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Exploration types of ectomycorrhizae

A proposal to classify ectomycorrhizal mycelial systems according to their patterns of differentiation and putative ecological importance

Abstract There is a need to quantify and qualify the ability of ectomycorrhizae to improve tree growth and nutrition and, in particular, to define criteria to classify ectomycorrhizae with respect to ecologically relevant features. Whereas the numbers of ectomycorrhizae and morphotypes give useful information when related to root biomass, root length or soil volume, the development and differentiation of the extramatrical mycelium may represent important predicative features relevant to the ecological classification of ectomycorrhizae. Here, different exploration types of ectomycorrhizae are distinguished based on the amount of emanating hyphae or the presence and differentiation of rhizomorphs. Their putative ecological importance is discussed.

Keywords Ecology · Ectomycorrhizae · Exploration types · Extramatrical mycelium · Rhizomorphs

Introduction

Ectomycorrhizae can differ in nutrient uptake and transfer capacities (Burgess et al. 1993) and in ability to promote tree growth (Burgess et al. 1994). This relates not only to the extent of root colonization but also to the development of hyphae in the soil (Colpaert et al. 1992; Thomson et al. 1994). The significance of mycelia in soils was highlighted for instance by Read (1992), who calculated a total hyphal length of 200 m per g dry soil for *Suillus bovinus* in forest soils of root chambers.

It is known since the work of Frank (1885) that ectomycorrhizae can differ greatly in their anatomy and this has been confirmed repeatedly (e.g. Agerer 1987–1998; Chilvers 1968; Fontana and Centrella 1967; Goodman et al. 1996–1999; Ingleby et al. 1990; Ogawa 1985;

Zak 1973). The extramatrical mycelia radiating into the soil and rhizomorph organization can vary considerably (Agerer 1987–1998, 1991a, 1995; Ogawa 1985; Raidl 1997; Schramm 1966; Zak 1973) and can spread in the soil over striking distances. For example, Schramm (1966) found rhizomorphs of *Pisolithus tinctorius* interconnecting *Pinus* seedlings over a distance of ca. 42 cm.

The function of extramatrical mycelia of ectomycorrhizae as transport structures has been well documented (Brownlee et al. 1983; Duddridge et al. 1980; Finlay and Read 1986; Read 1992; Skinner and Bowen 1974; Smith and Read 1997) and Kammerbauer et al. (1989) provided evidence of a relationship between the extent of rhizomorph organization and transport rates of phosphate therein. The ectomycorrhizal mantle itself does not have a large contact area with the soil, so that the emanating hyphae and rhizomorphs greatly increase the volume of exploited soil (Read 1992; Smith and Read 1997). However, when apparently smooth ectomycorrhizae formed by some *Lactarius* and *Russula* species are sandwiched between decomposing leaves (Brand 1991b), they can form a close contact with the nutrient source (Read 1992). In addition, emanating hyphae and rhizomorphs contribute to the colonization of newly formed roots (e.g. Allen 1991; Bowen 1994; Brundrett 1991; Cairney 1991; Fleming et al. 1984; Newton 1992; Read 1992; Schramm 1966).

As there is a great diversity of ectomycorrhizal structures, it is important to classify them with respect to their morphological and anatomical features (Meier 1991), especially with regard to emanating hyphae and rhizomorphs, since these may have putative ecological functions relevant to exploration of soil systems. A similar demand for defining functional groups of ectomycorrhizae has been published already by Newton (1992). He focused on whether rhizomorphs are formed to spread successfully in soil and on the question of replacing the terms "early-stage" and "late-stage" fungi.

Ectomycorrhizal fungi can explore the surrounding substrate by extramatrical mycelia which are either

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Fig. 1 Schematic drawings of different exploration strategies, represented by cross-sections of ectomycorrhizae and the extramatrical mycelium. *1* Contact exploration, *2* short-distance exploration, *3a, b* medium-distance fringe exploration and medium-distance mat exploration, *3c* medium-distance smooth exploration, *4* long-distance exploration, *5* pick-a-back exploration, shown as mycorrhiza and as soil hyphae in contact and intruding into rhizomorphs and ectomycorrhizae of a long-distance exploration type ectomycorrhiza. All figures are to scale (*Rh* rhizomorph, – rhizomorph lacking, A–F organization types of rhizomorphs according to Agerer 1987–1998, 1991a)
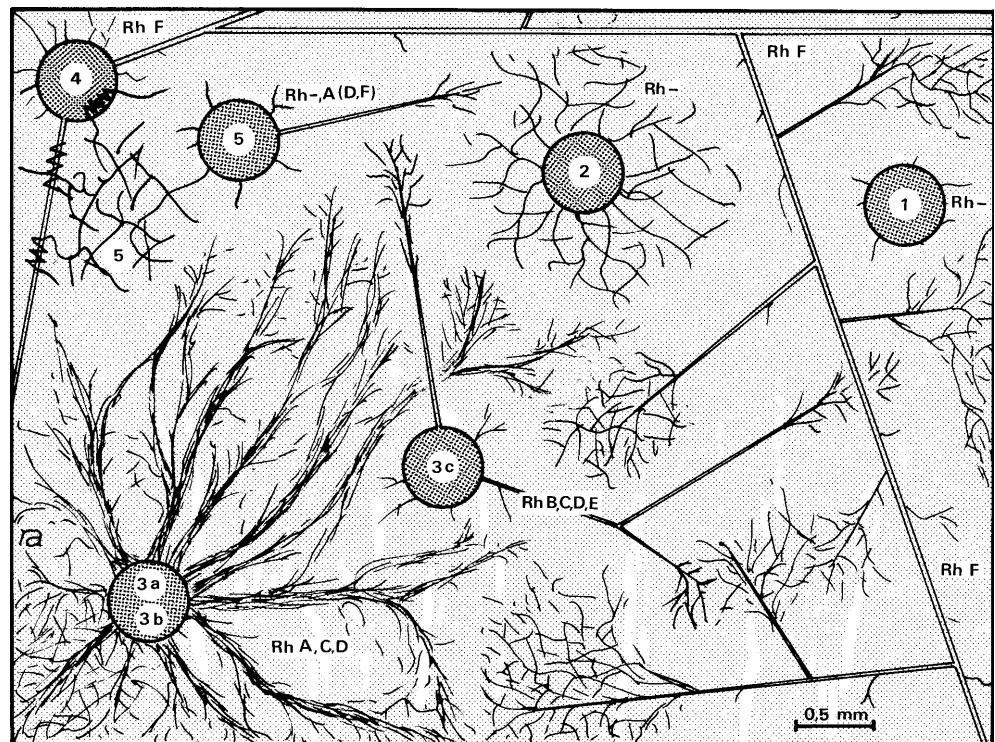
concentrated close to the mycorrhizal mantle or form far-reaching rhizomorphs (Figs. 1, 2). The distribution and differentiation of the mycelium can be used to distinguish so-called "exploration types", each of which may represent a distinct foraging strategy. The aim of the present contribution is to classify ectomycorrhizae into basic types with regard to their extramatrical mycelia in order to stimulate experimental analysis of the extent to which these are relevant to functional patterns of exploration and nutrient exploitation. The descriptions refer to selected fungal species so far studied.

Results and discussion

Contact exploration type

This type (Figs. 1, 2) is represented by ectomycorrhizae with a smooth mantle and only a few emanating hyphae. The ectomycorrhizal tips are often in close contact with the surrounding substrates (Brand 1991b) and emanating hyphae, where present, are in close contact with dead leaves.

Representatives of this group are ectomycorrhizae formed by the genera *Balsamia* (Palfner and Agerer 1998a), *Chroogomphus* (Agerer 1990), *Lactarius* pte. (e.g. Brand 1991a; Treu 1990a), *Leucangium* (Palfner and Agerer 1998b), *Russula* p. pte (e.g. Brand 1991a; Treu 1990a), *Tomentella* p. pte. (Danielson et al. 1984), and *Tuber* species with short cystidia (e.g. Rauscher et al. 1995; Zambonelli et al. 1995) (see also Agerer 1987–1998).

Short-distance exploration type

These ectomycorrhizae are characterized by a voluminous envelope of emanating hyphae, but rhizomorphs are not formed (Figs. 1, 2).

The most common fungal member of this group is *Cenococcum* (e.g. Ingleby et al. 1990). Further relationships to be included here are the majority of ascomycetous ectomycorrhizal species: *Elaphomyces* (Agerer 1999c; Brand 1991a; Haug and Pritsch 1992), *Genea* (Brand 1991a; Fontana and Centrella 1967; Jakucs et al. 1998), *Humaria* (Ingleby et al. 1990), *Sphaerosporella* (Danielson 1984), *Sphaerozone* (Brand 1991a), *Tricharina* (Ingleby et al. 1990), *Tuber* species with long cystidia (e.g. Rauscher et al. 1995; Zambonelli et al. 1995), and the basidiomycetous genera *Byssocorticium* (Brand 1991a), *Descolea* (Palfner 1997), *Hebeloma* (Treu 1990a), *Inocybe* (e.g. Beenken and Agerer 1996; Ingleby et al. 1990), *Rozites* (Agerer 1999a), *Tomentella* p. pte. (Agerer 1996a), and *Tylospora* (Haug and Pritsch 1992; Raidl 1997) (see also Agerer 1987–1998).

Medium-distance exploration type

The ectomycorrhizae of this exploration type form rhizomorphs and can be divided into three subtypes with respect to their rhizomorphal features (Figs. 1, 2).

Fringe subtype

In this subtype, the fungi often form fans of emanating hyphae and rhizomorphs which ramify and interconnect

Fig. 2 Examples of exploration strategies. *1 Lactarius* sp.: contact exploration, *2 "Quercirhiza squamosa"*: short-distance exploration, *3a Dermocybe cinnamomeolutea*: medium-distance fringe exploration, *3b Hysterangium stoloniferum*: medium-distance mat exploration, *3c Thelephora terrestris*: medium-distance smooth exploration, *4 Boletinus cavipes*: long-distance exploration, monopodial ectomycorrhizal system, *4' Suillus plorans*: long-distance exploration, tuberculate mycorrhizal system, *5 Chroogomphus helveticus* ssp. *tatrensis* primordium growing on a rhizomorph of *Rhizopogon* sp.: pick-a-back exploration, *5' Chroogomphus helveticus* ssp. *tatrensis* hyphae (stained blue with Melzer's reagent) in ectomycorrhiza of *Rhizopogon* sp.: pick-a-back exploration; *bars 1, 2, 3a, c, 4* 1 mm, *3b* 10 mm, *4', 5* 5 mm, *5'* 30 μm
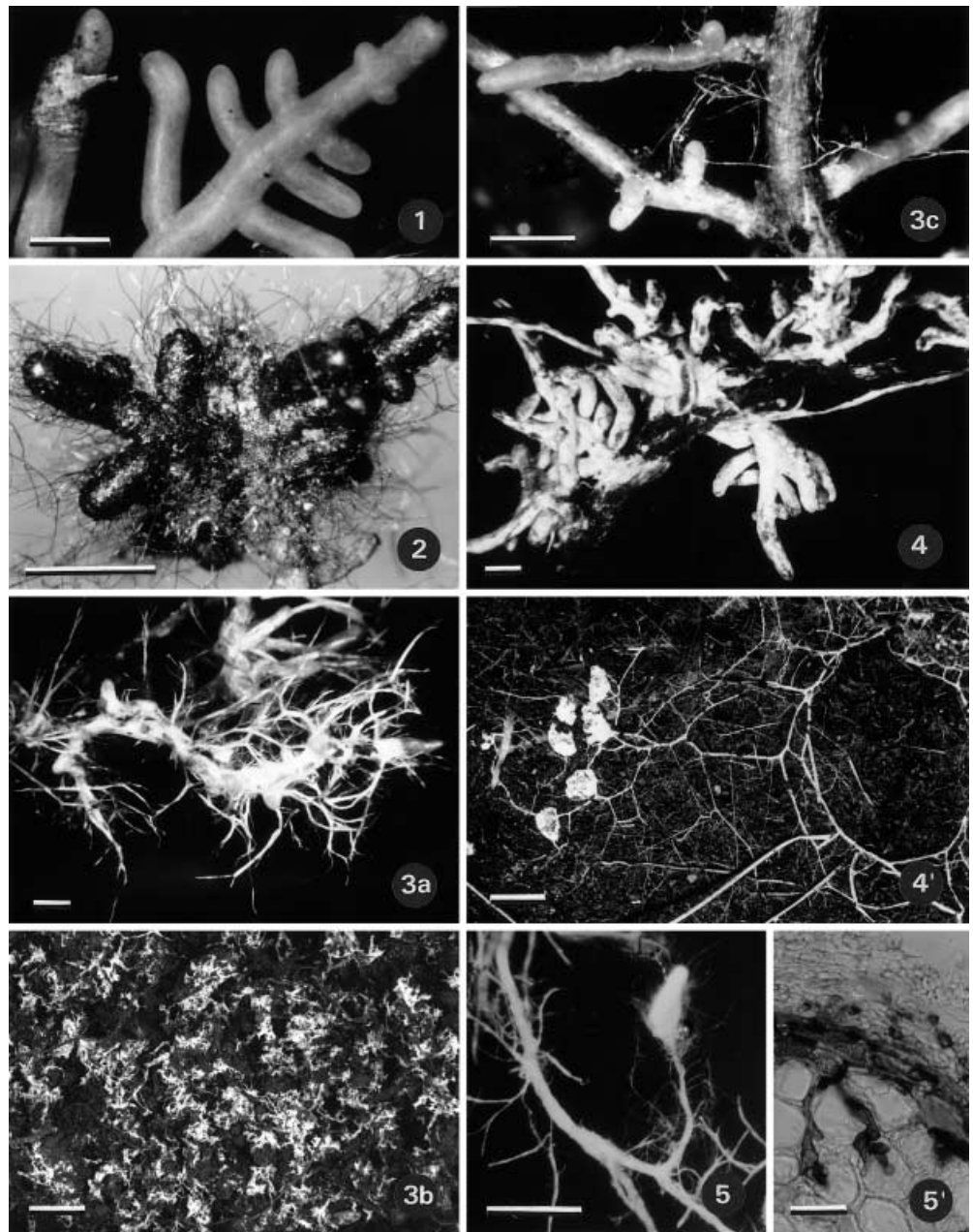
repeatedly. Frequently, rhizomorph surfaces are hairy and they form emanating hyphae with extended contact to the soil. The rhizomorphs are of organization type A (according to Agerer 1987–1998; uniform-loose according to Agerer 1999d) and, exceptionally, of type C, D (according to Agerer 1987–1998; thelephoroid, ramarioid, and phlegmacioid type, respectively, according to Agerer 1999d).

This category also includes ectomycorrhizal fungi of the genera *Amphinema* (e.g. Ingleby et al. 1990), *Dermocybe* (e.g. Uhl and Agerer 1987), *Cortinarius* (e.g. Egli 1992; Godbout and Fortin 1985; Gronbach 1988), *Entoloma* (Agerer 1997), *Laccaria* (Brand 1991a; Raidl 1997), *Lyophyllum* (Agerer and Beenken 1998b), *Pilo-*derma (Brand 1991c), and *Tricholoma* p. pte (e.g. Agerer 1987; Uhl 1988) (see also Agerer 1987–1998).

Mat subtype

Although mat-forming fungi can typically occupy large areas (Cromack et al. 1979), the individual mycorrhizae have only a rather limited range of exploration and their rhizomorphs are undifferentiated or, at most, slightly differentiated of types A, C and, exceptionally, D.

Known mat-forming genera are *Bankera* (Agerer and Otto 1997), *Boletopsis* (Agerer 1992a), *Gautieria* (Griffiths et al. 1991), *Geastrum* (Agerer and Beenken

1998b), *Gomphus* (Agerer et al. 1998b), *Hydnellum* (Agerer 1993), *Hysterangium* (e.g. Cromack et al. 1979; Müller and Agerer 1996), *Phellodon* (Agerer 1992b), *Piloderma* (e.g. Agerer, unpublished observation), *Ramaria* (e.g. Agerer 1996b), and *Sarcodon* (Agerer 1991c) (see also Agerer 1987–1998).

Smooth subtype

All rhizomorphs are internally undifferentiated, slightly differentiated or, very infrequently, with a central core of thick hyphae. Ectomycorrhizal mantles appear rather smooth with almost no or only a few emanating hyphae. Rhizomorphs belong to the types B (according to Agerer 1987–1998; uniform-compact according to Agerer 1999d), C and D. Exceptionally rhizomorphs are formed of type E (according to Agerer 1987–1998; russuloid rhizomorph type according to Agerer 1999d).

This subtype is formed at least by some species of *Albatrellus* (Agerer et al. 1996a), *Amanita* (Ingleby et al. 1990), *Gomphidius* (Agerer 1991b), *Lactarius* p. pte. (Brand 1991a; Godbout and Fortin 1985), *Polyporoletus* (Agerer et al. 1998a), *Thaxterogaster* (Palfner 1996), *Thelephora* (e.g. Agerer and Weiss 1989; Ingleby et al. 1990; Schramm 1966), *Tomentella* p. pte. (Raidl and Müller 1996), and *Tricholoma* p. pte (Raidl 1997; Uhl 1988) (see also Agerer 1987–1998).

Long-distance exploration type

This type (Figs. 1, 2) is characterized by rather smooth ectomycorrhizae with few but highly differentiated rhizomorphs of type F (according to Agerer 1991a, 1995, 1987–1998; boletoid rhizomorph type according to Agerer 1999d).

Examples of this group are the genera *Boletinus* (Treu 1990a), *Boletus* (e.g. Giovanetti and Fontana 1985; Gronbach 1988), *Chamonixia* (Raidl 1999), *Gyrodon* (Agerer et al. 1993), *Gyroporus* (Agerer 1999b), *Leccinum* (e.g. Fox 1987; Müller and Agerer 1990), *Paxillus* (e.g. Gronbach 1988), *Pisolithus* (e.g. Watling et al. 1995), *Rhizopogon* (e.g. Agerer et al. 1996b), *Scleroderma* (e.g. Waller et al. 1993), *Suillus* (e.g. Samson and Fortin 1988; Treu 1990a), *Tricholoma* p. pte. (Waller and Agerer 1993), *Tylopilus* (Uhl 1988), and *Xerocomus* (e.g. Brand 1989a, b; Palfner and Agerer 1995) (see also Agerer 1987–1998). This type of rhizomorph shows the greatest range of length. It spreads in the soil up to several decimetres (Raidl 1997; Schramm 1966; Skinner and Bowen 1974).

Ectomycorrhizae belonging to this type can be sparsely monopodially branched, like *Pisolithus tinctorius* (Mich.: Pers.) Coker & Couch on *Picea abies* (L.) Karst. (Weiss 1992), coralloid as for *Rhizopogon subcaerulescens* A. H. Smith on *Tsuga heterophylla* (Rafin.) Sarg. (Agerer et al. 1996b) and tuberculate like *Suillus plorans* (Roll.) Sing. on *Pinus cembra* L. (Treu 1990a, b).

Pick-a-back exploration type

This type (Figs. 1, 2) is typically formed by members of the Gomphidiaceae (Agerer 1990, 1991b, 1996c; Olsson et al. 2000). Although *Gomphidius* and *Chroogomphus* species form typical ectomycorrhizae, they can grow within rhizomorphs and/or mantles of *Suillus* and *Rhizopogon* ectomycorrhizae. They can become ectendomycorrhizal, often producing haustoria in the cortical cells of the root, in association with other ectomycorrhizae. They form typical ectomycorrhizae of the contact exploration type or the smooth subtype of the medium-distance exploration type. *Boletopsis leucomelaena* (Pers.: Pers.) Fayod has type D rhizomorphs and was reported to form haustoria in an unidentified ectomycorrhiza (Agerer 1992a). A similar situation without formation of haustoria has been found in the ectomycorrhizal fungus (according to Richter and Bruhn 1989) *Xerocomus parasiticus* (Bull.: Fr.) Quél. Raidl (1997) reported hyphae of *X. parasiticus*, possibly with type F rhizomorphs, to ramify repeatedly in contact with rhizomorphal hyphae of *Scleroderma citrinum* Pers.

Main differences between the exploration types
with respect to their possible ecological roles

There clearly exists a wide range of potential exploration strategies in ectomycorrhizae extending from the contact-exploration to the long-distance exploration types (Raidl 1997; Schramm 1966; Skinner and Bowen 1974). The distal ends of rhizomorphs frequently develop distinct fan-like structures (Raidl 1997; Read et al. 1985; Unestam and Sun 1995).

The extent of structural differentiation of the mycelia and their rhizomorphs could be of functional relevance. At one extreme, the surface area of the mantle or a few short hyphae provide contact exploration with the substrate, while at the other extreme, highly differentiated F-type rhizomorphs, producing vessel-like hyphae with partially or completely dissolved septa, could be relevant to long-distance exploration (Agerer 1988, 1991d; Brand 1989a; Brownlee et al. 1983). It can be hypothesized that loss of cross walls diminishes flow resistance of solutions, as in the vessels of angiosperms (Brownlee et al. 1983). Efficient water transport has been shown in F-type rhizomorphs of *Suillus bovinus* (L.: Fr.) O. Kuntze (Brownlee et al. 1983) and higher transport rates of phosphate have been observed in *S. bovinus* rhizomorphs than in the slightly differentiated C-type rhizomorphs of *Thelephora terrestris* Pers. (Kammerbauer et al. 1989). There appears to be a relationship between distance and the internal differentiation of rhizomorphs, the farthest-reaching types being the most differentiated (Fig. 1; Raidl 1997).

The distribution of hyphal biomass is also different in each type. In the contact exploration type, hyphae are concentrated in the mantle. Such hyphal distribution is also evident during ectomycorrhiza ontogeny in that a

long-distance exploration type commences its development with a short-distance type (Raidl 1997; Smith and Read 1997). Fungi of the pick-a-back exploration type have access to the fungal mantle and the rhizomorphs of the other fungi and even to the root cells (Agerer 1990, 1991b, 1992c, 1996c; Olsson et al. 2000; Raidl 1997). All the ectomycorrhizae exploited by pick-a-back fungi possess rhizomorphs of the most advanced F-type. Fruitbodies of these fungi can even form directly on foreign rhizomorphs, as can be seen in *Chroogomphus helveticus* (Sing.) Mos. ssp. *tatrensis* (Pilat) Kuth. & Sing. on *Rhizopogon* sp. (Fig. 2; Agerer 1990; Agerer and Rambold 1998) and in *Xerocomus parasiticus* on *Scleroderma citrinum* rhizomorphs (Engel et al. 1996). It may be that this behaviour enables such fungi to get better access to carbohydrates in the host roots or in the colonized ectomycorrhizal fungus.

A special situation occurs in tuberculate ectomycorrhizae. Densely branched and packed ectomycorrhizal tips are enveloped by a common sheath (Goodman 1996; Trappe 1965; Treu 1990b), similar to the peridial layer of a hypogeous fungus (Trappe 1965). Smith and Read (1997) pointed out a distinct compartment of function in such systems.

It has been suggested that acquisition and transport are performed exclusively by the fungal mycelium in the soil, especially by the most distal parts of rhizomorphal hyphae (cf. Raidl 1997; Unestam and Sun 1995), while the mantle is in fact an "outwardly sealed compartment solely involved with storage and exchange between the symbionts" (Smith and Read 1997).

Possible ecophysiological differences of extramatrical mycelium: hints for functional evidence of distinct exploration types

Regardless of the exploration type of an ectomycorrhiza, its most distant hyphae are on average much thinner than other hyphae of the mycelium and often have substrate particles glued to their surfaces (Raidl 1997). These hyphae, called "substrate adhesion hyphae" by Raidl (1997) or "exploiting hyphae" by Unestam and Sun (1995), appear to be hydrophilic (Raidl 1997; Unestam and Sun 1995) and are most likely responsible for the uptake of water and nutrients (Cairney and Burke 1996). The proximal parts of hyphae and rhizomorphs are relatively hydrophobic (Unestam and Sun 1995). Therefore, the formation of rhizomorphs will shift the zone of uptake from the direct vicinity of the mycorrhiza to more remote areas (Unestam and Sun 1995).

In a recent study on the production of oxidases of ectomycorrhizal fungi using highly turgescent, young and viable fruitbody explants, Agerer et al. (2000) found an evident correlation between fungal relationship, production of phenoloxidases and exploration type of their ectomycorrhizae.

Under the given experimental design, all *Lactarius* and *Russula* species revealed a high ability to produce extracellular phenoloxidases. Almost all members of the order Boletales lacked this feature. This correlates well with the exploration type of their ectomycorrhizae. Most species of the genera *Russula* and *Lactarius* belong to the contact exploration type, only some *Lactarius* species to the medium-distance smooth exploration type. The ectomycorrhizae of both genera are mostly hydrophilic and this is crucial for successfully exploring the substrate in their close vicinity. The ability to degrade lignin should increase access to nitrogen complexed to phenolic substances (Kuiters 1990) and could, therefore, support nutrient acquisition when squeezed between organic substrates. The Boletales, however, are all known to form ectomycorrhizae of the long-distance exploration type (Agerer 1999d, with the exception of Gomphidiaceae) and are hydrophobic at their proximal parts. Nutrient acquisition appears to be limited to the very distant hydrophilic substrate adhesion hyphae (Raidl 1997; Unestam and Sun 1995). A larger surface area and a greater range of spread (Raidl 1997) could, therefore, compensate for the lack of lignin degradation ability.

Laccaria species, possibly ascribable to the medium- or short-distance exploration type and generally hydrophilic, consistently produce extracellular phenoloxidases. However, the capacity to produce extracellular phenoloxidases was not generally related to the type of exploration. The genus *Dermocybe*, for example, with its medium-distance fringe exploration type, lacks phenoloxidases. Species- and strain-specific differences were apparent in other genera (Agerer et al. 2000).

Conclusions

Although differences in ectomycorrhizal effectiveness for tree growth and tree nutrition are often species specific (e.g. Dell et al. 1994) or even strain specific (e.g. Burgess et al. 1994; Dell et al. 1994), it is evident that the amount and differentiation of the extramatrical mycelium (Kammerbauer et al. 1988; Rousseau et al. 1992) is a very important ecological factor for tree performance, apart from the abundance of ectomycorrhizae (Thomson et al. 1994). The extramatrical mycelium is a sink for tree carbohydrates transferred to the root system (Cairney and Burke 1996; Rygiewicz and Andersen 1994; Söderström 1992) on the one hand but is also an important extension of the root system (Duddridge et al. 1980).

The distinction of exploration types might help to categorize ectomycorrhizae with respect to their ecophysiological effectivity, as limited evidence is available that this indicates functional differences. A few examples in addition to those above may underline this hypothesis.

Thelephora terrestris, a representative of the medium-distance smooth exploration type, reduced concentrations of nitrogen, phosphorus and potassium in a fermentation horizon organic matter to a considerably lower degree than *Suillus bovinus*, a representative of the long-distance exploration type (Bending and Read 1995).

Rousseau et al. (1994) studied the potential absorbing system area and the absorbing length of the extramatrical mycelium of *Pisolithus tinctorius* (Pers.) Coker & Couch (long-distance exploration type) and *Cenococcum geophilum* (short-distance exploration type) ectomycorrhizae. *Pisolithus tinctorius* was shown to produce 1.5 times the mycelial absorbing surface area and 3 times the mycelial length of *C. geophilum* Fr. It was concluded that the differences in these two values accounted for differences in P uptake.

Rousseau et al. (1992) obtained evidence that the amount of *Pisolithus tinctorius* mycelium (that of ectomycorrhizae including emanating elements) is strongly correlated with P nutrition of the seedlings. Although this study considers only different mycelial masses of the whole root system of only one species, it indicates that mycelial differences in exploration type may play a role in ecophysiology.

Pisolithus tinctorius and *Scleroderma verrucosum* (Vail.) Pers. on *Eucalyptus globulus* with long-distance exploration type ectomycorrhizae revealed a higher growth increase at least in a homogenized, sterile mineral soil than some species with a medium-distance smooth exploration type, for example *Hydnangium carneum* Wallr. & Dietr. (Burgess et al. 1993). But there were also species-specific differences unrelated to the exploration type of ectomycorrhizae. *Descolea maculata* Bougher & Malajczuk forming short-distance exploration type ectomycorrhizae appears to be as efficient as *S. verrucosum*. Strain-specific differences were evident in *Laccaria laccata* (Scop.: Fr.) Berk. *Eucalyptus* species-specific differences also occurred (Burgess et al. 1993). It would be interesting to test the performance of these ectomycorrhizae in natural soil.

Although the final structure of the extramatrical mycelium may indicate ecological specialization of the whole system, nothing is actually known about the internal physiological heterogeneity, which according to Cairney and Burke (1996) is a genuine feature of such dynamic systems with differential changes in gene expression. This biological feature might again influence the impact of the exploration types on plant growth and nutrition.

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