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Intracellular Colonization of *Rhododendron* and *Vaccinium* Roots by *Cenococcum geophilum*, *Geomyces pannorum* and *Meliniomyces variabilis*

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ABSTRACT. Four *in vitro* experiments were set up to verify the colonization potential of ectomycorrhizal (EcM) *Cenococcum geophilum* FR. (strain CGE-4), saprotrophic *Geomyces pannorum* (LINK) SIGLER & CARMICHAEL (GPA-1) and a frequent root-associated, potentially ericoid mycorrhiza (ErM)-forming *Meliniomyces variabilis* HAMBLETON & SIGLER (MVA-1) in roots of *Rhododendron* and *Vaccinium*. A typical ErM fungus, *Rhizoscyphus ericae* (READ) ZHUANG & KORF (RER-1), was included for comparison. All fungal strains intracellularly colonized rooted *Vaccinium* microcuttings: GPA-1 occasionally produced hyphal loops similar to ErM, MVA-1 and RER-1 exhibited a typical ErM colonization pattern. CGE-4 hyphae grew vigorously on and around newly formed roots and rarely penetrated turgescent rhizodermal cells forming intracellular loose loops. Rooting of *Rhododendron* sp. microcuttings was not promoted by any fungal strain except CGE-4, which also promoted the most vigorous growth of *Rhododendron ponticum* L. seedlings. The widespread EcM fungus *C. geophilum* has a potential to colonize non-EcM roots and support their development which may influence overall growth of ericaceous plants. As shown for *G. pannorum*, structures resembling ErM may be formed by fungi that are to date not regarded as ericoid mycorrhizal.

Abbreviations

DSE	dark septate endophytes	MMN	medium of Melin–Norkrans
EcM	ectomycorrhiza(l)	MMR	medium according to Mitchell and Read
ErM	ericoid mycorrhiza(l)		
CGE	*Cenococcum geophilum*	MVA	*Meliniomyces variabilis*
GPA	*Geomyces pannorum*		

Ericaceous plants form root-fungus associations mainly with ericoid mycorrhizal (ErM) fungi and dark septate endophytes (DSE), called ericoid mycorrhiza in the former and DSE-association in the latter case. An extensive body of literature shows that ErM plays a significant role in the life of ericaceous plants (Cairney and Meharg 2003; Read *et al.* 2004). Similarly to DSE (Jumpponen 2001; Mandyam and Jumpponen 2005), the significance of ectomycorrhizal (EcM) fungi (Dighton and Coleman 1992; Stoyke and Currah 1993; Midgley *et al.* 2004), unknown basidiomycetous fungi (Seviour *et al.* 1973; Bonfante-Fasolo 1980; Bougoure and Cairney 2005*a*,*b*) or saprotrophic ascomycetous fungi (Allen *et al.* 2003), which are occasionally found in roots of ericaceous species, remains obscure.

Even though mycorrhizal fungi influence various components of host-plant fitness (Jones and Smith 2004), their effect on the host-plant nutrient uptake and enhanced growth is usually sought, putting other factors aside (Johnson *et al.* 1997; Jones and Smith 2004). In ericaceous species, the primary effect of ErM fungi is in accessing organic nitrogen together with detoxication of the substrate (Perotto *et al.* 2002; Cairney and Meharg 2003). Other factors, such as involvement of ErM fungi in enhanced root development, are considerably less studied (Eccher and Noé 2002). In contrast, considerably more work has been focused on the influence of EcM fungi on rooting and root development of EcM host plants (*e.g.*, Gay 1990; Rudawska and Kieliszewska-Rokicka 1997; Niemi and Häggman 2002; Niemi *et al.* 2002); however, the experience and knowledge have not been transferred into the field of ErM symbiosis.

During our earlier unpublished aseptic syntheses several strains of different fungi, to date regarded as non-ErM, revealed a potential to intracellularly colonize roots of ericaceous hosts and positively influence their development. Among the most unexpected interactions, *Geomyces pannorum* (strain GPA-1), a soil-

borne fungus and an occasional human skin pathogen (Domsch et al 1980; Gianni *et al.* 2003), colonized newly formed roots of *Rhododendron* and *Vaccinium* microcutings. An EcM fungus, *Cenococcum geophilum* (strain CGE-4) and a frequent root-associated fungus, *Meliniomyces variabilis* (strain MVA-1) supported the root development of *Rhododendron ponticum* seedlings, both fungi also colonizing newly emerging roots. All three fungi were recently detected in ericaceous roots by different authors (Lacourt *et al.* 2001; Midgley *et al.* 2004; for details about *M. variabilis see* Hambleton and Sigler 2005) but without determination of their interaction with the host roots.

We conducted two *in vitro* experiments to describe the colonization potential of *C. geophilum*, *G. pannorum* and *M. variabilis* in ericaceous roots, paying special attention to the fungal structures formed inside the rhizodermal cells. Two further experiments screened their ability to influence the root development of the inoculated plants.

MATERIALS AND METHODS

The fungal isolates used are listed in Table I. GPA-1 was isolated from a contaminated *Rhododendron* tissue culture and MVA-1 from surface-sterilized *P. abies* roots. The strain RER-1, originally isolated from *Calluna vulgaris* HULL. roots by Pearson and Read (1973), was used as a representative of the typical ErM fungus *Rhizoscyphus ericae.*

Table I. Fungal isolates used

Genus and species	Isolate	Availability[a]	*GenBank*
Cenococcum geophilum FR.	CGE-4	*on request*	–
Geomyces pannorum (LINK) SIGLER & CARMICHAEL	GPA-1	CCF 3581	DQ494320
Meliniomyces variabilis HAMBLETON & SIGLER	MVA-1	CCF 3583	AM261523
Rhizoscyphus ericae (READ) ZHUANG & KORF	RER-1	UAMH 6735	AJ319078

[a]CCF – *Culture Collection of Fungi* (*Department of Botany, Faculty of Science, Charles University*, Prague, Czechia); UAMH – *University of Alberta Microfungus Collection and Herbarium* (*University of Alberta*, Edmonton, Canada)

Assessment of the fungal ability to colonize ericaceous roots

Experiment 1: Inoculation of rooted *Vaccinium* micro-cuttings. One compartment of each split Petri dish was filled with the modified MMN (Marx 1969) and inoculated with agar plugs overgrown with mycelium of CGE-4, GPA-1, MVA-1 and RER-1. The other compartment was left without the medium. Suitability of the MMN for growth of *Rhododendron* and/or *Vaccinium* seedlings and/or cuttings and the tested fungal strains was screened in advance with positive results. Despite the relatively high content of carbon, MMN supported ErM formation by *R. ericae* during the testing.

The dishes with the plugs were cultivated for one month at room temperature in the dark. One aseptic rooted *Vaccinium* cutting was then inserted into each dish so that its roots were placed on the surface of the fungal colonies and its shoot was accommodated in the empty compartment. There were three rooted microcuttings for each fungal strain including a non-inoculated control. Each dish was parafilm-sealed and placed in a growth chamber (16/8 h, 25/20 °C day-to-night, light intensity of 150 μmol m^{-2} s^{-1}). After 3 months, plants were removed from the dishes, their roots were cleared with 10 % KOH (20 min, 121 °C), washed with tap water, acidified (1 min, 3 % HCl), washed with tap water, stained with trypan blue (1 h, 121 °C) and de-stained overnight in lactoglycerol. Stained roots were observed with differential interference contrast at high magnifications (400× and 1000×).

Additionally, the ability of GPA-1 to colonize *Vaccinium* roots was screened in a peat + perlite substrate. Three 300-mL Erlenmeyer flasks filled with moistened autoclaved mixture of peat–perlite (1 : 1) were pre-inoculated for 1 month with GPA-1 and three flasks were left noninoculated. Three rooted microcuttings were inserted into each of the flasks, resulting in nine cuttings inoculated with GPA-1 and nine cuttings noninoculated. After 3 months of cultivation in the growth chamber, their roots were harvested, stained and evaluated (*see above*).

Experiment 2: Inoculation of *Rhododendron ponticum* seedlings. Germinating surface-sterilized seeds of *R. ponticum* were placed onto the margins of 1-month-old fungal colonies, actively growing on MMN. Each tested fungus plus noninoculated control was represented by three Petri dishes, each with four seed-

lings. After 3 months of cultivation in the growth chamber, the seedlings were extracted from the dishes and their roots were stained and evaluated for intracellular colonization by fungal hyphae.

Assessment of the fungal ability to support the development of ericaceous roots

Experiment 3. One compartment of each of 15 split Petri dishes with perforated central septa contained MMR (Mitchell and Read 1981), modified by Dalpé (1986), the other was left empty. Aseptic *Rhododendron* microcuttings without roots were inserted in triplicates through the perforated septa in a manner that ≈⅕ of their size was immersed into MMR. The dishes were inoculated with agar plugs collected from the margins of actively growing colonies of all four tested fungi, representing separate variants. Each variant including control had nine microcuttings. The dishes were parafilm-sealed and placed in a vertical position in the growth chamber. After 15 weeks, the number of rooted microcuttings was counted in each variant, and the length of their roots was measured. Roots were excised and treated as in *Experiment 1*.

Experiment 4. Aseptic *Rhododendron* microcuttings without roots, of the same origin as in the *Experiment 3*, were introduced into glass vessels (350 mL) with standard MS medium (Murashige and Skoog 1962) without growth regulators. The vessels with 50 microcuttings were inoculated with CGE-4, GPA-1, MVA-1 and RER-1, or left noninoculated, parafilm-sealed and placed in the growth chamber. After a 3-month cultivation, the number of rooted microcuttings, their length and colonization patterns in roots were assessed.

RESULTS

Assessment of the fungal ability to colonize ericaceous roots. All fungal strains intracellularly colonized roots of *Vaccinium* microcuttings and/or *R. ponticum* seedlings. Noninoculated plants remained without any fungal colonization.

GPA-1 intracellularly colonized the roots of *Vaccinium* microcuttings only in the peat + perlite substrate. Here it formed loose to dense trypan-blue-stained coils in the rhizodermal cells (Fig. 1) that resembled coils formed by ErM fungi in ericaceous roots. On the MMN, GPA-1 occasionally formed loose hyphal wefts around the roots of *Vaccinium* microcuttings but without apparent intracellular colonization. The development of the roots of *R. ponticum* seedlings in the presence of GPA-1 was reduced (Fig. 2, *see* p. 412) and the reduced roots were without any fungal colonization.

Dark-brown septate hyphae of CGE-4 formed a loose to dense mantle around the newly formed roots (Fig. 3A) and also around the base of stems of the microcuttings. Often, hyphae followed grooves between rhizodermal cells, occasionally penetrating turgescent cells with melanized or hyaline hyphae (Fig. 3B), forming loose hyphal loops inside (Fig. 3C).

Both MVA-1 and RER-1 colonized rhizodermal cells of rooted *Vaccinium* microcuttings in a manner typical of ErM fungi. Rhizodermal cells were filled with hyphal coils and the roots were often embedded in hyphal mantles. MVA-1 failed to colonize the roots of *R. ponticum* seedlings. In contrast with the CGE-4 and RER-1 variants, the roots of the seedlings did not penetrate through MVA-1 fungal colonies into the medium but developed extensively on the surface of the colonies. RER-1 was more efficient than MVA-1 in terms of root colonization levels, reaching ≈15 and 25 % of the total root length colonized in *Vaccinium* microcuttings and *R. ponticum* seedlings, respectively. Colonization level of GPA-1 was lower and reached ≈5 %. The intracellular colonization by CGE-4 was <1 %.

There were no apparent differences in the size of the *Vaccinium* microcuttings among all inoculation variants. The growth of *R. ponticum* seedlings was positively influenced by CGE-4 and negatively by GPA-1. In the presence of CGE-4, the seedlings developed apparently better than in the rest of the variants. In contrast, seedlings growing in the presence of GPA-1 had reduced roots and also their overall growth was reduced (Fig. 2).

Assessment of the fungal ability to support the development of ericaceous roots. In the CGE-4 variant of the *Experiment 3*, five of nine microcuttings developed three or four roots >10 mm. In the GPA-1 variant, one microcutting developed one root <5 mm without any fungal colonization; the same situation was in the RER-1 variant. The noninoculated microcuttings remained without any roots. There were no apparent differences in the growth of the cuttings between all variants.

In the CGE-4 variant of *Experiment 4*, 16 of 50 microcuttings produced abundant roots (Fig. 4), which were colonized in the same manner as in *Experiments 1–3*. The microcuttings in the other variants remained without any roots. The rooted CGE-4-inoculated microcuttings were ≈3× larger (90.6 ± 2.9 mm; mean ± SE) than the noninoculated cuttings (27.0 ± 2.5 mm) and the nonrooted CGE-4-inoculated microcut-

tings (26.0 ± 1.9 mm; Fig. 4). The cuttings inoculated with other fungi did not differ from the noninoculated ones.

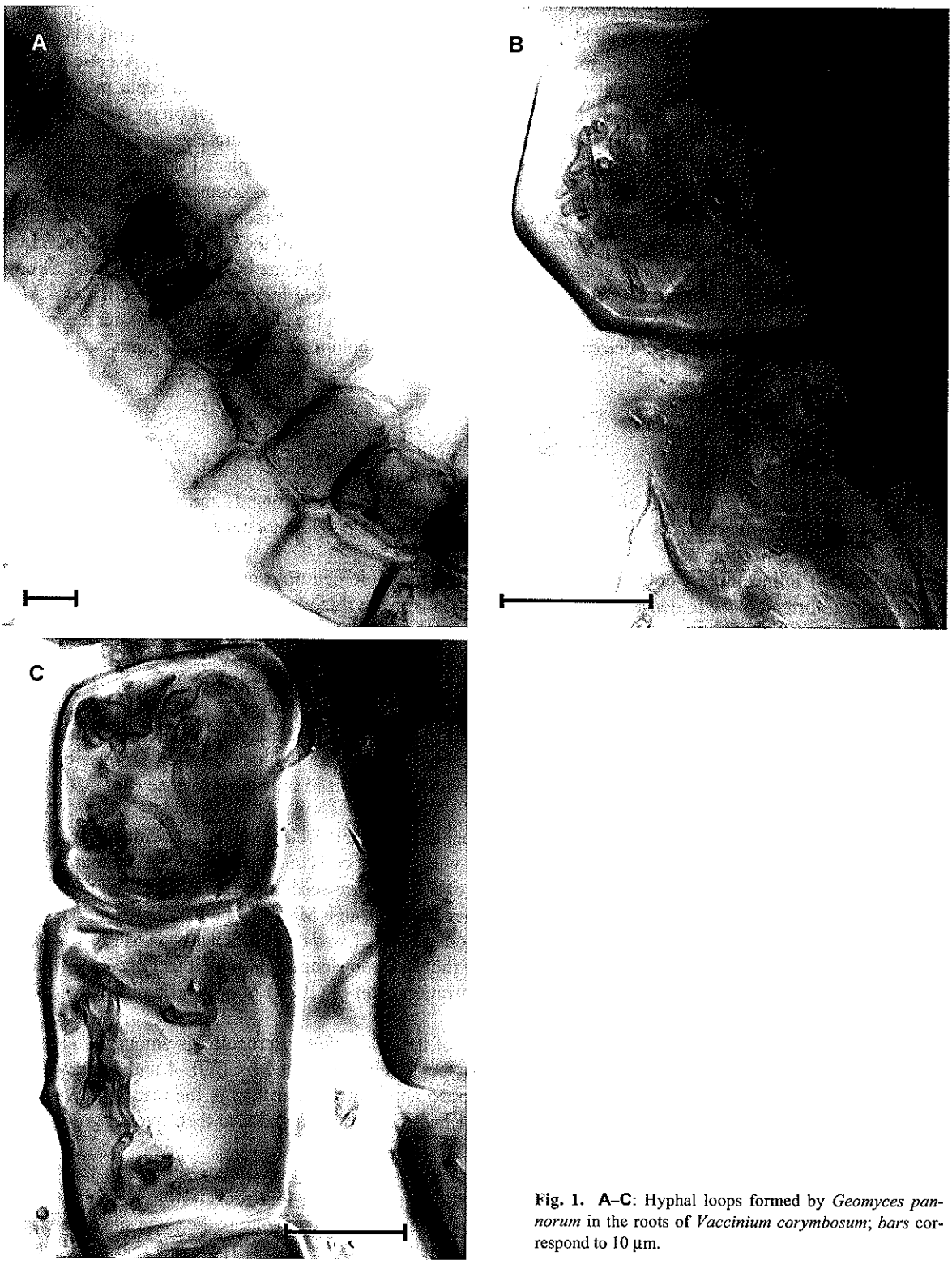

Fig. 1. A–C: Hyphal loops formed by *Geomyces pannorum* in the roots of *Vaccinium corymbosum*; *bars* correspond to 10 μm.

DISCUSSION

Even though *C. geophilum* (CGE) is an EcM fungus, it is occasionally detected in the surface-sterilized ericaceous roots (Midgley *et al.* 2004). Stoyke and Currah (1993) found in an aseptic re-synthesis trial

that CGE formed "*loose wefts of hyphae on root surfaces, but rarely penetrated the root cortex*" of *Menziesia ferruginea* SMITH (*Ericaceae*). The authors stated that the association between CGE and *M. ferruginea*

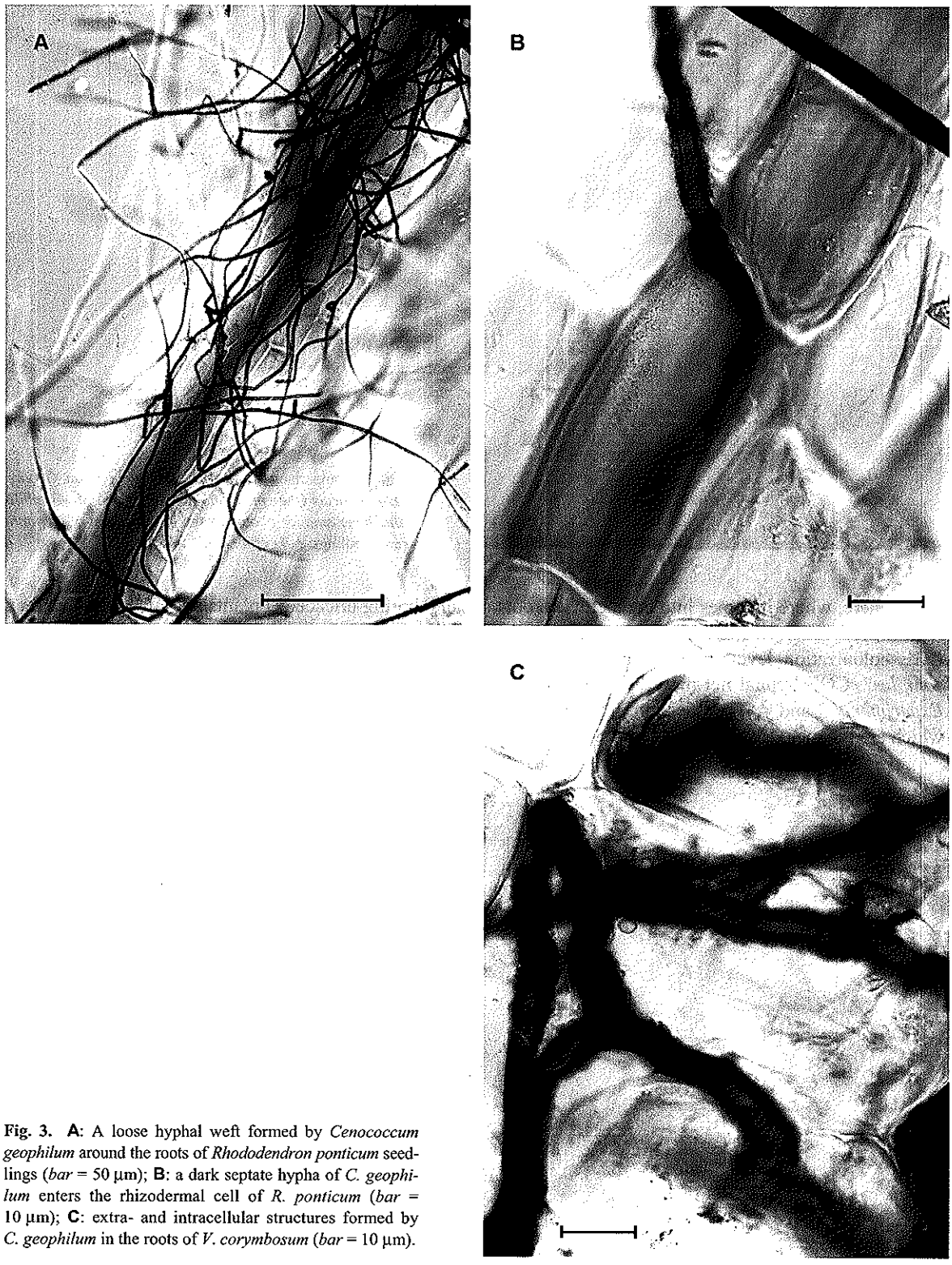

Fig. 3. **A**: A loose hyphal weft formed by *Cenococcum geophilum* around the roots of *Rhododendron ponticum* seedlings (*bar* = 50 µm); **B**: a dark septate hypha of *C. geophilum* enters the rhizodermal cell of *R. ponticum* (*bar* = 10 µm); **C**: extra- and intracellular structures formed by *C. geophilum* in the roots of *V. corymbosum* (*bar* = 10 µm).

appeared "*potentially mycorrhizal*", thus having beneficial character. Similarly, we observed that CGE-4 reached very low colonization levels and its extra- and intracellular colonization had a beneficial character, resulting in a stimulation of root development and improved growth of the inoculated plants.

CGE-4 influenced its hosts rather *via* ERM than *via* the infrequent intracellular structures. Such situation may occur under natural conditions, where EcM host plants spread their ERM through the mycor-

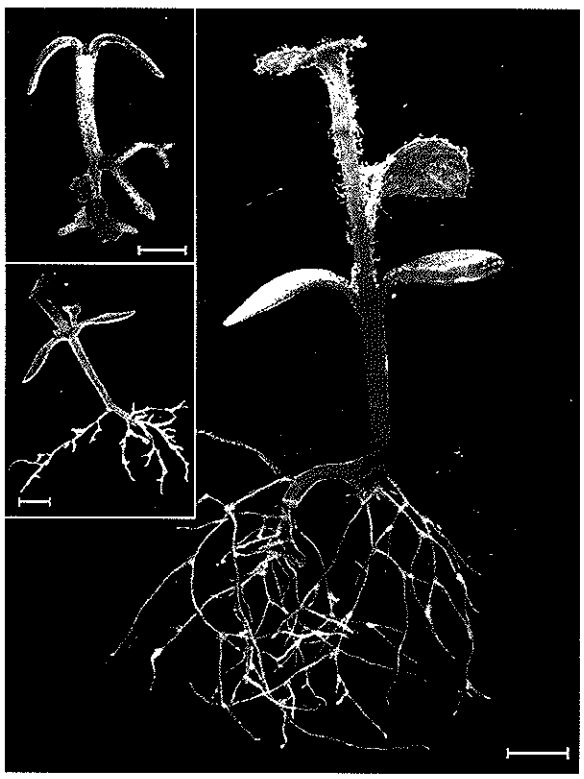

Fig. 2. Comparison of the effect of *C. geophilum*, *Geomyces pannorum* (*the upper smaller photo*) and *M. variabilis* (*the lower smaller photo*) on the development of *R. ponticum* seedlings; *bars* correspond to 1 mm.

rhizosphere, where it comes into contact with roots of neighboring ericaceous plants and may colonize their rhizodermal cells. This is supported by observations of Stoyke and Currah (1993) who noted that the low CGE colonization levels and pattern in *M. ferruginea* roots "*resembled associations observed in field samples*". CGE hyphal net may then positively interact with ericaceous plants in a similar manner as in *Experiments 3* and *4*. The question, however, remains about the interaction between CGE and ErM fungi, which are the most frequent colonizers of ericaceous roots.

Fig. 4. Comparison of the stimulation effect of *C. geophilum* on *Rhododendron* microcuttings (*smaller photo* – control cuttings); *bars* correspond to 10 mm.

EcM fungi are known to influence their hosts by production of phytohormones, auxins in particular (Nylund 1988; Gay 1990; Rudawska and Kieliszewska-Rokicka 1997; Niemi *et al.* 2002), but their effect on the root development has been studied only in typical EcM plants, *i.e.* species of *Pinus* and *Picea*. CGE-4 has relatively high intracellular levels of IAA (up to 21.4 pmol/g fresh mass), which is a probable cause of its root-stimulating effect. We show that this feature does not need to be limited to the roots of typical EcM hosts but may influence a broader spectrum of plants.

G. pannorum (GPA) is a common air- and soil-borne fungus with cellulolytic and keratinolytic abilities, frequently isolated from various substrates and niches, including rhizosphere of peat bog plants (Domsch *et al.* 1980). Lacourt *et al.* (2001) used a sequence of GPA strain CLM 323.96 (*GenBank* AF307760) and noted that this strain had been originally isolated from the roots of *Erica arborea* L. by Bergero *et al.* (2000). To our knowledge this study represents the first attempt to describe the interaction between GPA and ericaceous roots. However, GPA-1 formed intracellular coils in the rhizodermal cells of *Vaccinium* microcuttings only in the peat-based substrate. Similar structures formed by *Myxotrichum setosum* (EIDAM) ORR, KUEHN & PLUNKETT, *Gymnascella dankaliensis* (CASTELLANI) CURRAH (both with *Oidiodendron* anamorphs) and *Pseudogymnoascus roseus* RAILLO (with *Geomyces* anamorph) were observed in *Vaccinium angustifolium* AIT. roots by Dalpé (1989), who assigned them to ErM. The colonization potential of GPA-1 was low and the colonized *Vaccinium* microcuttings did not show any signs of improved fitness. Moreover, the overall growth of *R. ponticum* seedlings growing in contact with GPA-1 was depressed. On the other hand, also *M. setosum* and *P. roseus* reached low colonization levels (8–10 and 5–6 %, respectively) in the roots of *V. angustifolium*, without causing any apparent improvement of fitness of the host plants (Dalpé 1989), and the *in vitro* growth of rooted *Rhododendron* microcuttings can be depressed by *Oidiodendron maius* BARRON, which *ex vitro* forms ErM and improves nutrient uptake by *Rhododendron* cv. Azurro (Vohník *et al.* 2005). To conclude, the ability of GPA-1 to colonize rhizodermal cells of ericaceous plants together with its relatedness to *Oidiodendron* genera, containing many ErM fungi (Dalpé 1986 and 1991; Hambleton *et al.* 1998; Lacourt *et al.* 2001) may indicate that it is a putative ErM fungus.

M. variabilis (MVA), formerly known as the Variable White Taxon, is a fungus with an as yet not clear mycorrhizal status (Hambleton and Sigler 2005). MVA-1 did not influence rooting of *Rhododendron* microcuttings nor colonized the roots of *R. ponticum* seedlings nor apparently influenced their growth, but intracellularly colonized roots of *Vaccinium* microcuttings in a manner similar to ErM. On the other hand, RER-1 colonized also the *R. ponticum* seedlings, indicating that this typical ErM fungus is a more infective colonizer than MVA, at least under the chosen experimental conditions. Nevertheless, our results show that MVA apparently has the ability to form intracellular structures resembling ErM.

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