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Plants, Mycorrhizal Fungi, and Bacteria: A Network of Interactions

Paola Bonfante and Iulia-Andra Anca

ABSTRACT

This review focuses on interactions among plants, mycorrhizal fungi, and bacteria, testing the hypothesis whether mycorrhizas can be defined as tripartite associations. After summarizing the main biological features of mycorrhizas, we illustrate the different types of interaction occurring between mycorrhizal fungi and bacteria, from loosely associated microbes to endobacteria. We then discuss, in the context of nutritional strategies, the mechanisms that operate among members of the consortium and that often promote plant growth. Release of active molecules, including volatiles, and physical contact among the partners seem important for the establishment of the bacteria/mycorrhizal fungus/plant network. The potential involvement of quorum sensing and Type III secretion systems is discussed, even if the exact nature of the complex interspecies/interphylum interactions remains unclear.

INTRODUCTION

Bacteria seem to represent the third component of mycorrhizal associations, as they are loosely or tightly associated with mycorrhizal fungi and most likely play a role in mycorrhizal function. Garbaye (3) Bacteria seem to represent the third component of mycorrhizal associations, as they are loosely or tightly associated with mycorrhizal fungi and most likely play a role in mycorrhizal function. Garbaye (39) opened this field with the widely acknowledged term helper bacteria, which defined those bacteria that support mycorrhizal establishment; but now new knowledge and insight have been added, leading to a new scenario. There is increasing evidence that bacteria-fungi interactions are more widespread than expected and that their dynamics may be crucial in ecosystems (4, 32, 55).

We focus on interactions among plants, mycorrhizal fungi, and bacteria and assess whether mycorrhizas can be defined as tripartite associations. We first summarize the main biological features of mycorrhizas and then illustrate the different types of interaction occurring between bacteria and mycorrhizal fungi. Some of the mechanisms often lead to promotion of plant growth, and so nutritional strategies are discussed. Release of active molecules, including volatiles, and physical contact among the partners seem important for the establishment of the plant/bacteria/mycorrhizal fungus network.

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DEFINING MYCORRHIZAS

The term mycorrhiza comes from the Greek words for “fungus” and “root” and describes many diverse root-fungus associations. Mycorrhizas are found in many environments and their ecological success reflects a high degree of diversity in the genetic and physiological abilities of the fungal endophytes. About 6000 species in the Glomeromycotina, Ascomycotina, and Basidiomycotina have been recorded as mycorrhizal, and the advent of molecular techniques is increasing this number. The taxonomic position of the plant and fungal partners defines the types of mycorrhiza, for which the main distinction is between endomycorrhizas and ectomycorrhizas. In ectomycorrhizas (ECMs), which are characteristics of trees and shrubs, hyphae remain extracellular (Figure 1), inducing important changes to root morphogenesis, while their presence only leads to subtle modifications in epidermal or cortical cells (19). In endomycorrhizas, i.e., arbuscular (AMs), ericoid, and orchid mycorrhizas, the hyphae penetrate the root cells to establish an intracellular symbiosis (Figure 1), irrespective of the plant host. Whereas AMs are widespread among various plant taxa (21), ericoid and orchid mycorrhizas are restricted to the order Ericales and the family Orchidaceae, respectively (102).

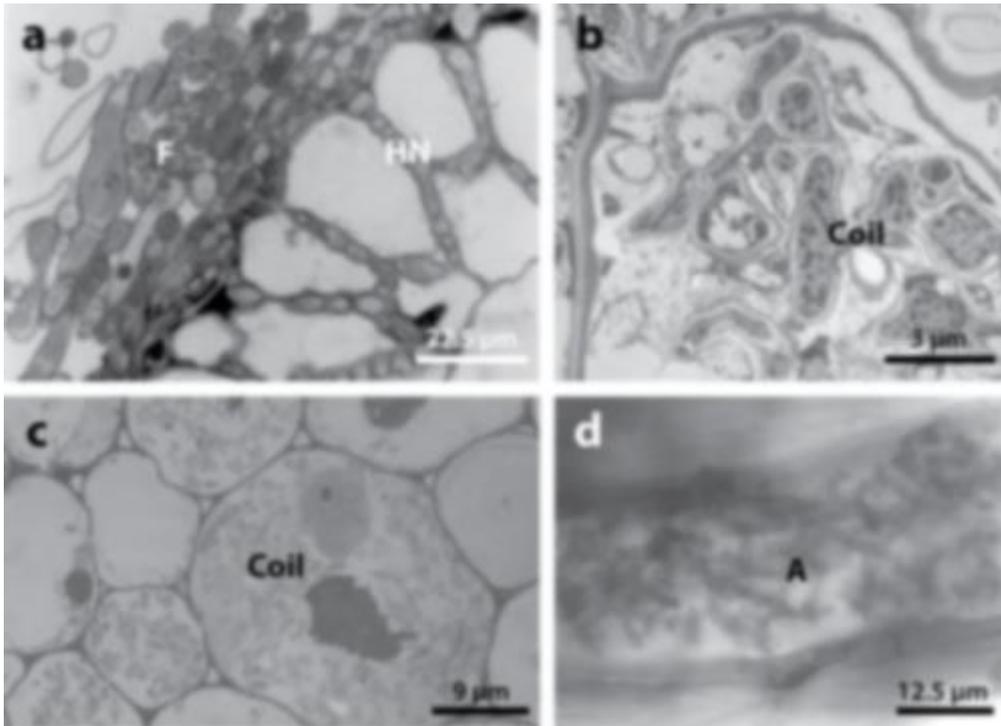


Figure 1 Micrographs illustrating the different mycorrhizal types and the main colonization structures. (a) The fungal mantle (F) and the Hartig net (HN) in *Tilia* ectomycorrhiza. (b) A coil produced by an ericoid fungus in a hair root of *Calluna vulgaris*. (c) A coil produced by an endophytic fungus inside an orchid root of *Cephalanthera*. (d) An arbuscule (A) of *Glomus versiforme* in the cortical cell of a leek root. Panel a reproduced from Reference 100, with permission.

The impressive diversity of plant and fungal taxa involved has led to morphological descriptions of the colonization process in many hosts since the start of the nineteenth century (101), while new information generated by the use of host plants or mycorrhizal fungi bearing GFP constructs and of plant mutants impaired in their symbiotic capabilities has been more recently reviewed (20, 42, 66).

Some aspects of the colonization process are common to all mycorrhizal fungi, whether they form ectomycorrhizas (ECMs), arbuscular (AMs), ericoid, or orchid mycorrhizas. Because they are soil fungi, fungal symbionts develop in the rhizosphere thanks to propagules (spores, hyphae, and rhizomorphs), which form the bridge between soil and plant roots. Such bridges are responsible for the so-called wood-wide web, network of connections among different plants forming a highway for horizontal nutrient movement (98). Many achlorophyllous heterotrophic plants obtain organic carbon by connecting to the wood-wide web through their mycorrhizal endophytes (95).

As a result of signaling events, which at the moment are best understood for AMs (10, 78, 80), hyphae contact the root surface, and colonization takes place according to steps that are strictly choreographed by the mycorrhizal type (102). ECM fungi produce a hyphal mantle that tightly covers the root tip, while epidermal (and in some cases also cortical) cells become separated by the development of labyrinth-like hyphae (the Hartig net), which increase the surface contact area with root cells (Figure 1a). In ericoid mycorrhizas, colonization is simple: The fungus develops inside epidermal cells, forming coils that gives rise to independent infection units. In orchid mycorrhizas, coils are produced mostly in the inner layers of the root (Figure 1b,c). Colonization by AM fungi is the most complex, leading to the development of hyphopodia (or appressoria) at the root surface, inter- and intracellular hyphae, coils, and characteristic branched structures called arbuscules (little trees) that develop inside cortical cells (Figure 1d). These structures, which give their name to the symbiosis, are considered the main site of nutrient exchange between the partners (45).

More than 200,000 plant species host mycorrhizal fungi, but a relatively small number of mycorrhizal types are known. Such basic information dates back many years (89), whereas the developmental processes that lead to colonization are still not fully known. Genetic, cellular, and molecular approaches, coupled with genome sequencing of model plants such as rice, poplar, and the ECM fungus *Laccaria laccata*, are now giving the first satisfying answers, at least for AMs and ECMs (65, 76,78).

WHAT MAKES A PLANT-FUNGUS INTERACTION A MYCORRHIZA?

Classically a mycorrhiza is defined as an interaction from which both partners benefit. Generally it is claimed that mycorrhizal fungi improve plant nutrient uptake thanks to fine exploration of the rhizosphere by the

hyphae, which in return receive plant carbohydrates that are essential for completion of the fungal life cycle. This retains the concept of mutualism, i.e., an interaction of net benefit to both parties (106), and poses questions about the molecular mechanisms that allow nutritional exchange.

A breakthrough on this front has come from some important findings: AM fungi possess active phosphate transporters that take up inorganic phosphate (Pi) from the soil, allowing its delivery to the plant (46). Furthermore, plants also possess phosphate transporters that are mycorrhiza specific. Their role is to receive Pi from the fungus and deliver it to plant cells. A *Medicago truncatula* Pi transporter exclusively expressed during AM symbiosis and located in the periarbuscular membrane (45) not only is essential for acquisition of Pi delivered by the AM fungus but is also required to maintain arbuscule vitality and sustain development of the fungus (50). Pi transport therefore seems to be a signal to sustain fungal growth inside the root and a determinant of arbuscule morphogenesis.

Nitrogen is the other important element taken up by most mycorrhizal fungi. Genes involved in organic and inorganic uptake of N have been identified in AM and ECM fungi (26, 59, 102). Many molecular and physiological data show that plant N transporters are activated during mycorrhization (43, 44, 102), suggesting that mycorrhizal fungi release a substantial amount of N to their hosts. While these fungal and plant transporters may be used as clear markers of mycorrhizal function, the reverse nutrient flow is not so clearly characterized.

Carbon transfer from plants to mycorrhizal fungi was demonstrated in the 1960s (102), but the molecular mechanisms are still unclear. With the exception of the gene described in the glomeromycotan *Geosiphon pyriforme* (94), which forms symbiosis with a cyanobacterium, and of the *AmMst1* gene from the ECM fungus *Amanita muscaria* (72), no other hexose transporter responsible for the uptake of C released by host cells has so far been characterized in mycorrhizal fungi. In addition, the transfer does not always go in the expected direction; for example, in orchid mycorrhizas or in other heterotrophic plants, C moves from the fungus toward the plant (95). In this case the nature of the benefit for the fungus is not obvious, although it might gain advantages, for example, by living within a protected niche.

A crucial consequence of nutrient exchange is that the partners must be living and in physical contact through their cell surfaces (19). The result is a specialized interface (Figure 2) that is particularly complex during intracellular interactions. Here, the fungus is in all cases engulfed by a plant-derived membrane, one result of a developmental program leading to intracellular accommodation of microbes by plants (77). In AM, this new compartment is known as the interfacial compartment (Figure 2) and consists of the invaginated host membrane, cell wall-like material, and the fungal wall and plasma membrane (19). Cellular and molecular approaches have provided many insights into the structure, function, and biogenesis of this complex compartment (40, 45, 78). Some fungi, such as *Piriformospora indica*, are sometimes defined as mycorrhizal because of their capacity to stimulate plant growth, even if an interface between living partners is not always present and the fungus may surprisingly cause the death of plant cells (33).

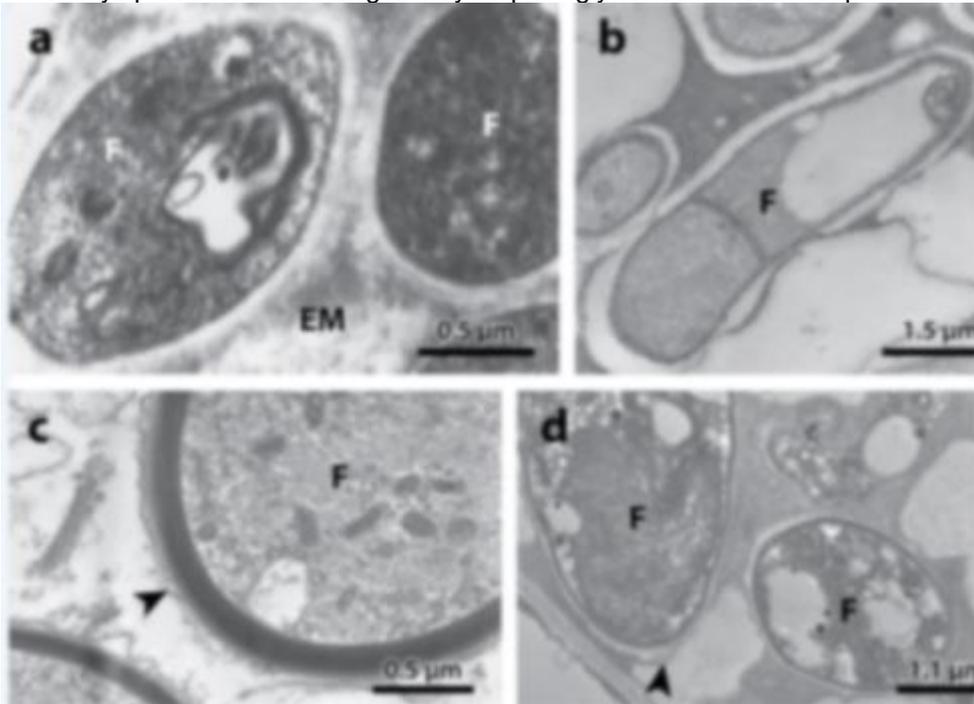


Figure 2 A gallery of interfaces established between plants and mycorrhizal fungi in the mycorrhizal types as seen at ultrastructural level. (a) Ultrastructural features of 90-day-old mantles of *Tuber borchii* in fully developed mycorrhizas. The mantle hyphae (F) are surrounded by abundant extracellular material (EM).

Panels b, c, and d illustrate interfaces of mycorrhizas where the fungus (F) develops intracellular structures. A membrane of host origin (arrowhead) constantly surrounds the fungal partners irrespective of their identity. (b) In the ericoid mycorrhizas, the fungus is an Ascomycete. (c) In the orchid mycorrhiza, the fungus is a Basidiomycete. (d) The arbuscule in the cortical cell of a leek root belongs to a Glomeromycete.

In conclusion, the borders that identify a plant-fungus interaction as a mycorrhiza are not always so clear-cut: The partners have to be alive; they are expected to exchange nutrients, the costs and benefits of which may change depending on ecological and genetic features, as in other cases of mutualism; the direction of nutrient flow may be inverted when a heterotrophic fungus may provide sugars to a photosynthetically inactive plant. Last, the exchanges require an active interface, which is guaranteed by the creation of a new compartment in the case of endomycorrhizas.

ASSOCIATED BACTERIA: THE THIRD COMPONENT OF FIELD-COLLECTED MYCORRHIZAS

In natural conditions, bacteria associated with mycorrhizal fungi colonize the surface of extraradical hyphae or, at least in some fungal taxa, live in the cytoplasm as endobacteria (Figure 3). Understanding the interactions between the microorganisms routinely found in the rhizosphere is essential for describing the nature of the soil-plant interface. A brief review of the predominant prokaryotic species thriving in the rhizosphere of mycorrhizal fungi is provided, followed by an analysis of their nutritional interactions.



Figure 3 Illustration of some interactions established in the rhizosphere among plants, mycorrhizal fungi, and bacteria. The two major types of mycorrhiza are illustrated: an ectomycorrhiza on the left and an arbuscular mycorrhiza (AM) on the right. The types of interacting bacteria are shown in relation to the text description: Endobacteria (white) are confined to AM fungi and grow from the spores toward the intraradical mycelium; rhizosphere bacteria (red) release diffusible factors that may be beneficial for (MHB) or detrimental to mycorrhization; other bacteria (green) establish physical contact with the fungus-root surface and may have positive effects or possess mycophagic activity. Arrows from roots and mycorrhizal fungi

illustrate the release of diffusible factors (strigolactones, Myc factors, volatiles, and auxin-like molecules) that are perceived by the reciprocal partners.

Predominant Prokaryotes in the Rhizosphere of Mycorrhizal Plants

Assessment of bacterial community structure in the soil is based mostly on the use of cultivation-dependent methods as well as cultivation-independent methods including soil metagenomics (30, 109).

Mycorrhiza-associated bacterial communities have been investigated according to established protocols, using microbiological (strain isolation and identification) and molecular screening of 16S rDNA libraries. These investigations, begun in the 1990s, have revealed a wide repertoire of microbes (Figure 4), including several bacterial taxa with a predominance of species from the genera *Pseudomonas*, *Burkholderia*, and *Bacillus* (32). Streptomycetes have been associated with ectomycorrhizal fungi and have been discussed as modulators of plant symbiosis (92), while Archaeobacteria thriving in the rhizosphere of mycorrhizal fungi have been reported only in boreal regions (18), and their limited distribution may be explained by their low preference for nonextreme environments and for rhizospheric soils in particular (74).

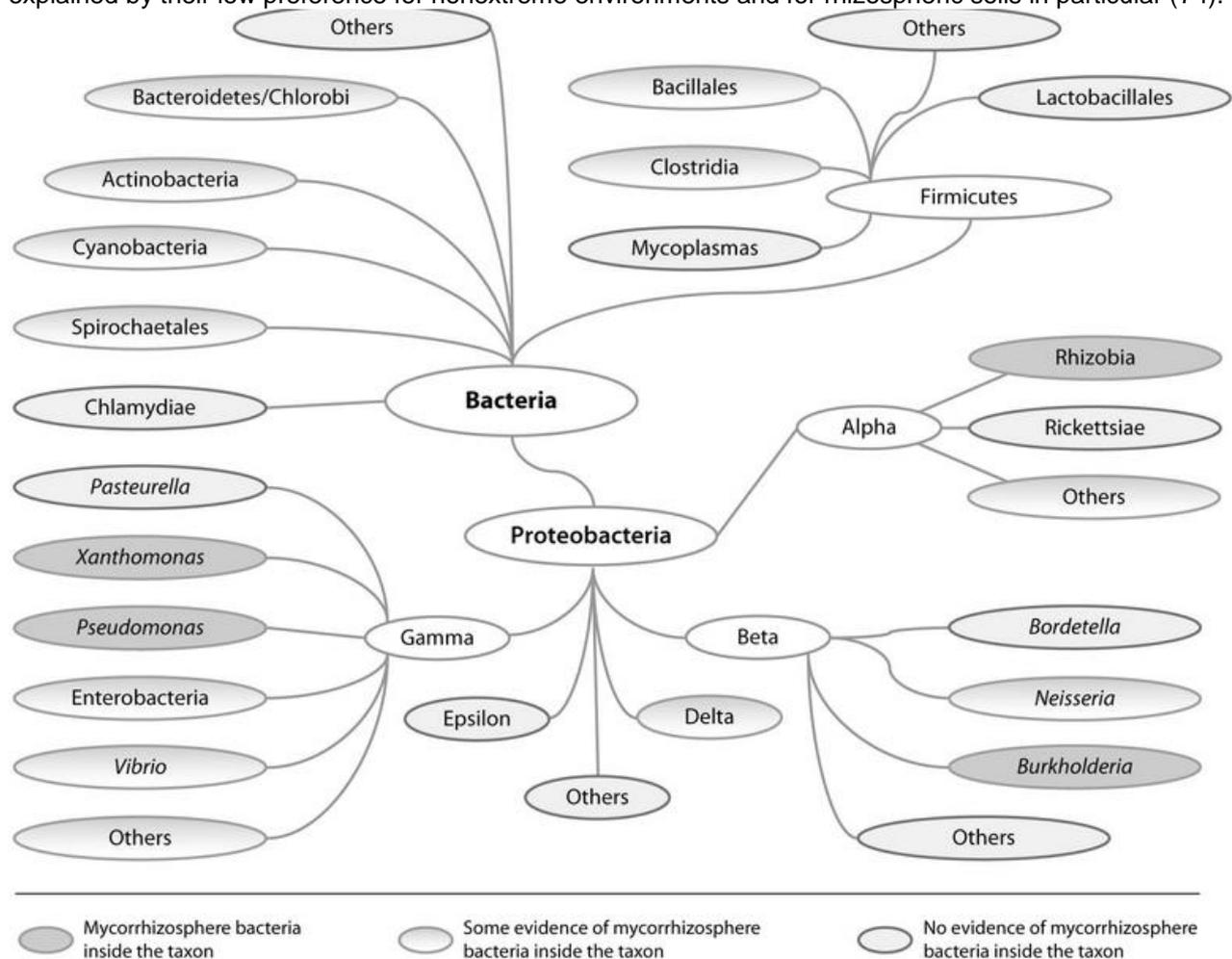


Figure 4 The tree modified from that present at http://www.ncbi.nlm.nih.gov/sutils/genom_tree.cgi illustrates the main bacterial groups so far identified as present in the mycorrhizosphere.

A detailed list of the bacteria present in the rhizosphere is outside the scope of this review. However, it is worth noting that prokaryotes are associated not only with the extraradical hyphae of mycorrhizal fungi, but also with mycorrhizal roots and sporocarps, i.e., the fruiting bodies of Ascomycota and Basidiomycota, suggesting that they accompany the symbiotic fungi during the various steps of their life cycle. Notably, the detection of rhizosphere bacteria is often dependent on the method of sampling. A significant difference in bacterial community composition associated with *Tuber* sp. fruiting bodies has been found, depending on the origin and preparation of the samples; a predominance of fluorescent pseudomonads in the culture-dependent samples was not confirmed by analysis of environmental samples that, in contrast, showed the predominance of Alphaproteobacteria represented by *Sinorhizobium/Ensifer* and *Rhizobium/Agrobacterium* groups as well as by the nitrogen-fixing *Bradyrhizobium* spp. (5, 6). This suggests that environmental sampling more accurately describes the

bacterial community, while culturing may be the best approach when selecting interesting mycorrhiza-associated species.

Investigation of the microbial diversity sheds light on whether bacterial communities are influenced by mycorrhizal fungi. Electron microscopy has shown that ectomycorrhizal fungi, such as *Suillus bovinus* and *Paxillus involutus*, host distinct populations of bacteria, suggesting spatially and physiologically different habitats in the mycorrhizospheres (73). Many other investigations have confirmed this finding using molecular approaches, stating that bacterial community structure depends more on AM fungi than on host plant identity (86). In a study observing the negative influence of the exotic tree *Eucalyptus camaldulensis* (51), AM fungal symbiosis was found to play a decisive role in the preservation of the soil microbial structure. Similarly, Singh et al. (99) showed that AM fungi are the major factor determining the bacterial assemblage on grass roots; they also found that this assemblage is influenced by soil pH and is spatially structured. However, the AM fungi themselves are influenced neither by the bacteria nor by soil pH; they are instead influenced by the plant community composition. Again, the dependence of the bacterial community composition on AMs was confirmed by Vestergård et al. (111).

In summary, it seems that bacterial biodiversity in the mycorrhizosphere reflects a considerable amount of bacterium/mycorrhiza and fungus/plant specificity. However, a central question basic to these studies remains unanswered: How do bacteria and mycorrhizal fungi associate and become mutual neighbors? Although some structural properties that regulate interspecies interactions inside microbial communities have been discussed and identified (58), the biological matrix that defines the rules of engagement (58) for the bacterial-mycorrhizal network is still obscure.

TROPHIC EVENTS IN THE SOIL: NUTRITIONAL INTERACTIONS BETWEEN MYCORRHIZAL FUNGI AND THEIR ASSOCIATED BACTERIA

As saprobic organisms, fungi and bacteria are at the base of the trophic pyramid. Their interactions have long been ignored, and only recently is it becoming clear that their nutritional dynamics may be ecologically important. Two classes represent these interactions: bacteria feeding on fungi (32, 55) and fungi feeding on bacteria (47, 48).

Consumption of fungus-derived substrates (or bacterial mycophagy) explains the ability of bacteria to obtain nutrients from the fungus and transform them into biomass. Leveau & Preston (55) recently identified three types of bacterial mycophagy: extracellular necrotrophy, extracellular biotrophy, and endocellular biotrophy. Studies of bacterial mycophagy among mycorrhizas are still in their infancy, but they suggest an overlap among these strategies.

There is evidence for necrotrophic and extracellular biotrophic activities of bacteria toward mycorrhizal fungi. Pathogenic and nonpathogenic soil bacteria (*Burkholderia* spp.) penetrated the spores of the AM fungus *Gigaspora decipiens* colonizing senescing spores and attaching to fungal hyphae, as detected in a spore lysis assay using GFP-tagged bacteria (56). Different kinetics in the attachment to living or nonliving *Glomus* spp. hyphae in five other GFP-tagged soil bacteria from the genera *Paenibacillus*, *Bacillus*, *Pseudomonas*, and *Arthrobacter* were described. These observations suggest that bacterial attachment to hyphae is regulated by two factors: species specificity and fungal vitality (107). Electron microscopy has revealed bacteria that probably feed on the outer hyaline spore layer of AM fungi (Figure 5a). As they represent several taxonomic groups of biodegraders such as *Cellvibrio*, *Chondromyces*, *Flexibacter*, *Lysobacter*, and *Pseudomonas*, it is not clear if their activity is beneficial (stimulation of spores germination) or parasitic (86).

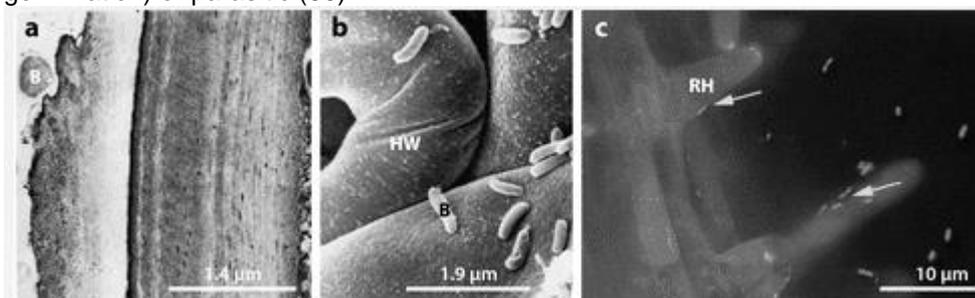


Figure 5 Electron microscopic features of some bacteria-fungi interactions. (a) A rhizospheric bacterium (B) is attacking the complex chitin-rich wall of *Glomus versiforme*, revealing a mycophagic habit. (b) A plant-growth-promoting bacterium (B) (*Pseudomonas* CHA0 strain) is seen strictly adhering to the hyphal wall (HW) of *Gigaspora margarita*. (c) The same bacteria (arrows) may adhere to the root hairs (RH) of the host plant, in addition to arbuscular mycorrhizal hyphae. Panels a, b, and c were reproduced from References 22, 17, and 12, respectively, with permission.

Although these reports offer good examples of bacterial mycophagy involving both necrotrophy and extracellular biotrophy, the observations are mostly descriptive and the controlling mechanisms are still unknown. Only in a few cases have molecular and biochemical mechanisms been clarified: Two mutant strains of *Pseudomonas fluorescens* CHA0 with increased capacity to produce extracellular polysaccharides display higher ability to adhere to the surface of AM fungi and plant roots (Figure 5b,c), compared with the nonmucoid wild type, showing the importance of cell wall composition for efficient bacterial adhesion (12). Another more recent example of a molecular determinant for fungal-bacterial attachment is given by a truffle-secreted protein, a lectin that binds *Rhizobium* sp. (27). Other molecules present in fungal exudates and potentially attractive for associated bacteria have been reviewed in Reference 32.

The third type of mycophagy, i.e., endocellular biotrophy, includes bacterial endosymbionts and free-living bacteria that penetrate and live inside mycorrhizal fungi. Among them, *in situ* hybridization has revealed the presence of cryptic bacteria from *Paenibacillus* sp. in the culture collection of the fungus *Laccaria bicolor* S238N (9). These bacteria are present in fungal mats and fruit bodies and grow in both live and dead fungal cells, but their presence inside hyphae is rare and erratic, and their role inside the fungus remains to be clarified (8). The *L. bicolor* genome assembly revealed high-GC sequences showing BlastX hits to rhizospheric bacteria proteins (65).

Interactions between AM fungi and bacteria imply both a beneficial effect of the fungi on bacterial development and vice versa (32). An interesting example is *Paenibacillus validus*, which when alone supports the growth and sporulation of *Glomus intraradices* independently of the presence of the plant (47). Two isolates of *P. validus* are highly efficient in sustaining fungal growth up to production of new germinating spores, probably owing to the release of raffinose and a still unidentified trisaccharide (48). This result shows that at least one AM fungus can grow independently of its plant host if in the presence of a bacterium. It might be interesting to see whether the still unknown bacterial compounds are mimicking plant molecules (23) and whether this bacterium is required for establishment of the mycorrhiza.

Helper Bacteria

Dupunnois & Garbaye (35) were the first to observe a significant stimulation of ectomycorrhiza formation by *Pseudomonas fluorescens* BBC6. This was experimental evidence for the so-called helper effect. Bacteria involved in mycorrhiza establishment and/or its functioning were therefore defined as mycorrhiza helper bacteria (MHB) by Garbaye (39) and are currently the most investigated group among bacteria interacting with mycorrhizas (37). Some species are responsible for multiple helper effects, because they influence both plants and associated mycorrhizal fungi. More recently, the stimulating effect of MHB has been evaluated mostly when symbiotic associations are exposed to stresses ranging from drought (114) to contamination with heavy metals such as Pb (112), Zn (113), and Cd(II) (54).

Frey-Klett et al. (37) proposed some mechanisms that may explain MHB success. These mechanisms involve the production of growth factors that might stimulate fungal spore germination, mycelial growth, increased root branching and greater root colonization, and reduction of soil-mediated stress through detoxification of antagonistic substances and inhibition of competitors and antagonists. A classical example illustrating the helper effect is given by rhizobia producing 1-aminocyclopropane-1-carboxylate (ACC) deaminase; the molecule modulates plant ethylene levels, increasing plant tolerance to environmental stress and stimulating nodulation (62). In agreement with this rationale, the ACC deaminase-producing *Pseudomonas putida* UW4 promotes mycorrhization with the AM *Gigaspora rosea* when inoculated into cucumber plants, whereas a bacterial mutant impaired in ethylene production causes decreased mycorrhization (38). In other cases, the beneficial effects of some MHB are related to changes in gene expression of the mycorrhizal fungus. In a study involving *L. bicolor* S238N and the MHB *P. fluorescens* BBc6R8, bacteria stimulated fungal growth and development as well as altered fungal gene expression. This led to activation of genes potentially involved in recognition processes, transcription regulation, and synthesis of primary metabolism proteins (34). Similarly, the MHB *Streptomyces* sp. AcH 505 promotes hyphal growth and symbiosis formation with spruce in the ECM *Amanita muscaria*, acting on basic cell growth processes. Immunofluorescence microscopy in fact revealed morphological changes in the actin cap of fungal hyphae in the presence of bacteria (91).

Taken together, these studies suggest that release of active diffusible molecules and physical contact between bacteria and mycorrhizal fungi are important for the establishment of their interactions (Figures 3 and 8). This recalls the major signaling mechanisms identified in rhizobia and legume plants (75) as well as in AMs. Here, the partners release active diffusible molecules that are reciprocally perceived (23), also activating Ca-mediated responses (20, 53, 71), while a physical contact between the fungus and the plant is required to elicit many of the plant responses that precede fungal colonization (40, 41).

Recent data also suggest that production of volatile organic compounds (VOCs) from all the members of the underground consortium may be important for inter- and intraorganismic communication (105). Splivallo et al. (103) demonstrated that truffle VOCs have biological activity, causing leaf bleaching and root inhibition of *Arabidopsis thaliana*. In the meantime, bacterial VOCs may affect soil fungi, including the mycorrhizal ones (105). In this context, such bioactive molecules can be regarded as important, even if poorly

understood, determinants for symbiosis establishment. Thus, integration of descriptive data with genomics, proteomics, and metabolomics is offering a first glimpse of the mechanisms taking place between plants and fungi, but there is still much to be done to identify the molecules that configure the basis of interaction between MHBs and their fungal and plant hosts.

ENDOBACTERIA: THE MOST INTIMATE INTERACTION BETWEEN PROKARYOTES AND MYCORRHIZAL FUNGI

Bacterial endosymbionts are widespread in the animal kingdom, where they offer excellent models for investigating important biological events. Organelle evolution, genome reduction, fast rates of evolution, and transfer of genetic information among host lineages are some of the main problems addressed in studies of endobacteria in insects (69). By contrast, examples of endobacteria living in fungi are limited (61) and those best investigated live in the cytoplasm of AM fungi, themselves obligate symbionts of plants.

Beginning in 1970 (70) many reports have noted the presence of bacterium-like objects (BLOs) inside endomycorrhizal fungi (63, 90). They were revealed by electron microscopy of AM roots and spores collected in the field and appeared as coccoid bodies with a typical gram-positive wall (Figure 6). No further information could be gathered at that time, as they could not be cultivated outside their hosts and identified (PCR-based protocols were not yet developed at that time). The glomeromycotan fungus *Geosiphon pyriformis* also contains similar BLOs, in addition to a photosynthetic species of *Nostoc* (cyanobacteria) (93). The presence of BLOs in fungi from phylogenetically distant Glomeromycota taxa suggests that they represent a vertically inherited population of uncultured bacteria and are an ancient trait of this unique group of fungi. BLOs may be of evolutionary importance for AM fungi speciation (M. Nauman, A. Schüssler & P. Bonfante, unpublished data).

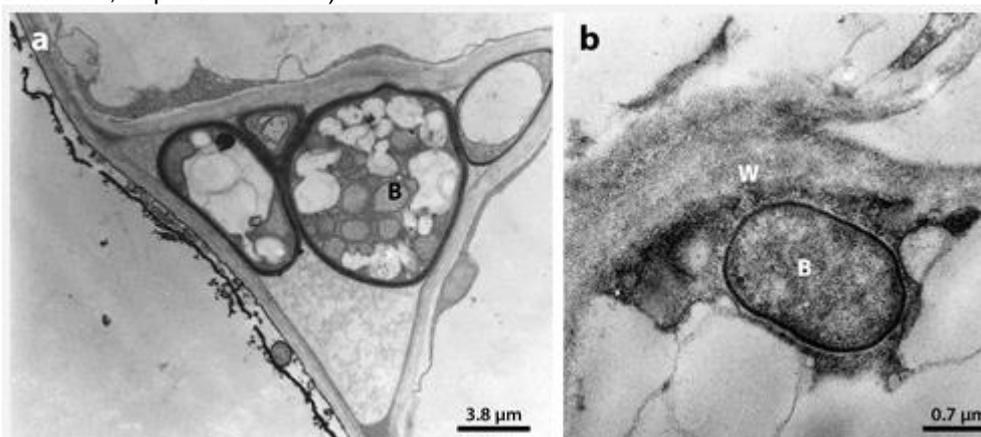


Figure 6 (a) Electron microscopy of bacterium-like objects (BLO) (B) inside an intercellular hypha of an arbuscular mycorrhizal fungus developing in the root. (b) A magnification of an intracellular BLO (B) close to the fungal cell wall (W).

Use of a combination of microscopy and molecular analysis of 16S rRNA has led to the description of organisms living inside different members of the Gigasporaceae as true bacteria related to *Burkholderia* (13). They were placed in a new taxon related to *Burkholderia* but named “*Candidatus Glomeribacter gigasporarum*” because of their unculturability (15). Investigations of members of the Gigasporaceae from different areas showed that 10 of 11 isolates contain endobacteria and at least 4 of them cluster together phylogenetically (16). Isolate BEG34 of *Gigaspora margarita* and its endobacterium “*Candidatus Glomeribacter gigasporarum*” are currently used as a model system to investigate endobacteria-AM fungi interactions.

“CANDIDATUS GLOMERIBACTER GIGASPORARUM”: THE ENDOSYMBIONT OF THE ARBUSCULAR MYCORRHIZAL FUNGUS GIGASPOA MARGARITA

“*Candidatus Glomeribacter gigasporarum*” is a stable component of the fungus *G. margarita* BEG34 in which it forms a homogenous population of about 20,000 individuals per fungal spore (14). Microscopy has shown that the endobacteria are gram negative and rod-shaped with an approximate size of 0.8–1.2×1.5–2.0 µm. They occur singly or in groups, often inside fungal vacuoles in both spores and hyphae (Figure 7). Their cytoplasm is rich in ribosomes; negative-staining electron microscopy has shown that flagella and pili are absent.

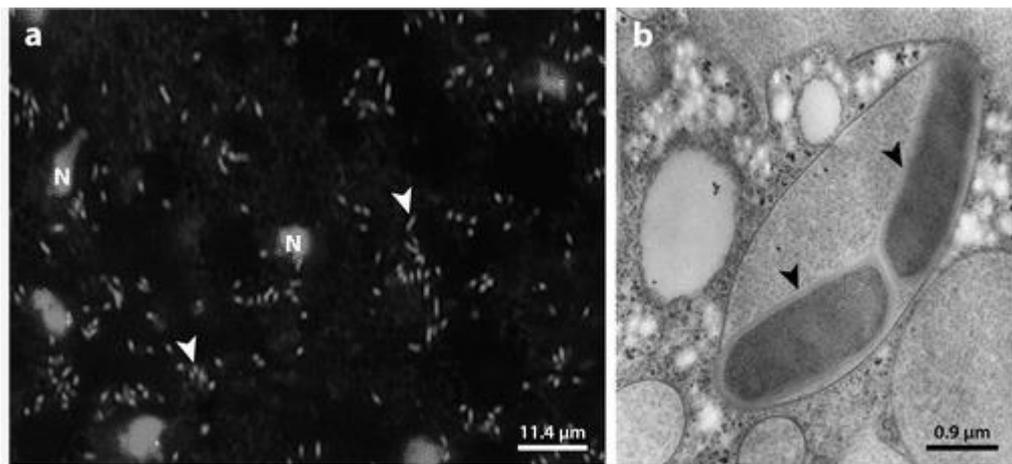


Figure 7 (a) A crushed spore of *Gigaspora margarita* reveals many rod-shaped bacteria inside its cytoplasm (arrowheads). After the staining with the Live/Dead BacLight kit, the bacteria appear green, while the fungal nuclei (N) are the red spots. The bacteria are identified as “*Candidatus Glomeribacter gigasporarum*.” (b) Two “*Candidatus Glomeribacter gigasporarum*” (arrowheads) located inside the vacuole of *G. margarita* when seen with an electron microscope. Panel are reproduced from Reference 16, with permission. Like many insect endosymbionts, “*Candidatus Glomeribacter gigasporarum*” is vertically transmitted through fungal generations. Its cytoplasmic stability in the fungal host and its transmission during asexual AM fungal reproduction have been investigated using transformed carrot roots and single-spore inocula of *G. margarita*. This sterile environment with no risk of horizontal contamination allowed monitoring of endobacterial propagation through several vegetative spore generations (SG0 to SG4), using amplification of the 16S and 23S ribosomal DNA genes. The endobacteria were consistently found through the fungal generations, demonstrating vertical transmission (14) and suggesting that they are obligate endocellular components of their hosts.

In an attempt to identify the fungal structures in which the endobacteria multiply, a marker of bacterial division (the *ftsZ* gene) was identified in “*Candidatus Glomeribacter gigasporarum*” and its transcript level was quantified with real-time RT-PCR at different stages of the fungus life cycle (2). Gene transcript level was higher during the symbiotic phase (i.e., when the fungus was plant associated) and peaked in the extraradical mycelium. Strigolactones, which are bioactive plant molecules that stimulate AM hyphal growth (11), caused a significant transcript increase in germinated spores, even in the absence of the plant. The transcript data were supported by quantification of the dividing bacteria, which again increased in number in strigolactone-treated spores. Strigolactone treatment did not lead to any change in the number of bacteria when isolated from the fungus, showing that the molecule alone does not allow the bacterium to be free-living (2). These results raise new questions about signal exchanges among plant, fungus, and endobacterium, and show that, even indirectly, “*Candidatus Glomeribacter gigasporarum*” may perceive signals of plant origin, as do fungal mitochondria (10, 11).

The vertical transmission experiment had a surprising second outcome. The number of endobacteria decreased during the fungal generations when a monosporal inoculum was used (14), eventually leading to cured spores lacking bacteria (60). Spores of this cured line have cells distinct in vacuole morphology, cell wall organization, lipid bodies, and pigment granules. The absence of bacteria severely affects presymbiotic fungal growth such as hyphal elongation and branching after root exudate treatment, suggesting that the endobacterium is important for optimal development of the fungal host. This experiment led to reliable quantification of the bacteria with a detection limit of 10 bacterial cells per spore (88) and gave the first indication of the influences of endobacteria on host physiology (60).

The main obstacle to studying “*Candidatus Glomeribacter gigasporarum*” is that it has not been cultivated cell-free, even after testing several different growth media (49). Although purification from the fungal host was only partially successful, a sufficient quantity of endobacterial DNA was obtained to estimate the genome size (49). By using $1-4 \times 10^4$ spores (manually collected), the genome size was estimated to be 1.35–2.35 Mb, depending on the method used (49). Thus, the genome can be considered small when compared with other Betaproteobacteria, but it is larger than that of obligate insect symbionts, whose genome size may be less than 1 Mb (28).

At the moment “*Candidatus Glomeribacter gigasporarum*” is being sequenced (S. Ghignone, I.-A. Anca, L. Lanfranco & P. Bonfante, unpublished data) by two complementary strategies: classical Sanger sequencing and 454 technology. Preliminary assembly and automatic annotation reveal large numbers of mobile elements, genes putatively involved in the pathways for vitamin B12 and antibiotic synthesis, such as streptomycin, as well as genes involved in secretion systems, such as the Type III secretion system (TTSS)

(I.-A. Anca, S. Ghignone, L. Lanfranco & P. Bonfante, unpublished data). This project is the first sequencing attempt for an endocellular organism living inside an AM fungus, and it may be crucial for further characterization of other endocellular bacteria inhabiting mycorrhizal fungi; it promotes "*Candidatus Glomeribacter gigasporarum*" as a model in the study of mycorrhizal fungi/bacteria symbionts.

The Case of *Rhizobium radiobacter*, the Endobacterium of *Piriformospora indica*

The order Sebaciniales comprise both endo- and ectomycorrhizal fungi, which are versatile plant symbionts impressive for their ability to establish associations with a wide range of plants such as ectomycorrhizal trees, orchids, and Ericaceae (96). An exception is members of the Brassicaceae, which are usually not colonized by AM fungi (81).

One of the most studied members is the endophytic fungus *Piriformospora indica*, which can colonize and promote the growth of plant roots (110) as well as induce resistance against biotic and abiotic stresses (115). Because the benefits provided by the plant to the fungus are not yet clearly defined, *P. indica* is a good example of those positive plant-fungi interactions that do not completely fit the mycorrhizal definition but that offer an experimental basis to the biological continuum existing between saprotrophism and mutualism.

An additional point of interest of *P. indica* is the presence of rod-shaped bacteria 1–1.5 μm in length recently found in its cytoplasm; the bacterium was identified as *Rhizobium radiobacter* (synonym of *Agrobacterium tumefaciens*) on the basis of its 16S rRNA sequence homology (97). Notwithstanding its supposed intimate association with the fungus, the bacterium is present in low numbers (2–20 per fungal cell) as detected by real-time RT-PCR and FISH analysis. In contrast to the obligate endobacteria of *G. margarita* BEG34, the *P. indica* bacteria can grow in pure culture. *R. radiobacter* detected inside *P. indica* possesses important features such as plant-growth-promoting properties and the ability to induce systemic resistance to fungal plant pathogens, such as powdery mildew. Because *P. indica* has similar properties, its endobacteria may well be responsible for these features (97).

Free-living *R. radiobacter* is well known as a soil-borne plant pathogen whose infection in dicotyledonous plants causes crown gall disease with the formation of neoplastic tissues. Infectivity is conferred by the virulent Ti plasmid, which contains genes coding for auxin and cytokinin synthesis (52, 57). The endocellular bacteria of *P. indica* seem to possess the vir D4 genes characteristic of the presence of the Ti plasmid, but not the *ips* gene, which codes for cytokinin synthesis. This might explain the lack of pathogenic effects by bacteria on barley as well as their capacity for auxin synthesis and growth promotion. Inoculation with a high concentration of bacteria seems to be harmful, if not lethal, to the fungus, raising questions on the role of the endobacterium, whether it is beneficial or pathogenic.

The *P. indica*–*R. radiobacter* association recalls the few examples of fungi and bacteria in which a precise role for the bacterium has been defined. *Rhizopus*, a rice pathogenic fungus, is pathogenic owing to the internal presence of a *Burkholderia* strain (79). Another example is that of a biocontrol strain of *Fusarium*. When cured of its associated bacteria, it becomes pathogenic (68). These examples suggest that the difference between a symbiont and a pathogen is not clear-cut, and may be influenced by many environmental and genetic factors.

In conclusion, bacteria living in the cytoplasm of mycorrhizal fungi still represent an unknown chapter in mycorrhizal biology: Some groups (the BLOs) seem to be widespread, and others appear to be limited to some fungal groups, as in the case of Gigasporaceae or Sebaciniales. However, irrespective of their ecological importance, the role of these endobacteria is still obscure. Novel insights are expected to be gained from the genome sequence of at least one endobacterium. Because the genome is the ultimate blueprint of a cell, we expect to understand for example how "*Candidatus Glomeribacter gigasporarum*" thrives in its peculiar ecological niche, the fungal cell.

TOWARD THE IDENTIFICATION OF POTENTIAL MECHANISMS

The way in which prokaryotes interact with eukaryotic cells is an important question regarding microbes that cause disease in animals, mostly humans, and in plants. Many reviews have recently illustrated the way in which microbes invade a host cell successfully, suppressing its defenses, often owing to the bacterial TTSS, which is central to the virulence of many gram-negative bacteria in plants and animals (1). In this way, bacterial pathogens directly inject effectors into the host cytoplasm. However, TTSS is not limited to pathogenic interactions: Many symbionts, such as nodulating rhizobia, rely on TTSS for communication (36, 64). TTSS genes have been reported in animal secondary symbionts such as *Sodalis glossinidius*, "*Candidatus Hamiltonella defensa*" and "*Candidatus Arsenophonus arthropodicus*" (29), whereas they were not detected in the genome of primary symbionts, such as *Buchnera*. The presence of TTSS might be an indication of more recent symbiosis, in contrast with ancient symbioses in which TTSS has probably been lost (28).

Although many bacteria living in the rhizosphere possess a TTSS (24), and considering the importance of this system in bacterial interaction with eukaryotic cells, little emphasis has so far been given to the role of TTSS in bacteria associated with mycorrhizal fungi. A large number of bacteria living in the *Laccaria proxima* mycorrhizosphere have been recently described as possessing a TTSS (116). This suggests that

TTSS with its effectors may be a specific way in which bacteria and fungi become associated. A TTSS has been detected in “*Candidatus Glomeribacter gigasporarum*” and is preferentially expressed when the fungal host is associated with the mycorrhizal plant (I.-A. Anca, S. Ghignone & P. Bonfante, unpublished data). The Type IV secretion system (TFSS) is another versatile bacterial system used to interact with eukaryotic cells. *R. radiobacter*, responsible for crown gall disease, possesses an efficient TFSS. The endocellular bacteria of the endophytic *P. indica* seem to possess similar genes (97). However, it is unclear if such a system is still functional.

In conclusion, we can hypothesize that at least in cases in which there is strict physical contact between a mycorrhizal fungus and an associated bacterium, effectors may be released by the microbe owing to activation of such powerful injection systems (Figure 8). This is still an area of research that needs urgent exploration.

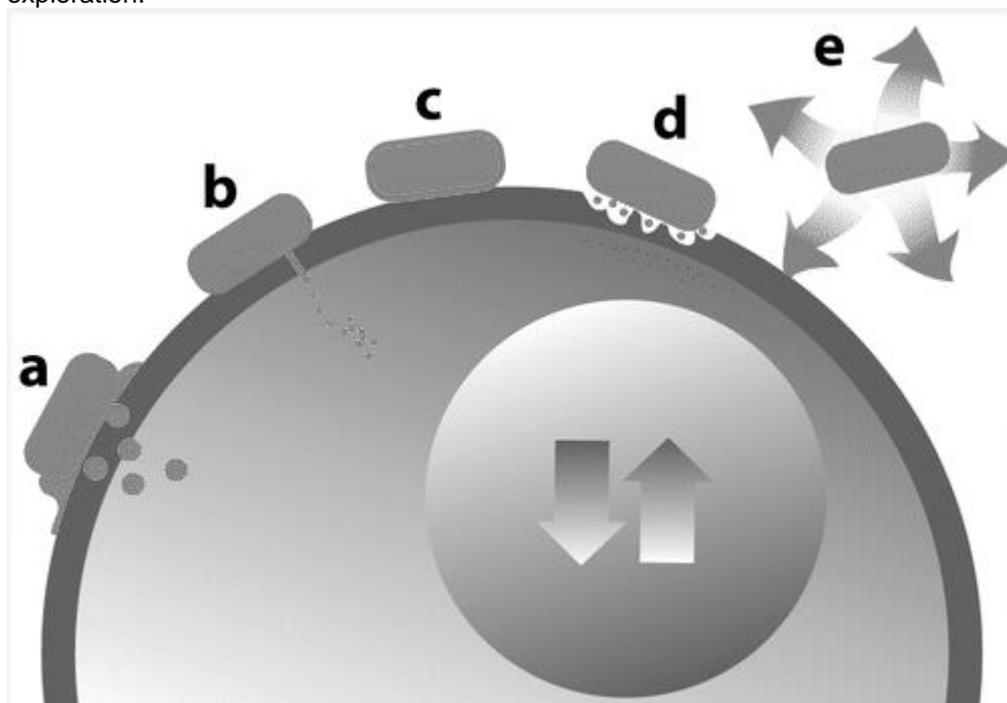


Figure 8 Schematic illustrating mechanisms that allow rhizosphere bacteria to adhere to the cell surface of mycorrhizal fungi, causing a change in fungal gene expression. (a) Bacteria may release effectors; (b) inject molecules via the Type III secretion system (TTSS); (c) bind to the fungal cell wall via lectins; or (d) degrade the fungal cell walls. (e) Alternatively, bacteria release volatile organic compounds (VOCs) that are perceived by the fungus, activating specific transcriptomics responses. All the illustrated mechanisms have an experimental basis with the exception of the still hypothetical TTSS.

Quorum sensing (QS) is another phenomenon basic to a wide range of bacterial activities including symbiosis, virulence, competence, conjugation, motility, sporulation, biofilm formation, and antibiotic production (67). QS has been defined as the regulation of bacterial gene expression in response to fluctuations in cell population density (67). QS was first described for *Vibrio fischeri*, the symbiont of the Hawaiian squid, which possesses a LuxI/LuxR type of QS (104). Among soil bacteria, the best-characterized QS mechanisms are those of *Rhizobium* sp., since QS has a crucial role in nodulation (85), nitrogen fixation, and symbiosome development (31), as well as nod gene control (83). QS is found in most gram-negative bacteria, whether they are versatile pathogens such as *Pseudomonas aeruginosa*, *R. radiobacter*, or *Erwinia carotovora*, or plant-growth promoters such as *Burkholderia graminis* (7).

Bacterial strains isolated from the mycorrhizosphere have never been checked for QS capacity. Artursson et al. (3) used a bromodeoxyuridine method to follow actively proliferating bacteria when associated with *Glomus mosseae*, but it is not clear whether the growth of mycorrhiza-associated bacteria is regulated to some degree by control of cell density. By contrast, there is a report that investigates the capacity of root-associated fungi to interfere with bacterial QS molecules; it seems that some mycorrhizal fungi possess enzymes that can degrade acyl-homoserine lactone (AHL) in vitro (108). It would be interesting to know whether fungal AHL-degrading activity is correlated with protection of plant roots against the pathogens or whether the mycorrhizal fungi are associated with bacteria responsible for such activity. AHL degradation is in fact unexpected for mycorrhizal fungi, as it was reported only in pathogenic fungi such as *Penicillium* (84). Important mechanisms like QS and TTSS, active in a wide range of bacterial interactions (from regulating density of bacterial communities to injecting effector proteins into hosts), may also operate in the specific

mycorrhizosphere habitat, where the importance of diffusible signals and physical contact between plant and fungal partners has already been noted.

CONCLUSIONS AND PERSPECTIVES

Analysis of the multiple interactions established by mycorrhizal fungi with plant and bacterial cells offers new understanding of the complexity of mycorrhizas. Simplified experimental models have provided many breakthroughs on the molecular and cellular bases that regulate plant-mycorrhizal fungi interactions as well as the signaling networks active in the rhizosphere (59, 66, 78). Studies of field-collected samples based on current molecular microbial ecology approaches are increasingly focusing on prokaryotes associated with mycorrhizal fungi. The constant finding of bacteria and the new roles attributed to them represent a paradigm shift in our way of viewing mycorrhizal symbioses. Although the exact nature of the complex interspecies/interphylum interactions remains unclear, much evidence supports the current trend to view mycorrhizas as tripartite associations. It is likely that the latest methods of high-throughput sequencing will allow us to develop integrated metagenomic and functional analyses that provide a complete scenario of the organisms that interact around a mycorrhizal plant. On the other hand, the availability of genome sequences of plants such as rice, poplar, and some legumes of mycorrhizal fungi such as *Laccaria* spp. and *Glomus* intraradices, and of the approximately 600 bacterial genome sequences available, will provide the tools to test functional hypotheses and to explore mycorrhizosphere biodiversity. The final goals will be to understand the pressures that push the organisms of three kingdoms to associate and produce a beneficial mycorrhizal symbiosis and to develop predictive models that can be used in sustainable agriculture. Although some of the mechanisms operating between fungus and plant have been deciphered (76), there is still much to do when the level of complexity increases and bacteria are considered as the third, stable component of the network.

SUMMARY POINTS

1. Mycorrhizas, the symbioses established between plant roots and soil fungi, represent a vital component in plant ecosystems.
2. An increasing amount of data suggest that bacteria, whether loosely or tightly associated with mycorrhizal fungi, represent the third component of mycorrhizas.
3. Understanding the interactions between bacteria and fungi living in the mycorrhizosphere is essential for describing the soil-plant interface.
4. Recent advances in molecular biology and genome sequencing have provided tools to address questions about the identity and role of bacteria associated with mycorrhizal fungi.
5. Investigation of microbial diversity demonstrates that bacterial communities are influenced by mycorrhizal fungi.
6. Nutritional interactions among plants, fungi, and bacteria in the mycorrhizosphere cover a range of trophic events (such as mutualism, mycoheterotrophy, bacterial mycophagy) and mirror the spatial location of the fungal and bacterial partners.
7. MHB are widespread among mycorrhizas: Many mechanisms have been proposed to explain their success. Release of active molecules, including VOCs and physical contact among the partners, seems to be important for the establishment of both plant-fungus and mycorrhiza-bacteria networks.
8. Endobacteria are consistently present in AM fungi, providing a sound demonstration of the tripartite nature of mycorrhizas.

disclosure statement

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1.

- Alfano JR, Collmer A. 2004. Type III secretion system effector proteins: double agents in bacterial disease and plant defense. *Annu. Rev. Phytopathol.* 42:385–414 [Abstract] [Medline] [Web of Science ®] OpenURL
 Universita Degli Studi di Torino - All Libraries
- 2.
- Anca IA, Lumini E, Ghignone S, Salvioli A, Bianciotto V, Bonfante P. 2009. The *ftsZ* gene of the endocellular bacterium *Ca. Glomeribacter gigasporarum* is preferentially expressed during the symbiotic phases of its host mycorrhizal fungus. *Mol. Plant Microbe. Interact.* 22:301–10 [CrossRef] [Web of Science ®] OpenURL
 Universita Degli Studi di Torino - All Libraries
- 3.
- Artursson V, Finlay RD, Jansson JK. 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.* 7:1952–66 [CrossRef] [Medline] [Web of Science ®] OpenURL
 Universita Degli Studi di Torino - All Libraries
- 4.
- Artursson V, Finlay RD, Jansson JK. 2006. Interactions between arbuscular mycorrhizal fungi and bacteria and their potential for stimulating plant growth. *Environ. Microbiol.* 8(1):1–10 [CrossRef] [Medline] [Web of Science ®] OpenURL
 Universita Degli Studi di Torino - All Libraries
- 5.
- Barbieri E, Bertini L, Rossi I, Ceccaroli P, Saltarelli R, et al. 2005. New evidence for bacterial diversity in the ascoma of the ectomycorrhizal fungus *Tuber borchii* Vittad. *FEMS Microbiol. Lett.* 247:23–35 [CrossRef] [Medline] [Web of Science ®] OpenURL
 Universita Degli Studi di Torino - All Libraries
- 6.
- Barbieri E, Guidi C, Bertaux J, Frey-Klett P, Garbaye J, et al. 2007. Occurrence and diversity of bacterial communities in *Tuber magnatum* during truffle maturation. *Environ. Microbiol.* 9:2234–46 [CrossRef] [Medline] [Web of Science ®] OpenURL
 Universita Degli Studi di Torino - All Libraries
- 7.
- Barriuso J, Ramos Solano B, Santamaría C, Daza A, Gutiérrez Mañero FJ. 2008. Effect of inoculation with putative plant growth-promoting rhizobacteria isolated from *Pinus* spp. on *Pinus pinea* growth, mycorrhization and rhizosphere microbial communities. *J. Appl. Microbiol.* 105:1298–309 [CrossRef] [Medline] [Web of Science ®] OpenURL
 Universita Degli Studi di Torino - All Libraries
- 8.
- Bertaux J, Schmid M, Hutzler P, Hartmann A, Garbaye J, et al. 2005. Occurrence and distribution of endobacteria in the plant-associated mycelium of the ectomycorrhizal fungus *Laccaria bicolor* S238N. *Environ. Microbiol.* 7:1786–95 [CrossRef] [Medline] [Web of Science ®] OpenURL
 Universita Degli Studi di Torino - All Libraries
- 9.
- Bertaux J, Schmid M, Prevost-Boure NC, Churin JL, Hartmann A, et al. 2003. In situ identification of intracellular bacteria related to *Paenibacillus* spp. in the mycelium of the ectomycorrhizal fungus *Laccaria bicolor* S238N. *Appl. Environ. Microbiol.* 69:4243–48 [CrossRef] [Medline] [Web of Science ®] OpenURL
 Universita Degli Studi di Torino - All Libraries
- 10.
- Besserer A, Bécard G, Jauneau A, Roux C, Séjalon-Delmas N. 2008. GR24, a synthetic analog of strigolactones, stimulates the mitosis and growth of the arbuscular mycorrhizal fungus *Gigaspora rosea* by boosting its energy metabolism. *Plant Physiol.* 148:402–13 [CrossRef] [Medline] [Web of Science ®] OpenURL
 Universita Degli Studi di Torino - All Libraries
- 11.
- Besserer A, Puech-Pagès V, Kiefer P, Gomez-Roldan V, Jauneau A, et al. 2006. Strigolactones stimulate arbuscular mycorrhizal fungi by activating mitochondria. *PLoS Biol.* 4:e226 Offers sound evidence of strigolactones as stimulators of mitochondrial activity and hyphal growth in AM fungi. [CrossRef] [Medline] [Web of Science ®] OpenURL
 Universita Degli Studi di Torino - All Libraries
- 12.
- Bianciotto V, Andreotti S, Balestrini R, Bonfante P, Perotto S. 2001. Mucoïd mutants of the biocontrol strain *Pseudomonas fluorescens* CHA0 show increased ability in biofilm formation on mycorrhizal and nonmycorrhizal carrot roots. *Mol. Plant. Microbe. Interact.* 14:255–60 [CrossRef] [Medline] [Web of Science ®] OpenURL
 Universita Degli Studi di Torino - All Libraries
- 13.
- Bianciotto V, Bandi C, Minerdi D, Sironi M, Tichy HV, et al. 1996. An obligately endosymbiotic fungus itself harbors obligately intracellular bacteria. *Appl. Environ. Microbiol.* 62:3005–10 [Medline] [Web of Science ®] OpenURL
 Universita Degli Studi di Torino - All Libraries
- 14.

- Bianciotto V, Genre A, Jargeat P, Lumini E, Bécard G, Bonfante P. 2004. Vertical transmission of endobacteria in the arbuscular mycorrhizal fungus *Gigaspora margarita* through generation of vegetative spores. *Appl. Environ. Microbiol.* 70:3600–8 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
- 15.
- Bianciotto V, Lumini E, Bonfante P, Vandamme P. 2003. 'Candidatus *Glomeribacter gigasporarum*', an endosymbiont of arbuscular mycorrhizal fungi. *Int. J. Syst. Evol. Microbiol.* 53:121–24 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
- 16.
- Bianciotto V, Lumini E, Lanfranco L, Minerdi D, Bonfante P, et al. 2000. Detection and identification of bacterial endosymbionts in arbuscular mycorrhizal fungi belonging to the family Gigasporaceae. *Appl. Environ. Microbiol.* 66:4503–9 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
- 17.
- Bianciotto V, Minerdi D, Perotto S, Bonfante P. 1996. Cellular interactions between arbuscular mycorrhizal fungi and rhizosphere bacteria. *Protoplasma* 193:123–31 [CrossRef] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
- 18.
- Bomberg M, Timonen S. 2007. Distribution of Cren- and Euryarchaeota in scots pine mycorrhizospheres and boreal forest humus. *Microb. Ecol.* 54:406–16 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
- 19.
- Bonfante P. 2001. At the interface between mycorrhizal fungi and plants: the structural organization of cell wall, plasma membrane and cytoskeleton. In *Mycota, IX Fungal Associations*, ed. B Hock, pp. 45–91. Berlin: Springer-Verlag OpenURL Università Degli Studi di Torino - All Libraries
- 20.
- Bonfante P, Balestrini R, Genre A, Lanfranco L. 2009. Establishment and functioning of arbuscular mycorrhizas. In *The Mycota, V: Plant Relationships*, ed. H Deising, pp. 257–72. Berlin: Springer-Verlag. 2nd ed. OpenURL Università Degli Studi di Torino - All Libraries
- 21.
- Bonfante P, Genre A. 2008. Plants and arbuscular mycorrhizal fungi: an evolutionary-developmental perspective. *Trends Plant Sci.* 13:492–98 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
- 22.
- Bonfante P, Vian B. 1984. Wall texture in the spore of a vesicular-arbuscular mycorrhizal fungus. *Protoplasma* 120:51–60 [CrossRef] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
- 23.
- Bouwmeester HJ, Roux C, Lopez-Raez JA, Bécard G. 2007. Rhizosphere communication of plants, parasitic plants and AM fungi. *Trends Plant Sci.* 12:224–30 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
- 24.
- Broughton WJ, Jabbouri S, Perret X. 2000. Keys to symbiotic harmony. *J. Bacteriol.* 182:5641–52 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
- 25.
- Bucher M. 2007. Functional biology of plant phosphate uptake at root and mycorrhiza interfaces. *New Phytol.* 173:11–26 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
- 26.
- Cappellazzo G, Lanfranco L, Fitz M, Wipf D, Bonfante P. 2008. Characterization of an amino acid permease from the endomycorrhizal fungus *Glomus mosseae*. *Plant Physiol.* 147:429–37 Identifies the first AM fungi transporter involved in the uptake of amino acids. [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
- 27.
- Cerigini E, Palma F, Barbieri E, Buffalini M, Stocchi V. 2008. The *Tuber borchii* fruiting body-specific protein TBF-1, a novel lectin which interacts with associated *Rhizobium* species. *FEMS Microbiol. Lett.* 284:197–203 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
- 28.
- Dale C, Moran NA. 2006. Molecular interactions between bacterial symbionts and their hosts. *Cell* 126:453–65 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
- 29.

- Dale C, Young SA, Haydon DT, Welburn SC. 2001. The insect endosymbiont *Sodalis glossinidius* utilizes a type III secretion system for cell invasion. *Proc. Natl. Acad. Sci. USA* 98:1883–88 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
- 30.
- Daniel R. 2005. The metagenomics of soil. *Nat. Rev. Microbiol.* 3:470–78 One of the first reviews on metagenomics. It describes how to construct complex libraries from soil samples, and how to use these libraries to unravel functions of soil microbial communities. [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
- 31.
- Daniels R, De Vos DE, Desair J, Raedschelders G, Luyten E, et al. 2002. The *cin* quorum sensing locus of *Rhizobium etli* CNPAF512 affects growth and symbiotic nitrogen fixation. *J. Biol. Chem.* 277:462–68 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
- 32.
- De Boer W, Folman LB, Summerbell RC, Boddy L. 2005. Living in a fungal world: impact of fungi on soil bacterial niche development. *FEMS Microbiol. Rev.* 29:795–811 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
- 33.
- Deshmukh S, Hüchelhoven R, Schäfer P, Imani J, Sharma M, et al. 2006. The root endophytic fungus *Piriformospora indica* requires host cell death for proliferation during mutualistic symbiosis with barley. *Proc. Natl. Acad. Sci. USA* 103:18450–57 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
- 34.
- Deveau A, Palin B, Delaruelle C, Peter M, Kohler A, et al. 2007. The mycorrhiza helper *Pseudomonas fluorescens* BBc6R8 has a specific priming effect on the growth, morphology and gene expression of the ectomycorrhizal fungus *Laccaria bicolor* S238N. *New Phytol.* 175:743–55 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
- 35.
- Duponnois R, Garbaye J. 1991. Mycorrhization helper bacteria associated with the Douglas fir–*Laccaria laccata* symbiosis: effects in aseptic and in glasshouse conditions. *Ann. Sci. For.* 48:239–51 [CrossRef] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
- 36.
- Freiberg C, Fellay R, Bairoch A, Broughton WJ, Rosenthal A, et al. 1997. Molecular basis of symbiosis between *Rhizobium* and legumes. *Nature* 387:394–401 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
- 37.
- Frey-Klett P, Garbaye J, Tarkka M. 2007. The mycorrhiza helper bacteria revisited. *New Phytol.* 176:22–36 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
- 38.
- Gamalero E, Berta G, Massa N, Glick BR, Lingua G. 2008. Synergistic interactions between the ACC deaminase-producing bacterium *Pseudomonas putida* UW4 and the AM fungus *Gigaspora rosea* positively affect cucumber plant growth. *FEMS Microbiol. Ecol.* 64:459–67 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
- 39.
- Garbaye J. 1994. Helper bacteria: a new dimension to the mycorrhizal symbiosis. *New Phytol.* 128:197–210 The first review in which the concept of helper bacteria was formalized. [CrossRef] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
- 40.
- Genre A, Chabaud M, Faccio A, Barker DG, Bonfante P. 2008. Prepenetration apparatus assembly precedes and predicts the colonization patterns of arbuscular mycorrhizal fungi within the root cortex of both *Medicago truncatula* and *Daucus carota*. *Plant Cell* 20:1407–20 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
- 41.
- Genre A, Chabaud M, Timmers T, Bonfante P, Barker DG. 2005. Arbuscular mycorrhizal fungi elicit a novel intracellular apparatus in *Medicago truncatula* root epidermal cells before infection. *Plant Cell* 17:3489–99 Demonstrates how plant cells actively control AM fungi development by forming an intracellular apparatus prior fungal invasion. [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
- 42.
- Gianinazzi-Pearson V, Séjalon-Delmas N, Genre A, Jeandroz S, Bonfante P. 2007. Plants and arbuscular mycorrhizal fungi: cues and communication in the early steps of symbiotic interactions. *Adv. Bot. Res.* 46:181–219 [CrossRef] OpenURL Università Degli Studi di Torino - All Libraries

43.
Guether M, Balestrini R, Hannah M, He J, Udvardi M, Bonfante P. 2009. Genome-wide reprogramming of regulatory networks, transport, cell wall and membrane biogenesis during arbuscular mycorrhizal symbiosis in *Lotus japonicus*. *New Phytol.* 182:200–12 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
44.
Guether M, Neuhauser B, Balestrini R, Dynowski M, Ludewig U, Bonfante P. 2009. A mycorrhizal specific ammonium transporter from *Lotus japonicus* acquires nitrogen. *Plant Physiol.* 150:74–83 [CrossRef] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
45.
Harrison MJ. 2005. Signaling in the arbuscular mycorrhizal symbiosis. *Annu. Rev. Microbiol.* 59:19–42 An excellent review that explores the signals and signaling pathways used by symbionts for the development of the AM symbiosis. [Abstract] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
46.
Harrison MJ, van Buuren ML. 1995. A phosphate transporter from the mycorrhizal fungus *Glomus versiforme*. *Nature* 378:626–29 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
47.
Hildebrandt U, Janetta K, Bothe H. 2002. Towards growth of arbuscular mycorrhizal fungi independent of a plant host. *Appl. Environ. Microbiol.* 68:1919–24 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
48.
Hildebrandt U, Ouziad F, Marner FJ, Bothe H. 2006. The bacterium *Paenibacillus validus* stimulates growth of the arbuscular mycorrhizal fungus *Glomus intraradices* up to the formation of fertile spores. *FEMS Microbiol. Lett.* 254:258–67 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
49.
Jargeat P, Cosseau C, Ola'h B, Jauneau A, Bonfante P, et al. 2004. Isolation, free-living capacities, and genome structure of “*Candidatus Glomeribacter gigasporarum*,” the endocellular bacterium of the mycorrhizal fungus *Gigaspora margarita*. *J. Bacteriol.* 186:6876–84 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
50.
Javot H, Varma Penmetsa R, Terzaghi N, Cook DR, Harrison MJ. 2007. A *Medicago truncatula* phosphate transporter indispensable for the arbuscular mycorrhizal symbiosis. *Proc. Natl. Acad. Sci. USA* 104:1720–25 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
51.
Kisa M, Sanon A, Thioulouse J, Assigbetse K, Sylla S, et al. 2007. Arbuscular mycorrhizal symbiosis can counterbalance the negative influence of the exotic tree species *Eucalyptus camaldulensis* on the structure and functioning of soil microbial communities in a sahelian soil. *FEMS Microbiol. Ecol.* 62:32–44 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
52.
Klee H, Montoya A, Horodyski F, Lichtenstein C, Garfinkel D, et al. 1984. Nucleotide sequence of the *tms* genes of the pTiA6NC octopine Ti plasmid: two gene products involved in plant tumorigenesis. *Proc. Natl. Acad. Sci. USA* 81:1728–32 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
53.
Kosuta S, Hazledine S, Sun J, Miwa H, Morris RJ, et al. 2008. Differential and chaotic calcium signatures in the symbiosis signaling pathway of legumes. *Proc. Natl. Acad. Sci. USA* 105:9823–28 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
54.
Kozdrój J, Piotrowska-Seget Z, Krupa P. 2007. Mycorrhizal fungi and ectomycorrhiza associated bacteria isolated from an industrial desert soil protect pine seedlings against Cd(II) impact. *Ecotoxicology* 6:449–56 [CrossRef] OpenURL Università Degli Studi di Torino - All Libraries
55.
Leveau JH, Preston GM. 2008. Bacterial mycophagy: definition and diagnosis of a unique bacterial-fungal interaction. *New Phytol.* 177:859–76 Offers precise definitions and analyses of the phenomenon of bacterial mycophagy, defined as a set of phenotypic behaviors that enable bacteria to obtain nutrients from living fungi. [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries
- 56.

Levy A, Chang BJ, Abbott LK, Kuo J, Harnett G, et al. 2003. Invasion of spores of the arbuscular mycorrhizal fungus *Gigaspora decipiens* by *Burkholderia* spp. *Appl. Environ. Microbiol.* 69:6250–56 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries

57.

Lichtenstein C, Klee H, Montoya A, Garfinkel D, Fuller S, et al. 1984. Nucleotide sequence and transcript mapping of the *tmr* gene of the pTiA6NC octopine Ti-plasmid: a bacterial gene involved in plant tumorigenesis. *J. Mol. Appl. Genet.* 2:354–62 [Medline] OpenURL Università Degli Studi di Torino - All Libraries

58.

Little AE, Robinson CJ, Peterson SB, Raffa KF, Handelsman J. 2008. Rules of engagement: interspecies interactions that regulate microbial communities. *Annu. Rev. Microbiol.* 62:375–401 Discusses working definitions of central ecological terms that have been used in various fashions in microbial ecology, and reviews the status of the interface between evolutionary and ecological study. [Abstract] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries

59.

Lucic E, Fourrey C, Kohler A, Martin F, Chalot M, et al. 2008. A gene repertoire for nitrogen transporters in *Laccaria bicolor*. *New Phytol.* 180:343–64 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries

60.

Lumini E, Bianciotto V, Jargeat P, Novero M, Salvioli A, et al. 2007. Presymbiotic growth and spore morphology are affected in the arbuscular mycorrhizal fungus *Gigaspora margarita* cured of its endobacteria. *Cell Microbiol.* 9:1716–29 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries

61.

Lumini E, Ghignone S, Bianciotto V, Bonfante P. 2006. Endobacteria or bacterial endosymbionts? To be or not to be. *New Phytol.* 170:205–8 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries

62.

Ma W, Penrose DM, Glick BR. 2002. Strategies used by rhizobia to lower plant ethylene levels and increase nodulation. *Can. J. Microbiol.* 48:947–54 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries

63.

MacDonald RM, Chandler MR. 1981. Bacterium-like organelles in the vesicular-arbuscular, mycorrhizal fungus *Glomus catenulatum*. *New Phytol.* 89:241–46 [CrossRef] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries

64.

Marie C, Broughton WJ, Deakin WJ. 2001. Rhizobium type III secretion systems: legume charmers or alarmers? *Curr. Opin. Plant Biol.* 4:336–42 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries

65.

Martin F, Aerts A, Ahrén D, Brun A, Danchin EG, et al. 2008. The genome of *Laccaria bicolor* provides insights into mycorrhizal symbiosis. *Nature* 452:88–92 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries

66.

Martin F, Kohler A, Duplessis S. 2007. Living in harmony in the wood underground: ectomycorrhizal genomics. *Curr. Opin. Plant Biol.* 10:204–10 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries

67.

Miller MB, Bassler BL. 2001. Quorum sensing in bacteria. *Annu. Rev. Microbiol.* 55:165–99 [Abstract] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries

68.

Minerdi D, Moretti M, Gilardi G, Barberio C, Gullino ML, et al. 2008. Bacterial ectosymbionts and virulence silencing in a *Fusarium oxysporum* strain. *Environ. Microbiol.* 10:1725–41 [CrossRef] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries

69.

Moran NA, McCutcheon AJ, Nakabachi P. 2008. Genomics and evolution of heritable bacterial symbionts. *Annu. Rev. Genet.* 42:165–90 [Abstract] [Medline] [Web of Science ®] OpenURL Università Degli Studi di Torino - All Libraries

70.

Mosse B. 1970. Honey-coloured sessile *Endogone* spores: II. Changes in fine structure during spore development. *Arch. Mikrob.* 74:129–45 [CrossRef] OpenURL Università Degli Studi di Torino - All Libraries

71.

Navazio L, Moscatiello R, Genre A, Novero M, Baldan B, et al. 2007. A diffusible signal from arbuscular mycorrhizal fungi elicits a transient cytosolic calcium elevation in host plant cells. *Plant Physiol.* 144:673–81 Provides the first experimental proof that a calcium transient in plant cells is caused by diffusible AM factors. [CrossRef] [Medline] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries

72.

Nehls U, Wiese J, Guttenberger M, Hampp R. 1998. Carbon allocation in ectomycorrhizas: identification and expression analysis of an *Amanita muscaria* monosaccharide transporter. *Mol. Plant Microbe Interact.* 11:167–76 [CrossRef] [Medline] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries

73.

Nurmiaho-Lassila EL, Timonen S, Haahtela K, 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 [CrossRef] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries

74.

Ochsenreiter T, Selezi D, Quaiser A, Bonch-Osmolovskaya L, Schleper C. 2003. Diversity and abundance of Crenarchaeota in terrestrial habitats studied by 16S RNA surveys and real time PCR. *Environ. Microbiol.* 5:787–97 [CrossRef] [Medline] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries

75.

Oldroyd GE, Downie JA. 2008. Coordinating nodule morphogenesis with rhizobial infection in legumes. *Annu. Rev. Plant Biol.* 59:519–46 [Abstract] [Medline] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries

76.

Oldroyd GE, Harrison MJ, Paszkowski U. 2009. Reprogramming plant cells for endosymbiosis. *Science* 324:753–55 [CrossRef] [Medline] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries

77.

Parniske M. 2000. Intracellular accommodation of microbes by plants: a common developmental program for symbiosis and disease? *Curr. Opin. Plant Biol.* 3:320–28 [CrossRef] [Medline] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries

78.

Parniske M. 2008. Arbuscular mycorrhiza: the mother of plant root endosymbioses. *Nat. Rev. Microbiol.* 6:763–75 A thorough, updated review on AMs and on their evolutionary and genetics implications. [CrossRef] [Medline] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries

79.

Partida-Martinez LP, Hertweck C. 2005. Pathogenic fungus harbours endosymbiotic bacteria for toxin production. *Nature* 437:884–88 [CrossRef] [Medline] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries

80.

Paszkowski U. 2006. A journey through signaling in arbuscular mycorrhizal symbioses. *New Phytol.* 172:35–46 [CrossRef] [Medline] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries

81.

Peskan-Berghöfer T, Shahollaria B, Giong PH, Hehl S, Markerta C, et al. 2004. Association of *Piriformospora indica* with *Arabidopsis thaliana* roots represents a novel system to study beneficial plant–microbe interactions and involves early plant protein modifications in the endoplasmic reticulum and at the plasma membrane. *Physiol. Plant* 122:465–77 [CrossRef] OpenURL Universita Degli Studi di Torino - All Libraries

82.

Pirozynski KA, Malloch DW. 1975. The origin of land plants: a matter of mycotropism. *Biosystems* 6:153–64 [CrossRef] [Medline] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries

83.

Pongsilp N, Triplett EW, Sadowsky MJ. 2005. Detection of homoserine lactone-like quorum sensing molecules in *Bradyrhizobium* strains. *Curr. Microbiol.* 51:250–54 [CrossRef] [Medline] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries

84.

Rasmussen TB, Skindersoe ME, Bjarnsholt T, Phipps RK, Christensen KB, et al. 2005. Identity and effects of quorum-sensing inhibitors produced by *Penicillium* species. *Microbiology* 151:1325–40 [CrossRef] [Medline] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries

85.

Rodelas B, Lithgow JK, Wisniewski-Dye F, Hardman A, Wilkinson A, et al. 1999. Analysis of quorum-sensing-dependent control of rhizosphere-expressed (*rhi*) genes in *Rhizobium leguminosarum* bv. *viciae*. *J. Bacteriol.* 181:3816–23 [Medline] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries

86.

Roesti D, Ineichen K, Braissant O, Redecker D, Wiemken A, et al. 2005. Bacteria associated with spores of the arbuscular mycorrhizal fungi *Glomus geosporum* and *Glomus constrictum*. *Appl. Environ. Microbiol.* 71:6673–79 [CrossRef] [Medline] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries

87.

Rosendahl S. 2008. Communities, populations and individuals of arbuscular mycorrhizal fungi. *New Phytol.* 178:253–66 [CrossRef] [Medline] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries

88.

Salvioli A, Lumini E, Anca IA, Bianciotto V, Bonfante P. 2008. Simultaneous detection and quantification of the unculturable microbe *Candidatus Glomeribacter gigasporarum* inside its fungal host *Gigaspora margarita*. *New Phytol.* 180:248–57 [CrossRef] [Medline] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries

89.

Scannerini S, Bonfante P. 1983. Comparative ultrastructural analysis of mycorrhizal associations. *Can. J. Bot.* 61:917–43 [CrossRef] OpenURL Universita Degli Studi di Torino - All Libraries

90.

Scannerini S, Bonfante P. 1991. Bacteria and bacteria like objects in endomycorrhizal fungi (Glomaceae). In *Symbiosis as Source of Evolutionary Innovation: Speciation and Morphogenesis*, ed. L Margulis, R Fester, pp. 273–87. Cambridge, MA: MIT Press OpenURL Universita Degli Studi di Torino - All Libraries

91.

Schrey SD, Salo V, Raudaskoski M, Hampp R, Nehls U, et al. 2007. Interaction with mycorrhiza helper bacterium *Streptomyces* sp. Ach 505 modifies organisation of actin cytoskeleton in the ectomycorrhizal fungus *Amanita muscaria* (fly agaric). *Curr. Genet.* 52:77–85 [CrossRef] [Medline] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries

92.

Schrey SD, Tarkka MT. 2008. Friends and foes: streptomycetes as modulators of plant disease and symbiosis. *Antonie van Leeuwenhoek* 94:11–19 [CrossRef] [Medline] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries

93.

Schüßler A. 2002. Molecular phylogeny, taxonomy, and evolution of arbuscular mycorrhiza fungi and *Geosiphon pyriformis*. *Plant Soil* 244:75–83 [CrossRef] OpenURL Universita Degli Studi di Torino - All Libraries

94.

Schüßler A, Martin H, Cohen D, Fitz M, Wipf D. 2006. Characterization of a carbohydrate transporter from symbiotic glomeromycotan fungi. *Nature* 444:933–36 [CrossRef] [Medline] OpenURL Universita Degli Studi di Torino - All Libraries

95.

Selosse MA, Roy M. 2009. Green plants that feed on fungi: facts and questions about mixotrophy. *Trends Plant Sci.* 14:64–70 [CrossRef] [Medline] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries

96.

Selosse MA, Setaro S, Glatard F, Richard F, Urcelay C, et al. 2007. Sebaciniales are common mycorrhizal associates of Ericaceae. *New Phytol.* 174:864–78 [CrossRef] [Medline] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries

97.

Sharma M, Schmid M, Rothballer M, Hause G, Zuccaro A, et al. 2008. Detection and identification of bacteria intimately associated with fungi of the order Sebaciniales. *Cell Microbiol.* 10:2235–46 [CrossRef] [Medline] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries

98.

Simard SW, Perry DA, Jones MD, Myrold DD, Durall DM, et al. 1997. Net transfer of carbon between ectomycorrhizal tree species in the field. *Nature* 388:579–82 [CrossRef] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries

99.

Singh BK, Nunan N, Ridgway KP, McNicol J, Young JP, et al. 2008. Relationship between assemblages of mycorrhizal fungi and bacteria on grass roots. *Environ. Microbiol.* 10:534–41 [CrossRef] [Medline] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries

100.

- Sisti D, Giomaro G, Cecchini M, Faccio A, Novero M, Bonfante P. 2003. Two genetically related strains of *Tuber borchii* produce *Tilia mycorrhizas* with different morphological traits. *Mycorrhiza* 13:107–15 [CrossRef] [Medline] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries
101.
- Smith FA, Smith SE. 1997. Structural diversity in (vesicular)-arbuscular mycorrhizal symbioses. *New Phytol.* 137:373–88 [CrossRef] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries
102.
- Smith SE, Read DJ. 2008. *Mycorrhizal Symbiosis*. New York: Academic. 3rd ed. OpenURL Universita Degli Studi di Torino - All Libraries
103.
- Splivallo R, Novero M, Berteza CM, Bossi S, Bonfante P. 2007. Truffle volatiles inhibit growth and induce an oxidative burst in *Arabidopsis thaliana*. *New Phytol.* 175:417–24 [CrossRef] [Medline] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries
104.
- Stevens AM, Greenberg EP. 1997. Quorum sensing in *Vibrio fischeri*: essential elements for activation of the luminescence genes. *J. Bacteriol.* 179:557–62 [Medline] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries
105.
- Tarkka MT, Piechulla B. 2007. Aromatic weapons: Truffles attack plants by the production of volatiles. *New Phytol.* 175:381–83 [CrossRef] [Medline] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries
106.
- Thompson JN, Cunningham BM. 2002. Geographic structure and dynamics of coevolutionary selection. *Nature* 417:735–38 [CrossRef] [Medline] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries
107.
- Toljander JF, Artursson V, Paul LR, Jansson JK, Finlay RD. 2006. Attachment of different soil bacteria to arbuscular mycorrhizal fungal extraradical hyphae is determined by hyphal vitality and fungal species. *FEMS Microbiol. Lett.* 254:34–40 [CrossRef] [Medline] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries
108.
- Uroz S, Heinonsalo J. 2008. Degradation of N-acyl homoserine lactone quorum sensing signal molecules by forest root-associated fungi. *FEMS Microbiol. Ecol.* 65:271–78 [CrossRef] [Medline] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries
109.
- van Elsas JD, Duarte GF, Rosado AS, Smalla K. 1998. Microbiological and molecular biological methods for monitoring microbial inoculants and their effects in the soil environment. *J. Microbiol. Methods* 32:133–54 [CrossRef] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries
110.
- Varma A, Savita Verma S, Sahay N, Butehorn B, Franken P. 1999. *Piriformospora indica*, a cultivable plant-growth-promoting root endophyte. *Appl. Environ. Microbiol.* 65:2741–44 [Medline] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries
111.
- Vestergård M, Henry F, Rangel-Castro JI, Michelsen A, Prosser JI, et al. 2008. Rhizosphere bacterial community composition responds to arbuscular mycorrhiza, but not to reductions in microbial activity induced by foliar cutting. *FEMS Microbiol. Ecol.* 64:78–89 [CrossRef] [Medline] OpenURL Universita Degli Studi di Torino - All Libraries
112.
- Vivas A, Azcón R, Biró B, Barea JM, Ruiz-Lozano JM. 2003. Influence of bacterial strains isolated from lead-polluted soil and their interactions with arbuscular mycorrhizae on the growth of *Trifolium pratense* L. under lead toxicity. *Can. J. Microbiol.* 49:577–88 [CrossRef] [Medline] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries
113.
- Vivas A, Barea JM, Biró B, Azcón R. 2006. Effectiveness of autochthonous bacterium and mycorrhizal fungus on *Trifolium* growth, symbiotic development and soil enzymatic activities in Zn contaminated soil. *J. Appl. Microbiol.* 100:587–98 [CrossRef] [Medline] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries
114.
- Vivas A, Marulanda A, Ruiz-Lozano JM, Barea JM, Azcón R. 2003. Influence of a *Bacillus* sp. on physiological activities of two arbuscular mycorrhizal fungi and on plant responses to PEG-induced drought

stress. *Mycorrhiza* 13:249–56 [CrossRef] [Medline] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries

115.

Waller F, Achatz B, Baltruschat H, Fodor J, Becker K, et al. 2005. The endophytic fungus *Piriformospora indica* reprograms barley to salt-stress tolerance, disease resistance, and higher yield. *Proc. Natl. Acad. Sci. USA* 102:13386–91 [CrossRef] [Medline] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries

116.

Warmink JA, van Elsas JD. 2008. Selection of bacterial populations in the mycosphere of *Laccaria proxima*: Is type III secretion involved? *ISME J.* 2:887–900 [CrossRef] [Medline] [Web of Science ®] OpenURL Universita Degli Studi di Torino - All Libraries