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Significance of Microbial Interactions in the Mycorrhizosphere

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I. Introduction

The living roots of most plant species are colonized by hyphae of nonpathogenic fungi to form structures known as mycorrhizas (from Greek meaning "fungus-root"; Frank, 1885). Mycorrhizas normally represent mutualistic interactions, the fungus receiving carbohydrate from its host plant, allowing it to form a mycelial network in the soil which assimilates nutrients (N, P, K, and some micronutrients) and water, a proportion of which is transferred directly to the host (Smith and Read, 1997).

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There are several major types of mycorrhiza, which are classified according to morphology and the types of fungi involved. The dominant type of mycorrhiza in terms of plant species and distribution are the arbuscular mycorrhizas (AM), which form between fungi from the Glomeromycota and angiosperms, gymnosperms, pteridophytes, and bryophytes. Based on taxonomy, approximately 160 species of AM fungus have been described, although this is likely to be a considerable underestimate of actual diversity (Johnson *et al.*, 2005a; Schussler *et al.*, 2001). In AM associations, the fungus penetrates root cortical cells in which it proliferates and forms arbuscules through which materials are exchanged between the symbionts. The fungus spreads into the soil where it forms extraradical mycelial networks of varying size and structural complexity (Hart and Reader, 2002).

The ectomycorrhizal (ECM) association forms largely between basidiomycete and ascomycete fungi and woody perennials, particularly members of the Pinaceae, Betulaceae, Fagaceae, and Dipterocarpaceae (Smith and Read, 1997). Between 5000 and 6000 fungal species may form ectomycorrhizas (Smith and Read, 1997). Hyphae penetrate the root cortex, ramifying between cells to form a ''Hartig net'' through which the symbionts exchange materials. The fungus forms a mantle of hyphae which covers the root, and an extraradical mycelial network of varying complexity (Agerer, 2001). There are a number of other mycorrhizal types which are limited to specific plant families, including the Ericaceae and Orchidaceae, which will not be considered in the current chapter.

Mycorrhizal fungi convey a range of benefits to their host plant in addition to providing nutrients and water, including increased resistance to foliar-feeding insects (Gange and West, 1994) and soilborne pathogens (Whipps, 2004), and tolerance to salinity (Feng *et al.*, 2002) and heavy metals (Diaz *et al.*, 1996). While plant diversity and age can influence the structure and diversity of AM and ECM fungus communities (Johnson *et al.*, 2005a), mycorrhizal fungi themselves may play a key role in determining the structure and diversity of aboveground plant communities (van der Heijden *et al.*, 1998). There is widespread interest in harnessing the benefits of mycorrhizal fungi in agricultural systems to reduce fertilizer and pesticide inputs, and improve the water relations of crop plants (Gosling *et al.*, 2006).

II. The Mycorrhizosphere as a Soil Compartment

Plants allocate between 5% and 30% of photosynthetic assimilate to their mycorrhizal fungus partner (Johnson *et al.*, 2005a), and mycorrhizal hyphae comprise a major proportion of the soil biomass in many

soil ecosystems. In boreal forests, ECM hyphae may comprise over 30% of the microbial biomass (Hogberg and Hogberg, 2002), and AM mycelium forms around 20% of the microbial biomass in prairie and pasture grasslands (Miller *et al.*, 1995). Mycorrhizas therefore have a central position in terrestrial nutrient cycling processes.

It has long been recognized that the physical, chemical, and biological interactions which occur in the soil surrounding mycorrhizas may be distinct from those of the nonmycorrhizal rhizosphere and bulk soil (Rambelli, 1973). Mycorrhizal roots and mycelium have the potential to affect, and be affected by, free-living and pathogenic microbes and fauna during the initiation and formation of mycorrhizas, as extraradical mycelium grows through the soil, and following hyphal and root senescence (Johansson *et al.*, 2004). Mycorrhizal fungi can directly affect soil organisms via nutritional interactions, including the production of hyphal exudates and the provision of living and senescent hyphae as a food source, competition for nutrients, changes in pH (via exudation and nutrient mobilization), and the production of inhibitory compounds. Since mycorrhizal fungi can change soil structure and affect the quality and quantity of rhizodeposits, plant growth and root:shoot ratio, they can also have indirect impacts on the soil microbiota. In turn, free-living soil organisms can directly influence mycorrhizal fungi and their host plant by stimulating the formation of mycorrhizas, changing nutrient availability, enhancing plant growth, changing root:shoot ratio, and using living fungal or plant tissues as a food source.

The region of soil inhabited by, surrounding and influenced by mycorrhizal roots and mycelium has been termed the ''mycorrhizosphere'' (Linderman, 1988). This includes the zone where the hyphae, spores, and fruit bodies of mycorrhizal fungi occur, and within the fungal mycelium and mycorrhizal roots themselves. The region of soil inhabited by extraradical mycelium alone is termed the ''hyphosphere.''

III. The Physical and Chemical Environment of the Mycorrhizosphere

A. Physicochemical Properties

Microbial communities inhabiting the rhizosphere and mycorrhizosphere are subject to spatial and temporal gradients and variation resulting from the uptake of oxygen, nutrients and water, and release of CO_2 by the plant and fungus (Hinsinger *et al.*, 2005). Mycorrhizal fungi also modify soil structure, with implications for aeration and water retention (Gosling *et al.*, 2006). Many studies have shown that the mycorrhizosphere has a lower pH than the rhizosphere and bulk

soil, with increased CO_2 concentrations resulting from the presence of mycorrhizal fungi proposed as one of the mechanisms responsible (Knight *et al.*, 1989). However, both nutrient uptake and exudation of organic acids (see Section III.B) can also contribute to mycorrhizosphere acidification. For example, Bago *et al.* (1998) showed that acidification arising from uptake of NH_4^+ was greater in an AM hyphosphere compartment than a nonmycorrhizal rhizosphere. Mycorrhiza-induced changes in soil physicochemical properties may influence the growth of microbial communities, although information on the direct impact of such changes on microbial community structure and functioning in the mycorrhizosphere is lacking.

B. Release of Organic Materials into the Mycorrhizosphere by Roots and Hyphae

Mycorrhizal colonization can induce a range of qualitative and quantitative changes in rhizodeposition (Jones *et al.*, 2004), although these have rarely been characterized. Several studies have shown that amounts of carbohydrates and amino acids exuded are lower in AM roots relative to nonmycorrhizal roots, with reductions in the amount of organic C exuded reported to be up to 78% (Bansal and Mukerji, 1994; Marschner *et al.*, 1997). Furthermore, these differences in exudation were associated with contrasting population densities of bacteria within the mycorrhizosphere. There are also reports of stimulated release of phenolics within the mycorrhizosphere (Mada and Bagyaraj, 1993). However, other studies have found no quantitative or qualitative impact of AM on rhizodeposition (Azaizeh *et al.*, 1995). A variety of factors could explain these contrasting results, including differences in the plant and fungus species involved, the experimental system used, and environmental conditions. ECM fungi can stimulate or inhibit rhizodeposition of carbohydrates and amino acids depending on the combination of plant and fungus (Leyval and Berthelin, 1993).

Living hyphae of ECM fungi have been shown to exude a variety of soluble organic materials, although there is little information available on exudation by the hyphae of AM fungi. Exudates may influence microbial communities in the mycorrhizosphere by direct impacts, such as by changing pH or by providing a substrate for microbial growth, although to date there is little direct evidence linking mycorrhizal fungus exudates to the structure or functioning of mycorrhizosphere communities (see Section V.A).

Most attention on exudation by ECM fungi has focused on organic acids. When grown *in vitro*, large amounts of oxalic and citric acids,

and smaller amounts of tartaric, glycolic, and formic acids can be exuded by a number of ECM fungi (Lapeyrie *et al.*, 1987). ECM roots increase the amount and change the composition of organic acids in soil (Griffiths *et al.*, 1994; van Hees *et al.*, 2003). While oxalic acid appears to be the major organic acid detected in soil supporting mycorrhizal plants, large amounts of propionic, formic, acetic, citric, shikimic, and lactic acid have also been detected (Ahonen-Jonnarth *et al.*, 2000; van Hees *et al.*, 2006). Although the relative contribution of the plant root and fungus mycelium to the elevated organic acid levels around mycorrhizal roots has not usually been determined, the precise types of organic acids exuded by mycorrhizal roots do depend on fungal species.

The role of organic acids exuded by ECM mycelium and roots appears to be to dissolve mineral nutrients, including K, Al, and Mg, increasing their availability for uptake (Jones *et al.*, 2004). The amount of organic acid exuded into soil by ECM mycelium can be large. van Hees *et al.* (2006) estimated that oxalic acid exudation by the ECM fungus *Hebeloma crustuliniforme* in symbiosis with *Pinus ponderosa* represented 2–4% of the total C received by the fungus, which was equivalent to 0.2% of the total C fixed by the plant. Organic acids produced by ECM plants are degraded rapidly in soil, with elevated degradation rates in the mycorrhizosphere compared to nonmycorrhizal rhizosphere soil (van Hees *et al.*, 2003).

The external mycelium of some hydrophobic and hydrophilic ECM fungi can exude drops of liquid at the hyphal tip (Unestam and Sun, 1995). In the case of *Suillus bovinus*, carbohydrates comprised 32% of the exudate mass. Ten different polyols (sugar alcohols) and sugars were identified, with the major components found to be inositol, erythritol, ribose, threitol, and mannose (Sun *et al.*, 1999). The drops also contained significant amounts of peptides, which accounted for up to 14% of the exudate mass. Oxalic and acetic acids were also detected in the hyphal drops, but no amino acids were found. The molecular and environmental factors controlling exudation, and the extent to which ECM hyphae exude carbohydrates while growing in symbiosis and in natural soil, is not known.

A number of hydroxymate siderophores have been detected in pure cultures of ECM fungi (Haselwandter, 1995) and soil colonized by ECM mycelium (van Hees *et al.*, 2006). These cyclic peptides sequester Fe when it is in short supply, making it more accessible for assimilation. The available data suggest that exudation rates of siderophores by ECM mycelia are small, and around 10,000 times lower than for oxalic acid (van Hees *et al.*, 2006). Although siderophores can be readily

catabolized by soil bacteria (Pierwola *et al.*, 2004), it seems that siderophore production by mycorrhizal mycelium does not represent a major C input to soil. However, by changing the availability of Fe, siderophores released by mycorrhizal fungi could influence the growth of free-living microbial communities, although this has not been tested.

A number of other organic materials are exuded by ECM hyphae. Some ECM fungi exude phenolic compounds when grown *in vitro* (Sun *et al.*, 1999). These compounds have antifungal activity against plant pathogens (Yamaji *et al.*, 2005), although the extent to which they suppress the growth of mycorrhizosphere organisms, or represent a substrate for saprophytic organisms, is not known. The ECM fungus *Pisolithus tinctorius* exudes an indole alkaloid, hypaphorine, which counteracts the action of the plant hormone indole-3-acetic acid (IAA), resulting in the inhibition of root hair development (Beguiristain and Lapeyrie, 1997). However, direct and indirect effects of hypaphorine on mycorrhizosphere microbes have not been studied.

Information on exudation from AM hyphae is scarce. Attention has focused on glomalin, a glycoprotein which has been shown to accumulate in concentrations up to 21 mg g^{-1} soil (Wright and Upadhyaya, 1999). Glomalin is highly persistent in soil, with a turnover time of 6–42 years (Rillig *et al.*, 2001). Alongside AM hyphae, glomalin may play a role in promoting soil aggregation. Analysis of glomalin production *in vitro* showed that less than 20% of glomalin produced by *Glomus intraradices* was exuded, with the remainder forming part of the hyphal and spore cell wall (Driver *et al.*, 2005). The significance of glomalin, and its impact on mycorrhizosphere organisms are unclear, and furthermore the processes controlling the fate of glomalin in soil are poorly understood.

IV. Interactions Between Microbes and Symbionts Prior to and During Mycorrhiza Formation

A. Mycorrhization Helper Bacteria

The term ''mycorrhization helper bacteria'' (MHB) was coined by Garbaye (1994) to describe bacteria which can enhance the rate of mycorrhiza formation. Such MHB may also suppress pathogens in mycorrhizosphere soil (Budi *et al.*, 1999; Schelkle and Peterson, 1996). The helper effect of soil bacteria on mycorrhiza formation was initially investigated in nursery soils (Garbaye, 1983; Ridge and Theodorou, 1972). In these soils, ECM formation was reduced following

fumigation with methyl bromide, suggesting that bacteria are important in the formation of mycorrhiza. Further work demonstrated that inoculation of microbial communities into sterilized soils containing *P. radiata* with either *Paxillus involutus, Rhizopogon luteolus*, or *H. crustuliniforme* resulted in enhanced mycorrhiza formation (Garbaye and Bowen, 1987).

In many subsequent studies, pure bacterial strains which promote mycorrhiza formation have been isolated and characterized. Early work on specific MHB interactions focused on the ECM symbiosis *Laccaria bicolor* S238N (formerly *Laccaria laccata*)–*Pseudotsuga menziesii* (Duponnois and Garbaye, 1990, 1991; Duponnois *et al.*, 1993), with bacteria isolated from either the sporocarp or the ECM mantle. Further MHB have been isolated from ECM symbioses involving the fungi *Lactarius rufus, Pisolithus* spp., *Suillus luteus*, and *Amanita muscaria* (Bending *et al.*, 2002; Founoune *et al.*, 2002b; Poole *et al.*, 2001; Schrey *et al.*, 2005). MHB have also been studied to a lesser extent in AM symbioses involving *Glomus* spp. (Duponnois and Plenchette, 2003; Mamatha *et al.*, 2002; Xie *et al.*, 1995).

For both ECM and AM symbioses, MHB strains are predominantly *Bacillus* and *Pseudomonas*, but examples have also been found in the genera *Bradyrhizobium, Burkholderia, Paenibacillus, Rhodococcus*, and *Streptomyces*. Bacteria have been categorized as MHB using a variety of contrasting experimental systems, including laboratory microcosms and glasshouse and nursery systems (Duponnois and Garbaye, 1991; Duponnois and Plenchette, 2003; Poole *et al.*, 2001). Examples of laboratory microcosm and glasshouse systems are shown in Figs. 1 and 2.

B. Characterizing Mycorrhization Helper Bacteria Effects

Numerous studies have been conducted to characterize the helper effect of specific MHB. For example, the bacterial strain BBc6 consistently stimulates mycorrhizal root formation in the *L. bicolor* S238N–*P. menziesii* symbiosis. In bare root forest nurseries, stimulation of mycorrhiza formation in the presence of this MHB is typically in the order of 20–30% over controls receiving no bacterial inoculum (Duponnois and Garbaye, 1991). Similarly, for *Acacia auriculiformis*–*Pisolithus alba*, mycorrhiza formation can be stimulated from 45.8% in controls to 70.3% in the presence of *Pseudomonas fluorescens* HR13 (Duponnois and Plenchette, 2003).

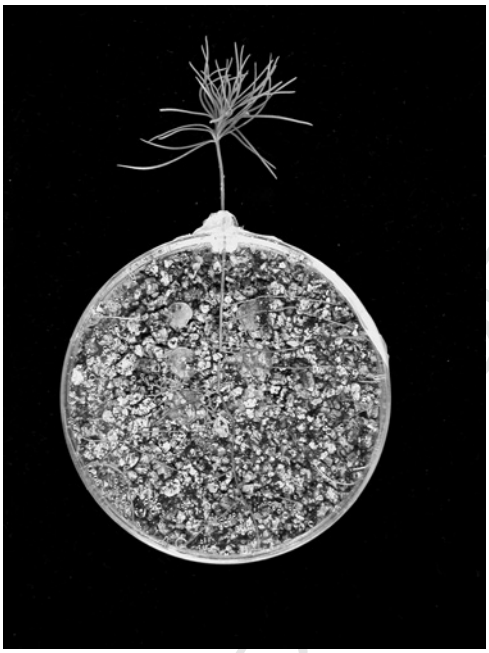

FIG. 1. Photograph of Poole microcosm. A Petri dish–based system containing peat vermiculate and inoculated with *P. sylvestris, L. rufus*, and, as appropriate, bacterial strains.

The concentration at which such MHB are applied has important consequences for the degree of stimulation. *P. fluorescens* BBc6R8 increased mycorrhiza formation to a greater extent at lower than high doses (Frey-Klett *et al.*, 1999). Similarly, Aspray *et al.* (2006) found using microcosms and the *P. sylvestris–L. rufus* symbiosis that for *Burkholderia* sp. EJP67 the effect on mycorrhiza formation was dependent on bacterial inoculation concentration, although in the same system, *Paenibacillus* sp. EJP73 stimulated mycorrhiza formation at a greater range of inoculum concentrations. Therefore, in terms of bacterial concentration it seems that a fine equilibrium must exist, as least for certain MHB, in order for the helper effect to be realized.

Although MHB were initially thought to be fungus specific (Dunstan *et al.*, 1998; Duponnois *et al.*, 1993), MHB strains have since been shown to stimulate mycorrhiza formation of several fungal strains. Duponnois and Plenchette (2003) found that MHB *P. fluorescens* HR13 was able to stimulate ectomycorrhiza formation by *P. alba* and

FIG. 2. Photographs of typical glasshouse experiment used to investigate MHB–ectomycorrhiza interactions, as conducted at INRA Nancy, Research Unit ''Tree-Microorganism Interactions, France'' (Courtesy of Béatrice Palin). Three-month-old *P. sylvestris* seedlings inoculated with ectomycorrhizal fungi and MHB.

Scleroderma spp. In fact, HR13 also stimulated mycorrhiza formation by the AM fungus *G. intraradices*. The nonfungal specificity of certain MHB has been confirmed using the strain *Paenibacillus* sp. EJP73, which stimulates *L. bicolor–P. sylvestris* mycorrhiza under glasshouse conditions and *L. rufus–P. sylvestris* mycorrhiza in laboratory microcosms (Poole *et al.*, 2001; Aspray *et al.,* in press).

C. Mycorrhization Helper Bacteria Mechanisms

A key focus for MHB research has been to understand the mechanisms responsible for producing the helper effect. Potential mechanisms were hypothesized by Garbaye (1994) to include: (1) enhancing receptivity of the root to colonization by mycorrhizal fungi, (2) affecting root-fungus recognition processes, (3) stimulating presymbiotic fungal growth, (4) affecting germination of fungal propagules, and (5) modifying soil properties. Garbaye (1994) provided a thorough overview of potential MHB mechanisms. As such, this section of the chapter will cover general concepts and focus on more recent developments in this area.

1. *Enhancing Receptivity of the Root to Colonization by Mycorrhizal Fungi*

One way in which MHB may enhance the colonization of plant roots by fungi is by increasing the actual number of short roots available for colonization (Garbaye, 1994). Bacteria can produce a wide array of molecules which may alter the physical and chemical properties of plant roots, including signaling molecules such as phytohormones, and enzymes. In particular, the phytohormone IAA is important in plants for controlling fundamental cellular processes, including cell division and tissue differentiation (Leveau and Lindow, 2005). Some MHB have been found to produce large amounts of IAA, which can stimulate the initiation of short roots by *P. menziessii* seedlings (Duponnois, 1992; Gamalero *et al.*, 2003).

MHB may also enhance the receptivity of the plant root by softening the cell wall and middle lamella of the root cortex (Duponnois, 1992), and making physical growth of the fungus through the root easier. Soil bacteria can produce a range of enzymes such as endoglucanases, cellobiose hydrolases, pectate lyases, and xylanases. The MHB *P. fluorescens* 92 and *P. fluorescens* BBc6 have both been shown to produce cellulase (Gamalero *et al.*, 2003), although its role in MHB activity has not been demonstrated. Enzymes such as endoglucanase and pectate lyase are also involved in virulence and pathogenicity of bacterial plant

pathogens (Ham *et al.*, 2004; Liao *et al.*, 1992), which could suggest a fine balance between helper and pathogenic effects.

Finally, one area recently receiving attention in relation to both pathogenic and mutualistic interactions between plants and microbes is the involvement of bacterial secretion systems. The type III secretion system (TTSS) in particular has been demonstrated to be involved both in pathogenic and mutualistic interactions with plant roots (Buttner *et al.*, 2006; Molina *et al.*, 2006). TTSS inject proteins into the cytosol of eukaryotic cells, where the translocated proteins interfere with host cell signal transduction and other cellular processes, resulting in changes to host physiology. Further work is needed to clarify the role of such systems in MHB interactions.

2. *Affecting Root-Fungus Recognition Processes*

In mycorrhizal symbioses, fungi and plants produce signal molecules such as phytohormones, enzymes, polysaccharides, phenolic compounds, adhesins, and volatiles during the initiation of mycorrhiza formation (Akiyama *et al.*, 2005; Smith and Read, 1997). Bacteria in the mycorrhizosphere may be able to synthesize many of these chemicals, and thereby affect mycorrhiza formation. In addition, degradation or transformation of signal molecules by bacteria could affect root-fungus recognition.

Production of IAA is a mechanism by which some plant growth-promoting bacteria operate (Patten and Glick, 2002), and production of IAA could also be an MHB mechanism. However, as the ECM fungus *L. bicolor* also produces IAA, it is not clear what contribution bacterially produced IAA has on enhancing this symbiosis. Bacteria, for example *Pseudomonas putida* strain 1290†, may also degrade IAA (Leveau and Lindow, 2005). However, whether such bacteria can enhance or inhibit mycorrhiza formation is unknown.

3. *Stimulating Presymbiotic Fungus Growth*

The third hypothesis, that MHB stimulate presymbiotic growth of the fungus, has been studied widely due to the simplicity of experiments involving cocultures of the fungus and bacterium. One way in which MHB can stimulate fungal growth is through the production of metabolites which can be used as nutrients or anabolic growth factors by the fungus. A variety of studies have shown that bacterial isolates or their culture filtrates can stimulate growth of ECM fungi on low nutrient agar (Brulé *et al.*, 2001; Duponnois and Garbaye, 1990). MHB may also detoxify metabolites produced by the fungus that inhibit mycelial growth (Duponnois and Garbaye, 1990).

Whether the stimulation of fungal growth on agar or in liquid media is an MHB mechanism remains to be proven conclusively. In the absence of the plant partner, enhancing presymbiotic fungus growth cannot be correlated with enhanced mycorrhiza formation. For example, *P. monteilii* HR13 stimulated radial growth of *Pisolithus* isolates, but not *Scleroderma dictyosporum* or *S. verrucosum*, and yet the bacterium significantly enhanced mycorrhiza formation of all three fungi (Duponnois and Plenchette, 2003).

4. *Affecting Germination of Fungal Propagules*

Bacteria have been shown to stimulate the germination of mycorrhizal fungus spores. For example, surface sterilization of *G. versiforme* spores reduced the rate of spore germination compared to those with naturally associated microbial communities (Mayo and Davis, 1986). Furthermore, the addition of bacteria (including *Pseudomonas* and *Corynebacterium* strains) isolated from nonsurface disinfected spores also increased spore germination compared to disinfected spores. Both volatile and nonvolatile metabolites released by bacteria have been suggested to be responsible for increased spore germination (Azcón, 1987; Carpenter-Boggs *et al.*, 1995; Mayo and Davis, 1986). However, like the previous hypothesis a clear link between enhanced spore germination and increased mycorrhiza formation remains to be demonstrated.

D. Mycorrhization-Inhibiting Bacteria

Some bacteria can have inhibitory effects on *in vitro* fungus growth or on mycorrhiza formation itself and have been termed mycorrhization-inhibiting bacteria (MIB; Bending *et al.*, 2002; Bowen and Theodorou, 1979; Varese *et al.*, 1996). MIB include strains of *Pseudomonas* sp. and *Bacillus* sp. The close phylogenetic similarity between MHB and MIB, and the fact that MHB are able to stimulate mycorrhiza formation of certain fungi and inhibit that of others suggests that bacteria are able to act both as MHB or as MIB, depending on the particular fungal and plant partners involved (Brulé *et al.*, 2001). Furthermore, Brulé *et al.* (2001) found that *P. fluorescens* BBc6R8 could act as an MHB or MIB of the *L. bicolor–P. menziesii* symbiosis under different environmental conditions. Such findings emphasize the dynamic nature of bacteria in the mycorrhizosphere rather than the presence of discrete functional groups.

V. Interactions Between Mycorrhizas and Free-Living Nonpathogenic Organisms

A. Bacterial Biomass and Community Structure

Most studies which have examined the impact of mycorrhizas on bacterial communities have compared the rhizosphere of mycorrhizal and nonmycorrhizal plants. Since colonization of roots by mycorrhizal fungi can alter root physiology, including patterns of rhizodeposition (see Section III.B), it is not clear to what extent these impacts reflect direct or indirect effects of mycorrhizal fungi. Furthermore, despite evidence that mycorrhizal fungi can alter the chemical and physical environment within the mycorrhizosphere (see Section III), most studies have failed to provide understanding of mechanisms driving community structure in the mycorrhizosphere, or in many instances the functional consequences of altered community structure.

Mycorrhizal fungi have been shown to have negative (Christensen and Jakobsen, 1993), neutral (Olsson *et al.*, 1998), and positive (Andrade *et al.*, 1998) effects on amounts or activity of total bacterial biomass, or specific genotypic groups. Using plating techniques, Meyer and Linderman (1986) showed that *G. fasciculatum* had no effect on the number of bacteria or actinomycetes in the rhizosphere of *Zea mays* or *Trifolium subterraneum*. However, relative to nonmycorrhizal plants, the rhizosphere of mycorrhizal plants supported higher populations of facultative anaerobic bacteria and chitinase-producing actinomycetes, but lower populations of fluorescent Pseudomonads. Numbers of bacteria in the mycorrhizosphere of ECM plants can also be higher than those of bulk soil or nonmycorrhizal rhizosphere, although the extent of differences can vary between mineral and humus horizons (Heinonsalo *et al.*, 2001).

Andrade *et al.* (1997) showed that more bacterial species occurred in soil from the hyphosphere relative to that from AM-colonized rhizosphere and that the precise communities found varied between AM fungus species. A number of specific bacterial genera have been found in greater abundance in the hyphosphere of AM fungi relative to nonmycorrhizal rhizosphere or bulk soil, including *Burkholderia* spp., *Arthrobacter* spp. (Andrade *et al.*, 1997), and *Paenibacillus* spp. (Artursson *et al.*, 2005). These genera, together with *Bacillus* spp., *Pseudomonas* spp., and *Rhodococcus* spp. can also be abundant within ECM roots (Bending *et al.*, 2002; Izumi *et al.*, 2006; Poole *et al.*, 2001). The mycorrhizosphere can also induce more subtle change to communities. Frey-Klett *et al.* (2005) found that both the genotypic and

functional diversity of *P. fluorescens* strains within the mycorrhizosphere was greater than in bulk soil.

In contrast to eubacteria, interactions between mycorrhizas and archaea have received little attention. In a humus soil, Bomberg *et al.* (2003) found greater diversity of archaea in mycorrhizal roots and soil colonized by ECM mycelium relative to uncolonized soil, with no archaea detected in nonmycorrhizal roots. However, the size of these communities and their significance is unclear.

B. Fungal Biomass and Community Structure

A variety of nonsymbiotic microfungi occur within ECM roots or in soil containing extraradical mycelium, although there is evidence that the size of the saprophytic fungus community is reduced in the mycorrhizosphere relative to the bulk soil or nonmycorrhizal roots (Olsson *et al.*, 1998; Summerbell, 2005). However, population sizes of individual fungus species can be inhibited, stimulated, or not affected by the presence of mycorrhizal mycelium (Larsen *et al.*, 1998; Tiunov and Scheu, 2005; Zadworny *et al.*, 2004). Intriguingly, the ECM fungus *L. laccata* has been shown to be a mycoparasite of the microfungus *Mucor hiemalis in vitro* (Werner and Zadworny, 2003), although an antagonistic interaction between these fungi, without mycoparasitism, occurred in the rhizosphere of *P. sylvestris* (Werner *et al.*, 2002). ECM fungi are known to compete with litter-inhabiting saprotrophic macrofungi, which can exploit the same spatial niche as ECM fungi. The outcome of competition between such ECM and saprotrophic macrofungi depends on the species involved and can also depend on C availability to each of the interacting fungi (Lindahl *et al.*, 2001). Much less is known about AM–saprophytic fungus interactions. Some microfungal inhabitants of the mycorrhizosphere are known to be antagonistic to AM fungi (McAllister *et al.*, 1997), and *Trichoderma harzianum* has been reported to be a mycoparasite of AM spores and mycelium (Rousseau *et al.*, 1996).

C. Interactions with Fauna

A variety of micro- and mesofauna inhabit the mycorrhizosphere, and these organisms are likely to affect microbial communities through feeding, inputs of fecal material, and disturbance, although these interactions are poorly understood. Mycorrhizal hyphae and their associated free-living bacterial and fungal communities are grazed by a variety of soil animals. Populations of protozoa have been found to be

both lower and higher in ECM roots and soil supporting extraradical mycelium relative to nonmycorrhizal roots (Jentschke *et al.*, 1995; Timonen *et al.*, 2004). Ronn *et al.* (2002) found that numbers of protozoa were reduced in the AM mycorrhizosphere relative to the nonmycorrhizal rhizosphere, with lower bacterial biomass in the presence of the AM fungus given as the reason.

Oribatid mites show varying feeding preferences for the mycelia of ECM fungi (Schneider *et al.*, 2005), while collembola can feed on the mycelium of both AM (Klironomos and Ursic, 1998) and ECM fungi (Hiol *et al.*, 1994) and may also physically sever hyphae as they move through soil (Johnson *et al.*, 2005b). Tiunov and Scheu (2005) showed that three species of collembola fed on saprotrophic rather than AM hyphae in the mycorrhizosphere of the grass *Cynodon dactylon*, altering community structure of the saprotrophic community. Additionally, the feeding preference for saprotrophic microfungi increased the extent to which *G. mosseae* altered the structure of the saprotrophic community. The direct and indirect impacts of collembola on bacterial community structure and functioning within the mycorrhizosphere are not known. Numbers of free-living nematodes can be stimulated in the mycorrhizosphere of ECM plants (Villenave and Duponnois, 2002), and furthermore AM fungi can override the selective influence of host plant on the structure of soil nematode communities (Villenave *et al.*, 2003). The effects of nematodes and other important faunal groups, such as enchytraeid worms (Didden, 1993), on the structure and functioning of microbial communities within the mycorrhizosphere have not been considered.

D. Decomposition Processes in the Mycorrhizosphere

Mycorrhizal fungi coexist with saprotrophic organisms, and interaction between these groups of organism can have consequences for the degradation of organic matter and xenobiotics (Cairney and Meharg, 2002). In forest soil, the presence of ECM roots can inhibit litter decomposition (Gadgil and Gadgil, 1971, 1975), an observation which has been termed the ''Gadgil effect.'' A number of mechanisms have been proposed for the apparent inhibition of saprotroph communities which underlies the Gadgil effect (Bending, 2003). The simplest explanation is that ECM fungi directly inhibit saprotrophic bacteria, fungi, and fauna (see Sections V.A–C). The capacity of ECM fungi to degrade litter components is low relative to saprotrophic fungi, and the colonization and exploitation of litter by ECM fungi in place of saprotrophic fungi would result in reduced rates of decomposition. Other explanations include

the selective exploitation and translocation of available forms of N and P by ECM fungi, which lower the quality of the substrate remaining to saprotrophs (Abuzinadah and Read, 1989; Bending and Read, 1995), and the uptake of water by ECM roots, which could result in availability of water limiting the activities of saprotrophic organisms (Koide and Wu, 2003). However, the Gadgil effect does not occur universally, and several studies have shown that the presence of mycorrhizal roots can enhance decomposition rates (Zhu and Ehrenfeld, 1996). Similarly, the presence of AM mycelium can stimulate decomposition rates of organic matter in soil (Hodge *et al.*, 2001).

The degradation of xenobiotics in the mycorrhizosphere has received little attention. The mycorrhizosphere is a compartment in which xenobiotic catabolizing communities can be enriched, and in which survival of inoculated catabolic communities can be enhanced (Sarand *et al.*, 1998). Joner and Leyval (2001) showed that the presence of *G. mosseae* increased the degradation of several polycyclic aromatic hydrocarbons (PAH) by up to 25% after 16 weeks, although using the same fungus species, Binet *et al.* (2000) found no difference in the catabolism of a mix of eight PAH between nonmycorrhizal rhizosphere and mycorrhizosphere soil. Genney *et al.* (2004) demonstrated that catabolism of the PAH fluorine was inhibited in the presence of ECM mycelium, extending the significance of the Gadgil effect. However, ECM roots may have no effect on degradation of other PAH (Genney *et al.*, 2004; Koivula *et al.*, 2004). Since mycorrhizal fungi are considered to have little or no capacity to degrade complex organic materials, direct stimulation of the activities of saprotrophic organisms by mycorrhizal fungi has been proposed as the mechanism responsible for enhanced organic matter or xenobiotic degradation in the mycorrhizosphere, although the communities involved, and the mechanisms underlying the interactions are unclear.

E. Interactions with Microbes Contributing to N and P cycling

Availability of N and P is commonly the factor most limiting to plant growth, and enhancing availability of these nutrients to the host is generally believed to be the key function of mycorrhizal fungi (Smith and Read, 1997). Many studies have indicated that organisms which improve N and P availability to mycorrhizal fungi are specifically enriched in the mycorrhizosphere. However, it is not clear whether these effects reflect direct effects of the mycorrhizal fungus, or indirect effects arising from mycorrhizal fungus-induced changes to soil moisture content or impacts on nutrient status.

Li *et al.* (1992) found that N_2 could be fixed by *Bacillus* spp. located within tuberculate ECM of *P. menziessii*. However, actual numbers of N_2 fixing bacteria in the mycorrhizosphere may be no different to those in nonmycorrhizal roots (Rozycki *et al.*, 1999). Amounts of N_2 fixed within the mycorrhizosphere are likely to contribute a relatively small proportion of total atmospheric N inputs to soil (Barkmann and Schwintzer, 1998). However, since the fixed N_2 directly enters the root zone, it could nonetheless be important for tree nutrition. The number of free-living N_2 fixing bacteria has been shown to be elevated in the mycorrhizosphere of several AM fungi growing individually with the grass *Panicum maximum* (Secilia and Bagyaraj, 1987), although N_2 fixation rates were not determined.

Many studies have shown that the AM symbiosis improves both nodulation and symbiotic N_2 fixation, with the extent to which this occurs depending on the specific strains of AM fungus and N_2 fixing bacteria involved (Requena *et al.*, 1997). Improved P and/or N nutrition of the host by the AM fungus is thought to be responsible for determining these interactions (Barea *et al.*, 2002). However, the relative competitiveness of nodule N_2 fixing bacteria can be altered within the mycorrhizosphere relative to the rhizosphere, with implications for patterns of nodulation and N_2 fixation (André *et al.*, 2003). AM colonization can also protect nodules and N_2 fixation from drought, although AM species vary in their effectiveness (Ruiz-Lozano *et al.*, 2001). Enhanced water uptake by AM fungi, in addition to reduction of oxidative damage, may be responsible for these effects.

The population sizes of other organisms involved in N cycling can be altered within the mycorrhizosphere. Numbers of autotrophic NH_4^+-oxidizing bacteria were higher in the mycorrhizosphere of *G. mosseae* and *G. fasciculatum* growing with *Z. mays* relative to nonmycorrhizal rhizosphere soil, with the reverse situation for numbers of denitrifying and NH_4^+-producing organisms (Amora-Lazcano *et al.*, 1998). However, actual rates of N transformation processes were not determined in this study, so the significance is unclear.

The main functional role of AM is thought to be to enhance P uptake to the host plant by obtaining P from beyond the depletion zone surrounding plant roots (Smith and Read, 1997). A variety of free-living soil bacteria and fungi are extremely effective at mobilizing P from insoluble minerals through the production of organic acids (Richardson, 2001), and there has been much interest in the interaction of native and coinoculated P-solubilizing bacteria with AM fungi. In *Medicago sativa*, populations of native P-solubilizing bacteria can be enhanced in the mycorhizosphere of *G. mosseae* relative to the nonmycorrhizal

rhizosphere (Toro *et al.*, 1998), while Frey-Klett *et al.* (2005) showed that the ectomycorrhizosphere selected P-mobilizing strains of *P. fluorescens*. Furthermore, several studies have found that the effectiveness of inoculated P-solubilizing bacteria (Villegas and Fortin, 2002) and fungi (Osorio and Habte, 2001; Tarafdar and Marschner, 1995) is stimulated within the mycorrhizosphere, with the inoculants acting synergistically with AM fungi to enhance P uptake by the host plant. However, in other studies, no interactive relationships between AM fungi and inoculant P-solubilizing bacterial strains have been found (Toro *et al.*, 1998).

F. Localization of Microbes Within the Mycorrhizosphere

There is considerable spatial variability in the localization of bacteria within the mycorrhizosphere. Nurmiaho-Lassila *et al.* (1997) showed that within the *S. bovinus–P. sylvestris* mycorrhizosphere, bacteria occurred inter- and intracellularly within the mantle and Hartig net of the root, and while fungal rhizomorphs supported few bacteria, the fungal front, which was composed of dense mycelium, supported an extensive biofilm of bacteria. The localization of bacteria on *P. involutus–P. sylvestris* mycorrhizas was shown to be different, with bacteria mostly absent from mycorrhizal roots. Furthermore, the precise structure of bacterial communities can vary between root and hyphosphere locations within the mycorrhizosphere (Timonen *et al.*, 1998).

The spores and hyphae of some AM fungi, including *Gigaspora margarita*, contain obligate endocellular bacteria, which have been identified as a new taxon, *Candidatus Glomeribacter gigasporarum* (Jargeat *et al.*, 2004). Similarly, living hyphae of the ECM fungus *L. bicolor* can harbor diverse endobacteria, mainly belonging to the α-proteobacteria (Bertaux *et al.*, 2005). However, the functional significance of endocellular bacteria within mycorrhizal hyphae has yet to be elucidated.

Much less is known of the localization of fungi within the mycorrhizosphere. Bending and Read (1995) showed that conidiophores of *Penicillium* sp. were associated with senescent areas of mycelium behind the fungal front and were absent from active mycelium.

G. Nutritional Aspects of Mycorrhizosphere Interactions

Frey *et al.* (1997) demonstrated that the structure of fluorescent Pseudomonad communities associated with *P. menziesii–L. bicolor* mycorrhizas and mycorrhizosphere soil was different to that of the bulk soil, and that those from mycorrhizal compartments preferentially

utilized the fungus sugar trehalose. Similarly, Izumi *et al.* (2006) found that diverse endophytic bacteria isolated from a range of *P. sylvestris* mycorrhizas had a preference for trehalose relative to plant sugars. These studies indicate that exudation and specific nutrient availability could be a key driver determining the community structure of organisms inhabiting the mycorrhizosphere surrounding active hyphae, although such links remain to be proven.

The major routes by which C is released from mycorrhizal roots and hyphae into the soil are likely to be through senescence and following ingestion by fauna. The impact of these processes in determining the structure and functioning of mycorrhizosphere bacterial and fungal communities is poorly understood. In the case of AM, hyphae have been shown to have a life span of just 5–6 days, following which they senesce (Staddon *et al.*, 2003). Many ECM fungus species form dense mycelia at the foraging front, connected to plant roots by rhizomorphs (Agerer, 2001). For *S. bovinus*, the time from initial colonization of substrate by the fungal front to senescence was less than 40 days (Bending and Read, 1995). Chitinolytic bacteria are frequently encountered within the mycorrhizosphere of ECM (Bending *et al.*, 2002) and AM fungi (Meyer and Linderman, 1986), and these organisms could potentially utilize chitin from living or senescent mycorrhizal hyphae. Some microfungi which show antagonism to AM fungi have been shown to penetrate living spores and hyphae, and proliferate inside, although chitinolytic activity only occurred at the infection point (Rousseau *et al.*, 1996). Endophytic bacteria associated with ECM and AM fungi must clearly derive all their nutrition from their host fungus, although it is not clear how this is achieved. Furthermore, it remains to be seen whether endophytic bacteria have any positive or negative impact on the mycorrhizal fungus itself. Although *Candidatus Glomeribacter gigasporarum* has been shown to possess N_2 fixation genes (Minerdi *et al.*, 2001), their significance is not known.

VI. Pathogen Interactions with Mycorrhizas

A. Control of Pathogens by Mycorrhizas

The majority of studies concerning pathogen–mycorrhiza interactions have been focused on developing mycorrhizal fungi for biological disease control and this topic has been comprehensively reviewed in recent years (Harrier and Watson, 2004; Whipps, 2004). Consequently, in the main, only general concepts and principles associated with this

topic are presented with key or more recent references cited where necessary.

Both AM and ECM fungi have been reported to provide control of numerous plant pathogens and some examples are given in Table I. There is considerable diversity in mycorrhizal fungi capable of reducing diseases caused by a number of different plant pathogens, but *Glomus* spp., especially *G. intraradices* and *G. mosseae* are the most studied AM fungi and *L. bicolor, L. laccata*, and *P. involutus* are the most widely studied ECM fungi. Fungal pathogens, such as *Fusarium* spp., *Rhizoctonia solani, Cylindrocarpon destructans*, and *Phytophthora* spp., have been examined numerous times along with nematodes including *Meloidogyne* spp. and *Pratylenchus* spp., reflecting their widespread nature and economic importance. Control of bacterial diseases has been little studied, although there are a few examples (Garcia-Garrido and Ocampo, 1989; Zhu and Yao, 2004).

The level of control achieved by any AM or ECM fungus can depend on the cultivar of plant (Duchesne, 1994; Mark and Cassells, 1996), the aggressiveness of the pathogen (Strobel and Sinclair, 1991), the isolate of mycorrhizal fungus, and the substrate and environment used for plant cultivation, but control is never complete. Combinations of mycorrhizal fungi may also give improved control of pathogens in comparison with those used individually (Requena *et al.*, 2001). However, it should be noted that there are reports that some soilborne diseases are increased by mycorrhizal infection (Davis and Menge, 1980; Garmendia *et al.*, 2004; Ross, 1972) suggesting that, in some instances, a healthy mycorrhizal plant may be more susceptible than a poorly developed nonmycorrhizal one (Dehne, 1982).

B. Mechanisms and Microbial Interactions Associated with Disease Control

Research on mycorrhiza–pathogen interactions has focused on understanding the mechanisms by which mycorrhizal roots resist attack by a plant pathogen. But more recently, it has been realized that complex interactions of mycorrhizal fungi with other microorganisms in the mycorrhizosphere can also influence the ability of a pathogen to infect a plant, particularly where bacterial and fungal biocontrol agents are combined with mycorrhizal fungi as inocula. These areas are considered below.

Four major groups of modes of action have been identified (Whipps, 2004): (1) direct competition or inhibition; (2) enhanced or altered plant growth, nutrition, and morphology; (3) biological changes associated

TABLE I

EXAMPLES OF MYCORRHIZAS EXHIBITING CONTROL OF PLANT PATHOGENS

Mycorrhizal fungus	Pathogen	Host plant	References
Arbuscular mycorrhizal fungi			
Gigaspora margarita	*Fusarium oxysporum* f. sp. *asparagi*	*Asparagus officinalis* (Asparagus)	Matsubara *et al.* (2001)
	Meloidogyne incognita	*Gossypium hirsutum* (Cotton)	Roncardori and Hussey (1977)
Glomus spp.	*Meloidogyne incognita*	*Lycopersicon esculentum* (Tomato)	Talavera *et al.* (2001)
	Pratylenchus penetrans	*Daucus carota* (Carrot)	Talavera *et al.* (2001)
Glomus aggregatum	*Cylindrocarpon destructans*	*Prunus persicaria* (Peach)	Traquair (1995)
Glomus clarum	*Rhizoctonia solani*	*Vigna unguiculata* (Cowpea)	Abdel-Fattah and Shabana (2002)
Glomus coronatum	*Rhizoctonia solani*	*Vigna radiata* (Mung bean)	Kasiamdari *et al.* (2002)
Glomus etunicatum	*Phytophthora fragariae* var. *fragariae*	*Fragaria x ananassa* (Strawberry)	Norman *et al.* (1996)
Glomus fasciculatum	*Fusarium oxysporum* f. sp. *asparagi*	*Asparagus officinalis* (Asparagus)	Matsubara *et al.* (2001)
	Radopholus similis	*Musa acuminata* (Banana)	Umesh *et al.* (1988)
Glomus fistulosum	*Phytophthora fragariae var. fragariae*	*Fragaria vesca* (Wild strawberry)	Mark and Cassells (1996)
Glomus intraradices	*Fusarium solani* f. sp. *phaseoli*	*Phaseolus vulgaris* (Bean)	Filion *et al.* (2003)
	Meloidogyne javanica	*Musa* sp. (Banana)	Pinochet *et al.* (1997)
Glomus mosseae	*Aphanomyces euteiches*	*Pisum sativum* (Pea)	Larsen and Bødker (2001)
	Pratylenchus vulnus	*Prunus domestica* (Plum)	Camprubi *et al.* (1995)
Glomus proliferum	*Cylindrocladium spathyphylli*	*Musa acuminata* (Banana)	Declerk *et al.* (2002)

(*continued*)

TABLE I (*Continued*)

Mycorrhizal fungus	Pathogen	Host plant	References
Glomus versiforme	*Ralstonia solanacearum*	*Lycopersicon esculentum* (Tomato)	Zhu and Yao (2004)
	Verticillium dahliae	*Gossypium hirsutum* (Cotton)	Liu (1995)
Ectomycorrhizal fungi			
Clitocybe claviceps	*Fusarium moniliforme*	*Picea glauca* (White spruce)	Chakravarty *et al.* (1999)
Hebeloma crustiliniforme	*Phytophthora cambivora*	*Castanea sativa* (Chestnut)	Brazanti *et al.* (1999)
Hebeloma sinapizans	*Phytophthora cambivora*	*Castanea sativa* (Chestnut)	Brazanti *et al.* (1999)
Laccaria bicolor	*Fusarium moniliforme*	*Picea glauca* (White spruce)	Chakravarty *et al.* (1999)
Laccaria laccata	*Phytophthora cinnamomi*	*Castanea sativa* (Chestnut)	Brazanti *et al.* (1999)
	Rhizoctonia solani	*Pinus sylvestris* (Scots pine)	Chakravarty and Unestam (1987)
Paxillus involutus	*Cylindrocladium floridanum*	*Picea mariana* (Clack spruce)	Morin *et al.* (1999)
	Phytophthora cinnamomi	*Castanea sativa* (Chestnut)	Brazanti *et al.* (1999)
Pisolithus spp.	Natural plant parasitic nematodes	*Acacia* spp.	Founoune *et al.* (2002a)
	Meloidogyne javanica	*Acacia* spp.	Duponnois *et al.* (2000)
Pisolithus tinctorius	*Rhizoctonia solani*	*Pinus sylvestris* (Scots pine)	Chakravarty and Unestam (1987)
Scleroderma spp.	*Tylenchorenchus gladiolatus*	*Afzelia africana* (African hardwood)	Villenave and Duponnois (2002)

with plant defense mechanisms and induced resistance; and (4) development of an antagonistic microbiota. Thus, in (1) the mycorrhizal fungus acts directly on the pathogen, in (2) and (3) it acts on the plant, and in (4) it acts on the microbiota around the root.

Direct competition or inhibition may involve competition for photosynthate in or on the root, or for exudates and rhizodeposits external to the roots. There may also be competition for infection sites or space on the roots, and for ECM fungi, mechanical sheathing of the root forming a defensive barrier. The quantity and quality of exudates from the roots or mycorrhizal fungus could inhibit the pathogen including production of low levels of antibiotics or defense compounds, and there may be direct competition in the soil.

Enhanced or altered plant growth, nutrition, and morphology can involve increased nutrient uptake (particularly P), increased uptake of trace elements, drought tolerance, and decreased toxicity to salt and heavy metals, all providing alleviation of abiotic stress. The age of the plant when a pathogen attacks the root can also influence the biocontrol level seen (Idoia *et al.*, 2004). Similarly, there may be changes in plant hormone levels and damage compensation. All these effects would provide a healthier plant potentially more tolerant to pathogen attack.

Biochemical changes associated with plant defense mechanisms and induced resistance have been a major focus in recent years. Production of phenolics, terpenes, phytoalexins, specific amino acids, internal structural barriers, defense-related proteins, and increased DNA methylation and respiration have all been reported as involved in pathogen control. Combinations of these responses may also give rise to systemic-induced resistance throughout the plant. Potentially, colonization by mycorrhizal fungi could enable the plant to respond more rapidly to subsequent pathogen challenge by resistance mechanisms being preactivated.

Molecular approaches are now being applied to dissect the changes in signaling and defense mechanisms related to disease resistance induced in response to mycorrhizal colonization (Colditz *et al.*, 2005; Pozo *et al.*, 2002; Requena *et al.*, 1999). In a proteomics study, the proteins expressed in *G. intraradices*-colonized *Medicago truncatula* roots in response to infection by *Aphanomyces euteiches* showed similar changes to those induced by *A. euteiches* alone except for a proteasome subunit alpha type 4 which was increased in abundance (Colditz *et al.*, 2005). This protein is involved in protein degradation by the ATP/ubiquitin-mediated proteolysis pathway, which has been shown to play a key role in regulation of plant disease resistance responses in

other systems, with ubiquitin-associated proteins acting as signaling components in defense response signal cascades.

Development of a microbiota antagonistic to pathogens in soil around roots in response to mycorrhiza formation is a relatively recent concept (Andrade *et al.*, 1998) but as evidence has accumulated that the microbiota around the root can be changed in the presence of mycorrhizal fungi (see Section V), the need for further work in this area has been highlighted. One result of this has been the concept of utilizing combinations of biological disease control agents with mycorrhizal fungi to enhance disease control. A huge number of potential candidates that control soilborne plant pathogens when applied to seeds, roots, or soil are known (Whipps, 2001), but relatively few have so far been tested with mycorrhizal fungi. Dual inoculations of *Glomus* spp. with a variety of bacteria, including *Azospirillum* spp., *Bacillus* spp., *Pseudomonas* spp., and *Rhizobium* spp., and fungi, such as *Gliocladium* and *Trichoderma* spp., have resulted in either improved plant growth or decreased severity of several pathogens (Berta *et al.*, 2005; Whipps, 2004). With ECM fungi, a number of bacteria have been utilized as ECM helper bacteria (see Section IV) resulting in enhanced plant growth but there have been no studies involving pathogen control. Combinations of ECM fungi with other fungi are restricted to a single *in vitro* synthesis experiment involving *P. sylvestris, L. laccata*, and *Trichoderma virens* (Werner *et al.*, 2002) but there were no significant effects of the introduction of *T. virens*.

An important feature of these studies is to ensure that the biocontrol agents do not affect the activity of the mycorrhizal fungi and vice versa. Numerous studies have investigated these interactions and there are examples of bacteria and fungi stimulating, having no effect or inhibiting growth of mycorrhizal fungi; bacteria and fungi enhancing mycorrhiza formation and development; and cases where bacteria and fungi inhibit mycorrhizal formation (Barea *et al.*, 2005; Whipps, 2004). Similarly, mycorrhizal fungi can also stimulate or inhibit specific bacteria and saprotrophic fungi (see Section V.A and B), illustrating the diversity of interactions that are possible between mycorrhizal fungi and the soil microbiota including plant pathogens. These deserve further study.

VII. Conclusions

There is clearly considerable spatial and temporal variability of microbial community structure and functioning within the mycorrhizosphere with the region representing a mosaic of spatial habitats,

resulting from rhizoexudation and hyphal exudation, hyphal and root senescence, and the feeding habits of grazers. The mycorrhizosphere microbial community may play a role in supporting plant growth, by mobilizing nutrients and suppressing plant pathogens. The importance of these processes clearly depends on the characteristics of the mycorrhizal fungus species itself, but also on the host plant and soil and environmental variables.

The biological and chemical interactions which take place within the mycorrhizosphere are still largely unexplored, and furthermore the relative importance of the host and mycorrhizal fungus mycelium for directing interactions largely remains to be resolved. One of the key research challenges is to elucidate the mechanisms driving microbial community structure and functioning within the mycorrhizosphere, including the role of exudates and signal molecules. A variety of techniques have recently become available which will prove valuable to address these issues. These include stable isotope probing (Radajewski *et al.*, 2000) and the use of bromodeoxyuridine immunocapture and mRNA (Artursson and Jansson, 2003) to identify metabolically active organisms, and microarrays (Wu *et al.*, 2001) and metagenomic techniques (Tringe *et al.*, 2005) to profile microbial community structure and functioning. Furthermore, transcriptional profiling of mycorrhizosphere interactions (Duplessis *et al.*, 2005; Morel *et al.*, 2005; Schrey *et al.*, 2005), and the genome sequencing of mycorrhizal fungi and their host plants (Town, 2006; Tuskan *et al.*, 2004) will generate understanding of the mechanisms involved in mycorrhiza formation, including the role of free-living mycorrhizosphere organisms. Ultimately, this information should provide new possibilities to exploit biological interactions within the mycorrhizosphere for agricultural and environmental management.

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References

Abdel-Fattah, G. M., and Shabana, Y. M. (2002). Efficacy of the arbuscular mycorrhizal fungus *Glomus clarum* in protection of cowpea plants against root rot pathogen *Rhizoctonia solani*. *J. Plant Dis. Prot.* **109,** 207–215.

Abuzinadah, R. A., and Read, D. J. (1989). The role of proteins in the nitrogen nutrition of ectomycorrhizal plants. 4. The utilization of peptides by birch (*Betula pendula* L.) infected with different mycorrhizal fungi. *New Phytol.* **112,** 55–60.

Agerer, R. (2001). Exploration types of ectomycorrhizae: A proposal to classify ectomycorrhizal mycelial systems according to their patterns of differentiation and putative ecological importance. *Mycorrhiza* **11,** 107–114.

Ahonen-Jonnarth, U., van Hees, P. A. W., Lundstrom, U. S., and Finlay, R. D. (2000). Organic acids produced by mycorrhizal *Pinus sylvestris* exposed to elevated aluminium and heavy metal concentrations. *New Phytol.* **146,** 557–567.

Akiyama, K., Matsuzaki, K., and Hayashi, H. (2005). Plant sesquiterpenes induce hyphal branching in arbuscular mycorrhizal fungi. *Nature* **435,** 824–827.

Amora-Lazcano, E., Vazquez, M. M., and Azcon, R. (1998). Response of nitrogen-transforming microorganisms to arbuscular mycorrhizal fungi. *Biol. Fert. Soils* **27,** 65–70.

Andrade, G., Mihara, K. L., Linderman, R. G., and Bethlenfalvay, G. J. (1997). Bacteria from rhizosphere and hyphosphere soils of different arbuscular-mycorrhizal fungi. *Plant Soil* **192,** 71–79.

Andrade, G., Linderman, R. G., and Bethlenfalvay, G. J. (1998). Bacterial associations with the mycorrhizosphere and hyphosphere of the arbuscular mycorrhizal fungus *Glomus mosseae*. *Plant Soil* **202,** 79–87.

André, S., Neyra, M., and Duponnois, R. (2003). Arbuscular mycorrhizal symbiosis changes the colonization pattern of *Acacia tortilis* spp. *Raddiana* rhizosphere by two strains of rhizobia. *Microb. Ecol.* **45,** 137–144.

Artursson, V., and Jansson, J. K. (2003). Use of bromodeoxyuridine immunocapture to identify active bacteria associated with arbuscular mycorrhizal hyphae. *Appl. Environ. Microbiol.* **69,** 6208–6215.

Artursson, V., Finlay, R. D., and Jansson, J. K. (2005). Combined bromodeoxyuridine immunocapture and terminal-restriction fragment length polymorphism analysis highlights differences in the active soil bacterial metagenome due to *Glomus mosseae* inoculation or plant species. *Environ. Microbiol.* **7,** 1952–1966.

Aspray, T. A., Frey-Klett, P., Jones, J. E., Whipps, J. M., Garbaye, J., and Bending, G. D (2007). Mycorrhization helper bacteria: Non-specificity for enhancing mycorrhiza formation but specific effect on mycorrhiza architecture. *Mycorrhiza* (in press).

Aspray, T. A., Jones, E., Whipps, J. M., and Bending, G. D. (2006). Importance of mycorrhization helper bacteria cell density and metabolite localization for the *Pinus sylvestris-Lactarius rufus* symbiosis. *FEMS Microbiol. Ecol.* **56,** 25–33.

Azaizeh, H. A., Marschner, H., Romheld, V., and Wittenmayer, L. (1995). Effects of a vesicular-arbuscular mycorrhizal fungus and other soil-microorganisms on growth, mineral nutrient acquisition and root exudation of soil-grown maize plants. *Mycorrhiza* **5,** 321–327.

Azcón, R. (1987). Germination and hyphal growth of *Glomus mosseae in vitro*: Effects of rhizosphere bacteria and cell-free culture media. *Soil Biol. Biochem.* **19,** 417–419.

Bago, B., Azcon-Aguilar, C., and Piche, Y. (1998). Architecture and developmental dynamics of the external mycelium of the arbuscular mycorrhizal fungus *Glomus intraradices* grown under monoxenic conditions. *Mycologia* **90,** 52–62.

Bansal, M., and Mukerji, K. G. (1994). Positive correlation between VAM-induced changes in root exudation and mycorrhizosphere mycoflora. *Mycorrhiza* **5,** 39–44.

Barea, J. M., Toro, M., Orozco, M. O., Campos, E., and Azcón, R. (2002). The application of isotopic (^{32}P and ^{15}N) dilution techniques to evaluate the interactive effect of phosphate-solubilizing rhizobacteria, mycorrhizal fungi and *Rhizobium* to improve the agronomic efficiency of rock phosphate for legume crops. *Nutr. Cycl. Agroecosyst.* **63,** 35–42.

Barea, J. M., Pozo, M. J., Azcón, R., and Azcon-Aguilar, C. (2005). Microbial co-operation in the rhizosphere. *J. Exp. Bot.* **56,** 1761–1778.

Barkmann, J., and Schwintzer, C. R. (1998). Rapid N_2 fixation in pines? Results of a Maine field study. *Ecology* **79,** 1453–1457.

Beguiristain, T., and Lapeyrie, F. (1997). Host plant stimulates hypaphorine accumulation in *Pisolithus tinctorius* hyphae during ectomycorrhizal infection while excreted fungal hypaphorine controls root hair development. *New Phytol.* **136,** 525–532.

Bending, G. D. (2003). Litter decomposition, ectomycorrhizal roots and the 'Gadgil' effect. *New Phytol.* **158,** 228–229.

Bending, G. D., and Read, D. J. (1995). The structure and function of the vegetative mycelium of ectomycorrhizal plants. 5. Foraging behavior and translocation of nutrients from exploited litter. *New Phytol.* **130,** 401–409.

Bending, G. D., Poole, E. J., Whipps, J. M., and Read, D. J. (2002). Characterisation of bacteria from *Pinus sylvestris-Suillus luteus* mycorrhizas and their effects on root-fungus interactions and plant growth. *FEMS Microbiol. Ecol.* **39,** 219–227.

Berta, G., Sampo, S., Gamalero, E., Massa, N., and Lemanceau, P. (2005). Suppression of *Rhizoctonia* root-rot of tomato by *Glomus mosseae* BEG12 and *Pseudomonas fluorescens* A6RI is associated with their effect on the pathogen growth and on root morphogenesis. *Eur. J. Plant Pathol.* **111,** 279–288.

Bertaux, J., Schmid, M., Hutzler, P., Churin, J. L., Hartmann, A., Garbaye, J., and Frey-Klett, P. (2005). Occurrence and distribution of endobacteria in the plant-associated mycelium of the ectomycorrhizal fungus *Laccaria bicolor* S238N. *Environ. Microbiol.* **7,** 1786–1795.

Binet, P., Portal, J. M., and Leyval, C. (2000). Fate of polycyclic aromatic hydrocarbons (PAH) in the rhizosphere and mycorrhizosphere of ryegrass. *Plant Soil* **227,** 207–213.

Bomberg, M., Jurgens, G., Saano, A., Sen, R., and Timonen, S. (2003). Nested PCR detection of archaea in defined compartments of pine mycorrhizospheres developed in boreal forest humus microcosms. *FEMS Microbiol. Ecol.* **43,** 163–171.

Bowen, G. D., and Theodorou, C. (1979). Interactions between bacteria and ectomycorrhizal fungi. *Soil Biol. Biochem.* **11,** 119–126.

Branzanti, M. B., Rocca, E., and Pisi, A. (1999). Effect of ectomycorrhizal fungi on chestnut ink disease. *Mycorrhiza* **9,** 103–109.

Brulé, C., Frey-Klett, P., Pierrat, J. C., Courrier, S., Gérard, F., Lemoine, M. C., Rousselet, J. L., Sommer, G., and Garbaye, J. (2001). Survival in the soil of the ectomycorrhizal fungus *Laccaria bicolor* and the effects of a mycorrhiza helper *Pseudomonas fluorescens*. *Soil Biol. Biochem.* **33,** 1683–1694.

Budi, S. W., van Tuinen, D., Martinotti, G., and Gianinazzi, S. (1999). Isolation from the *Sorghum bicolor* mycorrhizosphere of a bacterium compatible with arbuscular mycorrhiza development and antagonistic towards soilborne fungal pathogens. *Appl. Environ. Microbiol.* **65,** 5148–5150.

Buttner, D., Lorenz, C., Weber, E., and Bonas, U. (2006). Targeting of two effector protein classes to the type III secretion system by a HpaC- and HpaB-dependent protein complex from *Xanthomonas campestris* pv. *vesicatoria*. *Mol. Microbiol.* **59,** 513–527.

Cairney, J. W. G., and Meharg, A. A. (2002). Interactions between ectomycorrhizal fungi and soil saprotrophs: Implications for decomposition of organic matter in soils and degradation of organic pollutants in the rhizosphere. *Can. J. Bot.* **80,** 803–809.

Camprubí, A., Calvet, C., and Estaún, V. (1995). Growth enhancement of *Citrus reshni* after inoculation with *Glomus intraradices* and *Trichoderma aureoviride* and associated effects on microbial populations and enzyme activity in potting mixes. *Plant Soil* **173,** 233–238.

Carpenter-Boggs, L., Loynachan, T. E., and Stahl, P. D. (1995). Spore germination of *Gigaspora margarita* stimulated by volatiles of soil-isolated actinomycetes. *Soil Biol. Biochem.* **27,** 1445–1451.

Chakravarty, P., and Unestam, T. (1987). Differential influence of ectomycorrhizae on plant growth and disease resistance in *Pinus sylvestris* seedlings. *J. Phytopathol.* **120,** 104–120.

Chakravarty, P., Khasa, D., Dancik, B., Sigler, L., Wichlacz, M., Trifonov, L. S., and Ayer, W. A. (1999). Integrated control of *Fusarium* damping-off in conifer seedlings. *J. Plant Dis. Prot.* **106,** 342–352.

Christensen, H., and Jakobsen, I. (1993). Reduction of bacterial-growth by a vesicular-arbuscular mycorrhizal fungus in the rhizosphere of cucumber (*Cucumis-sativus* L.). *Biol. Fert. Soils* **15,** 253–258.

Colditz, F., Braun, H. P., Jacquet, C., Niehaus, K., and Krajinski, F. (2005). Proteomic profiling unravels insights into the underlying increased *Aphanomyces euteiches*-tolerance of *Medicago truncatula*. *Plant Mol. Biol.* **59,** 387–406.

Davis, R. M., and Menge, J. A. (1980). Influence of *Glomus fasciculatus* and soil phosphorus on Phytophthora root rot of citrus. *Phytopathology* **70,** 447–452.

Declerck, S., Risede, J. M., Rufyikiri, G., and Delvaux, B. (2002). Effects of arbuscular mycorrhizal fungi on severity of root rot of bananas caused by *Cylindrocladium spathiphylli*. *Plant Pathol.* **51,** 109–115.

Dehne, H. W. (1982). Interaction between vesicular-arbuscular mycorrhizal fungi and plant pathogens. *Phytopathology* **72,** 1115–1119.

Diaz, G., Azcon-Aguilar, C., and Honrubia, M. (1996). Influence of arbuscular mycorrhizae on heavy metal (Zn and Pb) uptake and growth of *Lygeum spartum* and *Anthyllis cytisoides*. *Plant Soil* **180,** 241–249.

Didden, V. A. M. (1993). Ecology of terrestrial enchytraedae. *Pedobiology* **37,** 2–29.

Driver, J. D., Holben, W. E., and Rillig, M. C. (2005). Characterization of glomalin as a hyphal wall component of arbuscular mycorrhizal fungi. *Soil Biol. Biochem.* **37,** 101–106.

Duchesne, L. C. (1994). Role of ectomycorrhizal fungi in biocontrol. *In* ''Mycorrhizae and Plant Health'' (F. L. Pfleger and R. G. Linderman, eds.), pp. 27–45. APS Press, St. Paul, MN.

Dunstan, W. A., Malajczuk, N., and Dell, B. (1998). Effects of bacteria on mycorrhizal development and growth of container grown *Eucalyptus diversicolor* F. Muell. seedlings. *Plant Soil* **201,** 241–249.

Duplessis, S., Courty, P. E., Tagu, D., and Martin, F. (2005). Transcript patterns associated with ectomycorrhiza development in *Eucalyptus globulus* and *Pisolithus microcarpus*. *New Phytol.* **165,** 599–611.

Duponnois, R. (1992). Les bactéries auxiliaires de la mycorhization du Douglas Fir (*Pseudotsuga menziesii* (Mirb.) Franco) par *Laccaria laccata* souche S238, l'Université de Nancy, France.

Duponnois, R., and Garbaye, J. (1990). Some mechanisms involved in growth stimulation of ectomycorrhizal fungi by bacteria. *Can. J. Bot.* **68,** 2148–2152.

Duponnois, R., and Garbaye, J. (1991). Effect of dual inoculation of Douglas fir with the ectomycorrhizal fungus *Laccaria laccata* and mycorrhization helper bacteria (MHB) in two bare-root forest nurseries. *Plant Soil* **138,** 169–176.

Duponnois, R., and Plenchette, C. (2003). A mycorrhiza helper bacterium enhances ectomycorrhizal and endomycorrhizal symbiosis of Australian *Acacia* species. *Mycorrhiza* **13,** 85–91.

Duponnois, R., Garbaye, J., Bouchard, D., and Churin, J. L. (1993). The fungus-specificity of mycorrhization helper bacteria (MHBs) used as an alternative to soil fumigation for ectomycorrhizal inoculation of bare-root Douglas-fir planting stocks with *Laccaria laccata*. *Plant Soil* **157,** 257–262.

Duponnois, R., Founoune, H., Lesueur, D., Thiolouse, J., and Neyra, M. (2000). Ectomycorrhization of six *Acacia auriculiformis* provenances from Australia, Papua New Guinea and Senegal in glasshouse conditions: Effect on the plant growth and on the multiplication of plant parasitic nematodes. *Aust. J. Exp. Agric.* **40,** 443–450.

Feng, G., Zhang, F. S., Li, X. L., Tian, C. Y., Tang, C., and Rengel, Z. (2002). Improved tolerance of maize plants to salt stress by arbuscular mycorrhiza is related to higher accumulation of soluble sugars in roots. *Mycorrhiza* **12,** 185–190.

Filion, M., St-Arnaud, M., and Jabaji-Hare, S. H. (2003). Quantification of *Fusarium solani* f. sp. *phaseoli* in mycorrhizal bean plants and surrounding mycorrhizosphere soil using real-time polymerase chain reaction and direct isolations on selective media. *Phytopathology* **93,** 229–235.

Founoune, H., Duponnois, R., and Ba, A. M. (2002a). Ectomycorrhization of *Acacia mangium*, Willd. and *Acacia holosericea*, A. Cunn ex G. Don in Senegal. Impact on plant growth, populations of indigenous symbiotic microorganisms and plant parasitic nematodes. *J. Arid. Environ.* **50,** 325–332.

Founoune, H., Duponnois, R., Meyer, J. M., Thioulouse, J., Masse, D., Chotte, J. L., and Neyra, M. (2002b). Interactions between ectomycorrhizal symbiosis and fluorescent pseudomonads on *Acacia holosericea*: Isolation of mycorrhiza helper bacteria (MHB) from a Soudano-Sahelian soil. *FEMS Microbiol. Ecol.* **41,** 37–46.

Frank, B. (1885). Ueber die auf Wurzelsymbiose beruhende Ernährung gewisser Bäume durch unterirdische Pilze. *Ber. Dtsch. Bot. Ges.* **3,** 128–145.

Frey, P., Frey-Klett, P., Garbaye, J., Berge, O., and Heulin, T. (1997). Metabolic and genotypic fingerprinting of fluorescent pseudomonads associated with the Douglas fir-*Laccaria bicolor* mycorrhizosphere. *Appl. Environ. Microbiol.* **63,** 1852–1860.

Frey-Klett, P., Churin, J. L., Pierrat, J. C., and Garbaye, J. (1999). Dose effect in the dual inoculation of an ectomycorrhizal fungus and a mycorrhiza helper bacterium in two forest nurseries. *Soil Biol. Biochem.* **31,** 1555–1562.

Frey-Klett, P., Chavatte, M., Clausse, M. L., Courrier, S., Le Roux, C., Raaijmakers, J., Martinotti, M. G., Pierrat, J. C., and Garbaye, J. (2005). Ectomycorrhizal symbiosis affects functional diversity of rhizosphere fluorescent pseudomonads. *New Phytol.* **165,** 317–328.

Gadgil, R. L., and Gadgil, P. D. (1971). Mycorrhiza and litter decomposition. *Nature* **233,** 133.

Gadgil, R. L., and Gadgil, P. D. (1975). Suppression of litter decomposition by mycorrhizal roots of *Pinus radiata*. *NZ J. For. Sci.* **5,** 33–41.

Gamalero, E., Fracchia, L., Cavaletto, M., Garbaye, J., Frey-Klett, P., Varese, G. C., and Martinotti, M. G. (2003). Characterisation of functional traits of two fluorescent pseudomonads isolated from basidiomes of ectomycorrhizal fungi. *Soil Biol. Biochem.* **35,** 55–65.

Gange, A. C., and West, H. M. (1994). Interactions between arbuscular mycorrhizal fungi and foliar-feeding insects in *Plantago lanceolata* L. *New Phytol.* **128,** 79–87.

Garbaye, J. (1983). Premiers résultats de recherche sur la compétitivité des champignons ectomycorhiziens. *Plant Soil* **71,** 303–308.

Garbaye, J. (1994). Tansley review No. 76. Helper bacteria: A new dimension to the mycorrhizal symbiosis. *New Phytol.* **128,** 197–210.

Garbaye, J., and Bowen, G. D. (1987). Effect of different microflora on the success of ectomycorrhizal inoculation of *Pinus radiata*. *Can. J. For. Res.* **17,** 941–943.

Garcia-Garrido, J. M., and Ocampo, J. A. (1989). Effect of VA mycorrhizal infection of tomato on damage caused by *Pseudomonas syringae*. *Soil Biol. Biochem.* **21,** 165–167.

Garmendia, I., Goicoechea, N., and Aguirreolea, J. (2004). Effectiveness of three *Glomus* species in protection of pepper (*Capsicum annuum* L.) against verticillium wilt. *Biol. Control* **31,** 296–305.

Genney, D. R., Alexander, I. J., Killham, K., and Meharg, A. A. (2004). Degradation of the polycyclic aromatic hydrocarbon (PAH) fluorene is retarded in a Scots pine ectomycorrhizosphere. *New Phytol.* **163,** 641–649.

Gosling, P., Hodge, A., Goodlass, G., and Bending, G. D. (2006). Arbuscular mycorrhizal fungi and organic farming. *Agric. Ecosyst. Environ.* **113,** 17–35.

Griffiths, R. P., Baham, J. E., and Caldwell, B. A. (1994). Soil solution chemistry of ectomycorrhizal mats in forest soil. *Soil Biol. Biochem.* **26,** 331–337.

Ham, J. H., Cui, Y., Alfano, J. R., Rodriguez-Palenzuela, P., Rojas, C. M., Chatterjee, A. K., and Collmer, A. (2004). Analysis of *Erwinia chrysanthemi* EC16 pelE: UidA, peIL: UidA, and hrpN : UidA mutants reveals strain-specific a typical regulation of the Hrp type III secretion system. *Mol Plant Microbe Interact.* **17,** 184–194.

Harrier, L. A., and Watson, C. C. (2004). The potential role of arbuscular mycorrhizal (AM) fungi in the bioprotection of plants against soil-borne pathogens in organic and/or other sustainable farming systems. *Pest Manag. Sci.* **60,** 149–157.

Hart, M. M., and Reader, R. J. (2002). Taxonomic basis for variation in the colonization strategy of arbuscular mycorrhizal fungi. *New Phytol.* **153,** 335–344.

Haselwandter, K. (1995). Mycorrhizal fungi-siderophore production. *Crit. Rev. Biotech.* **15,** 287–291.

Heinonsalo, J., Jorgensen, K. S., and Sen, R. (2001). Microcosm-based analyses of Scots pine seedling growth, ectomycorrhizal fungal community structure and bacterial carbon utilization profiles in boreal forest humus and underlying alluvial mineral horizons. *FEMS Microbiol. Ecol.* **36,** 73–84.

Hinsinger, P., Gobran, G. R., Gregory, P. J., and Wenzel, W. W. (2005). Rhizosphere geometry and heterogeneity arising from root-mediated physical and chemical processes. *New Phytol.* **168,** 293–303.

Hiol, F. H., Dixon, R. K., and Curl, E. A. (1994). The feeding preference of mycophagous collembola varies with the ectomycorrhizal symbiont. *Mycorrhiza* **5,** 99–103.

Hodge, A., Campbell, C. D., and Fitter, A. H. (2001). An arbuscular mycorrhizal fungus accelerates decomposition and acquires nitrogen directly from organic material. *Nature* **413,** 297–299.

Hogberg, M. N., and Hogberg, P. (2002). Extramatrical ectomycorrhizal mycelium contributes one-third of microbial biomass and produces, together with associated roots, half the dissolved organic carbon in a forest soil. *New Phytol.* **154,** 791–795.

Idoia, G., Nieves, G., and Jone, A. (2004). Plant phenology influences the effect of mycorrhizal fungi on the development of *Verticillium*-induced wilt in pepper. *Eur. J. Plant Pathol.* **110,** 227–238.

Izumi, H., Anderson, I. C., Alexander, I. J., Killham, K., and Moore, E. R. B. (2006). Endobacteria in some ectomycorrhiza of Scots pine (*Pinus sylvestris*). *FEMS Microbiol. Ecol.* **56,** 34–43.

Jargeat, P., Cosseau, C., Ola'h, B., Jauneau, A., Bonfante, P., Batut, J., and Becard, G. (2004). Isolation, free-living capacities, and genome structure of ''*Candidatus*

glomeribacter gigasporarum,'' the endocellular bacterium of the mycorrhizal fungus *Gigaspora margarita*. *J. Bacteriol.* **186,** 6876–6884.

Jentschke, G., Bonkowski, M., Godbold, D. L., and Scheu, S. (1995). Soil protozoa and forest tree growth-non-nutritional effects and interaction with mycorrhizae. *Biol. Fert. Soils* **20,** 263–269.

Johansson, J. F., Paul, L. R., and Finlay, R. D. (2004). Microbial interactions in the mycorrhizosphere and their significance for sustainable agriculture. *FEMS Microbiol. Ecol.* **48,** 1–13.

Johnson, D., Ijdo, M., Genney, D. R., Anderson, I. C., and Alexander, I. J. (2005a). How do plants regulate the function, community structure, and diversity of mycorrhizal fungi? *J. Exp. Bot.* **56,** 1751–1760.

Johnson, D., Krsek, M., Wellington, E. M. H., Stott, A. W., Cole, L., Bardgett, R. D., Read, D. J., and Leake, J. R. (2005b). Soil invertebrates disrupt carbon flow through fungal networks. *Science* **309,** 1047–1047.

Joner, E. J., and Leyval, C. (2001). Influence of arbuscular mycorrhiza on clover and ryegrass grown together in a soil spiked with polycyclic aromatic hydrocarbons. *Mycorrhiza* **10,** 155–159.

Jones, D. L., Hodge, A., and Kuzyakov, Y. (2004). Plant and mycorrhizal regulation of rhizodeposition. *New Phytol.* **163,** 459–480.

Kasiamdari, R. S., Smith, S. E., Smith, F. A., and Scott, E. S. (2002). Influence of the mycorrhizal fungus, *Glomus coronatum*, and soil phosphorus on infection and disease caused by binucleate *Rhizoctonia* and *Rhizoctonia solani* on mung bean (*Vigna radiata*). *Plant Soil* **238,** 235–244.

Klironomos, J. N., and Ursic, M. (1998). Density-dependent grazing on the extraradical hyphal network of the arbuscular mycorrhizal fungus, *Glomus intraradices*, by the collembolan, *Folsomia candida*. *Biol. Fert. Soils* **26,** 250–253.

Knight, W. G., Allen, M. F., Jurinak, J. J., and Dudley, L. M. (1989). Elevated carbon-dioxide and solution phosphorus in soil with vesicular-arbuscular mycorrhizal western wheatgrass. *Soil Sci. Soc. Am. J.* **53,** 1075–1082.

Koide, R. T., and Wu, T. (2003). Ectomycorrhizas and retarded decomposition in a *Pinus resinosa* plantation. *New Phytol.* **158,** 401–407.

Koivula, T. T., Salkinoja-Salonen, M., Peltola, R., and Romantschuk, M. (2004). Pyrene degradation in forest humus microcosms with or without pine and its mycorrhizal fungus. *J. Environ. Qual.* **33,** 45–53.

Lapeyrie, F., Chilvers, G. A., and Bhem, C. A. (1987). Oxalic acid synthesis by the mycorrhizal fungus *Paxillus involutus* (Batsch ex Fr) Fr. *New Phytol.* **106,** 139–146.

Larsen, J., and Bødker, L. (2001). Interactions between pea root-inhabiting fungi examined using signature fatty acids. *New Phytol.* **149,** 487–493.

Larsen, J., Olsson, P. A., and Jakobsen, I. (1998). The use of fatty acid signatures to study mycelial interactions between the arbuscular mycorrhizal fungus *Glomus intraradices* and the saprotrophic fungus *Fusarium culmorum* in root-free soil. *Mycol. Res.* **102,** 1491–1496.

Leveau, J. H. J., and Lindow, S. E. (2005). Utilization of the plant hormone indole-3-acetic acid for growth by *Pseudomonas putida* strain 1290†. *Appl. Environ. Microbiol.* **71,** 2365–2371.

Leyval, C., and Berthelin, J. (1993). Rhizodeposition and net release of soluble organic-compounds by pine and beech seedlings inoculated with rhizobacteria and ectomycorrhizal fungi. *Biol. Fert. Soils* **15,** 259–267.

Li, C. Y., Massicote, H. B., and Moore, L. V. H. (1992). Nitrogen-fixing *Bacillus* sp. associated with Douglas-fir tuberculate ectomycorrhizae. *Plant Soil* **140,** 35–40.

Liao, C. H., Sasaki, K., Nagahashi, G., and Hicks, K. B. (1992). Cloning and characterisation of a pectate lyase gene from the soft-rotting bacterium *Pseudomonas viridiflava*. *Mol. Plant Microbe Interact.* **5,** 301–308.

Lindahl, B., Stenlid, J., and Finlay, R. (2001). Effects of resource availability on mycelial interactions and ^{32}P transfer between a saprotrophic and an ectomycorrhizal fungus in soil microcosms. *FEMS Microbiol. Ecol.* **38,** 43–52.

Linderman, R. G. (1988). Mycorrhizal interactions with the rhizosphere microflora-the mycorrhizosphere effect. *Phytopathology* **78,** 366–371.

Liu, R. J. (1995). Effect of vesicular-arbuscular mycorrhizal fungi on *Verticillium* wilt of cotton. *Mycorrhiza* **5,** 293–297.

Mada, R. J., and Bagyaraj, D. J. (1993). Root exudation from *Leucaena leucocephala* in relation to mycorrhizal colonization. *World J. Microb. Biotech.* **9,** 342–344.

Mamatha, G., Bagyaraj, D. J., and Jaganath, S. (2002). Inoculation of field-established mulberry and papaya with arbuscular mycorrhizal fungi and a mycorrhiza helper bacterium. *Mycorrhiza* **12,** 313–316.

Mark, G. L., and Cassells, A. C. (1996). Genotype-dependence in the interaction between *Glomus fistulosum, Phytophthora fragariae* and the wild strawberry (*Fragaria vesca*). *Plant Soil* **185,** 233–239.

Marschner, P., Crowley, D. E., and Higashi, R. M. (1997). Root exudation and physiological status of a root-colonizing fluorescent pseudomonad in mycorrhizal and non-mycorrhizal pepper (*Capsicum annuum* L.). *Plant Soil* **189,** 11–20.

Matsubara, Y., Ohba, N., and Fukui, H. (2001). Effect of arbuscular mycorrhizal fungus infection on the incidence of fusarium root rot in asparagus seedlings. *J. Jpn. Soc. Hortic. Sci.* **70,** 202–206.

Mayo, K., and Davis, R. E. (1986). Stimulation of germination of spores of *Glomus versiforme* by spore-associated bacteria. *Mycologia* **78,** 426–431.

McAllister, C. B., Garcia-Garrido, J. M., Garcia-Romera, I., Godeas, A., and Ocampo, J. A. (1997). Interaction between *Alternaria alternata* or *Fusarium equiseti* and *Glomus mosseae* and its effects on plant growth. *Biol. Fert. Soils* **24,** 301–305.

Meyer, J. R., and Linderman, R. G. (1986). Selective influence on populations of rhizosphere or rhizoplane bacteria and actinomycetes by mycorrhizas formed by *Glomus fasciculatum*. *Soil Biol. Biochem.* **18,** 191–196.

Miller, R. M., Reinhardt, D. R., and Jastrow, J. D. (1995). External hyphal production of vesicular-arbuscular mycorrhizal fungi in pasture and tallgrass prairie communities. *Oecologia* **103,** 17–23.

Minerdi, D., Fani, R., Gallo, R., Boarino, A., and Bonfante, P. (2001). Nitrogen fixation genes in an endosymbiotic *Burkholderia* strain. *Appl. Environ. Microbiol.* **67,** 725–732.

Molina, M. A., Ramos, J. L., and Espinosa-Urgel, M. (2006). A two-partner secretion system is involved in seed and root colonization and iron uptake by *Pseudomonas putida* KT2440. *Environ. Microbiol.* **8,** 639–647.

Morel, M., Jacob, C., Kohler, A., Johansson, T., Martin, F., Chalot, M., and Brun, A. (2005). Identification of genes differentially expressed in extraradical mycelium and ectomycorrhizal roots during *Paxillus involutus-Betula pendula* ectomycorrhizal symbiosis. *Appl. Environ. Microbiol.* **71,** 382–391.

Morin, C., Samson, J., and Dessureault, M. (1999). Protection of black spruce seedlings against *Cylindrocladium* root rot with ectomycorrhizal fungi. *Can. J. Bot.* **77,** 169–174.

Norman, J. R., Atkinson, D., and Hooker, J. E. (1996). Arbuscular mycorrhizal fungal-induced alteration to root architecture in strawberry and induced resistance to the root pathogen *Phytophthora fragariae*. *Plant Soil* **185,** 191–198.

Nurmiaho-Lassila, E. L., Timonen, S., Haahtela, K., and Sen, R. (1997). Bacterial colonization patterns of intact *Pinus sylvestris* mycorrhizospheres in dry pine forest soil: An electron microscopy study. *Can. J. Microbiol.* **43,** 1017–1035.

Olsson, P. A., Francis, R., Read, D. J., and Soderstrom, B. (1998). Growth of arbuscular mycorrhizal mycelium in calcareous dune sand and its interaction with other soil microorganisms as estimated by measurement of specific fatty acids. *Plant Soil* **201,** 9–16.

Osorio, N. W., and Habte, M. (2001). Synergistic influence of an arbuscular mycorrhizal fungus and a P solubilizing fungus on growth and P uptake of *Leucaena leucocephala* in an oxisol. *Arid Land Res. Manag.* **15,** 263–274.

Patten, C. L., and Glick, B. R. (2002). Role of *Pseudomonas putida* indoleacetic acid in development of the host plant root system. *Appl. Environ. Microbiol.* **68,** 3795–3801.

Pierwola, A., Krupinski, T., Zalupski, P., Chiarelli, M., and Castignetti, D. (2004). Degradation pathway and generation of monohydroxamic acids from the trihydroxamate siderophore deferrioxamine B. *Appl. Environ. Microbiol.* **70,** 831–836.

Pinochet, J., Fernandez, C., Jiazme, M. D., and Tenoury, P. (1997). Micropropagated banana infected with *Meloidogyne javanica* responds to *Glomus intraradices* and phosphorus. *HortScience* **32,** 101–103.

Poole, E. J., Bending, G. D., Whipps, J. M., and Read, D. J. (2001). Bacteria associated with *Pinus sylvestris-Lactarius rufus* ectomycorrhizas and their effects on mycorrhiza formation *in vitro*. *New Phytol.* **151,** 743–751.

Pozo, M. J., Slezack-Deschaumes, S., Dumas-Gaudot, E., Gianinazzi, S., and Azcón-Aguilar, C. (2002). Plant defense responses induced by arbuscular mycorrhizal fungi. *In* ''Mycorrhizal Technology in Agriculture from Genes to Bioproducts'' (S. Gianinazzi, H. Schüepp, J. M. Barea and K. Haselwandter, eds.), pp. 103–111. Birkhäuser Verlag, Basel.

Radajewski, S., Ineson, P., Parekh, N. R., and Murrell, J. C. (2000). Stable-isotope probing as a tool in microbial ecology. *Nature* **403,** 646–649.

Rambelli, A. (1973). The rhizosphere of mycorrhizae. *In* ''Ectomycorrhizae: Their Ecology and Physiology'' (G. C. Marks and T. T. Kozlowski, eds.), pp. 299–349. Academic Press, New York.

Requena, N., Jimenez, I., Toro, M., and Barea, J. M. (1997). Interactions between plant-growth-promoting rhizobacteria (PGPR), arbuscular mycorrhizal fungi and *Rhizobium* spp. in the rhizosphere of *Anthyllis cytisoides*, a model legume for revegetation in mediterranean semi-arid ecosystems. *New Phytol.* **136,** 667–677.

Requena, N., Fuller, P., and Franken, P. (1999). Molecular characterization of GmFOX2, an evolutionarily highly conserved gene from the mycorrhizal fungus *Glomus mosseae*, down-regulated during interaction with rhizobacteria. *Mol. Plant Microbe Interact.* **12,** 934–942.

Requena, N., Perez-Solis, E., Azcón-Aguilar, C., Jeffries, P., and Barea, J. M. (2001). Management of indigenous plant-microbe symbioses aids restoration of desertified ecosystems. *Appl. Environ. Microbiol.* **67,** 495–498.

Richardson, A. E. (2001). Prospects for using soil microorganisms to improve the acquisition of phosphorus by plants. *Aust J. Plant Physiol.* **28,** 897–906.

Ridge, E. H., and Theodorou, C. (1972). The effect of soil fumigation on microbial recolonisation and mycorrhizal infection. *Soil Biol. Biochem.* **4,** 1507.

Rillig, M. C., Wright, S. F., Nichols, K. A., Schmidt, W. F., and Torn, M. S. (2001). Large contribution of arbuscular mycorrhizal fungi to soil carbon pools in tropical forest soils. *Plant Soil* **233,** 167–177.

Roncardori, R. W., and Hussey, R. S. (1977). Interaction of the endomycorrhizal fungus *Gigaspora margarita* and the root knot nematode on cotton. *Phytopathology* **67,** 1507–1511.

Ronn, R., Gavito, M., Larsen, J., Jakobsen, I., Frederiksen, H., and Christensen, S. (2002). Response of free-living soil protozoa and microorganisms to elevated atmospheric CO_2 and presence of mycorrhiza. *Soil Biol. Biochem.* **34,** 923–932.

Ross, J. P. (1972). Influence of *Endogone* mycorrhiza on *Phytophthora* rot of soybean. *Phytopathology* **62,** 896–897.

Rousseau, A., Benhamou, N., Chet, I., and Piche, Y. (1996). Mycoparasitism of the extramatrical phase of *Glomus intraradices* by *Trichoderma harzianum*. *Phytopathology* **86,** 434–443.

Rozycki, H., Dahm, H., Strzelczyk, E., and Li, C. Y. (1999). Diazotrophic bacteria in root-free soil and in the root zone of pine (*Pinus sylvestris* L.) and oak (*Quercus robur* L.). *Appl. Soil Ecol.* **12,** 239–250.

Ruiz-Lozano, J. M., Collados, C., Barea, J. M., and Azcón, R. (2001). Arbuscular mycorrhizal symbiosis can alleviate drought-induced nodule senescence in soybean plants. *New Phytol.* **151,** 493–502.

Sarand, I., Timonen, S., Nurmiaho-Lassila, E. L., Koivula, T., Haahtela, K., Romantschuk, M., and Sen, R. (1998). Microbial biofilms and catabolic plasmid harbouring degradative fluorescent pseudomonads in Scots pine mycorrhizospheres developed on petroleum contaminated soil. *FEMS Microbiol. Ecol.* **27,** 115–126.

Schelkle, M., and Peterson, R. L. (1996). Suppression of common root pathogens by helper bacteria and ectomycorrhizal fungi *in vitro*. *Mycorrhiza* **6,** 481–485.

Schneider, K., Renker, C., and Maraun, M. (2005). Oribatid mite (Acari, Oribatida) feeding on ectomycorrhizal fungi. *Mycorrhiza* **16,** 67–72.

Schrey, S. D., Schellhammer, M., Ecke, M., Hampp, R., and Tarkka, M. T. (2005). Mycorrhiza helper bacterium *Streptomyces* AcH 505 induces differential gene expression in the ectomycorrhizal fungus *Amantia muscaria*. *New Phytol.* **168,** 205–216.

Schussler, A., Schwarzott, D., and Walker, C. (2001). A new fungal phylum, the Glomeromycota: Phylogeny and evolution. *Mycol. Res.* **105,** 1413–1421.

Secilia, J., and Bagyaraj, D. J. (1987). Bacteria and actinomycetes associated with pot cultures of vesicular arbuscular mycorrhizas. *Can. J. Microbiol.* **33,** 1069–1073.

Smith, S. E., and Read, D. J. (1997). ''Mycorrhizal Symbiosis.'' Academic Press, London.

Staddon, P. L., Ramsey, C. B., Ostle, N., Ineson, P., and Fitter, A. H. (2003). Rapid turnover of hyphae of mycorrhizal fungi determined by AMS microanalysis of C^{14}. *Science* **300,** 1138–1140.

Strobel, N. E., and Sinclair, W. A. (1991). Influence of temperature and pathogen aggressiveness on biological control of *Fusarium* root rot by *Laccaria bicolor* in Douglas-fir. *Phytopathology* **81,** 415–420.

Summerbell, R. C. (2005). From Lamarckian fertilizers to fungal castles: Recapturing the pre-1985 literature on endophytic and saprotrophic fungi associated with ectomycorrhizal root systems. *Studies Mycol.* **53,** 191–256.

Sun, Y. P., Unestam, T., Lucas, S. D., Johanson, K. J., Kenne, L., and Finlay, R. (1999). Exudation-reabsorption in a mycorrhizal fungus, the dynamic interface for interaction with soil and soil microorganisms. *Mycorrhiza* **9,** 137–144.

Talavera, M., Itou, K., and Mizukubo, T. (2001). Reduction of nematode damage by root colonisation with arbuscular mycorrhiza (*Glomus* spp.) in tomato-*Meloidogyne incognita* (Tylenchida: Meloidogynidae) and carrot-*Pratylenchus penetrans* (Tylenchida: Pratylenchidae). *Appl. Entomol. Zool.* **36,** 387–392.

Tarafdar, J. C., and Marschner, H. (1995). Dual inoculation with *Aspergillus fumigatus* and *Glomus mosseae* enhances biomass production and nutrient-uptake in wheat (*Triticum aestivum* L) supplied with organic phosphorus as Na phytate. *Plant Soil* **173,** 97–102.

Timonen, S., Jorgensen, K. S., Haahtela, K., and Sen, R. (1998). Bacterial community structure at defined locations of *Pinus sylvestris-Suillus bovinus* and *Pinus sylvestris-Paxillus involutus* mycorrhizospheres in dry pine forest humus and nursery peat. *Can. J. Microbiol* **44,** 499–513.

Timonen, S., Christensen, S., and Ekelund, F. (2004). Distribution of protozoa in Scots pine mycorrhizospheres. *Soil Biol. Biochem.* **36,** 1087–1093.

Tiunov, A. V., and Scheu, S. (2005). Arbuscular mycorrhiza and Collembola interact in affecting community composition of saprotrophic microfungi. *Oecologia* **142,** 636–642.

Toro, M., Azcon, R., and Barea, J. M. (1998). The use of isotopic dilution techniques to evaluate the interactive effects of *Rhizobium* genotype, mycorrhizal fungi, phosphate-solubilizing rhizobacteria and rock phosphate on nitrogen and phosphorus acquisition by *Medicago sativa*. *New Phytol.* **138,** 265–273.

Town, C. D. (2006). Annotating the genome of Medicago truncatula. *Curr. Opin. Plant Biol.* **9,** 122–127.

Traquair, J. A. (1995). Fungal biocontrol of root diseases: Endomycorrhizal suppression of cylindrocarpon root rot. *Can. J. Bot.* **73,** S89–S95.

Tringe, S. G., von Mering, C., Kobayashi, A., Salamov, A. A., Chen, K., Chang, H. W., Podar, M., Short, J. M., Mathur, E. J., Detter, J. C., Bork, P., Hugenholtz, P., *et al.* (2005). Comparative metagenomics of microbial communities. *Science* **308,** 554–557.

Tuskan, G. A., DiFazio, S. P., and Teichmann, T. (2004). Poplar genomics is getting popular: The impact of the poplar genome project on tree research. *Plant Biol.* **6,** 2–4.

Umesh, K. C., Hkrisshnappa, K., and Bagyarai, D. J. (1988). Interaction of burrowing nematode, *Radophilus similes* (Cobb, 1983) Thorne 1949, and VA mycorrhiza *Glomus fasciculatum* (Thaxt.) Gerd. & Trappe in banana (*Musa acuminata* Colla). *Ind. J. Nematol.* **18,** 6–11.

Unestam, T., and Sun, Y. P. (1995). Extramatrical structures of hydrophobic and hydrophilic ectomycorrhizal fungi. *Mycorrhiza* **5,** 301–311.

van der Heijden, M. G. A., Klironomos, J. N., Ursic, M., Moutoglis, P., Streitwolf-Engel, R., Boller, T., Wiemken, A., and Sanders, I. R. (1998). Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* **396,** 69–72.

van Hees, P. A. W., Godbold, D. L., Jentschke, G., and Jones, D. L. (2003). Impact of ectomycorrhizas on the concentration and biodegradation of simple organic acids in a forest soil. *Eur. J. Soil Sci.* **54,** 697–706.

van Hees, P. A. W., Rosling, A., Essen, S., Godbold, D. L., Jones, D. L., and Finlay, R. D. (2006). Oxalate and ferricrocin exudation by the extramatrical mycelium of an ectomycorrhizal fungus in symbiosis with *Pinus sylvestris*. *New Phytol.* **169,** 367–378.

Varese, G. C., Portinaro, S., Trotta, A., Scannerini, S., Luppi Mosca, A. M., and Martinotti, M. G. (1996). Bacteria associated with *Suillus grevillei* sporocarps and ectomycorrhizae and their effect on *in vitro* growth of the mycobiont. *Symbiosis* **21,** 129–147.

Villegas, J., and Fortin, J. A. (2002). Phosphorus solubilization and pH changes as a result of the interactions between soil bacteria and arbuscular mycorrhizal fungi on a medium containing NO_3^- as nitrogen source. *Can. J. Bot.* **80,** 571–576.

Villenave, C., and Duponnois, R. (2002). Interactions between ectomycorrhizal fungi, plant-parasitic and free-living nematodes and their effects on seedlings of the hardwood *Afzelia africana* Sm. *Pedobiologia* **46,** 176–187.

Villenave, C., Leye, K., Chotte, J. L., and Duponnois, R. (2003). Nematofauna associated with exotic and native leguminous plant species in West Africa: Effect of *Glomus intraradices* arbuscular mycorrhizal symbiosis. *Biol. Fert. Soils* **38,** 161–169.

Werner, A., and Zadworny, M. (2003). *In vitro* evidence of mycoparasitism of the ectomycorrhizal fungus *Laccaria laccata* against *Mucor hiemalis* in the rhizosphere of *Pinus sylvestris*. *Mycorrhiza* **13,** 41–47.

Werner, A., Zadworny, M., and Idzikowska, K. (2002). Interaction between *Laccaria laccata* and *Trichoderma virens* in co-culture and in the rhizosphere of *Pinus sylvestris* grown *in vitro*. *Mycorrhiza* **12,** 139–145.

Whipps, J. M. (2001). Microbial interactions and biocontrol in the rhizosphere. *J. Exp. Bot.* **52,** 487–511.

Whipps, J. M. (2004). Prospects and limitations for mycorrhizas in biocontrol of root pathogens. *Can. J. Bot.* **82,** 1198–1227.

Wright, S. F., and Upadhyaya, A. (1999). Quantification of arbuscular mycorrhizal fungi activity by the glomalin concentration on hyphal traps. *Mycorrhiza* **8,** 283–285.

Wu, L. Y., Thompson, D. K., Li, G. S., Hurt, R. A., Tiedje, J. M., and Zhou, J. Z. (2001). Development and evaluation of functional gene arrays for detection of selected genes in the environment. *Appl. Environ. Microbiol.* **67,** 5780–5790.

Xie, Z. P., Staehelin, C., Vierheilig, H., Wiemken, A., Jabbouri, S., Broughton, W. J., Vogellange, R., and Boller, T. (1995). Rhizobial nodulation factors stimulate mycorrhizal colonization of nodulating and nonnodulating soybeans. *Plant Physiol.* **108,** 1519–1525.

Yamaji, K., Ishimoto, H., Usui, N., and Mori, S. (2005). Organic acids and water-soluble phenolics produced by *Paxillus* sp. 60/92 together show antifungal activity against *Pythium vexans* under acidic culture conditions. *Mycorrhiza* **15,** 17–23.

Zadworny, M., Werner, A., and Idzikowska, K. (2004). Behaviour of the hyphae of *Laccaria laccata* in the presence of *Trichoderma harzianum in vitro*. *Mycorrhiza* **14,** 401–405.

Zhu, H. H., and Yao, Q. (2004). Localized and systemic increase in phenols in tomato roots induced by *Glomus versiforme* inhibits *Ralstonia solanacearum*. *J. Phytopathol.* **153,** 537–542.

Zhu, W. X., and Ehrenfeld, J. G. (1996). The effects of mycorrhizal roots on litter decomposition, soil biota, and nutrients in a spodosolic soil. *Plant Soil* **179,** 109–118.