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Review. The role of the arbuscular mycorrhiza-associated rhizobacteria in the biocontrol of soilborne phytopathogens

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Abstract

The mutualistic symbiosis of most land plants with arbuscular mycorrhizal (AM) fungi has been shown to favor mineral and water nutrition and to increase resistance to abiotic and biotic stresses. This review reports the main mechanisms involved in the control of the disease symptoms and of the intraradical proliferation of soilborne phytopathogens by root colonization with AM fungi, with a special emphasis on the role of the rhizobacteria shown to be specifically associated with the AM extraradical network and the mycorrhizosphere (the soil zone with particular characteristics under the influence of the root/AM association). The mycorrhizosphere would constitute an environment conducive to microorganisms antagonistic to pathogen proliferation. Moreover, attempts to identify rhizobacteria from AM structures and/or the mycorrhizosphere often lead to the isolation of organisms showing strong properties of antagonism on various soilborne pathogens. The ability of AM fungi to control soilborne diseases would be strongly related to their capacity to specifically stimulate the establishment of rhizobacteria unfavorable to pathogen development within the mycorrhizosphere before root infection. Current knowledge concerning the mechanisms involved in AM/rhizobacteria interactions are also described in this review.

Additional key words: AM-associated bacteria (AMB), arbuscular mycorrhizal fungi, biocontrol, mycorrhizosphere, *Paenibacillus,* soilborne pathogens.

Resumen

Revisión. El papel de las rizobacterias asociadas a micorrizas arbusculares en el control biológico de fitopatógenos del suelo

La simbiosis micorriza arbuscular (MA), presente en la mayoría de las plantas terrestres, favorece la nutrición mineral, la captación de agua e incrementa la resistencia a estreses abióticos y bióticos. En esta revisión se recogen los principales mecanismos, ligados a la colonización de las raíces por hongos MA, implicados en el control de síntomas ligados a enfermedades y en el control de la proliferación intraradical de fitopatógenos del suelo. Se hace un énfasis especial en el papel de las rizobacterias asociadas específicamente a la red de micelio extraradical de los hongos MA y a la micorrizosfera (zona de suelo con características especiales debidas a la influencia de la asociación hongo/planta). La micorrizosfera constituiría un entorno propicio para el desarrollo de microorganismos antagónicos a la proliferación de patógenos. Los estudios realizados sobre rizobacterias asociadas a estructuras de hongos MA o de la micorrizosfera han conducido en muchas ocasiones al aislamiento de organismos con características antagonistas frente a patógenos del suelo. La capacidad de los hongos MA para controlar enfermedades de suelo estaría fuertemente relacionada con su capacidad para estimular específicamente el establecimiento de rizobacterias en la micorrizosfera desfavorables para el desarrollo de patógenos antes de que estos puedan infectar la raíz. En esta revisión también se describen los conocimientos actuales sobre los mecanismos implicados en las interacciones entre hongos MA y rizobacterias.

Palabras clave adicionales: bacterias asociadas a micorrizas arbusculares (AMB), control biológico, hongos micorrizógenos arbusculares, micorrizosfera, *Paenibacillus*, patógenos del suelo.

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Abbreviations used: AM (arbuscular mycorrhizal), AMB (AM-associated rhizobacteria), API (analytical profile index), Ecc (*Erwinia carotovora* var *carotovora*), EPS (extracellular polysaccharide), Foc (*Fusarium oxysporum o.* f.sp. *chrysanthemi*), fol (*Fusarium oxysporum* f. sp. *lycopersici*), fsp (*Fusarium solani* f. sp. *phaseoli*), ISR (induced systemic resistance), MHB (mycorrhization helper bacteria), PCR-DGGE (polymerase chain reaction-denaturing gradient gel electrophoresis), PGPR (plant growth promoting rhizobacteria), PLFA (phospholipid fatty acid analysis), PR proteins (pathogenesis related proteins).

Introduction

In symbiotic association with roots of a large majority of land plants, arbuscular mycorrhizal (AM) fungi increase the nutrient absorptive root surface area, through soil exploration by the external mycelium, favoring in this manner access to nutrients and water to the host plant (Rhodes and Gerdemann, 1975; Smith and Read, 2008). Moreover, as the largest component of the soil microbial biomass (Kabir *et al.*, 1997; Olsson *et al.*, 1999), they form extensive mycelial networks within the soil matrix and hyphae constitute important sites for interactions with other soilborne microorganisms. The narrow zone of soil surrounding living roots is called the rhizosphere (Hiltner, 1904) characterized by increased microbial activity and by a specific microbial community structure (Duineveld *et al.*, 2001; Kim *et al.*, 2006). The root-AM fungi association constitutes the major factor influencing the community structure and the biomass of soil microorganisms leading to the establishment of the so-called mycorrhizosphere (Linderman, 1988; Marschner *et al.*, 2001; Marschner and Timonen, 2005; Lioussanne *et al.*, 2009a). The zone of soil influenced by only AM fungi is named the mycosphere. From mycorrhizosphere and AM structures, various rhizobacteria (named AM-associated rhizobacteria, AMB) (especially Paenibacilli, Bacilli and Pseudomonas spp.) were identified by classical culture-dependant methods (Andrade *et al.*, 1997; Budi *et al.*, 1999; Mansfeld-Giese *et al.*, 2002; Lioussanne, 2007; Bharadwaj *et al.*, 2008b), phospholipid fatty acid analysis (PLFA) (Rillig *et al.*, 2005) and PCR-DGGE (Polymerase chain reaction-Denaturing gradient gel electrophoresis; Xavier and Germida, 2003; Roesti *et al.*, 2005; Lioussanne, 2007) reinforcing the hypothesis that AM structures constitute important nutrient-rich niches for soilborne microorganisms. *Candidatus* Glomeribacter gigasporarum (proposed as a new taxon of *Burkholderiaceae*) was even described as a Gram- non-cultivable (thus obligatory) bacterial endosymbiot of spore vacuoles, mycelium and intraradical hyphae of *Gigaspora margarita* colonizing clover plants (Bianciotto *et al.*, 1996b; Bianciotto and Bonfante, 2002). This endobacteria was later phenotypically described in details (Jargeat *et al.*, 2004), shown to be widespread within *Gigasporaceae* (Bonfante, 2003), to be vertically transmitted (Bianciotto *et al.*, 2004) and to contain nitrogen fixation genes instead of *Gi. margarita*, suggesting that this AM fungus might fix nitrogen and then deliver it to the symbiotic plant through the associated bacterial population (Minerdi *et al.*, 2001). Consequently, some of the effects on the host-plant physiology attributed to the mycorrhizal root colonization might, at least partially, be the consequence of the activity of specifically AM-associated rhizobacteria.

Among the beneficial effects of AM fungi on the host-plant physiology, the decrease of the intraradical and/or mycorrhizosphere population and/or of the disease symptoms of soilborne pathogens was shown in many biological systems but according to yet partially described but probably synergistic mechanisms (St-Arnaud and Vujanovic, 2007; Lioussanne *et al.*, 2009b). Since chemical pesticide use is more and more restricted due to its risks to human health and the environment, implementation of sustainable agriculture has become imperative in crop industry. The understanding of the mechanisms involved in the AM-mediated biocontrol will permit the performance of an adequate management of such agroecosystems and then permit the maximization of AM benefits (Gosling *et al.*, 2006).

The present article aims to review the main mechanisms involved in the biological control of diseases induced by soilborne phytopathogens after root colonization with AM fungi, especially the role of the AM-associated rhizobacteria which would constitute major elements implicated in this phenomenon.

Mechanisms involved in the AM-mediated biocontrol

Reduction in the deleterious effects of soilborne pathogens after root colonization with AM fungi was described a long time ago (Gerdemann, 1968, 1974) and has been observed on various fungi, stramenopiles, nematodes and bacteria (for review see Whipps, 2004). *Glomus mosseae* in symbiosis with clover plants cv. Sonja was even able to totally prevent infection by *Pythium ultimum* (Carlsen *et al.*, 2008). The characteristics of this biological control regarding to its amplitude related to the pathogen/AM fungus/plant taxa association, conditions of culture, level of root colonization, time of AM/pathogen inoculation and harvest, etc. and the mechanisms hypothesized to be involved were described in various reviews (Harrier and Watson, 2004; Whipps, 2004; St-Arnaud and Vujanovic, 2007; Avis *et al.*, 2008; Vierheilig *et al.*, 2008; Akhtar and Siddiqui, 2009; Lioussanne *et al.*, 2009b,c; for the most recently published ones). The disease symptoms

induced were even shown to be systemically reduced in non-mycorrhizal roots of plants grown in split-root systems inoculated with AM fungi (Pozo *et al.*, 2002; Zhu and Zao, 2004; Khaosaad *et al.*, 2007).

Various hypotheses have been put forward in an attempt to explain the AM-mediated biocontrol of soilborne phytopathogens. The fact that pathogen induced symptoms are systemically regulated by AM colonization suggests the establishment of induced systemic resistance (Pozo and Azcón-Aguilar, 2007) [ISR defined as resistance mechanisms induced upon plant pre-treatment with a variety of organisms and compounds (Van Loon *et al.*, 1998)]. New isoforms of superoxide dismutases and peroxidases (Pozo *et al.*, 2002; Garmendia *et al.*, 2006), PR-1 proteins (pathogenesis-related proteins type 1; Cordier *et al.*, 1998) and higher concentrations of phenolic acids (Singh *et al.*, 2004; Zhu and Zao, 2004) (ISR-related compounds) were detected in plants colonized with AM species with biocontrol activities. Accumulation of jasmonic acid involved in the rhizobacteria-mediated ISR (Pozo *et al.*, 2004) in mycorrhizal roots (Hause *et al.*, 2002, 2007; Isayenkov *et al.*, 2005) could be related to the systemic pathogen biocontrol. Additionally, Cordier *et al.* (1998) identified local cell-wall modifications such as callose accumulation around arbuscule-containing cortical cells of tomato roots. Furthermore, the synthesis of constitutively and additional isoforms of defense related enzymes such as chininases, chitosanases, β-1,3-glucanases, peroxydases and superoxide dismutase has been locally detected in mycorrhizal roots (Pozo *et al.*, 1996, 1998, 1999). Nonetheless, the level of production of these enzymes or of flavonoïds was shown to be unrelated to the capacity of biocontrol of the AM species (Pozo *et al.*, 2002; Carlsen *et al.*, 2008). Moreover, transcript profiling and real-time quantitative PCR used to explore the transcriptional changes triggered by AM colonization revealed a complex pattern of local and systemic changes in gene expression in roots of *Medicago trunculata* (Liu *et al.*, 2007) but, transcripts for defense-related proteins were only locally expressed. Furthermore, concentrations of defense related compounds such as rosmarinic and caffeic acids, phenolics and essential oils were not increased by colonization with *G. mosseae* protecting basil plants against *Fusarium oxysporum* f. sp. *basilica* highlighting the role of other mechanisms in the AM-mediated biocontrol than the stimulation of systemic and localized plant defense mechanisms (Toussaint *et al.*, 2008).

The most frequently documented response to AM colonization is an increase in phosphorus nutrition of the host plant which would consequently be more vigorous and more resistant to pathogen invasion. Nonetheless, the AM mediated biocontrol was shown to be unrelated to the soil P availability and/or the P status in plant tissues and then more dependent on other mechanisms (Trotta *et al.*, 1996; Yao *et al.*, 2002; St-Arnaud and Elsen, 2005; Toussaint *et al.*, 2008).

AM fungi would compete for space and nutrients with soilborne pathogens within the mycorrhizosphere and the host roots. Larsen and Bødker (2001), using signature fatty acids profiles, demonstrated the decrease in biomass and energy reserves of both *G. mosseae* and *Aphanomyces euteiches* co-occupying pea roots. Cordier *et al.* (1996) also showed that *Phytophthora nicotianae* and *G. mosseae* never occupied simultaneously the same tomato root tissues. A reduction in the extent of mycorrhizal colonization by different plant pathogens has been reported (Davis and Menge, 1980; Bååth and Hayman, 1983; Krishna and Bagyaraj, 1983) indicating the possible occurrence of competitive interactions. Because of this competition, the AM fungus is often inoculated before the pathogen in order to favor biocontrol efficiency. However, *F. solani* f. sp. *phaseoli* (Fsp) genomic DNA quantified using quantitative real time PCR was significantly reduced not only in the mycorrhizosphere and the mycosphere but also in the bulk soil of a compartmentalized soil-root system inoculated with *G. intraradices* (Filion *et al.*, 2003). In this study, the AM genomic DNA was not significantly modified by the pathogen in the soil. Reduction in Fsp growth as well as root rot symptoms as a result of colonization with *G. intraradices* would not be the consequence of competition for resources and habitat between the two fungi but mostly caused by the biotic and/or abiotic characteristics of the established mycorrhizosphere.

The *G. intraradices* extraradical network has been shown to directly reduce the growth of the nematodes *Radopholus similis* and *Pratylenchus coffeae* and of conidial formation of the fungus *F. o.* f.sp. *chrysanthemi* (Foc) in root and other microorganism-free *in vitro* conditions (St-Arnaud *et al.*, 1995; Elsen *et al.*, 2001, 2003). However, these negative impacts were not significant for all nematode developmental stages and were unrelated to the AM fungus mycelial or spore densities (Elsen *et al.*, 2001, 2003). Furthermore, the Foc spore germination and hyphal growth were significantly increased in presence of the AM fungus suggesting that the direct inhibition of pathogen development by AM

structures would be weakly involved in biocontrol (St-Arnaud *et al.*, 1995).

Studies on the impact of exudates from extraradical AM network or mycorrhizal roots both grown *in vitro* on pathogen can lead to results in contradiction. Crude extracts from *G. intraradices* extraradical network unambiguously reduced Foc conidia germination (Filion *et al.*, 1999). Analogous inhibitive effects were observed with exudates liberated by strawberry roots colonized by *G. etunicatumn* and *G. monosporum* on the pathogen *P. fragariae* sporulation (Norman and Hooker, 2000). Meanwhile, depending on the harvest time, exudates from *in vitro* grown tomato roots colonized with *G. intraradices* were repulsive or more attractive than exudates from non-AM inoculated roots to *P. nicotianae* zoospores (Lioussanne *et al.*, 2008). Moreover, microconidia germination of F. o. f. sp. *lycopersici* (Fol) was more than doubled in the presence of root exudates from tomato plants grown in soil and colonized with *G. mosseae* compared with exudates from non-mycorrhizal plants (Scheffknecht *et al.*, 2006). The only study of the direct impact of exudates from mycorrhizal plants in the AM mediated biocontrol directly measured in soil conditions by quantification of the capacity of root infection by the pathogen was performed by Lioussanne *et al.* (2009d). Application of root exudates from tomato plants colonized with *G. intraradices* or *G. mosseae* on tomato roots had no impact on *P. nicotianae* intraradical growth while direct inoculation of these AM fungi significantly reduced this data suggesting that exudates from mycorrhizal plants would not directly or indirectly (through stimulation of other beneficial microorganisms) inhibit the capacity of pathogen intraradical proliferation. Furthermore, no compound antagonistic to pathogen development directly exuded by AM fungi has yet been identified.

In summery, none of the above-cited mechanisms proposed to be involved in the AM-mediated biocontrol has been shown to happen in every biological system studied: a mechanism described in a system is shown not to happen in another one. These mechanisms might thus act in synergy with each other, with one mechanism becoming preponderant depending on the environmental conditions and the plant cultivar-pathogen/AM fungus strain studied. Nonetheless, another mechanism related to the capacity of interaction of AM fungi with other soil microorganisms would be importantly and even represent a main mechanism involved in the control of soilborne diseases by AM fungi.

The mycorrhizosphere: a zone unfavorable to pathogen development

The mycorrhizosphere has been hypothesized to constitute an environment conducive to microorganisms antagonistic to soilborne pathogen proliferation. Indeed, co-culture of the non-mycorrhizal species *Dianthus caryophyllus* with the mycorrhizal species *Tagetes patula* in presence of *G. intraradices* clearly reduced the disease caused by *F. o. dianthi* in *D. caryophyllus* in a manner clearly unrelated to plant nutrition which suggests a reduction in the pathogen development within the mycorrhizosphere (St-Arnaud *et al.*, 1997). Moreover, a reduction in the number of infection loci of tomato roots pre-colonized with *G. mosseae* and inoculated with *P. nicotianae* zoospores infers that the pathogen may be affected prior to root penetration in the mycorrhizosphere (Vigo *et al.*, 2000).

The mycorrhizosphere influenced by the rhizobacteria-AM-root tripartite association presents specific characteristics, in which each actor influences the others growth and health. Notably through the liberation of glycoproteins such as glomalin, AM fungi favor the formation of aggregates which provide stable microsites favorable to root and microbe establishment (Rillig and Mummey, 2006). The AM extraradical network also constitutes specific microsites which favor the growth of some bacteria. Among Plant growth promoting rhizobacteria [PGPR (Bowen and Rovira, 1999)], P-solubilizing and N-fixing-bacteria have been shown to synergistically interact with AM fungi, increasing P and N availability to the plant and promoting its growth and probably favoring its capacity to counteract pathogen impact on plant growth (Johansson *et al.*, 2004; Barea *et al.*, 2005; Artursson *et al.*, 2006; Lioussanne *et al.*, 2009b). PGPR can also display biocontrol properties and impact pathogen proliferation through direct liberation of toxic compounds, competition for space and nutrients, reduction of Fe and Mn availability, modification of the plant hormone balance and stimulation of plant defense mechanisms (Nehl *et al.*, 1997; Bowen and Rovira, 1999). A synergistic or additive control of pathogen impact on plant growth by dual inoculation of AM fungi with rhizobacteria showing biocontrol properties would depend on the bacterial/fungal species combination used, the soil nutritional status and probably other environmental conditions (Barea *et al.*, 2005). Maximum reduction in galling and nematode multiplication causing root-rot in chick pea was observed with combined inoculation

of *G. intraradices* with the biocontrol agents *Pseudomonas straita* and *Rhizobium* sp. (Akhtar and Siddiqui, 2008) and dual inoculation of *G. mosseae* with *Pseudomonas fluorescens* (Siddiqui and Mahmood, 1998). Järderlund *et al*. (2008) showed that interactions between the two PGPR *P. fluorescens* SBW25 and *Paenibacillus brasilensis* PB177 with *G. mosseae* and *G. intraradices* investigated on winter wheat infested with *Microdochium nivale* were fungal and bacterial species specific. Several studies have demonstrated that microbial antagonists to pathogens, either fungi or PGPR, do not exert any negative effect against AM fungi (Barea *et al.*, 2005). Mycorrhization Helper Bacteria (MHB), defined by Garbaye (1994) as bacteria which consistently promote mycorrhizal development, would even increase AM impact on pathogens. Rhizobacteria and conditions of stimulation of mycorrhizal symbiosis have been listed by Frey-Klett and colleagues (2007).

Mechanisms of interactions between AMB and AM extraradical network

Bacterial communities associated with various AM inocula or spores have been shown to diverge, with some rhizobacterial taxa specifically associated with one mycorrhizal isolate and others more largely encountered in the mycosphere of several AM taxa (Rillig *et al.*, 2005). Recently, Bharadwaj *et al.* (2008b) found that species assemblages of cultivable bacteria from surface-disinfected spores of *G. mosseae* and *G. intraradices* were influenced both by fungal and plant species, with spore-type being the most prominent factor. This specificity of interaction AM species dependent was hypothesized to be related to spore size and surface roughness. Physical interactions between bacteria and AM fungi have been described. Bacterial adherence to spores and/or hyphae of several AM species, under sterile conditions, was demonstrated to be specific to the fungal and bacterial isolate and to depend on the fungal vitality (Bianciotto *et al.*, 1996a; Artursson and Jansson, 2003; Toljander *et al.*, 2006). The association capacity of rhizobacteria to AM surfaces would be dependant on their ability to form biofilms, a structured community of microbial cells encased in a self-produced extracellular matrix (Rudrappa *et al.*, 2008). The rhizobacteria with biocontrol abilities *P. fluorescens* CHAO formed sparse spots while two mucoid mutants of this strain (with increased production of acidic extracellular polysaccharides (EPS), essential for biofilm formation) formed a large number of clusters on non-mycorrhizal carrot roots, on roots colonized with *Gi. margarita* and extraradical hyphae of this AM fungus, demonstrating that EPS are involved in the *in vitro* association of *P. fluorescens* CHAO to these biological surfaces (Bianciotto *et al.*, 2001b). Moreover, mutants of *Azospirilum brasilense* and *Rhizobium leguminosarum* affected in EPS production were strongly impaired in the capacity to attach to mycorrhizal root, AM and inert structures (Bianciotto *et al.*, 2001a). Various strains of Burkholderia inoculated on germinating spores of *Gi. decipiens* were able to colonize the interior of the spores demonstrating AM colonization does not occur on AM surfaces only through biofilm formation (Levy *et al.*, 2003). Bacterial saprophytic activity was also suggested by scanning electron microscopy observations of *G. geosporum* spores (Roesti *et al.*, 2005). The spore's outer layer was shown to be eroded and to be covered by mucilaginous products suggesting that AM fungi can be directly consumed by bacteria. Growth of *Pseudomonas chlororaphis* was stimulated in presence of crude extracts (containing not only AM exudates but also mycelial compounds) from the extraradical network of *in vitro* grown *G. intraradices* (Filion *et al.*, 1999).

The hypothesis that AM fungi would stimulate the growth of rhizobacteria by serving of nutritional source through the liberation of exudates has also been emitted. Sood (2003) proved a stronger attraction of *Azotobacter chrococcum* and *P. fluorescens* by exudates collected from tomato roots colonized by *G. fasciculatum* than by exudates collected from non-colonized roots. Recently, a bacterial community extracted from soil was shown to be significantly affected after 48 h when inoculated with exudates produced by AM mycelia in comparison to a control composed of culture medium (Toljander *et al.*, 2007). Nonetheless, in soil, reduction in exudation through defoliation of pea plants did not modify the PCR-DGGE profile of rhizosphere bacteria, whereas missing and additional bands where observed from the rhizosphere of plants precolonized with *G. intraradices* (Vestergård *et al.*, 2008). PCR-DGGE analysis showed that enrichment with root exudates collected from roots colonized with *G. intraradices* or *G. mosseae* had no effect on the bacterial community structure of tomato rhizosphere while direct root colonization with these AM fungi induced significant changes compared to non-mycorrhizal plants (Lioussanne *et al.*, 2009a). This study suggests that rhizobacterial

community structure modification by AM colonization would be poorly related to exudate liberation from mycorrhizal roots and/or AM mycelium and importantly dependant on their physical presence and to specific direct interactions.

Nonetheless, the impact of AM colonization on other soil microorganisms can be negative. The overall decrease of microbial activity described after root colonization with AM fungi has been proposed to be due to competition for substrates (Christensen and Jakobsen, 1993; Raiesi and Ghollarata, 2006). *G. intraradices* in association with cucumber had a negative effect on the population of *P. fluorescens* DF57 (antagonistic to *Pythium* sp.) both in the rhizosphere and the mycosphere (Ravnskov *et al.*, 1999).

AMB with biocontrol activities

Most AMB described so far in details showed antagonistic characteristics towards soilborne pathogens or behaved as MHB (Xavier and Germida, 2003). Studies performed in parallel and aiming to identify AMB particularly isolated *Paenibacillus* spp. with biocontrol activities. *Paenibacillus* sp. B2, isolated from the mycorrhizosphere of *G. mosseae* and identified by phylogenetic comparison of the 16S rRNA gene sequence and analytical profile index (API, analytical profile index) system, was antagonistic against various soilborne pathogens *in vitro* and reduced tomato root necrosis caused by *P. nicotianae* (Budi *et al.*, 1999). This isolate displayed cellulolytic, proteolytic, chitinolytic and pectinolytic activities and was shown to liberate the antibiotic polymixin B1 and two other polymyxin-like compounds antagonistic among *F. solani* and *F. acuminatum* (Budi *et al.*, 2000; Selim *et al.*, 2005). Moreover, its presence resulted in disorganization of cell walls and/or cell contents of *P. nicotianae* and *F. oxysporum* observed by electron microscopy. It also increased the root and shoot fresh weights of mycorrhizal tomato plants and stimulated tomato root colonization by *G. mosseae* (Budi *et al.*, 1999). Through the use of a compartmentalized growth system, Mansfeld-Giese *et al.* (2002) particularly identified *Paenibacillus polymyxa* and *Paenibacillus macerans* from the mycorrhizosphere, the hyphosphere (root free soil and sand compartments) and from a root-free sand compartment abundantly washed to collect bacterial isolates closely associated with *G. intraradices* mycelium (called mycosphere). All Paenibacilli strains tested from these AM influenced soil zones prevented pre-emergence damping-off caused by *Py. aphanidermatum* (Li *et al.*, 2007). Out of eighteen cultivable isolates from surface disinfected spores of *G. mosseae*, fourteen (especially isolates identified as *Bacillus simplex* but also as *B. niacini*, *B. drententis*, *Paenibacillus* spp. and *Methylobacterium* sp.) showed antagonism against various soilborne pathogens (*P. nicotianae* particularly, but also *F. solani* and three stains of *F. oxysporum*) (Lioussanne, 2007). Bacteria isolated from surface-decontaminated spores of *G. intraradices* and *G. mosseae* extracted from field rhizospheres of *Festuca ovina* and *Leucanthemum vulgare* were classified within two phylogenic clusters: A, corresponding to Proteobacteria and B, Actinobacteria and Firmicutes (Bharadwaj *et al.*, 2008b). Bacteria from both clusters were antagonistic against *Rhizoctonia solani* in dual culture *in vitro* assays. In further studies, selected bacteria (two isolates of *Stenotrophomonas maltophilia*, three *Pseudomonas* spp., one *B. subtilis* and one *Arthrobacter ilicis*) were all antagonistic against *Erwinia carotovora* var *carotovora* (Ecc), *Verticillium dahliae*, *P. infestans* and *R. solani in vitro,* produced siderophores and proteases and decreased the weight of rotten potato tissues caused by Ecc (Bharadwaj *et al.*, 2008a). The ability of AM fungi to specifically harbor and then to stimulate rhizobacteria with biocontrol properties suggests that these bacteria would directly reduce pathogen development within the mycorrhizosphere and would consequently strongly contribute to the biocontrol mediated by AM fungi on soilborne diseases.

Conclusion

The capacity of AM fungi to control disease symptoms and the intraradical and rhizosphere proliferation of soilborne pathogens is complex and influenced by various mechanisms probably acting in synergy with each others. Among these mechanisms, the capacity of the AM extraradical network to stimulate beneficial microorganisms would be strongly involved. Various bacteria with high capacities of antagonism against several soilborne pathogens have been identified within AM extraradical structures or in the mycorrhizosphere of several AM species. The AM-mediated biocontrol would not be the fruit of the AM-fungus function only but would be strongly related to the capacity of the AM fungus to constitute an environment

favourable to the establishment of rhizobacteria with biocontrol abilities. Ongoing studies on the specificity of AM-other beneficial microorganism interactions (probably related to the bacterial capacity of attachment and/or grazing of AM structures) will permit to increase the understanding of the AM mediated biocontrol. Further identification of AMB will permit not only effective inoculations of new biocontrol agents easier to grow in artificial conditions than AM fungi and but also powerful synergistic controls of soilborne pathogens by dual-inoculation of AM fungi with other biocontrol agents which establish preferentially in the mycorrhizosphere, in an environmentally friendly but profitable sustainable agriculture.

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