11 Ectendomycorrhizas: Occurrence, Structural Characteristics, and Possible Roles

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CONTENTS

I. Introduction

Plants interact with a diverse assemblage of soil fungi, some of which colonize roots to form mycorrhizas. Mycorrhizas have traditionally been categorized partially on the identity of the fungal partner(s) but mainly on the modifications of these fungi and their associated roots that lead to the distinct mature structure (Brundrett 2004; Peterson and Massicotte 2004; Smith and Read 2008). **Ectendomycorrhiza**, one of approximately seven currently recognized mycorrhiza categories (Peterson et al. 2004; Smith and Read 2008), has been defined either broadly (Smith and Read 2008) or narrowly (Yu et al. 2001; Peterson et al. 2004). The **broad classification** includes arbutoid mycorrhizas that are characteristic of several genera in the large family, Ericaceae (Smith and Read 2008). The **narrow view** confines the term ectendomycorrhizas to specialized associations that form primarily with two conifer genera, *Pinus* and *Larix*, and a limited number of ascomycete fungal species (Yu et al. 2001). Yu et al. (2001) summarized the *Pinus* and *Larix* species as well as several angiosperm species that have been reported to have ectendomycorrhizas. They pointed out, however, that the evidence for some of these reports is not particularly strong because observations were based on field-collected material of unknown age and the fungal symbionts were not identified.

There has been debate as to whether ectendomycorrhiza should be considered a separate category or a developmental phase or evolutionary stage of ectomycorrhizas (Egger and Fortin 1988). More recently, Brundrett (2004) argued that since ectendomycorrhizas do not occur in a distinct and separate plant lineage, they should be considered as a 'fungal morphotype' included within the category, ectomycorrhiza. The examination of root systems and their associated symbiotic fungi of plant species in parts of the world that until now have been poorly studied may lead to a reassessment, not only of the category, ectendomycorrhiza, but also of other categories of mycorrhizas.

Beck et al. (2005) have used the term to describe the morphological features of mycorrhizas formed by two members of the Glomeromycota with the tropical tree species (*Alzatea verticillata*). The evidence cited for designating the mycorrhiza as an ectendomycorrhiza is the occurrence of highly branched intercellular hyphae resembling Hartig net hyphae in ectomycorrhizas as well as the presence of intracellular structures, in this case typical arbuscules.

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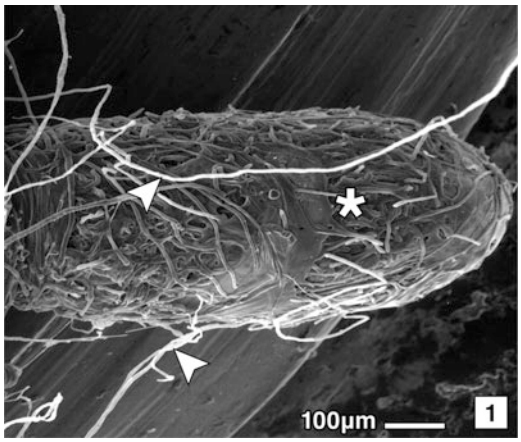

Fig. 11.1. Scanning electron microscopy image of a *Pinus banksiana* monopodial short root colonized by *Wilcoxina mikolae* var. *mikolae*. The mantle (*) consists of loosely arranged hyphae. A few extraradical hyphae (*arrowheads*) are present

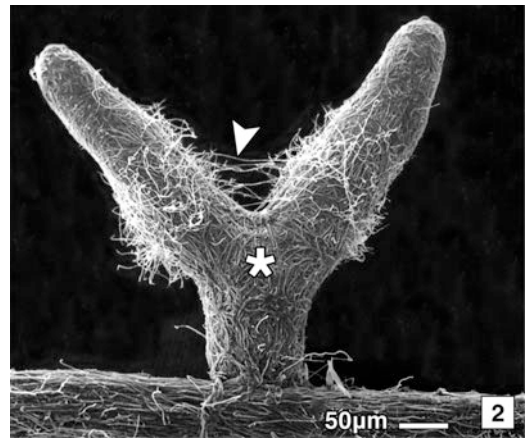

Fig. 11.2. Scanning electron microscopy image of a *Pinus banksiana* dichotomous short root colonized by *Wilcoxina mikolae* var. *mikolae*. The mantle (*) consists of loosely arranged hyphae. A few extraradical hyphae (*arrowhead*) are present

In this chapter, ectendomycorrhizas will be considered from a narrow perspective keeping in mind that, with new evidence, this category may not be maintained (Brundrett 2004) or may be expanded to include a broader range of plant species and fungal symbionts. Arbutoid mycorrhizas and similar mycorrhizas of members of the Ericaceae (see Setaro et al. 2006) will not be discussed in this chapter since they are covered elsewhere in this volume.

II. Structural Characteristics of Ectendomycorrhizas

The short roots of pine species colonized by ectendomycorrhizal fungal species are usually monopodial (Fig. 11.1) but dichotomies may occur (Fig. 11.2). **Ectendomycorrhizas share two important characteristics with ectomycorrhizas**: a **fungal mantle** and **Hartig net**. The mantle, however, may be poorly developed (Figs. 11.1, 11.2, 11.3) or in some cases absent (Smith and Read 2008). The mantle of an E-strain fungal species associated with *Pinus strobus* has been described, using laser scanning confocal microscopy, as a loosely organized net prosenchyma (Schelkle et al. 1996). Mantle hyphae are frequently embedded in surface mucigel (Scales and Peterson 1991b; Fig. 11.3). Hartig net hyphae develop between the epidermal and cortical cells in *Pinus* spp. (Mikola 1965; Wilcox 1969; Wilcox and Ganmore-Neumann 1974; Piché et al. 1986; Ivory and Pearce 1991; Scales and Peterson 1991a; Ursic and Peterson 1997; Peterson et al. 2004; Figs. 11.3 and 11.4) and in *Larix occidentalis* (Laiho 1965). An additional feature, **intracellular hyphae within root epidermal and cortical cells**, distinguishes ectendomycorrhizas from typical ectomycorrhizas (Yu et al. 2001; Peterson and Massicotte 2004; Smith and Read 2008; Figs. 11.3 and 11.4). These hyphae are formed by the ingress of Hartig net hyphae through epidermal and cortical cell walls and, once within these cells, the hyphal diameter increases substantially (Piché et al. 1986; Scales and Peterson 1991a; Figs. 11.4 and 11.5). **Ultrastructural details** of the intracellular hyphae of *Wilcoxina mikolae* var. *mikolae* within *Pinus banksiana* root cells close to the apical meristem showed that they are rich in cytoplasmic organelles and are separated from host cell cytoplasm by the development of a host-derived plasma membrane and interfacial matrix material (Scales and Peterson 1991a; Fig. 11.6). The nature of the matrix material

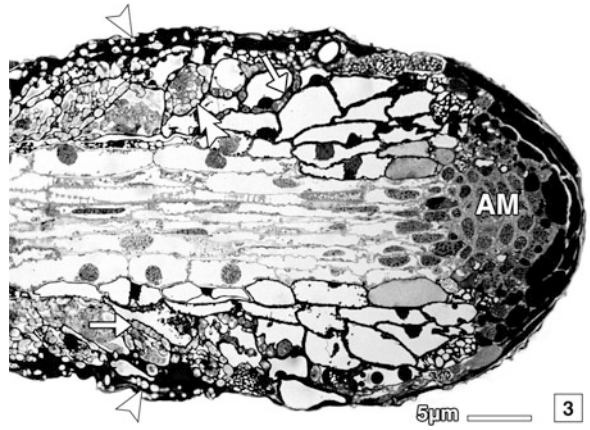

Fig. 11.3. Light microscopy of a longitudinal section of a monopodial short root of *Pinus resinosa* colonized by *Wilcoxina mikolae* var. *mikolae*. Mantle hyphae (*arrowheads*) are embedded in mucilage. Hartig net hyphae (*arrows*) and intracellular hyphae (*double arrowhead*) are present. Colonization has occurred close to the root apical meristem (*AM*)

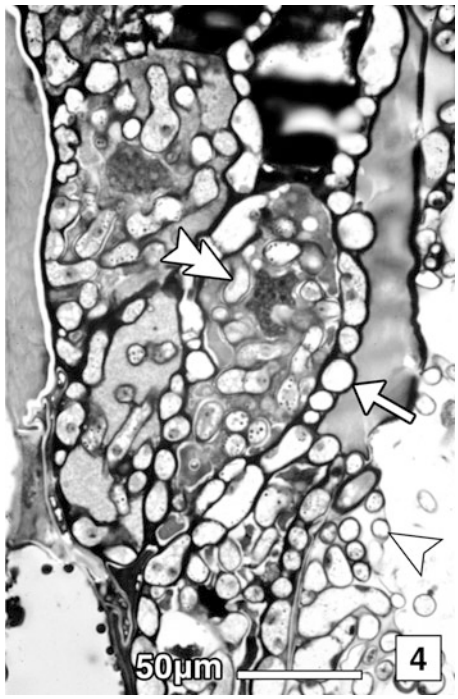

Fig. 11.4. Light microscopy of a longitudinal section of a monopodial short root of *Pinus resinosa* colonized by *Wilcoxina mikolae* var. *mikolae*. Few mantle hyphae (*arrowhead*), Hartig net hyphae (*arrow*) and intracellular hyphae (*double arrowhead*) are evident

has not been determined but its presence, along with the host-derived plasma membrane, suggests that intracellular hyphae may play a role in nutrient exchange between the symbionts; this has not been shown experimentally. Microtubules are closely associated with the intracellular hyphae and these may be involved in the formation of the interface between the symbionts (Kuga-Uetake et al. 2004).

The same isolate of *W. mikolae* var. *mikolae* that forms ectendomycorrrhizas with *P. banksiana* (Scales and Peterson 1991a) forms typical ectomycorrhizas with *Picea mariana* and *Betula alleghaniensis* (Scales and Peterson 1991b), indicating the importance of the host genome in the type of mycorrhiza formed. Similar results were reported previously with other E-strain fungi (Laiho 1965) and these observations led Molina et al. (1992) to conclude that ectendomycorrhizal fungi show broad host range responses with species in which ectomycorrhizas typically form but intermediate specificity with *Pinus* and *Larix* species in which ectendomycorrhizas form. This observation was confirmed experimentally by Massicotte et al. (1999) by growing seedlings of three conifer species (*Abies grandis*, *Pseudotsuga menziesii*, *Pinus ponderosa*) and two angiosperm species (*Lithocarpus densiflora*, *Arbutus menziesii*) in soil collected from three forest sites in southwestern Oregon, United States. The authors suggested that one of the morphotypes formed on all species was consistent with descriptions of that formed by *W. mikolae*.

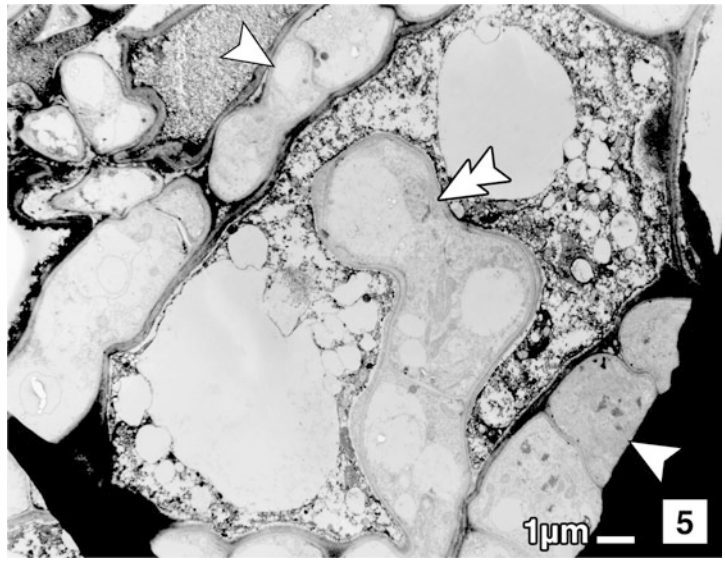

Fig. 11.5. Transmission electron micrograph of cortical cells in of a *Pinus banksiana* short root colonized by *Wilcoxina mikolae* var. *mikolae* showing Hartig net hyphae (*arrowheads*) and an enlarged intracellular hypha (*double arrowhead*)

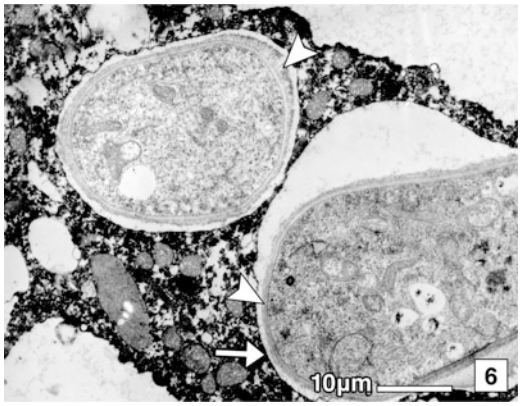

Fig. 11.6. Transmission electron micrograph of a cortical cell in a *Pinus banksiana* short root colonized by *Wilcoxina mikolae* var. *mikolae* showing enlarged intracellular hyphae each surrounded by interfacial material (*arrowheads*) and a host-derived plasma membrane (*arrow*). Some plasmolysis has occurred during fixation

III. Fungal Species Involved

A. Systematics

A detailed discussion of the history of the classification of fungi reported to be involved in the formation of ectendomycorrhizas can be found in Yu et al. (2001). Many of the early studies identified the fungi based on morphological characteristics either of sterile hyphae of isolates cultured from roots of various gymnosperm species or from soil-borne mycelium (e.g. Wilcox et al. 1974; Danielson 1982). These fungi comprised a number of problematic taxonomic isolates that were originally placed into a broad group, 'E-strain' fungi (Laiho and Mikola 1964). They were determined to be ascomycetes based on diagnostic features of hyphae, including the presence of Woronin bodies and regular septation (Danielson 1982). Later studies (Egger and Fortin 1990; Egger et al. 1991) comparing poymorphisms in nuclear and mitochondrial rRNA genes, placed most of the E-strain fungi into two species *W. mikolae* and *W. rehmii* in the ascomycete order Pezizales. Sequence analysis of *W. mikolae* identified two varieties *W. mikolae* var. *mikolae* and var. *tetraspora* (Egger 1996).

Other fungal species that are known to form ectendomycorrhizas under some conditions include *Phialophora finlandia* and *Chloridium paucisporum* (Wang and Wilcox 1985; Wilcox and Wang 1987a, b). In a study of the colonization of *Pinus contorta* (lodgepole pine) roots by a number of post-fire

ascomycetes in the Pezizales, Egger and Paden (1986) found that one species, *Sphaerosporella brunnea* formed typical ectendomycorrhizas. This was confirmed for this host species as well as for *P. banksiana* (Jack pine; Iwanyzki 1992). The mycorrhizal status of *S. brunnea* may, however, vary depending on the host species and conditions during mycorrhiza formation (Danielson 1984).

B. Physiology

Physiological aspects of ectendomycorrhizal fungi have not been studied to the same extent as ectomycorrhizal fungi. Mikola (1965) determined the **carbon, nitrogen, and pH requirements** for a number of E-strain isolates from pine and observed that none could use cellulose as a carbon source. However, Caldwell et al. (2000) found that an isolate of *Phialophora finlandia*, when grown in vitro, utilized cellulose, laminarin, starch, and xylan as a carbon source. This isolate also was capable of hydrolyzing protein, ribonucleic acids, and a fatty acid ester. Redlak et al. (2001) found that *Wilcoxina* spp. produced cellulolytic, pectolytic, proteolytic and chitinolytic activity in culture medium but at very low levels. Phenolic compounds had various effects on enzyme production in three ectendomycorrhizal fungal species; this depended on the particular phenolic compound and the enzyme being assayed (Dahm and Redlak 2000). For example, there was no effect on the production of β-glucosidases or pectolytic enzymes by any of the phenolic compounds but endocellulases were inhibited. It is not clear how these results relate to the colonization of roots by ectendomycorrhizal fungi.

Sphaerosporella brunnea is able to hydrolyze complex compounds such as gelatin, cellulose, oil, and pectins, depending on the pH of the medium (Egger 1986). It is not known whether carbon compounds resulting from the breakdown of complex organic compounds could be transported to host roots under certain conditions.

Martin et al. (1988), using ^{13}C-labeled glucose, found evidence for a direct pathway from glucose to mannitol, the main carbohydrate reserve substance in *S. brunnea*, as well as evidence for a lesser accumulation of glycogen and trehalose. In addition, as much as 40% of the ^{13}C-labeled glucose ended up in the free amino acid pools in mycelium.

Ectendomycorrhizal fungi, like other mycorrhizal symbionts, are likely to **benefit plant species by the increased uptake of various nutrients from the substrate**. Mycorrhizal fungi have access to inorganic and organic nitrogen sources in various ecosystems (Smith and Read 2008), an important feature since nitrogen is often limiting to plant growth in many of these ecosystems. Rudawska et al. (1994) confirmed that the ectendomycorrhizal fungal isolate MrgX obtained originally from roots of *Pinus sylvestris* (Pachlewski 1983), grew on medium with ammonium as the source of nitrogen and that this fungus possessed ammonium assimilation enzymes with the glutamine synthetase (GS-GOGAT) pathway being the most important. Prabhu et al. (1995) provided the first evidence for the presence of a NADPH-specific nitrate reductase which catalyzes the first step in nitrate assimilation, in an ectendomycorrhizal ascomycete fungal species, *W. mikolae* var. *mikolae*. By using urea, a neutral nitrogen source, in the culture medium Prabhu et al. (1996a) showed that this enzyme was induced by nitrate and repressed by ammonium.

Two isolates of *W. mikolae* and one of *W. rehmii* were shown to produce the siderophore, ferricrocin (Prabhu et al. 1996b). Siderophores act as chelating agents solubilizing ferric iron and therefore increasing iron absorption by mycorrhizal plants (Haselwandter 1995).

The ectendomycorrhizal fungal isolate MrgX is capable of synthesizing a number of indole compounds (Rudawska et al. 1992). Of these, indole-3-acetic acid (auxin) and indole-3-carboxyl acid are produced in the greatest amounts.

IV. Factors Affecting Mycorrhiza Formation

Temperature has been shown to **affect growth of E-strain fungal isolates** in culture with isolates from northern United States growing

better at 20 °C and isolates from southern United States growing better at 24 °C (Wilcox et al. 1983). Northern isolates showed some growth at 4 °C but southern isolates failed to grow at this temperature. Northern isolates formed ectendomycorrhizas with *Pinus resinosa* whereas a southern isolate formed ectomycorrhizas with the same pine species (Wilcox et al. 1983).

Exposure of *P. halepensis* to the **atmospheric pollutants**, ozone and sulfur dioxide in combination, resulted in a decrease in the percentage of mycorrhizal colonization and a change in the morphological appearance of mycorrhizas, with fewer coralloid morphotypes and more simple morphotypes formed (Díaz et al. 1996). Although the fungal symbionts were not identified, structural features of the latter morphotype included a thin mantle, Hartig net hyphae, and intracellular hyphae, typical of ectendomycorrhizas.

Pine nurseries are frequently treated with **herbicides** as a weed control measure and, in a *P. resinosa* nursery in Victoria, Australia, two herbicides, propazine and chlorthal dimethyl are widely used (Marks and Becker 1990). These authors showed that both herbicides suppressed mycorrhiza formation in greenhouse experiments and that in both control and herbicide treatments only two unidentified morphotypes formed, an ectomycorrhiza and an ectendomycorrhiza. The ratio of the ectomycorrhiza morphotype to the ectendomycorrhiza morphotype was reduced in both herbicide treatments. The structure of the ectendomycorrhiza morphotype was modified in the chlorthal dimethyl treatment with only the development of a Hartig net without an evident mantle or intracellular hyphae.

Pathogenic fungi are often problematic in conifer nurseries leading to the use of various **fungicides** to minimize seedling loss. The effect of two fungicides, benomyl and oxine benzoate, on mycelial growth of four ectendomycorrhizal fungal species was studied by Chakravarty et al. (1990). Treatments with both fungicides at 50 ppm and above significantly reduced mycelial growth, indicating that the much higher recommended field rates of both fungicides are likely detrimental to these fungi in nurseries.

There is increasing evidence that the mycorrhizosphere and the hyphosphere host a variety of bacteria (Bending et al. 2006; Smith and Read 2008), some of which have been designated as **'mycorrhiza helper bacteria'** since they have a positive effect on the formation of ectomycorrhizas (Garbaye 1994). Bending et al. (2006) provide a thorough discussion of the diverse interactions that occur between bacteria and the two most prevalent mycorrhizas: ectomycorrhizas and arbuscular mycorrhizas. Research on interactions between bacteria and ectendomycorrhizal fungi is limited. Chanway and Holl (1991) determined the effect of a plant growth promoting *Bacillus* isolate, either alone or in combination with *W. mikolae*, on the growth and nutrient status of *P. contorta* seedlings. Treatment with *Bacillus* alone had no effect on shoot and root biomass or total leaf nitrogen content, whereas treatment with *W. mikolae* alone reduced shoot biomass and total leaf nitrogen content. Inoculation with both resulted in higher root and shoot biomass but lower foliar nitrogen content compared with controls.

Chitinase genes have been **inserted into a number of plant species** in attempts to increase their resistance to pathogenic fungi. The endochitinase gene ech-42 has been transferred into *Picea glauca* (white spruce) and subsequently the transformed seedlings were shown to be more resistant to the root fungal pathogen *Cylindrocladium floridanum* than controls (Noël et al. 2005). Transformed white spruce with the same inserted gene was recently tested for mycorrhiza formation by ectendomycorrhizal *Wilcoxina* spp. (Stefani et al. 2010). The authors showed that mycorrhization was not affected, with roots of transformed seedlings developing a Hartig net and intracellular hyphae. It is of interest however, that *Wilcoxina* spp. usually form ectomycorrhizas with *Picea* spp. (Mikola 1988; Scales and Peterson 1991b).

V. Occurrence and Ecological Considerations

Early studies by Laiho (1965) and Mikola (1965) and later by Mikola (1988) and Lehto (1989) established that ectendomycorrhizas

formed on pine seedlings by E-strain fungi were common in Finnish and other European nurseries. A number of other reports confirm the **prevalence of ectendomycorrhizas in pine nurseries** in Canada (Danielson and Visser 1989a; Ursic and Peterson 1997; Ursic et al. 1997), the United States (Laiho 1965; Wilcox 1971; Wilcox et al. 1983), several African countries, New Zealand, and Australia (Mikola 1980). Ectendomycorrizas have also been reported in pine plantations in the United States (Menge and Grand 1981).

There is some evidence that **pine seedlings colonized with ectendomycorrhizal fungi** are more **resistant to harsh environments** than those colonized by ectomycorrhizal fungi. For example, *Pinus resinosa* seedlings inoculated with either the E-strain fungus BDG-58 or *Phialophora finlandia*, both shown to produce typical ectendomycorrhizas with this pine species, had better survival rates than seedlings inoculated with two ectomycorrhizal fungal species when grown on iron tailings (LoBuglio and Wilcox 1988). In a study of survival of *Pinus banksiana* seedlings inoculated with 11 mycorrhizal fungal species and outplanted to oil-sands tailings, only E-strain ectendomycorrhizas were present in substantial numbers after 3 years (Danielson and Visser 1989b).

In a study of successional changes in mycorrhizas of a chronological sequence of *P. banksiana* stands following a wild fire, **E-strain fungi** were **prevalent as early-stage fungi** (Visser 1995) in 6-year-old plantations; these were replaced in older stands, primarily by ectomycorrhizal basidiomycete species. In bioassays with *P. halepensis* seedlings grown in soil collected from two sites in which fire had killed all conifer and shrub species, E-strain morphotypes were up to 20 times more frequent than all ectomycorrhizal morphotypes combined after 1 and 2 years growth (Torres and Honrubia 1997). Also, *W. rehmii*, a known ectendomycorrhizal fungus on pine species, was the most common ascomycete identified by analysis of 18S rDNA and ITS 1 data collected from colonized root tips of *P. ponderosa* after a prescribed burn in eastern Oregon, United States (Fujimura et al. 2005).

The **widespread occurrence of ectendomycorrhizas** geographically, their occurrence in pine seedlings under nursery conditions, and the resilience of ectendomycorrhizal fungal species following various disturbance events, suggests that they **may play important roles in conifer seedling establishment**. However, more controlled experiments are needed before decisions are made to use these fungal species as inoculum for outplanted seedlings.

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