrålstad et al. 2000), *O. maius* from ectomycorrhizas (Perotto et al. 1995), and a fungus resembling VWT from *Picea* roots (Summerbell 1987), are noteworthy, because fungi with mitosporic states are generally associated with a saprobic or parasitic niche rather than a mycorrhizal one, at least with ectotrophic hosts (Hutchison 1989).

We were thus prompted to compare the relationship of *H. ericae*, *O. maius*, and VWT with an ericaceous host, a coniferous ectotrophic host, and a non-living, organic substrate. In boreal Alberta, extensive stands of *Picea mariana* (Mill.) BSP. and *Rhododendron groenlandicum* (Oeder) Kron and Judd co exist in some peatlands, rooted in thick mats of *Sphagnum* moss. These ecosystems provide a relatively simple system in which ericoid and ectotrophic mycorrhizal fungi can be compared and also tested with respect to their relationship with the substrate. Here we demonstrate the relative abilities of *H. ericae*, *O. maius*, and VWT to form associations with

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Table 1 Fungi used to inoculate roots of *Picea mariana* and *Rhododendron groenlandicum*, and plant species and location from which they were isolated. Strains are accessioned at the University of Alberta Microfungus Collection and Herbarium (UAMH)

Taxon	Strain	Source	Location
Hymenoscyphus ericae	UAMH 8680	*R. groenlandicum*	Acidic peatland (bog) near Athabasca, Alberta, Canada
H. ericae	UAMH 8872	*Oxycoccus quadripetalus* Gilib	Acidic peatland (bog) near Athabasca, Alberta, Canada
Oidiodendron maius	UAMH 8919	*Chamaedaphne calyculata* Moench	Acidic peatland (bog) near Athabasca, Alberta, Canada
O. maius	UAMH 8920	*Oxycoccus quadripetalus*	Acidic peatland (bog) near Athabasca, Alberta, Canada
Variable White Taxon (VWT)	UAMH 8863	*Phyllodoce empetriformis* (Smith) D. Don	Alpine heathland, Jasper National Park, Alberta, Canada
VWT	UAMH 8864	*Empetrum nigrum* L.	Alpine heathland, Jasper National Park, Alberta, Canada

the roots of *R. groenlandicum* and *P. mariana* and compare their effectiveness as saprobes on a substrate of *Sphagnum fuscum* (Schimp.) Klinggr. plants.

Materials and methods

Preparation of *Sphagnum* substrate, culture tubes and jars, and axenic seedlings

Sphagnum substrate was prepared by collecting approximately 4 l of living *Sphagnum* plants from a peatland 10 km west of Entwistle, Alberta. Coarse debris, such as roots and twigs, was removed prior to drying the bryophyte substrate for 2 weeks at 38°C. It was then homogenized in a blender, hydrated to 80% water by weight, and sterilized by autoclaving twice at 121°C for 15 min (liquid cycle).

Culture tubes and jars were prepared as follows. Pyrex culture tubes (10 mm ×50 mm) were quarter-filled with approximately 15 ml of modified Melin-Norkrans medium [MMN: 1.0 g D-glucose anhydrous, 2.0 g Difco malt extract agar, 1.0 g Difco yeast extract, 10.0 g KH_2PO_4, 5.0 g $(NH_4)HPO_4$, 3.0 g $MgSO_4 \cdot 7H_2O$, 1.0 g $CaCl_2$, 0.5 g NaCl, 0.115 g Sigma bovine albumin, 12.0 g Difco bacto-agar, 1 l distilled water (d-H_2O)]. Each of three sets of 20 tubes was inoculated with a 0.5 mm^3 plug of mycelium from stock plates of each fungal strain (Table 1) so that there were 10 tubes for each of the six fungal strains. Tubes were filled to one-third with processed *Sphagnum* moss. Mycelium grew through this substrate for 10 days at room temperature before seedlings were added to the culture tubes. Twenty uninoculated culture tubes served as controls.

To prepare jars for paired plantings (see below), 30 ml of MMN medium was poured into 35 60 cm ×25 cm glass jars (Sigma V0633) with clear, vented, polypropylene caps (Sigma B3031). Jars were inoculated with a 0.5 mm^3 agar plug at the center and then filled to one-third with processed *Sphagnum*.

To grow sterile seedlings, *P. mariana* seeds were soaked in a 1:1 solution of double-distilled water (dd-H_2O):5.25% hypochlorite bleach for 120 s and *R. groenlandicum* seeds were soaked in a 2:1 solution of dd-H_2O:5.25% hypochlorite bleach for 90 s. Surface-sterilized seeds were rinsed with sterilized d-H_2O for 120 s and placed on malt extract agar (MEA; 15 g Difco malt extract, 20 g Difco bacto-agar, 1 l d-H_2O) under a 6 h dark (18°C):18 h light (23°C) regime until roots and green cotyledons developed (approximately 5 weeks). Six- to eight-week-old seedlings of *P. mariana* and *R. groenlandicum* were transplanted into the *Sphagnum* in culture tubes individually and in pairs (one plant of each species) in jars. Fungal strains were obtained from the University of Alberta Microfungus Collection and Herbarium (UAMH). One set of tubes containing each plant species was inoculated with *H. ericae* (ten with UAMH 8680, ten with UAMH 8872), a second set with *O. maius* (ten with UAMH 8919, ten with UAMH 8920), and a third set with VWT (ten with UAMH 8863, ten with UAMH 8864). A fourth set was left uninoculated and served as a control. This inoculation process was repeated with the jars to produce 30 cultures containing two plant species per fungal strain. Tubes and jars were incubated under a 6 h dark (18°C):18 h light (23°C) regime for approximately 8 weeks.

At the end of the incubation periods, plants were compared visually with the controls, removed from the tubes and jars, and cleaned from *Sphagnum* debris. The fine structure of the roots (especially in *Rhododendron*) required that measurements be made as follows. Roots were photographed with a scale bar to determine total root lengths. The photographs were projected onto a white screen, root images were traced and used to calculate root length.

Roots were cleared by autoclaving in 20 ml 10% KOH for 5 (*R. groenlandicum*) or 20 min (*P. mariana*) at 121°C (liquid cycle). Cleared roots were washed with d-H_2O, placed in a solution of 10 ml 0.1% Chlorazol Black E in equal parts water, glycerine, and 80% lactic acid, and autoclaved for 5 (*R. groenlandicum*) or 15 min (*P. mariana*) at 121°C (liquid cycle). Colonization was assessed by phase contrast (LM) and scanning electron microscopy (SEM) using a Jeol Model JSM 6301FXV with cryostage. Some roots were freeze-fractured to visualize the positions of fungal cells within root tissues.

Relative saprobic abilities of the six fungal strains were determined by placing a 0.5 mm^3 plug of mycelium of each strain onto 2 g dry weight of processed *Sphagnum* moistened with 15 ml d-H_2O in 90×15 mm Pyrex Petri dishes. Ten replicates were prepared for each strain and ten uninoculated plates served as controls. Plates were sealed with Parafilm and incubated at room temperature in the dark for 70 days. To ensure plates had remained uncontaminated during the incubation period, a small sample (<0.01 g) of *Sphagnum* taken from three points in each plate was placed on corn meal agar (CMA; 15 g Difco corn meal agar, 1 l d-H_2O)and incubated for 28 days. After 70 days, the plates of substrate were autoclaved (liquid cycle) at 121°C for 20 min, dried to constant mass at 38°C, and weighed. Mass losses were expressed as percentages.

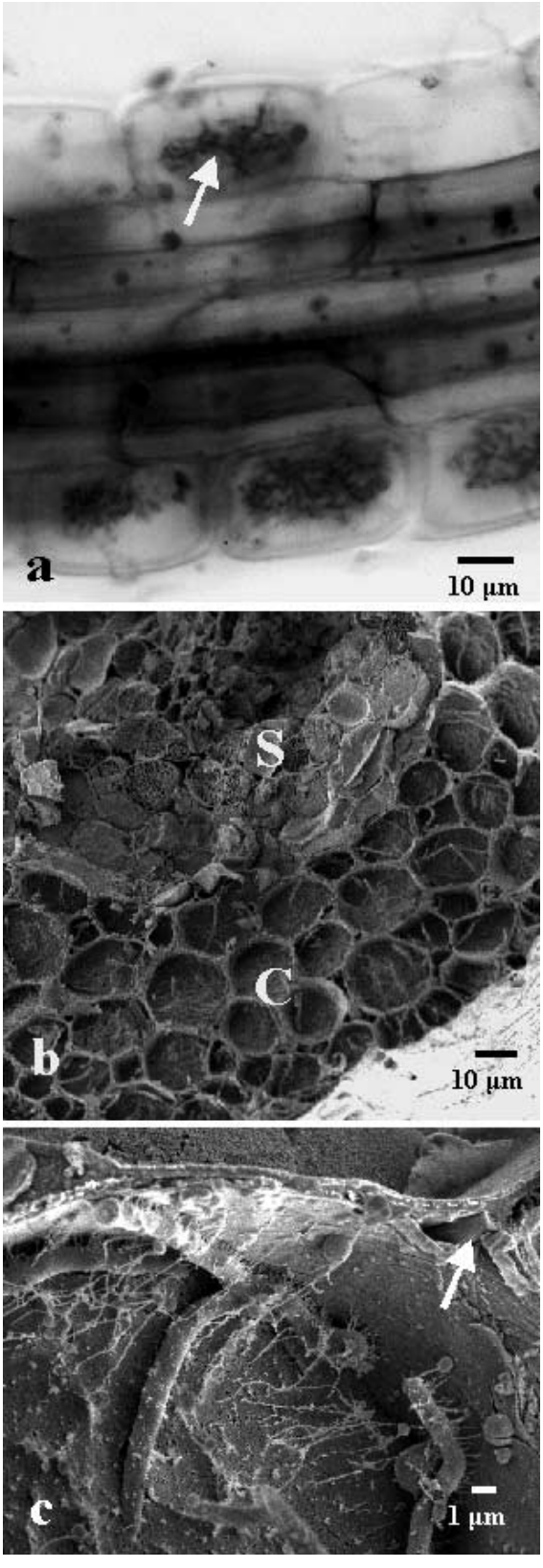
Statistical analyses

Differences in average root length and average *Sphagnum* mass loss values among treatment groups were analyzed using a Kruskal-Wallis test because of lack of normality and the heterogeneity of variances. If significant differences were detected, the Kruskal-Wallis test was followed by a post hoc Tukey-type test.

Results

Characteristics of fungal interactions with roots

Intracellular coils formed within the root epidermal cells of *R. groenlandicum* inoculated with VWT (8863) and



either strain of *H. ericae* (8680 and 8872) (Fig. 1a). These structures were not seen in plants grown with either strain of *O. maius* (8919 and 8920) or with VWT (8864). A small number of epidermal cells of *R. groenlandicum* inoculated with *O. maius* (8919) contained some hyphae that were not coiled. In both strains of *O. maius*, conidiophores bearing conidia developed on the surface of *R. groenlandicum* roots.

In *P. mariana*, all six strains formed hyphae across the root surface. Freeze-fracturing of *P. mariana* roots inoculated with *H. ericae* (8872) or VWT (8863 and 8864) showed intracellular and intercellular hyphae in the epidermal and outer cortical cell layers. Hyphae were not observed within the stele (Fig. 1b). By SEM and LM, there was no indication of cellular damage or degeneration in colonized cells, even with extensive intracellular colonization (Fig. 1c). Light microscopic comparisons of *P. mariana* roots grown with *H. ericae* (8680 and 8872) showed that the mode of ingress of the two strains was identical. There was no evidence of hyphae within root cells of *P. mariana* in plants inoculated with either strain of *O. maius*, although hyphae and conidiophores were numerous on, and in, the mucoid layer of the root surface.

Roots of *P. mariana* and *R. groenlandicum* growing together in jar cultures and inoculated with VWT (8863) and either strain of *H. ericae* showed hyphae among and within cells of the epidermis and cortex. Coiled hyphae of these strains were also in the roots of *R. groenlandicum*. Intracellular hyphae were not found in *R. groenlandicum* roots inoculated with VWT (8864), although *P. mariana* root cells were colonized as described above. Both strains of VWT and both strains of *H. ericae* grew within the roots of *R. groenlandicum*. Hyphae of *O. maius* (8919) were detected, but uncommon, in roots of only two *R. groenlandicum* plants. Hyphae of *O. maius* (8920) were not found in the roots of *R. groenlandicum*.

Roots of control *R. groenlandicum* plants were short and stunted. *Rhododendrom groenlandicum* roots inoculated with either strain of *O. maius* were similar to those of control roots. Comparisons of measured root lengths indicate that roots inoculated with either strain of *H. ericae* were longer than control roots but those inoculated with either strain of VWT were not significantly longer (Fig. 2). The *Rhododendron* roots broke easily when removed from the *Sphagnum* substrate and washed, therefore sample sizes ranged from three to five intact roots per treatment. Due to small sample size, the data could not be statistically analyzed. Comparisons of *P. mariana*

Fig. 1a–c Fungal endophytes within the roots of *Rhododendron groenlandicum* and *Picea mariana* (grown in vitro). **a** Light micrograph showing an infection unit (*arrow* coiled intracellular hyphae). *Hymenoscyphus ericae* (UAMH 8872) in hair root of *R. groenlandicum*. **b** Scanning electron micrograph (SEM) of freeze fractured *Picea mariana* root inoculated with *H. ericae* (UAMH 8872), showing hyphae within the cortical cells (*C*) but not within the stele (*S*). **c** SEM of freeze-fractured *P. mariana* root inoculated with *H. ericae* (UAMH 8872), showing intracellular and intercellular (*arrow*) hyphae in outer cortical cells

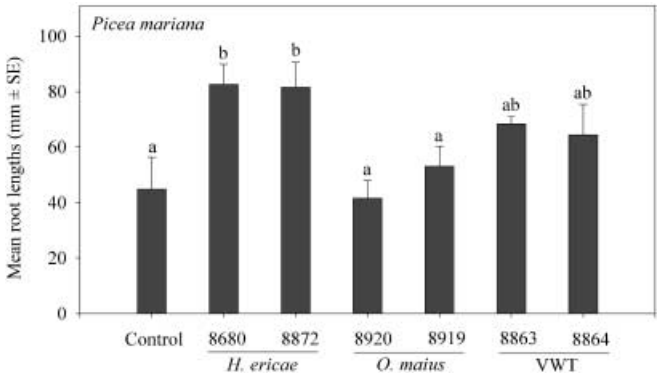


Fig. 2 Mean root lengths of *P. mariana* (mm±SE) following inoculation and approximately 8 weeks incubation with *H. ericae* UAMH 8680 and 8872, *Oidiodendron maius* UAMH 8919 and 8920, and Variable White Taxon (VWT) UAMH 8863 and 8864. Values with same letter do not differ significantly (α =0.10)

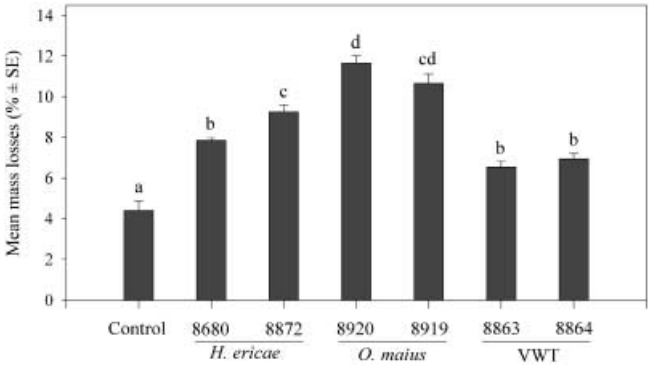


Fig. 3 Mass losses of *Sphagnum fuscum* (%±SE) caused by *H. ericae* UAMH 8680 and 8872, *Oidiodendron maius* UAMH 8919 and 8920, and VWT UAMH 8863 and 8864 following a 70 day incubation. Values with same letter do not differ significantly (α =0.05)

Table 2 Relative abilities of six fungal isolates from ericoid mycorrhizal roots to form mycorrhizas with *P. mariana* and *R. groenlandicum*

Taxon	Strain	Infection unit formation with *R. groenlandicum*	Colonization of *P. mariana* roots	Simulataneous association between fungus, *Picea* and *Rhododendron* demonstrated in culture
H. ericae	UAMH 8680	+	(+)[a]	+
H. ericae	UAMH 8872	+	+	+
O. maius	UAMH 8919	–	–	–
O. maius	UAMH 8920	–	–	–
VWT	UAMH 8863	+	(+)	+
VWT	UAMH 8864	–	+	(+)

[a] Indicates an inconsistent response

root lengths (Fig. 2) indicated that roots inoculated with *H. ericae* were significantly longer than control roots (P<0.10). These results are summarized in Table 2.

Relative abilities of fungi to degrade *Sphagnum*

Following 70 days incubation, *O. maius* (8920) caused the greatest mass loss of *S. fuscum* (11.65±1.13%), followed by (in descending order) *O. maius* (8919) (10.65±1.49%), *H. ericae* (8872) (9.25±1.09%), *H. ericae* (8680) (7.85±0.41%), VWT (8864) (6.94±0.77%), and VWT (8863) (6.55±0.90%) (Fig. 3). A small decrease in mass (4.40±1.45%) was noted in control plates, but contaminant organisms were not found. Mass losses in all treatments differed significantly from the control group after incubation for 70 days (P <0.001, *df* 6). Differences between the two strains of *O. maius* and of VWT were not significant (P =0.11, *df* 17, and P =0.32, *df* 17, respectively). However, there was a significant difference between the mass losses caused by the two strains of *H. ericae* (P =0.002, *df* 12).

Discussion

Hymenoscyphus ericae

In *R. groenlandicum*, intracellular hyphae of *H. ericae* conformed to the "infection unit" morphology (coiled hyphae within individual root cortical cells) indicative of an ericoid mycorrhizal relationship (Read 1996). Within *P. mariana* roots, intracellular hyphae of *H. ericae* were abundant but not coiled. Hyphae ramified from cell to cell within the epidermis and cortex, but did not penetrate the stele (Fig. 1b). An ectomycorrhizal relationship was not evident since hyphae growing among cortical cells did not form a Hartig net, nor was a mantle formed. However, heavy colonization of this type did not seem to adversely affect the host plants, and roots colonized by *H. ericae* were significantly longer than control roots (Fig. 2), suggesting either the production of a diffusible growth-promoting compound or that nutrients being released from moribund root tissues by the fungus are being resorbed by the roots (Fernando and Currah 1996).

Instances of ascomycetous fungi with inoperculate affinities being implicated in the formation of ectomycorrhizas are uncommon (e.g., Fernando and Currah 1996). Analyses of nuclear ribosomal DNA sequences suggested the fungus forming the ectomycorrhizal morphotype *Piceirhiza bicolorata* (Agerer 1987–99, plate 73) is part

of the *H. ericae* aggregate (Vrålstad et al. 2000). However, members of the *H. ericae* aggregate isolated from ericoid mycorrhizal roots failed to form typical ectomycorrhizas with ectotrophic hosts but rather formed superficial hyphal associations with the ectotrophic roots (Vrålstad et al. 2002). In this study, *H. ericae* did not form typical ectomycorrhizas with *P. mariana*, nor did it form a mantle morphotype similar to *P. bicolorata*, i.e., hyaline hyphae at the root apex and dematiaceous hyphae at the proximal end of the root (Brand et al. 1992). Instead, hyphae of *H. ericae* grew abundantly within and among root cortical cells without formation of a mantle.

Variable White Taxon

Abundant intracellular hyphae of VWT (8863), another inoperculate ascomycete (Hambleton 1998), were observed within the root cortical cells of *P. mariana*, although typical ectomycorrhizal structures were not formed. The taxon represented by the VWT strains is highly variable in culture (Hambleton and Currah 1997) and variation in the ability to colonize roots under a given set of conditions might be expected. VWT resembles both "Sterile white 1" and "Sterile dark 1" from *P. mariana* roots (Summerbell 1987). He indicated that these isolates might be conspecific since the white colony gave rise to dark patches and vice versa, and they did not differ significantly in isolation frequency. Strains labeled "VWT" also varied in colony color and the light and dark morphs did not differ significantly in isolation frequency (Hambleton 1998). The association of VWT with ericaceous plants and with ectotrophic hosts could be widespread, but the significance of this association remains unclear. Transmission electron microscopy of the fungus-root cell interface would help clarify the nature of these intracellular associations formed by both VWT and *H. ericae* in *Picea* roots.

Oidiodendron maius

Oidiodendron maius (8920) failed to form mycorrhizas with either plant species, while *O. maius* (8919) formed very few infection units in the root cortical cells of two (of ten) *R. groenlandicum* seedlings. The scant colonization by *O. maius* (8920) in *R. groenlandicum* was atypical for an ericoid mycorrhizal morphology because hyphae were few, short, and uncoiled. Roots of both species colonized by *O. maius* resembled those of control plants and did not differ significantly in length, suggesting *O. maius* was having little effect on the roots. These results agree with those of Bergero et al. (2000), who found that *O. maius* (and *Oidiodendron griseum* Robak) isolated from roots of *Erica arborea* L. and reinoculated onto axenic plants formed few infection units after a prolonged incubation (6–9 months). Furthermore, these results correlate well with results from the decomposition experiment. The relative abilities of *H. ericae* and VWT to decompose *Sphagnum* were low compared to *O. maius* (Fig. 3) and suggest that *H. ericae* and VWT could depend more heavily on carbon from host plants than *O. maius*.

Simultaneous associations between *Picea*, *Rhododendron* and fungi

The jar cultures contained a single, continuous fungal colony and two plant seedlings of different species. Simultaneous colonization of *P. mariana* and *R. groenlandicum* by either of two strains of *H. ericae* or one strain of VWT suggest that hyphal links could form between conifers and ericoid mycorrhizal plants in situ, and that both fungal taxa have the ability to associate with the roots of both ectotrophic and ericoid plants.

In this study, the fungal isolates were obtained from ericalean hosts only. Resynthesis of typical ericoid mycorrhizas might have been obtained with *O. maius* if isolates from *R. groenlandicum* had been used, although provenance did not prevent *H. ericae* (8872 from *Oxycoccus quadripetalus*) and VWT (8863 from *Phyllodoce empetriformis*) from forming typical infection units in *R. groenlandicum*. Vrålstad et al. (2002) found that strains of the *H. ericae* aggregate isolated from ericoid mycorrhizas failed to form ectomycorrhizas with *Betula*, *Picea*, or *Pinus* hosts, and strains isolated from ectomycorrhizal root tips failed to form ericoid mycorrhizas with *Vaccinium vitis-idaea*. The morphology of the association observed in the *Picea* roots of this study may have been affected by provenance, but rationalizing the interaction of provenance of both hosts and fungi against the artificial nature of experimental conditions would be moot.

In summary, these data show that *H. ericae*, an arthroconidial representative of the inoperculate discomycetes and a well-studied ericoid mycorrhizal fungus, can develop an intracellular association with roots of *P. mariana*. It is not known if this association is of benefit to the ectotrophic host, although there is considerable data showing that the fungus can benefit its ericaceous host (see Smith and Read 1997). An ectomycorrhizal morphotype, *P. bicolorata*, attributed previously to *H. ericae* based on molecular data (Vrålstad et al. 2000), was not formed in our study. We also show that a widespread but unnamed inoperculate taxon (VWT) can grow within the root cells of both conifers and ericaceous plants. Two strains of *O. maius*, another arthroconidial fungus allied with the inoperculate discomycetes and often implicated as an ericoid mycorrhizal fungus (Douglas et al. 1989; Xiao and Berch 1995; Perotto et al. 1996; Currah et al. 1999), did not form typical infection units in *R. groenlandicum*. *O. maius* did not colonize the root cells of *P. mariana* although both strains grew and sporulated along root surfaces. Mass losses incurred by these three fungal taxa using sterilized *S. fuscum* plants as a substrate indicated that *Oidiodendron maius* was more efficient as a free-living saprobe on this material than either *H. ericae* or VWT, and may be less reliant on

a plant host to obtain carbon than the other two taxa. This evidence suggests that the simultaneous colonization of an ericaceous shrub and an ectotrophic tree by a single fungus may occur in boreal peatlands, where nutrients are in short supply, primarily in organic forms, and thus inaccessible by vascular plants.

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