MINI-REVIEW

Interactions between arbuscular mycorrhizal fungi and soil bacteria

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Abstract The soil environment is interesting and complicated. There are so many interactions taking place in the soil, which determine the properties of soil as a medium for the growth and activities of plants and soil microorganisms. The soil fungi, arbuscular mycorrhiza (AM), are in mutual and beneficial symbiosis with most of the terrestrial plants. AM fungi are continuously interactive with a wide range of soil microorganisms including nonbacterial soil microorganisms, plant growth promoting rhizobacteria, mycorrhiza helper bacteria and deleterious bacteria. Their interactions can have important implications in agriculture. There are some interesting interactions between the AM fungi and soil bacteria including the binding of soil bacteria to the fungal spore, the injection of molecules by bacteria into the fungal spore, the production of volatiles by bacteria and the degradation of fungal cellular wall. Such mechanisms can affect the expression of genes in AM fungi and hence their performance and ecosystem productivity. Hence, consideration of such interactive behavior is of significance. In this review, some of the most important findings regarding the interactions between AM fungi and soil bacteria with some new insights for future research are presented.

Keywords Arbuscular mycorrhizal fungi · Beneficial and deleterious effects · Soil bacteria · Agricultural implications

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Introduction

Soil biological behavior is a key parameter affecting soil health, quality and production. Evaluating such effects can be beneficial to enhance ecological and agricultural efficiency. For example, more optimized use of agrochemicals as a result of promoting soil biological properties, including the interactions among different soil microbes can significantly affect environment and crop production (Artursson et al. 2006). This is also biotechnologically important as such interactions can affect the rate of input necessary for a successful and sustainable production (Barea et al. 2005). In other words, the recognition of positive and negative interactions between AM fungi and different soil microbes may result in the identification of microbial genes, significantly contributing to the enhanced soil production.

Soil rhizosphere is interesting and complicated by surrounding plant roots. There are so many different types of microorganisms in the soil rhizosphere interacting with the other soil microbes and with plant roots. The properties of soil rhizosphere make it a unique and active area. The activity and interactions of rhizotrhophic microorganisms can influence soil conditions and hence plant growth and microorganisms' activities (Zaidi et al. 2003).

AM fungi are among the most important and influential soil microbes, significantly affecting the growth of plants and other soil microorganisms. The soil environment around the plant roots and AM hyphae, where AM fungi and soil bacteria are interactive, is called "mycorrhizosphere" (Linderman 1988). There are different types of soil bacteria in the soil, interacting with AM fungi, particularly in the rhizosphere. In most cases, the interactions are synergistic (Smith and Read 2008).

Consideration of the rhizotrhophic interactions and their consequent effects on the soil properties and hence plant growth can have important implications in agriculture and ecology. Such interactions can result in the modification of soil structural properties (Rillig and Mummey 2006) as well as the enhanced availability of nutrients (Marschener and Dell 1994). Thus, it is important to precisely evaluate such interactions and consider their implications in agriculture. This may result in some new perspectives for future research, leading to rapid advancements in the field and more efficient agricultural strategies.

Arbuscular mycorrhizal fungi

Arbuscular mycorrhizal fungi are soil fungi belonging to the phylum Glomeromycota (Schußler et al. 2001). According to both fossil discoveries and DNA sequences, the appearance of both AM fungi and plants is almost 400 million years old (Parniske 2000). AM fungi are able to develop a symbiotic association with most terrestrial plants (van der Heijden 1998b; Pongrac et al. 2007; Feddermann et al. 2010), and usually their symbiosis with the host plant is not host-specific. In their symbiosis, the host plants provide the fungi with their hydrocarbon needs in exchange for nutrients, including phosphorous (P) (Harrison 1999a, 1999b; Hause et al. 2002). Compared with most species of Ectomycorrhiza, AM species develop nonspecific association with their host plant (Zhou and Hyde 2001). The level of specificity is determined by the two symbionts and the ecological parameters. However, some combination of AM–host plant may result in a more efficient symbiosis under different conditions including stress (Daei et al. 2009; Feddermann et al. 2010).

The fungal hyphae grow into the cellular cortex of host plant roots, eventually forming the arbuscules and the vesicles. Arbuscules are branched structural hyphaee, exchanging nutrient with the plant roots. Vesicles are the specialized storage organelles with numerous large vacuoles. They can help the host plant improve its growth under different conditions including stress. For example, the presence of a high number of vacuoles in the vesicles can store salt ions such as sodium and chloride under salinity stress or heavy metals in the polluted soils. This can alleviate the unfavorable effects of stress on plant growth (Smith and Read 2008).

Development of AM symbiosis with the host plant results in some alterations in the physiology of the host plant. For example, plants must behave in a way that could handle the incorporation of enhanced absorbed water and nutrient uptake into their biochemical compounds and physiological functions. Under stress, AM can alter plant physiology in a way, which enables the host plant to cope with the stress (Miransari et al. 2008).

Relative to the complete recognition of symbiotic stages, activated during the process of N fixation between rhizobium (including *Sinorhizobium*, *Bradyrhizobium*, *Mezorhizobium*, and *Azorhizobium*) and the specific host plant, including the exchange of the signal molecules between the two partners (Lindstrom et al. 2002; Miransari and Smith 2007, 2008, 2009), there are numerous other factors regarding the symbiosis of AM fungi with the host plant that have yet be elucidated (Bonfante 2003; Barea et al. 2005).

Communication of some signal molecules between AM and the host plant is necessary for the onset of symbiosis and the beneficial mutualism between the two symbionts (Harrison 1999a; Matusova et al. 2005). It has been recently indicated that plant roots produce a new class of phytohormoens called strigolactones. In addition to stimulating the seed germination of parasitic weeds called *Striga*, these hormones are also able to stimulate fungal metabolism as well as hyphael branching (Akiyama et al. 2005).

The symbiotic signals produced by the fungi are "Myc factors," resulting in the response of symbiotic roots including the plant genes to the fungal presence. Such plant genes have been recently recognized and are necessary for AM symbiosis. In other words, there are plant genes that are expressed by "Myc factors" at the onset of AM-host plant symbiosis. The plant genes activities result in some structural and physiological alterations in the host plant. For example, during the inoculation of root cells by AM fungi, the modification of microtubules is necessary for the growth of AM hyphae into the cells and development of symbiotic mutualism with the host plant (Akiyama and Hayashi 2006; Parniske 2008; Feddermann et al. 2010). On the other hand, the physiological functions of the host plant must also be modified so that the host plant can provide the fungi with the required hydrocarbons in exchange for water and nutrients. Interestingly, there are some common plant genes, expressed during the AM symbiosis and rhizobium N fixation (Akiyama and Hayashi 2006; Parniske 2008; Feddermann et al. 2010).

The mandatory biotrophic nature and the cellular structure of AM fungi have slowed down the pace of advancements in this field, relative to the rhizobim–legume symbiosis (Hijri et al. 1999; Bonfante 2003). Although AM fungal genome (15 Mb) is large, the heterogeneity of a single strain regarding the multitude of its genome (nuclei) has made the performance of AM genomic projects unlikely (Bonfante 2003); however, the significance of the host plant should also be considered. The first plant that has been genetically sequenced is *Arabidopsis taliana*, which is not a host to AM fungi (the *Arabidopsis* Genome Initiative 2000). However, other model plants including rice are host to AM fungi and, hence, the research related to rice

genomic data can illustrate some important knowledge regarding AM symbiosis (Goodman et al. 2002).

Different researchers have indicated that there are about 100,000 genes related to AM plant host symbiosis (Hosny et al. 1999; Bridge and Spooner 2001; Stracke et al. 2002; Bonfante and Genre 2008; Genre et al. 2009). Additionally, using mutants have indicated the presence of proteins, which are communicated between the two partners at the time of symbiosis establishment (Stracke et al. 2002; Grunwald et al. 2009; Hata et al. 2010). The discovery of genes such as NORK and SYMRK have also made the identification of pathways related to signal perception by the host plant, bacteria, and AM fungi likely (Bonfante 2003; Gutjahr et al. 2008, Guether et al. 2009).

The unique characters of AM fungi make them important components of the ecosystem as their activities can contribute to the enhanced plant growth and health (Barea et al. 2005). Inoculating plants with AM inoculum may be a good method for enhancing the efficiency of crop plants. There are three essential parameters affecting the performance of AM inoculum in agriculture: appropriate AM species (Estaun et al. 2002), the quality of AM inoculum (Von Alten et al. 2002), and their ecological properties (Feldman and Grotkass 2002).

AM fungi are able to enhance plant tolerance to different stresses such as soil salinity and drought, soil compaction, heavy metals, and pathogens (Davies et al. 1993; Auge 2001; Feng et al. 2002; Citterio et al. 2005; Hildebrandt et al. 2007; Miransari et al. 2007, 2008). Plant responses to different species of AM fungi are different, and since AM fungi significantly affect the diversity, biomass, and nutrients uptake of plants, AM species determine the structure of plant communities (van der Heijden et al. 1998a, 1998b; Scheublin et al. 2004). The efficiency of plants species in symbiosis with AM species affects their ecological functioning (Davies et al. 1993; van der Heijden et al. 1998a, 1998b; Scheublin et al. 2004; Miransari et al. 2007, 2008).

AM fungi influence the plant community structure by enhancing the growth of their host plant. Hence, recognition of the proper combination of AM species with their host plant is important. Although AM–plant symbiosis is not specific, the probability of some symbiotic combinations is more likely. Compared with other AM–plant symbiosis, some combinations are more common under field conditions (Scheublin et al. 2004). For example, it has been indicated that some AM–host plant symbioses (specific wheat varieties and Glomus mosseae) may be more efficient in enhancing crop yield under stress (Daei et al. 2009).

Application of AM mutualism in agriculture

The practical aspects of AM fungi in the field have been attracting attention for a long time. AM fungi are able to enhance plant water and nutrient uptake. They can increase the solubility and hence the uptake of different macro- and micronutrients by the host plant. For example, P is among the most important nutrients, whose absorption is considerably increased by the host plant. The reason is the production of phosphatase enzymes by AM fungi. This can indicate the significance of AM fungi in agriculture for biological fertilization, which is among the most important applications of AM fungi for crop production (Miransari 2010b). AM fungi can also induce plant systemic resistance as a necessary tool for the host plant to resist plant pathogens in the soil (Hause and Fester 2005; Liu et al. 2007). In addition, AM fungi can also alleviate the unfavorable effects of soil stresses on plant growth and crop production, indicating the significant role of AM fungi as bioprotectors (Xavier and Boyetchko 2002). Improved soil structure is also another benefit resulting from the presence of AM in the soil (Azcón-Aguilar and Barea 1997). These factors indicate the importance of AM biotechnology in the field.

There are different agricultural practices adversely affecting AM functioning in the field including soil tillage, chemical fertilization, biocides, monocropping and non-mycorrhizal plants. Accordingly, organic farming may be a useful alternative to alleviate the unfavorable effects of the above-mentioned practices on AM symbiosis in the field. However, whether organic farming can significantly affect AM colonization in the field, has yet to be indicated (Gosling et al. 2006). Therefore, the selection of appropriate agricultural practices is a must for the enhanced efficiency of AM symbiosis in field when using biological fertilization (Sawers et al. 2008).

AM fungi interactions with other nonbacterial soil microorganisms

Root rhizosphere is important because its properties are significantly different from those of the bulk soil. This is because a continuous flux of carbon is exuded into the rhizosphere environment by plant roots, significantly affecting soil microorganisms and their competition. Although AM fungi are interactive with soil bacteria in the rhizosphere, they are also interactive with nonbacterial soil fauna (Bais et al. 2006).

Protozoa and nematodes are among the most important soil fauna feeding on soil microflora (Bamforth 1985; Ingham et al. 1985; Richardson et al. 2009). Soil nematodes can influence the activities of soil microbes in the rhizosphere by feeding on the roots and hence increasing C allocation to the soils and subsequent enhanced root leakage (Bardgett et al. 1998). Surprisingly, although AM fungi are one of the most important components of the soil

ecosystem and a high range of fungivorous species are found in the soil, little is known about the interactions between AM species and soil fauna (Finlay 1985; Paulitz and Linderman 1991).

Soil nematodes such as *Meloidogyne javanica* are the most effective soil microfauna interacting with AM species as hyphae feeders and root parasites. AM species can also affect nematodes activities and population by enhancing plant growth and hence increasing plant resistance to pathogens including nematodes. Soil protozoa are also interactive with AM species and research has indicated that AM species can positively affect their activities and population (Jentschke et al. 1995; Bonkowski et al. 2000). Among soil mesofauna, collembola may be interactive with soil fungi. However, it has been indicated that feeding on AM species is not their preference and even their feeding on nonmycorrhizal fungi may enhance AM functioning in the field (Bonkowski et al. 2000; Gange 2000).

AM fungi and soil bacteria

Although AM fungi are important symbionts to plants and their symbiosis can significantly enhance the growth of the host plant, they are also interactive with different soil bacteria. These bacteria include both the bacterial strains in the rhizosphere and the bacterial strains in the cytoplasm of some fungal species (Bonfante 2003). Understanding such interactions (Table 1), particularly in agricultural areas with little resources of input, is of significance in the field of molecular microbe–plant interactions (Bonfante 2003; Sanon et al. 2009).

Accordingly, as plant physiology is affected by AM symbiosis, root exudates are also influenced with the production of some new biochemicals, resulting in the alteration of microbial populations in the rhizosphere, relative to a nonmycorrhizal plant (Johansson et al. 2004). AM hyphae are able to produce C products as a source of energy for soil microbes in the mycorrhizosphere, although at a little amount, relative to the rhizosphere (Andrade et al. 1997).

Soil microbes are able to produce products that enhance the amounts of root exudates resulting in the activation of AM hyphae and hence higher rate of root colonization (Barea et al. 2005). Additionally, soil microbes produce plant hormones, which can influence AM establishment as well as spore and hyphal growth (Barea et al. 2005).

The interactions between AM fungi and soil bacteria are influenced by different factors. For example, the ability of bacteria in attachment to the AM hyphae differs among different bacteria and is also affected by the hyphal physiological stage (Artursson et al. 2006). The other related parameters include the AM species and bacterial strains, plant species, rhizosphere, and climate properties (Sanon et al. 2009). So far, no details have been reported regarding the importance of bacterial attachment on AM activities (Artursson et al. 2006). Hence, future research must highlight such effect as well as whether such interactions and attachments can influence soil productivity.

Additionally, it has been stated that bacterial genera are more frequent in the rhizosphere than hyphosphere, indicating that root exudates can be more beneficial to the bacteria than hyphal products (Artursson et al. 2006). There are different examples of enhanced associations between different bacterial strains including *Bacillus*, *Paenibacillus*, *Pseudomonas* and *Rhizobia* and different AM species including *G. calrum*, *G. intraradices*, *G. mosseae*, and *G. versiforme* (Artursson et al. 2006). These stimulating effects include the growth and germination of fungi and spores, respectively, root colonization of the host plant by AM fungi, the solubilization of phosphate, and the suppression of pathogens (Artursson et al. 2006).

Plant growth promoting rhizobacteria (PGPR) are among the most important soil bacteria significantly enhancing plant growth and crop production. They can: (1) alleviate the adverse effects of soil stresses on plant growth, (2) produce plant hormones, (3) increase the solubility of different nutrients by producing different enzymes as well as siderophores, (4) control pathogens, and (5) interact with AM fungi (Glick 2005; Artursson et al. 2006; Jalili et al. 2009; Abbas-Zadeh et al. 2010; Arzanesh et al. 2010; Zabihi et al. 2010).

Researchers have stated that PGPR can have some stimulatory effects on AM growth (Linderman 1997). This indicates that the coinoculation of AM and specific PGPR can enhance the activity of AM during the symbiosis with the host plant (Artursson et al. 2006). This is because, for example, some PGPR such as *Pseudomonas putida* are able to stimulate the root colonization of host plants by AM fungi (Meyer and Linderman 1986). The interaction between AM fungi and soil bacteria, particularly PGPR (von Alten et al. 1993; Kloepper 1996), and N-fixing bacteria are beneficial to the host plants. There is little information regarding the simultaneous and enhancing effects of AM fungi and PGPR on plant growth. It has just been recently that these effects have simultaneously been tested (Artursson et al. 2006).

Major groups of bacteria interacting with AM fungi

Interaction of AM fungi and PGPR

The bacteria that are able to enhance plant growth through interacting with plant roots are called PGPR. As previously mentioned, PGPRs are beneficial bacteria enhancing plant

Table 1 Major groups of bacteria interacting with AM fungi

Bacteria	Effects in soil	Examples	References
PGPR	(1) Nutrient solubility	*Pseudomonas* spp.	Artursson et al. (2005)
	(2) Production of phytohormones	*Bacillus* spp.,	Glick (2005)
	(3) Controlling pathogens	*Rhizobium* spp.	Kohler et al. (2006)
	(4) Production of siderophores	*Burkholderia* spp.	Jalili et al. (2009)
	(5) Interacting with AM fungi	*Methylobacterium* spp.	Richardson et al. (2009)
		Azospirillum spp.	Kim et al. (2010)
		Serratia spp.	(del Mar Alguacil et al. 2009)
		Streptomyces spp.	
		Trichoderma spp.	
		Paenibacillus spp.	
MHB	(1) Spore germination	PGPR	Rillig et al. (2005)
	(2) Fungal growth		Barea et al. (2005)
	(3) Stress alleviation		Frey-Klett (2007), Richardson et al. (2009)
	(4) Controlling pathogens		
	(5) Nutrient availability		Pivato et al. (2009)
	(6) Interacting with AM fungi		
NFB	(1) Fixing atmospheric N$_2$	Rhizobium	Aryal et al. 2003;
	(2) Acting as PGPR		Miransari and Smith (2007), 2008, 2009)
	(3) Interacting with AM fungi		
			Mortimer et al. 2008
			Richardson et al. (2009)
			Franzini et al. (2010)
DB	(1) Production of phytotoxins	Rhizobacteria	Nehl et al. (1997) Francis et al. (2010)
	(2) Competing with other microbes		
	(3) Inhibitory effects on AM fungi		

PGPR plant growth promoting rhizobacteria, *MHB* mycorrhiza helper bacteria, *NFB* nitrogen fixing bacteria, *DB* deleterious bacteria
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growth through different mechanisms including: (1) the production of plant hormones, (2) enhanced solubility of nutrients in soil, (3) controlling pathogens and (4) alleviating stresses (Glick 2005; Kohler et al. 2006, 2009; Jalili et al. 2009; del Mar Alguacil et al. 2009).

PGPR are able to increase AM fungal development by affecting root colonization as well as by enhancing plant N and P uptake (Artursson et al. 2006; Richardson et al. 2009). Although it has been indicated that some of the PGPRs are able to perfectly inoculate plants roots, data related to the inoculation intensity of AM hyphae by PGPR is limited (Hartmann et al. 2009).

Production of extracellular polysaccharides by two PGPRs, *Azospirillum* and *Rhizobium*, significantly enhanced the attachment of bacterial strains to mycorrhizal roots and AM fungal structures. This can significantly influence the movement of bacterial strains into new rhizospheres and is also important for the effective production of microbial inoculums (Bianciotto et al. 2001b).

Kim et al. (2010) found that the synergetic effects of the PGPR *Methylobacterium* oryzae and different species of AM fungi significantly affected plant growth and chlorophyll content. In addition, the rate of root colonization by AM fungi and the number of spores as well as plant uptake of macro- and micronutrients were also significantly higher using the combined inoculation of the two microbes. Such results indicate the presence of a mutualism between the two microbes, which is of significance for inoculums production and hence AM fungi biotechnology.

The strength of bacterial binding to AM hyphae differs during the different physiological stages of attachment including a weak electrostatic attachment in the first stage followed by a strong attachment in the second stage, which is related to the production of cellulose or other extracellular products by bacteria (Artursson et al. 2006). This hypothesis is supported by the less strong attachment of bacterial mutants, which were not able to produce such products, in the presence of the AM hyphae (Artursson et al. 2006). Because some bacterial strains such as *Pseudomonas* spp. are able to colonize both plant roots and AM hyphae, it has been suggested that the related processes can be relatively similar.

Gram-positive bacterial association with AM fungi is higher, related to the Gram-negative bacteria, but has yet to be verified (Artursson et al. 2005). The significance of such interactions is because some of the most important PGPRs including *Bacillus* spp., which are in synergistic interaction with AM fungi, are Gram-positive bacteria (Frey-Klett et al. 2007; Francis et al. 2010). In addition, it has been indicated that some of the plant cell programmes may be common for bacteria such as PGPRs and AM fungi (Sanchez et al. 2004). Soil bacteria and AM fungi can also influence the decomposition of organic matter in the soil, which is affected by their enzyme production (de Boer et al. 2005).

There are some bacteria (P solubilizing bacteria) in the soil that are able to enhance P uptake by AM species and plant through enhancing the solubility of soil P, present in organic and inorganic forms (Zabihi et al. 2010; Salimpour et al. 2010). Organic and inorganic P are made available by phosphatase and organic acid producing bacteria, respectively. This significantly increases P uptake by AM hyphae and hence the symbiotic host plant (Smith and Read 2008). The soil inorganic form of P, which is not available to plants, is strongly bound in the insoluble structures of P and is also attached to the clay surface layers (Zabihi et al. 2010; Salimpour et al. 2010).

The synergistic effects of AM fungi and soil solubilizing P bacteria has been indicated (Kim et al. 1998). Under limited P availability, the interaction effects between P solubilizing bacteria and AM fungi result in the enhanced plant colonization by AM fungi and the increased bacterial population in the rhizosphere. The coinoculation of AM fungi and P solubilizing bacteria increased plant N and P uptake, relative to control plants (Artursson et al. 2006). The combined inoculation of AM fungi and P solubilizing bacteria was the most efficient treatment, significantly enhancing P absorption by plant. P solubilizing bacteria increased the amount of available P from the rock phosphate, absorbed by AM hyphae (Barea et al. 2005; Zabihi et al. 2010; Salimpour et al. 2010). This can be of particular significance for the proper development of P fertilization.

Mycorrhiza helper bacteria

There are a large number of bacteria, including PGPR and *Rhizobium*, called mycorrhiza helper bacteria (MHB), which promote the activity and development of AM fungi (Frey-Klett et al. 2007; Richardson et al. 2009). They are usually fungal-specific but not plant-specific (Rillig et al. 2005). In other words, they can promote the growth of specific AM fungi, in symbiosis with their nonspecific host plant. Such specificity has been attributed to the size of spore and the roughness of spore surface (Bharadwaj et al. 2008). Accordingly, the term "mycorrhization helper

bacteria" was suggested by Frey-Klett et al. (2007), indicating a broader concept compared with MHB as it also includes the onset of AM symbiosis as well as the biocontrolling effects of MHB on other fugal species with regard to their specificity.

They can influence spore germination by affecting the spore wall (Maia and Kimbrough 1998; de Boer et al. 2005), stimulate spore germination by producing stimulants such as CO_2 (Carpenter-Boggs et al. 1995), or by affecting the AM fungal P absorption (Ruiz-Lozano and Bonfante 2000). Interestingly, the in vitro germination of AM spores was dependent on the presence of *Streptomyces orientalis* as the fungi were able to germinate in the presence of bacteria (Mugnier and Mosse 1987). This may be useful for the in vitro production of AM inoculum. Ames et al. (1989) indicated that most of the AM spores were colonized by different microbes including chitin-mineralizing microbes, actinomycetes, bacteria and fungi affecting spore germination.

Additionally, AM can also alter the combination of bacteria in the rhizosphere through competition for soil nutrients (Christensen and Jakobsen 1993). Researchers have stated that the association of some bacteria with AM is specific (Artursson et al. 2005) indicating that there are some kind of communication between the bacteria and AM fungi, stimulated by fungal exudates (Artursson et al. 2006). This is also verified by results that some bacterial genera including *Arthrobacter* and *Bacillus* were most common in the hyphosphere or the soil around specific AM hyphae, while *Pseudomonas spp.* were most distributed in the *Sorghum bicolour* rhizosphere (Artursson et al. 2005).

The significance of bacterial attachment to the AM hyphae and whether it can affect hyphal growth has yet to be elucidated. However, if this is so, the coinoculation of appropriate bacteria with AM can significantly contribute to enhanced plant growth (Artursson et al. 2006). For example, the bacteria present in the water soluble aggregates are different from the bacteria present in non-soil water aggregates (Artursson et al. 2006). Bacterial types, which are interactive with AM species are saprophytes and symbionts, some of which are unfavorable, some are neutral and some are favorable (Johansson et al. 2004). According to Bianciotto et al. (1996a), the attachment intensity of some strains of *Rhizobium* and *Pseudomonas* to AM germinating spore and hyphae under sterilized conditions was different depending on the strains of bacteria; however, the level of specificity was not recognized.

For PGPRs, their adherence to AM is determined by the formation of biofilms, which are extracellular matrixes including bacteria, produced by the bacteria (Seneviratne et al. 2009). In their experiment, Pivato et al. (2009) examined the effects of different bacterial strains on the saprophytic

and root colonization of AM *G. mosseae*. They tested strains belonging to *Comamonadaceae* (isolated from non-mycorrhizal roots) and the *Comamonadaceae* and *Oxalobacteraceae* families (isolated from mycorrhizal roots) as well as two reference strains *Collimonas fungivorans* Ter331 and *Pseudomonas fluorescens* C7R12. They found that only the *Oxalobacteraceae* family and *P. fluorescens* C7R12 enhanced the in vitro saprophytic growth of *G. mosseae* and root colonization of *Medicago truncatula* indicating that they are MHB.

MHB mostly include *Bacillus* and *Pseudomonas*. MHB can affect AM fungal functioning by influencing root cell permeability, root exudation, entrance of fungi into the host root, phytohormone production; alleviating the adverse effects of environmental parameters on hyphal growth; and stimulating the growth of plant root hairs. Some rhizobial strains are also able to affect the presymbiotic stages in AM fungi by influencing spore germination and hyphal growth (Barea et al. 2005; Frey-Klett et al. 2007). The other recently recognized effects of MHB on AM include their formation and functioning as well as their effects on nutrient availability, N_2 fixation and controlling root pathogens (Frey-Klett et al. 2007).

Nitrogen fixing *Rhizobium*

The other interesting part related to the AM fungal interaction with other soil microbes is the formation of tripartite symbiosis between AM fungi, rhizobium and legumes. The enhancing effects of coinoculation with AM fungi and rhizobium on the growth and yield of legume have been well known. AM fungi can significantly increase legume growth by enhancing water and nutrients uptake. The enhanced P uptake can also positively affect rhizobium N-fixation by affecting the energy producing pathways (Barea et al. 1992; Aryal et al. 2003; Mortimer et al. 2008).

Hormonal effects on the development of root and nodules may also affect the N_2-fixation by legume in the tripartite symbiosis (Richardson et al. 2009; Franzini et al. 2010). The efficiency of the tripartite symbiosis is affected by parameters such as plant variety, *Rhizobium* strains, AM species and the related interactions as well as their growth stage (Marulanda et al. 2006; Mortimer et al. 2008). AM mutants (Myc$^-$) that are also Nod mutants are not able to produce Nod factors and can be used for: (1) the elucidation of both cellular and molecular processes, necessary for legume symbiosis, and (2) for the recognition of the common trusdacution pathways between plants and microbes during symbiosis (Gollotte et al. 2002).

With respect to the significance of both AM symbiosis and *Rhizobium* N fixation environmentally and economically, consideration of parameters, which enhance their tripartite symbiosis can be important. N and P are two necessary macronutrients for plant growth and yield production (Richardson et al. 2009). Chemical fertilization especially at excess amounts is not recommendable; hence, providing N and P biologically by AM fungi and rhizobium may greatly contribute to the increased yield production while making them agriculturally and environmentally sustainable (Miransari 2010b; Miransari and Mackenzie 2010a, b, c).

It is also important that the tripartite symbiosis be tested under different conditions including stress to evaluate if its efficiency can be enhanced. As AM fungi and *rhizobium* bacteria are morphologically and physiologically different, their response is also different under stress conditions. Under stress, AM fungi are more resistant and can help their host plants grow more effectively (Miransari 2010a); however, rhizobium are not tolerant to stress and their efficiency decreases under stress (Miransari and Smith 2007, 2008, 2009). Hence, in a tripartite symbiosis, it can be useful if the N-fixing capacity of rhizobium is increased by AM symbiosis. This is also important for the production of inoculum, meaning that biotechnologically the two microbes have to be treated in a way that results in the highest efficiency of the host plant symbiosis under different conditions including stress.

Deleterious bacteria

Root rhizosphere is interactive and complicated determining the activities of soil microbes and hence plant growth. Among the different bacterial strains found in the rhizosphere are deleterious bacteria (DB), which adversely affect plant growth. Such unfavorable effects are due to the production of different unfavorable compounds by the bacteria including phytotoxins, competition for food resources with other soil microorganisms as well as their inhibitory effects on AM fungal activities. Parameters such as microbial growth stage, environmental conditions, plant varieties, and AM growth and development determine if the bacteria may act as deleterious. AM fungi are able to induce plant systemic resistance in the presence of DB by affecting the cross-talk between the salicylic acid and jasmonate pathways (Pozo and Azcón-Aguilar 2007).

Interestingly, depending on the conditions, rhizobacteria may act as deleterious or PGPR by both inhibiting plant growth and controlling plant pathogens in soil. Such characteristics indicate the importance of proper management of rhizobacteria for inoculum production to achieve sustainable agriculture (Nehl et al. 1997; Francis et al. 2010). In other words, it is important that bacterial inoculums be produced depending on the present conditions with respect to their physiological properties. Hence, the biotechnological aspects related to the handling of soil microbes for inoculum production must also be determined so that appropriate inoculums can be produced.

AM fungi and endosymbiotic bacteria

The interactions between AM fungi and endosymbiotic bacteria can influence their performance and the pathogenic microbes as well as plant growth and development. There are different mechanisms by which the attached bacteria to the fungal spore can affect fungal performance including: (1) release of substances, which affect fungal gene expression, (2) injection of molecules into the fungal spore, (3) attachment to the fungal surface by producing lectins, (4) degradation of fungal cell wall and (5) production of volatiles affecting fungal gene expression (Bonfante and Anca 2009).

Although there are research work regarding the association of endosymbiotic bacteria with *Glomus* species, but the most findings are related to the interactions between endosymbiotic bacteria and mycorrhizal fungi *Gigaspora margarita* (Bianciotto et al. 1996b; Bharadwaj et al. 2008; Bonfante and Anca 2009).

Ecological and agricultural significance of interactions between AM fungi and soil bacteria

Microhabitats occupied by the interacting bacteria with AM fungi

The microhabitats, which are commonly occupied by soil bacteria interacting with AM fungi (Dumbrell et al. 2010) include surface of plant roots (nonsymbiotic bacteria), plant root cells (symbiotic bacteria), AM hyphae (DB, MHB, PGPR) and the rhizosphere surrounding plant roots (different kinds of bacteria). Hence, the microhabitats occupied by bacteria are determined based on their feeding properties, their kind of symbiosis, soil and climate properties and their host specifications (Nazir et al. 2010).

AM are also great niches for other soil microbes and while some of the bacteria are attached to AM hyphae, some of them are bound to plant roots (Bianciotto et al. 2001a; Bonfante 2003). While for other eukaryotic cells the association with bacteria is common (Moran and Wernegreen 2000), for AM fungi only a few strains of bacteria are integrated into the fungi (Ruiz-Lozano and Bonfante 2000; Levy et al. 2003; de Boer et al. 2005). There are bacteria-like structures in the cytoplasm of AM fungi (Mosse 1970; Artursson et al. 2006).

Effects of the microbial community on AM fungi

In brief, it can be mentioned that there is a high rate of interactions between the soil microbial community and AM fungi (Dumbrell et al. 2010). As previously mentioned, soil microbial community can positively or adversely affect AM

fungal efficiency. Accordingly, it is important that the deleterious effects of microbial community on AM performance can be diminished under different conditions including stress. Soil microbial communities can also adversely affect AM fungal activities in soil by: (1) competing for different sources, (2) reducing plant growth (pathogens), (3) interacting with other soil microbes, and (4) producing unfavorable chemicals (Nehl et al. 1997; Glick 2005). However, soil microbial communities can also exert positive effects on AM fungi are by: (1) producing plant hormones, (2) affecting the solubility of soil nutrients, (3) improving soil structure, (4) controlling plant pathogens, and (5) affecting plant growth (Glick 2005; Rillig and Mummey 2006; Jalili et al. 2009; Abbas-Zadeh et al. 2010).

Effects of AM fungi on the microbial community

In most cases, AM fungi can positively affect the microbial community. AM fungi have several interesting abilities, which can help the host plant grow under stress and hence provide more favorable conditions for the activity of the microbial community. In most cases, AM fungi can synergistically affect the microbial community and hence increase the efficiency of soil production. The growth of AM hyphae into the mycorhizosphere (the rhizosphere around mycorrhizal roots affected by root activities, for example, rhizodeposition; Jones et al. 2009) can affect its properties and hence soil microbial communities through the following: (1) production of different enzymes such as phosphatases and hence the solubility of different nutrients including P, (2) production of glomalin and hence improving soil structure, (3) controlling plant pathogens in soil and (4) interacting with plant roots and other soil microbes (Rillig and Mummey 2006; Cheng and Baumgartner 2006; Haung et al. 2009).

Specific aspects

There are several specific aspects related to the interactions between AM fungi and soil microbes including: (1) how the synergistic interactions between AM fungi and soil microbes can be improved; (2) how the adverse effects of DB on AM fungal activity and hence plant growth can be alleviated; (3) which combination of soil microbes are the most optimum for plant inoculation; (4) how the soil microbes must be biotechnologically treated so that the inoculum efficiency can increase; and (5) how the specificity of interactions can affect soil efficiency.

Importance of AM fungi and soil microbes' interactions in agriculture

The previously mentioned microbial interactions can affect agricultural efficiency. If AM fungi and soil microbes can

interact synergistically, higher yield production can result, which at the same time can be agriculturally sustainable. Microbes are abundant in the soil and continuously interacting; therefore, it is important to treat soil conditions in a way that soil microbes can positively interact, resulting in more favorable conditions for plant growth and yield conditions.

Among the most important implications of microbial interactions in agriculture is the alleviation of different soil stresses including salinity, drought, acidity, compaction and heavy metals. For example, how the use of soil microbes including arbuscular mycorrhizal fungi and other soil microbes can alleviate the unfavorable effects of heavy metals on plant growth or how such a technique can be used for the remediation of polluted soils (Berg 2009; Joner and Leyval 2009). Extensive research has been done on use of AM fungi for treating heavy metals in soil. Although AM has been proved to be effective on the alleviation of stress, it would be interesting to investigate how such abilities can be improved when using AM fungi in combination with other soil microbes. AM fungi are able to alleviate the stress by enhancing plant growth, storing heavy metals in the vacuoles of their vesicles and binding them by the production of the insoluble glycoprotein, glomalin (Khan 2005).

One of the most important mechanisms by which AM fungi are able to enhance plant resistance to plant pathogens in soil is through altering the microbial combination in the mycorrhizosphere. The related effects also include bacterial activities and their production that usually contains pathogen-controlling products (Barea et al. 2005). Hence, it would be interesting to investigate the right species of AM fungi, and which of these can have the highest impact on soil bacterial activities, including their eventual control of soil pathogens.

The activities of soil microbes including AM fungi and bacteria can influence soil structure through the production of bacterial metabolites including polysaccharides, formation of AM hyphae and production of the glycoprotein, glomalin (Rillig and Mummey 2006). Such products are able to bind soil particles and form soil aggregates, resulting in improved soil structure (Andrade et al. 1998; Barea et al. 2005). Accordingly, such effects also indicate the beneficial effects of coinoculation with AM fungi and bacteria on the improvement of soil structural properties and fertility in desertified areas.

Using several legume species tolerant under drought conditions, Jeffries and Barea (2001) indicated that soil properties including nutritional values were improved upon coinoculation with AM fungi and rhizobium. These include enhanced N fixation as well as improved soil structure. Hence, as a useful biotechnological method, coinoculation of drought-tolerant plants with AM fungi and bacteria

including rhizobium can contributes to the enhanced recovery of desertified and self-sustaining ecosystems (Barea et al. 2005). It is important to determine the bacterial population with the highest physiological activities, in association with AM fungi. This indicates the bacterial strains that are more efficient, particularly when interacting with AM fungi, and can likely make the use of effective coinoculation (Hartmann et al. 2009; Franzini et al. 2010).

There are different methods used to determine bacterial association with AM fungi. For example, for tagging and visualizing the bacterial strain *Paenibacillus brasilensis*, which has suppressing effects on the activity of plant pathogens and can stimulate the activity of some specific AM species, von der Weid et al. (2005) used the green fluorescent protein technique. In this method, marker gens (*gfp*) are used to tag the bacteria. Such genes lead to the production of green fluorescent and hence make it likely to investigate the bacterial behavior interacting with AM fungi or other soil microbes including pathogens. The other molecular techniques include staple isotope probing, DNA sequencing and PCR (Johnson et al. 2001; Griffiths et al. 2004).

The interactions between AM fungi and bacteria can take place in the rhizosphere before the onset of inoculation or after the establishment of the tripartite symbiosis between AM fungi, bacteria and the host plant (Garbaye 1994; Gryndler et al. 2000; Artursson et al. 2006). As previously mentioned, the synergistic interactions of AM fungi and bacteria can stimulate plant growth through enhancing processes such as nutrients uptake and controlling plant pathogens. These processes are of significance, especially in agricultural cropping strategies (such as organic farming), which do not depend much on agrochemicals to maintain soil fertility and health. In addition, AM fungi are also able to influence the combinations of soil bacterial populations (Artursson et al. 2005). These effects can be related to the alteration of root physiology by affecting the chemical combination of root products (Gryndler 2000; Linderman 2000).

Although extensive research has been carried out on the interactive activities between AM fungi and bacteria, more research must be conducted to more clearly elucidate the processes involved in the interactions between AM fungi and soil bacteria. This can be useful for the optimum determination of bioinoculants combination, which is necessary for sustainable agricultural cropping strategies (Artursson et al. 2006).

AM fungi and other soil fungi

The presence of other soil fungi in plant rhizosphere can affect the level of symbiotic efficiency between AM fungi

and the host plant depending on the properties of soil fungi. In other words, there may be direct interactions between AM fungi and other soil fungi or AM fungi, and the other fungi such as pathogenic fungi can interact through their effects on plant growth. Both types of fungi can induce plant systemic resistance through different ways including their effects on plant hormone pathways. Although in the presence of pathogenic fungi, plant resistance can be positively affected by AM fungi, pathogenic fungi may adversely affect such type of symbiosis by inducing plant resistance (Harman et al. 2004; Kloepper et al. 2004; Waller et al. 2005; Van Wees et al. 2008).

AM fungi and plant hormones

One of the different enhancing effects of AM fungi and soil bacteria on plant performance is by inducing plant systemic resistance, which is also influenced by plant hormones (Van Wees et al. 2008). AM fungi can also alter the amount of plant hormones, which has been extensively investigated for jasmonic acid (JA) and abscisic acid (ABA) (Ludwig-Muller 2000; Hause et al. 2007; Grunwald et al. 2009). Both hormones are necessary for the establishment of AM symbiosis (Isayenkov et al. 2005).

In addition, the newly classified plant hormones, strigolactones, can also affect mycorrhization in plants, which is also influenced by mitochondrial activities (Akiyama et al. 2005; Akiyama and Hayashi 2006; Besserer et al. 2009). Under the stress of nutrient deficiency, plants may increase the level of strigolactones, resulting in the reduction of shoot branching and enhancement of mycorrhization. The elucidation of interactions between auxin, cytokinins and strigolactones may provide more details regarding root branching (Shimizu-Sato et al. 2009) as well as the establishment of mycorrhizal establishment.

Interestingly, under stress AM fungi can also influence plant physiology in a way, which helps the host plant handle the stress (Miransari et al. 2008). Such effects can be exerted through the alteration of plant hormone activities in plants. For example, Aroca et al. (2008) indicated that by altering the activity of ABA in plant, AM fungi can alleviate the unfavorable effects of stress on plant growth. Accordingly, it may be mentioned that the interactions between AM fungi and plant hormones may effectively influence the symbiosis between AM fungi and the host plant under different conditions including stress.

Conclusion

The interactions between AM fungi and bacteria in soil are of significant importance. These interactions must be clearly elucidated as they can have some significant implications in agriculture and ecology. Such interactions, which are fulfilled by different means such as bacterial attachment to the fungal spore and hypha, injection of molecules into the fungal spore by bacteria, degradation of fungal cell wall and production of volatiles, influence fungal gene expression. Thus, the symbiosis between the fungi and the host plant and hence ecosystem productivity is also affected. In addition to their individual functioning in the soil, the combined effects of soil microbes are also important for the production of bioinoculants. Therefore, future research may be directed on the more detailed illustration of interactions between the host plant, AM fungi and soil bacteria by using different molecular techniques. This may result in a more efficient—and at the same time agriculturally and environmentally sustainable—use of soil microorganisms for crop production. The use of new techniques related to molecular ecology and metagenomic analyses may yield further details regarding the interactions between different organisms and AM fungi.

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