

SHORT NOTE

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Fungi in ectomycorrhizal associations of silver fir (*Abies alba* Miller) in Central Italy

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Abstract Naturally occurring ectomycorrhizas of silver fir (*Abies alba* Miller) were studied in two stands, one natural and one artificial, situated in Central Italy. A total of 25 mycorrhizal types was classified, for eight of which the mycobiont was identified at the species level. Analysis of macroscopic and microscopic features and matching of field-collected carpophores with associated mycorrhizas led to the tentative identification of several other types encountered during this study, at least at the genus level. No significant differences were noticed between natural and artificial stands in the relative richness of mycorrhizal types found on *A. alba*, indicating the maturity of the artificial stand with regard to succession of ectomycorrhizal fungi. Confocal laser scanning microscopy was used for visualization of mycorrhizal structures formed by *Lactarius* spp., without the need for specific staining with a fluorochrome, thanks to latex autofluorescence. This technique allowed observation of several structures in greater detail than with conventional light microscopy.

Key words Ectomycorrhizas · *Abies alba* · Characterization · Ecology · Confocal microscopy

Introduction

Silver fir (*Abies alba* Miller) is an ecologically valuable and indigenous tree species in many mountainous re-

gions of eastern, western, southern and central Europe. During the last century, silver fir populations have suffered several episodes of widespread decline and are currently scattered throughout the entire European range (Konnert and Bergmann 1995).

Although this decline is probably due to a combination of biotic and abiotic factors (Sierpinski 1981; Larsen 1986), attention has been drawn recently to the status of the fine root system of declining trees. In this relation, ectomycorrhizas are of special interest as they make up the largest part of very fine, absorptive roots. Over the last two decades, studies have been conducted on the mycorrhizal status (Blaschke 1981), mycorrhizal dynamics (Fontana et al. 1982), and vitality of ectomycorrhizas (Ritter et al. 1989) of silver fir, but these efforts were severely hampered by inadequate identification and recognition of ectomycorrhizas, due to difficulties in evaluating the individual contributions of diverse symbionts in these ecological processes.

During the last 2 years, we have investigated, both macroscopically and microscopically, naturally occurring ectomycorrhizas associated with silver fir in one artificial and one natural stand in Central Italy. We classified 25 mycorrhizal types, eight of which were identified to the level of the species. The individual descriptions of the fully characterized ectomycorrhizas will be presented elsewhere. In this paper, we briefly review the present status of knowledge on the naturally occurring ectomycorrhizal associations of silver fir and discuss the general implications of our recent findings. We also report the application of confocal laser scanning microscopy (CLSM) to the characterization of morphological features of some ectomycorrhizal types (Schelkle et al. 1996).

Materials and methods

The material examined was collected during the growing seasons 1995–1996 and originates from two silver fir stands situated in the Gran Sasso-Laga National Park, Central Italy: “Fonte Gelata” (artificial stand planted in early 1950s; 1000 m a.s.l.) and “Colle

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Plato" (natural stand; 1100 m a.s.l.). Details of the two study areas, including mycocoenological, phytosociological and pedological aspects, have been reported by Comandini (1997).

Soil cores under carpophores of known and putatively mycorrhizal fungi were taken weekly. Subsequently, samples were carefully washed in water and ectomycorrhizal roots were separated under a dissecting microscope (Leica Wild M 10) for macroscopical characterization, as described by Agerer (1991). Particular care was taken to isolate mycorrhizal roots of *A. alba* from those of other host trees in the sampling sites (mainly *Fagus sylvatica* L.). Methods to characterize ectomycorrhizas have been comprehensively explained by Agerer (1986, 1987–1993, 1991), and the glossary of all terms used has been published by the same author (Agerer 1987–1993). For a better characterization of ectomycorrhizas, Munsell Soil Color Charts (1954) were used as a reference.

Mantle preparations of fresh ectomycorrhizas were fixed on slides with polyvinyl lactophenol for both light and CLSM investigations. For light microscopy, observations were made with a Leitz Laborlux S microscope and photographs were taken with Kodak Ektachrome 160 T film. For CLSM, observations were made using a Molecular Dynamics Sarastro 2000 microscope equipped with a Nikon Optiphot fluorescence microscope (Planapo 60/1.4 lens) and an Argon gas laser (25 mW). Laser excitation wavelength was fixed at 488 nm and images were recorded using Kodak Elite 100 film. Cross and longitudinal sections (2–3 µm thick) of smooth mycorrhizas were cut on a cryotome (Frigocut 2800, Reichert-Jung), while mycorrhizas with a rather loose mantle were embedded in historesin (Technovit 7100, Heraeus Kulzer) and sections cut on a Leitz 1512 microtome. Voucher specimens are deposited in AQUI (Herbarium Micologicum Aquilinum) as fixed material (4% glutaraldehyde) together with slides.

The identity of ectomycorrhizas was proved by macroscopic and microscopic analysis, evaluation of consistent features, in par-

ticular those in common with carpophores of the correspondent fungal symbionts, by tracing hyphal connections between mycorrhizas and carpophores, and by matching of field-collected carpophores with associated mycorrhizas.

Results and discussion

Table 1 reports 25 mycorrhizal types classified for the two stands. Several mycobionts responsible for particular ectomycorrhizal types on silver fir were identified at the species level and include: *Cenococcum geophilum* Fr., *Byssocorticium atrovirens* (Fr.) Bond. et Sing. ex Sing., *Phellodon niger* (Fr.:Fr.) Karst, *Laccaria amethystina* (Bolt.) Murr., *Tricholoma bufonium* (Pers.:Fr.) Gillet, *Lactarius ichoratus* (Batsch) Fr., *Lactarius salmonicolor* Heim et Lec., *Lactarius scrobiculatus* (Scop.:Fr.) Fr.. All other fungal symbionts were *Basidiomycetes*, as evidenced by clamp connections in mantle hyphae and, if present, extramatrical hyphae.

Type 14 was tentatively believed to be formed by *Russula viscida* Kuhn, although carpophores were not encountered in the field. In fact, several morphological features of the mantle surface of this type, including the typical slimy appearance, match those described for the cuticle of *R. viscida* carpophores (Romagnesi 1967). Despite the fact that a general viscid appearance is typical also of other *Russula* species (Ro-

Table 1 Main macroscopic and microscopic features of the ectomycorrhizal types of *Abies alba* occurring in a natural (N) and an artificial (A) stand. Terminology according to Agerer (1987–1993)

Type	Macroscopic features		Microscopic features				Cystides	Fungal symbiont	Stand	
	Mantle surface	Rhizomorphs ^a	Mantle structure ^b SV	ML	IV	Laticifers ^c			N	A
1	Smooth	–	Pl	Pl	Pl	–	–	<i>Cenococcum geophilum</i>	+	+
2	Cottony	–	Pl	Pl	Pl	–	–	<i>Byssocorticium atrovirens</i>	+	+
3	Smooth to grainy	a-B	Pl	Pl	T	–	–	<i>Phellodon niger</i>	+	+
4	Velvety to cottony	c-A	Pl	Pl	Ps	–	–	<i>Laccaria amethystina</i>	+	+
5	Cottony	a-B	Pl	Pl	T	–	–	<i>Tricholoma bufonium</i>	+	+
6	Cottony	a-B	Pl	Pl	T	–	–	<i>Tricholoma</i> sp. 1	–	+
7	Cottony	a-A	Pl	Pl	T	–	–	<i>Tricholoma</i> sp. 2	–	+
8	Cottony	a-A	Pl	Pl	T	–	–	<i>Tricholoma</i> sp. 3	+	+
9	Smooth to cottony	–	Pl	T	Ps	–	–	<i>Inocybe</i> sp.	+	+
10	Cottony	f-A	Pl	T	Pl	–	–	<i>Cortinarius</i> sp. 1	+	+
11	Smooth to cottony	f-D	Pl	Pl	Pl	–	–	<i>Cortinarius</i> sp. 2	+	–
12	Short-spiny	–	Pl	Ps	Ps	c-IV	+	<i>Russula</i> sp. 1	+	+
13	Smooth to woolly	–	Pl	Ps	Ps	c-SV, ML	+	<i>Russula</i> sp. 2	+	–
14	Viscid	–	Pl	Ps	T	c-ML, IV	+	<i>Russula</i> sp. 3	–	+
15	Smooth	–	Ps	–	Pl	a-IV	–	<i>Lactarius ichoratus</i>	+	+
16	Smooth	rr-B	Pl	Pl	Pl	a-IV	–	<i>Lactarius salmonicolor</i>	+	+
17	Smooth	r-A	T	Pl	Pl	a-ML	–	<i>Lactarius scrobiculatus</i>	+	+
18	Cottony	a-E	Pl	T	Pl	–	–	<i>Hysterangium</i> sp.	+	+
19	Smooth	–	Pl	Pl	Pl	–	–	<i>Basidiomycetes</i>	+	–
20	Short spiny	–	Pl	Ps	T	–	+	<i>Basidiomycetes</i>	+	–
21	Grainy to woolly	–	Pl	Ps	T	–	–	<i>Basidiomycetes</i>	–	+
22	Short spiny	–	Ps	Ps	T	–	+	<i>Basidiomycetes</i>	–	+
23	Cottony	–	Pl	Ps	T	–	–	<i>Basidiomycetes</i>	–	+
24	Cottony	a-B	Pl	Pl	Pl	–	–	<i>Basidiomycetes</i>	+	–
25	Cottony	a-E	Pl	Pl	T	–	–	<i>Basidiomycetes</i>	–	+

^a rr/r/c/f/a: very rare, rare, common, frequent, abundant – A/B/D/E: types of rhizomorph organization

^b Pl/T/Ps: plectenchymatous, transitional type, pseudoparenchymatous

^c IV/ML/SV: inner view, middle layer, surface view

magnesi 1967), the identification of type 14 as *R. viscida* is indirectly corroborated by the reported association of this mycobiont with silver fir in mycocoenological studies (Kost and Haas 1989; Perini et al. 1995). Given the presence of abundant calcium oxalate crystals on the hyphal surface, type 18 was likely formed by *Hysterangium* sp. (Müller and Agerer 1996), but no carpophores belonging to this genus were found. Although it is presently not clear whether such crystals are a genus characteristic, the attribution of type 18 to *Hysterangium* sp. is supported also by the strong resemblance of morphological and anatomical characters (mycorrhizal systems; color, shape and structure of rhizomorphs; structure of mantle layers; reagent reactions of crystals) with those of the only fully-described ectomycorrhiza of this genus *H. crassirhachis* Zeller & Dodge + *Pseudotsuga menziesii* (Mirb.) Franco (Müller and Agerer 1996). From comparison of macroscopical and microscopical features with those reported in the literature, several other ectomycorrhizal types could be reasonably assigned to *Tricholoma* spp. (6–8), *Inocybe* sp. (9), *Cortinarius* spp. (10–11), and *Russula* spp. (12–13). In all these cases, collections were taken under carpophores of identified mycorrhizal fungi: *Tricholoma aurantium* (Sch.:Fr.) Ricken, *Tricholoma orirubens* Quélet, *Tricholoma scalpturatum* (Fr.) Quélet, *Inocybe geophylla* (Fr.:Fr.) Kummer, *Cortinarius decipiens* (Pers.:Fr.) Fr., *Cortinarius dibaphus* Fr., *Russula fragilis* (Pers.:Fr.) Fr., *Russula olivacea* (Sch.) Pers.. However, the definitive match of a mycorrhizal type with the correspondent mycobiont was impaired by lack of recognizable features common to both the mycorrhiza and the carpophore, and by the presence of more than one mycorrhizal type of the same genus in a single soil core. Other ectomycorrhizal types (19–25) were readily recognizable but the mycobiont was unknown. Type 20, found several times in samples collected under different mycorrhizal fungi, shows some particular characters in common with *Fagirhiza globulifera*, an unidentified mycorrhiza described by Brand (1991) with *Fagus sylvatica*. Despite the presence of some macroscopical differences, especially concerning the color, it can be reasonably suggested that the two mycorrhizal types are formed by the same fungal species.

As outlined above, in several cases the occurrence of striking similarities between ectomycorrhizas and carpophores proved to be very helpful, although not sufficient in all instances, for the correct identification of mycobionts. The most frequently observed characters common to both mycorrhizas and carpophores were: general aspect and color (*Byssocorticium atrovirens*, *Phellon niger*, *Laccaria amethystina*, *Tricholoma bufonium*, *Russula* sp. 3 - cfr. *viscida*); characters of latex, including color and change in color on exposure to air, and response to chemical reagents (*Lactarius ichoratus*, *Lactarius salmonicolor*, *Lactarius scrobiculatus*); structure of rhizomorphs (*Tricholoma bufonium*, *Tricholoma* sp. 2 - cfr. *orirubens*, *Tricholoma* sp.3 - cfr. *scalpturatum*).

No significant differences were noticed between natural and artificial stands for the number of mycorrhizal types present on *A. alba* (Table 1). This finding is not surprising if one takes into account the age of the artificial stand (planted in the early 1950s). From studies on succession of ectomycorrhizal fungi, it has become evident that one of the main factors determining the composition of the ectomycorrhizal flora is the age of the associated host trees (Dighton and Mason 1985; Mason et al. 1987). As shown by research on plots of *Picea abies* (L.) Karst. (Ricek 1981), *Pinus sylvestris* L. (Hintikka 1988), and *Pseudotsuga menziesii* (Jansen 1991), the usual process in forest stands seems to be a fairly rapid increase in species richness and sporocarp productivity during 30–40 years and a more gradual decrease afterwards to an intermediate, rather constant level. Although no similar investigations have been carried out in silver fir stands so far, a similar trend can be reasonably expected also for *A. alba* woods. Thus, the artificial stand of Fonte Gelata should be regarded as “mature”, with a richness in ectomycorrhizal species approaching the rather constant level typical of natural stands.

Prior to this study, numerous ectomycorrhizal fungi have been reported in association with silver fir, mainly on the basis of field observations (Trappe 1962; Romagnesi 1967; Moser 1983; Stangl 1988; Kost and Haas 1989; Brandrud et al. 1989–1992). However, complete descriptions of ectomycorrhizas of *A. alba* are available only for very few mycobionts: *Cortinarius odorifer* Britz. (Egli 1992), *Russula ochroleuca* (Hall.) Pers. (Pillukat and Agerer 1992), *Lactarius salmonicolor* (Pillukat 1996). In all other cases, efforts to characterize mycorrhizas of silver fir resulted in the report of “mycorrhizal types”, for some of which only a tentative identification was proposed (Dominik 1958; Hu 1980; Fontana et al. 1982; Berndt et al. 1990; Berndt and Oberwinkler 1992; Riess 1993; Paoletti et al. 1994). Mycocoenological studies of silver fir woods in different parts of Europe (Haas 1932; Smarda 1969, 1973; Bon and Géhu 1973; Wojewoda 1974, 1975; Bujakiewicz 1979, 1981, 1982; Kost and Haas 1989; Comandini et al. 1993; Perini et al. 1995) revealed the presence of a relatively large number of ectomycorrhizal fungi, with a rather low degree of similarity between the study areas. Although these findings are consistent with the fact that the silver fir woods investigated so far belong to different community types in which, apart *A. alba*, several other ectomycorrhizal trees are present, they also suggest that the number of actual mycobionts of silver fir has been somewhat underestimated. The results of the present study are in good agreement with this hypothesis, in that 10 out of 18 mycorrhizal types for which an identification was possible or could be suggested are reported here for the first time (as far as we know) as directly associated with *A. alba*: *Byssocorticium atrovirens*, *Phellodon niger*, *Laccaria amethystina*, *Tricholoma aurantium*, *Tricholoma bufonium*, *Tricholoma scalpturatum*, *Inocybe geophylla*, *Cortinarius decipiens*, *Russu-*

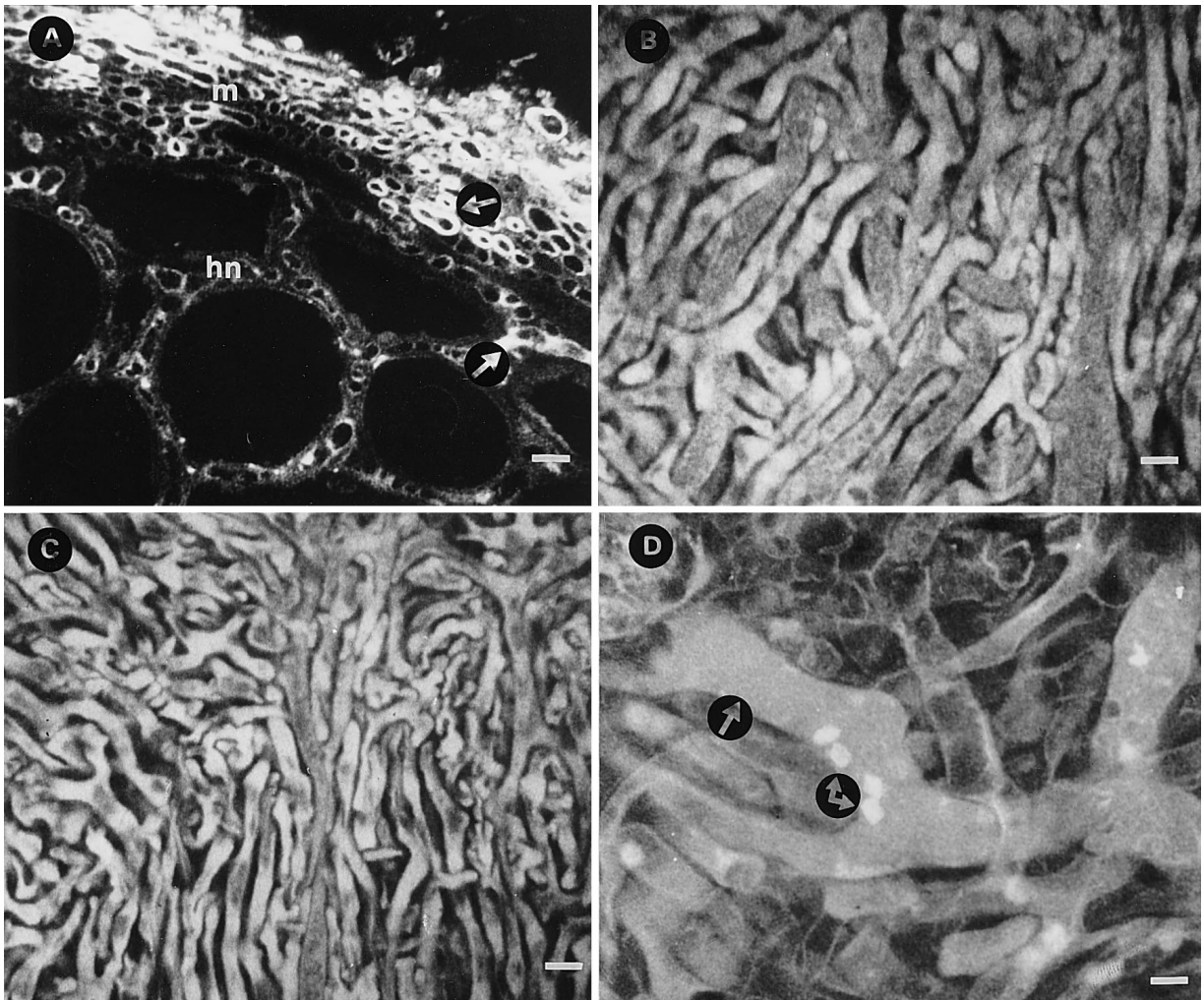
la fragilis, *Russula olivacea*. These identifications, although tentative in most cases, provide much information about the fungal species that colonize silver fir and their host specificity and ecology.

Five mycorrhizal types identified during our study have been already described in association with host trees other than silver fir: *Laccaria amethystina* + *Fagus sylvatica* (Brand and Agerer 1986), *Cenococcum geophilum* + *Picea abies* (Gronbach 1988); *Byssocortium atrovirens* + *Fagus sylvatica* (Brand 1991), *Lactarius scrobiculatus* + *Picea abies* (Amiet and Egli 1991); *Phellodon niger* + *Picea abies* (Agerer 1992). The main macroscopic and microscopic features described for these mycorrhizal types were very similar to those identified for *A. alba*. This confirms previous observations of host-dependent variability of ectomycorrhizas formed by *Russula ochroleuca* (Pillukat and Agerer 1992). In fact, the features originating from the fungus were almost identical in all mycorrhizas, with only minor host-dependent differences (type of ramification, shape and dimensions of mycorrhizas, occurrence of tannin cells, shape and orientation of cortical cells, depth of the Hartig net) (Pillukat and Agerer 1992). As already stated, other mycorrhizal types have

been reported for silver fir, but the descriptions are in these cases too poor to allow matching with types encountered during our study.

Considerable help in the identification process for some types came from CLSM. The advantages offered by CLSM over more conventional microscopy techniques for visualizing diagnostic features of ectomycorrhizas have been explained previously (Schelkle et al. 1996). One characteristic of CLSM is that it requires bright fluorescence of the tissues or structures of interest. To overcome this problem, Schelkle and co-workers tested several fluorochromes for staining fungal tissues of ectomycorrhizas formed by four fungal species and found that the most effective stain was trypan blue.

Fig. 1 Morphological features of *Lactarius salmonicolor* mycorrhizas viewed with confocal laser scanning microscopy. **A** Cross section showing the bright autofluorescence of the latex (*arrows*), clearly observed both in the Hartig net (*hn*) and the mantle (*m*). **B** Surface view of the very tip mantle showing a rather loose plectenchymatous structure. **C** Inner view of the very tip mantle showing a more compact plectenchymatous structure. **D** Reconstructed three-dimensional image of laticifers (*arrow*), particularly abundant in the middle layer of the mantle, containing latex remnants (*double arrow*); bars 5 μm



However, the fluorescence activity of trypan blue strictly required fresh preparations and observations had to be made immediately following staining (Schelkle et al. 1996).

In the present study, we used CLSM to corroborate observations of ectomycorrhizas of *Lactarius* spp. made using conventional light microscopy and to help identify mycobionts at the species level. Given the relatively high autofluorescence of latex (Fig. 1A), no specific staining with a fluorochrome was necessary and fresh ectomycorrhizas were simply fixed on slides with polyvinyl lactophenol. Thus, this procedure for CLSM observation of mycorrhizas has the double advantage of being extremely rapid in the preparation of material and giving permanently fixed slides for future control and comparison; it is applicable to all those fungal species that possess laticifers (*Lactarius* spp.) or latex-containing cells (*Russula* spp.). In our experience, CLSM allowed the study of mantle structures through non-destructive and ultra-thin (less than 1 µm) optical sections, permitting the observation of the distinct mantle layers in the same x-y location but at different depths (Fig. 1B, C). At the same time, CLSM can reconstruct the separate optical sections to form three-dimensional images, thus helping the observation of such elements as laticifers (Fig. 1D).

The identifications of ectomycorrhizas on silver fir reported here is the result of a 2-year study of two stands. Additional morphological types may be encountered in different years and at different sampling sites, and new clues may be obtained to help correctly identify the types already known. Further studies are in progress in this direction.

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