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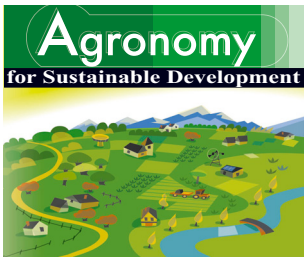

Review article

Arbuscular mycorrhizal networks: process and functions. A review

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Abstract – An unprecedented, rapid change in environmental conditions is being observed, which invariably overrules the adaptive capacity of land plants. These environmental changes mainly originate from anthropogenic activities, which have aggravated air and soil pollution, acid precipitation, soil degradation, salinity, contamination of natural and agro-ecosystems with heavy metals such as cadmium (Cd), lead (Pb), mercury (Hg), arsenic (As), global climate change, etc. The restoration of degraded natural habitats using sustainable, low-input cropping systems with the aim of maximizing yields of crop plants is the need of the hour. Thus, incorporation of the natural roles of beneficial microorganisms in maintaining soil fertility and plant productivity is gaining importance and may be an important approach. Symbiotic association of the majority of crop plants with arbuscular mycorrhizal (AM) fungi plays a central role in many microbiological and ecological processes. In mycorrhizal associations, the fungal partner assists its plant host in phosphorus (P) and nitrogen (N) uptake and also some of the relatively immobile trace elements such as zinc (Zn), copper (Cu) and iron (Fe). AM fungi also benefit plants by increasing water uptake, plant resistance and biocontrol of phytopathogens, adaptation to a variety of environmental stresses such as drought, heat, salinity, heavy metal contamination, production of growth hormones and certain enzymes, and even in the uptake of radioactive elements. The establishment of symbiotic association usually involves mutual recognition and a high degree of coordination at the morphological and physiological level, which requires a continuous cellular and molecular dialogue between both the partners. This has led to the identification of the genes, signal transduction pathways and the chemical structures of components relevant to symbiosis; however, scientific knowledge on the physiology and function of these fungi is still limited. This review unfolds our current knowledge on signals and mechanisms in the development of AM symbiosis; the molecular basis of nutrient exchange between AM fungi and host plants; and the role of AM fungi in water uptake, disease protection, alleviation of various abiotic soil stresses and increasing grain production.

arbuscular mycorrhiza / environmental stresses / phytopathogens / sustainable agriculture

Contents

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1. INTRODUCTION

There is a pressing need to strike a balance between food production for the ever-increasing world population and conserving biodiversity, as well as supply of organic or low-input products for the markets (Dodd, 2000). Earlier, soil was treated as a 'resource base' with its function of support subordinate to the production of food and fiber, and on the scale of priorities, the soil had always taken second place (Bethlenfalvay and Schüepp, 1994). Recently, scientists have recognized the importance of the soil not only as an agricultural resource base (Stewart et al., 1991), but as a complex, living and fragile system that must be protected (Reagnold et al., 1990) and managed for its own sake (Pierce and Lal, 1991) to guarantee its long-term stability and productivity (Aryal and Xu, 2001).

Increased environmental awareness has progressively led to a shift from conventional intensive management to low-input, sustainable crop production agroecosystems. In low-input cropping systems the natural activities of microorganisms contribute to the biocontrol of plant pathogens and improved supply of nutrients, thus maintaining crop health and production. Symbiotic mycorrhizal fungi, such as arbuscular mycorrhizal (AM) fungi, form a key component of the microbial populations influencing plant growth and soil productivity (Johansson et al., 2004). The multifunctional nature of AM fungi include weathering, dissolution and cycling of mineral nutrients (Finlay and Rosling, 2006; Wallander, 2006; Helgason and Fitter, 2009), nutrient mobilization from organic substrates (Finlay, 2008), carbon cycling (Johnson et al., 2002), effects on plant communities and ecosystems, and mediation of plant responses to various environmental stresses, such as soil salinity, heavy metal toxicity, drought and heat stress, soil acidification, and plant pathogens (Colpaert, 2008; Finlay et al., 2008), as well as a range of possible interactions with groups of other soil microbes (Finlay, 2008). The natural roles of these microorganisms may have been marginalized in intensive agriculture, since microbial communities in conventional farming systems have been modified due to tillage (Sturz et al., 1997; McGonigle and Miller, 1996) and high inputs of inorganic fertilizers, herbicides and pesticides (Gianinazzi and Schuepp, 1994; Gianinazzi et al., 2002). A better understanding of the microbial interactions is therefore crucial for the development of sustainable management of soil fertility and crop production.

The vast majority of plant species in terrestrial ecosystems form symbioses with rhizosphere microbes to take up essential nutrients (Bonfante and Genre, 2008; Parniske, 2008; Helgason and Fitter, 2009). A number of these microbes inhabit the rhizosphere, including mycorrhizal fungi, nitrogen-fixing bacteria and other plant-growth-promoting rhizobacteria (van der Putten et al., 2007). The endosymbiosis formed between roots of more than 80% of land plant species and arbuscular mycorrhizal (AM) fungi is ubiquitous and the most widespread symbiotic association in the plant kingdom (Redecker et al., 2000; Helgason and Fitter, 2009). The AM fungi were formerly included in the order Glomales in the Zygomycota (Redecker et al., 2000; Bonfante and Genre, 2008), but they have recently been moved to a newly ascribed phylum, Glomeromycota (Garg et al., 2006; Parniske, 2008; Smith and Read, 2008). Arbuscular mycorrhizal fungi develop extensive, below-ground extraradical hyphae fundamental for the uptake of inorganic phosphate and other immobile nutrients from the soil and their translocation to the host plant (Giovannetti et al., 2006; Smith and Read, 2008). Fungal penetration and establishment in the host roots involve a complex sequence of events and intracellular modifications (Bonfante-Fasolo and Perotto, 1992). In contrast, the nitrogen-fixing root nodule symbiosis is almost completely restricted to the legumes (Zhu et al., 2006). The symbiotic relationships between legumes and rhizobacteria involve extensive signaling between the two organisms (Smit et al., 2005). These microbes can stimulate plant growth and reproduction by providing their hosts with services such as increased access to limiting nutrients (phosphorus and nitrogen) and enhanced uptake of water. In exchange, the plants provide these microbes with carbon (Parniske, 2008; Smith and Read, 2008). An important characteristic of legumes is that they utilize more nitrogen and phosphorus from the environment with the help of nodulation bacteria and mycorrhizal fungi living in their roots (Smith and Read, 1997). Thus, dual application of AM fungi and *Rhizobium* acts as biological fertilization in legumes. Moreover, there are ameliorative synergistic effects of this dual application (Abd-Alla et al., 2000).

2. A JOURNEY THROUGH MYCORRHIZAL SYMBIOSIS

The term 'mycorrhiza' originates from the Greek *mycos*, meaning 'fungus', and *rhiza* meaning 'root', and was first used in 1885 (Frank, 1885) to describe the intimate association between biotrophic mycorrhizal fungi and plant roots. Approximately 80% of land plant species that have been studied form the mycorrhizal symbiosis (and 92% of plant families), which exist everywhere, from tiny home-gardens to large ecosystems (Wang and Qiu, 2006; Helgason and Fitter, 2009). Six types of mycorhizas; arbuscular, arbutoid, ecto-, ericoid, monoptropoid and orchid, are categorized by their distinct morphological characteristics (Wang and Qiu, 2006; Garg et al., 2006). Of them, arbuscular mycorrhiza (AM) is the most common and predominant type (Fig. 1). Arbuscules, specific 'little-tree-shaped' fungal structures, serve as the main sites of nutrient exchange between the plant and the fungus (He and Nara, 2007). They are branched, microscopic haustorial structures of the fungal symbiont that form within living cortical cells of the root (Manchanda and Garg, 2007). This structure is common to all associations of this type of mycorrhiza (Franken et al., 2007). AM fungi are soil inhabitants with a presumed origin at least 460 million years ago (Redecker et al., 2000; Bonfante and Genre, 2008). Perhaps due to this ancient association with plants, AM fungi have lost their ability to live and complete their life cycle in the absence of a green partner (Requena et al., 2007). The Glomeromycota consists of approximately 150 isolates which colonize a wide range of both mono- and dicotyledonous plant species (Paszkowski, 2006). These AM fungi communities influence a number of important

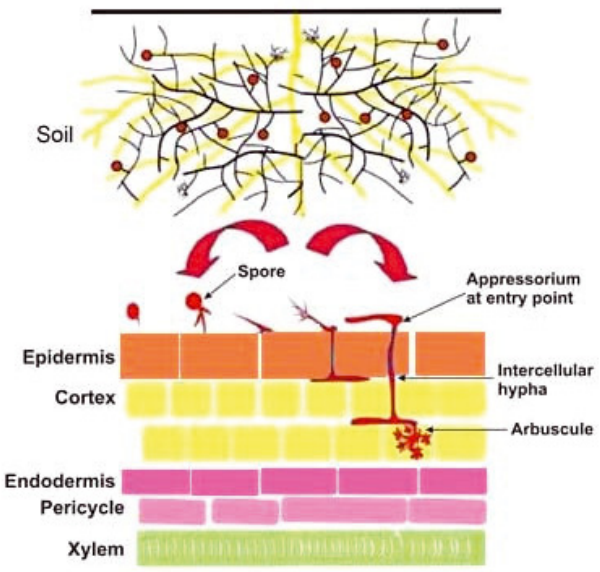

Figure 1. Sequence of events leading to the formation of arbuscular mycorrhizal (AM) symbiosis (schematic representation).

ecosystem processes, including plant productivity, plant diversity and soil structure (van der Heijden et al., 1998). So, not only do the activities of AM fungi have multiple functions that enhance plant performance, but they also play crucial roles in the development of soil properties and the health of the entire ecosystem.

2.1. Arbuscular mycorrhizal development

The establishment of AM symbiosis can be envisaged as a programed sequence of phenotypic changes, corresponding to distinct recognition events which lead the two partners, host plant and fungal symbiont, to a high degree of morphological and physiological integration.

2.1.1. Early stages of fungal asymbiotic growth

Arbuscular mycorrhizal fungi are obligate biotrophs, unable to complete their life cycle during asymbiosis (Bonfante and Bianciotto, 1995). AM fungal spores are the only plant-independent phase of the mycobiont. They are round-shaped structures with a thick cell wall and average diameters between 50 and 100 μm. They contain a very large number of nuclei, up to 2000 per spore (Becard and Pfeffer, 1993). After germination, hyphae are always coenocytic. Studies on two AM fungal species have shown that these are haploids with an unusually high genetic variation (Hijri and Sanders, 2004; Hosny et al., 1997). Assessments of the genome size of these fungi have shown extreme variations between different species ranging from about 16.5 Mb in *Glomus intraradices* (Hijri and Sanders, 2004) up to 1058.4 Mb in *Scutellospora gregaria* (Hosny et al., 1998). AM spores germinate under appropriate water and temperature conditions and hyphae grow for about 2–3 weeks. Several nuclei from the spore move into the extending mycelium and some of them undergo mitosis (Requena et al., 2000). During this time the fungal colonies extend a few centimeters, showing a characteristic growth pattern with marked apical dominance and infrequent hyphal branching. In the absence of a host root, growth ceases after about 2–4 weeks and hyphal septation from the apex occurs (Mosse, 1988). The apical septation is accompanied by extensive vacuolization and retraction of protoplasm towards the spore (Logi et al., 1998). During this asymbiotic phase, the fungus lives mainly on its triacylglyceride reserves. This phase of growth in the absence of signals from the plant is what is known as the asymbiotic stage (Requena et al., 2007). Thus, in the asymbiotic stage, spores germinate and AM fungi show limited hyphal development in the absence of a host plant.

2.1.2. Arbuscular mycorrhizal life cycle

The establishment of the AM symbiosis begins with the colonization of a compatible root by the hyphae produced by AM fungal soil propagules, asexual spores or mycorrhizal roots (Requena et al., 1996). After attachment of a hypha to the root surface by means of an appressorium, the fungus penetrates into the cortex and forms distinct morphologically specialized structures: inter- and intracellular hyphae, coils and arbuscules. Arbuscules are specialized hyphae, similar to haustoria from the plant pathogenic fungi, formed as intercalary structures between the coil hyphae, and are the site of mineral nutrient transfer to the plant and potentially the site of carbon acquisition by the fungus (Requena et al., 2007; Pumplin and Harrison, 2009). After host colonization, the fungal mycelium grows out of the root exploring the soil in search of mineral nutrients, and it can colonize other susceptible roots. The fungal life cycle is completed after formation of asexual chlamydospores on the external mycelium. Distinct morphological stages can therefore be identified during the life cycle of arbuscular mycorrhizal fungi (Requena and Breuninger, 2004). This clearly shows that the host plant plays a key role in orchestrating the AM infection process (Eckardt, 2005).

The sequence of steps leading to an AM symbiosis is largely conserved among different combinations of fungal and plant species. Overall, these developmental processes require molecular communication between the AM fungus and the plant, including exchange and perception of signals by the symbiotic partners (Bucher, 2007). Thus, the complex morphological and physiological alterations of both symbiotic partners accompanied by the recognition process suggest that AM symbiosis is the result of multifaceted, fine-tuned signaling events (Paszkowski, 2006).

2.2. Plant signal and fungal perception

This phase of mycorrhizal fungi can be divided into three steps.

2.2.1. Pre-symbiotic phase

2.2.1.1. Fungal responses to plant-derived signals

For both symbionts, the period before physical contact (appressorium formation) involves recognition and attraction of appropriate partners and other events promoting an alliance. There is increasing evidence showing that the fungus and plant start to recognize each other long before the first colonization structures on the root epidermis appear (Requena et al., 2007). Spores of AM fungi persist in the soil and germinate spontaneously, independently of plant-derived signals. However, root exudates and volatiles may promote or suppress spore germination, indicating the existence of the presence of spore 'receptors' responsive to alterations in the chemical composition of the environment (Bécard et al., 2004; Harrison, 2005). It has been known for a long time that germinating hyphae from spores respond to the presence of roots in their vicinity. In the vicinity of a host root, fungal morphology shifts towards enhanced hyphal growth and extensive hyphal branching (Giovannetti et al., 1993b; Buee et al., 2000). Although no directional growth has been observed towards the root, several experiments showed that exudates from the host root elicit growth stimulation in contrast to non-host root exudates (Giovannetti et al., 1993a, b, 1996). These observations suggest that the fungus senses a host-derived signal; ('branching factor'), leading to intensified hyphal ramification that is likely to increase the probability of contact with a host root. Hence, distinction between host and non-host occurs to a certain degree at this early point in the interaction (Paszkowski, 2006).

In many plant-microbe interactions, the dialogue between the two symbionts is initiated by the presence of plant phenolic substances such as flavonoids. Interestingly, there are many reports showing that, indeed, flavonoids (exogenously applied to spores) exert a positive effect on hyphal growth during asymbiosis (Akiyama et al., 2002). However, flavonoids might not be essential for the plant-fungal recognition since a study using maize mutant plants impaired in flavonoid production showed that they were able to form mycorrhizal symbiosis similarly to wild-type plants (Bécard et al., 1995). A major step forward in deciphering the molecular cross-talk in the AM symbiosis was the identification of a branching factor present in root exudates as a strigolactone (5-deoxy-strigol) (Akiyama et al., 2005). Strigolactones have been isolated from a wide range of mono- and dicotyledonous plants and were previously found to stimulate seed germination of parasitic weeds such as *Striga* and *Orobranche* (Bouwmeester et al., 2003). Strigolactones were previously described as sesquiterpenes (Akiyama et al., 2005); however, the use of carotenoid mutants of maize and inhibitors of isoprenoid pathways in maize, sorghum and cowpea showed that strigolactones are derived from the carotenoid biosynthetic pathway (Matusova et al., 2005). Nevertheless, the results do indicate that processed carotenoid derivatives are involved at multiple stages in the development of the AM symbiosis, possibly by stimulating intraradical fungal branching (Paszkowski, 2006). It is likely that other signals, such as thigmotrophic signals from the plant surface or secondary metabolites produced in plants after perception of the fungus, are required for appressorium formation and symbiosis progression (Requena et al., 2007). These chemical signals exuded by the plant and the thigmotrophic signals from the rhizodermis are possibly recognized by receptor proteins associated with the fungal plasma membrane (Requena et al., 2007). Requena et al. (2002) used suppressive subtractive hybridization (SSH) to create a subtractive cDNA library from *Glomus mosseae* enriched in genes induced during the asymbiotic phase. With this approach, a novel gene (GmGin1) encoding a two-domain protein with a putative role in signaling was identified. Expression analyses showed that GmGin1 was downregulated upon entry into symbiosis, suggesting it could play a role at the plant recognition stage (Requena et al., 2002). GmGin1 could be a sensor for plant signals and is located at the cell membrane. It undergoes splicing in response to signals from the plant. These interesting results show that the chemical communication with the plant symbiont not only modifies fungal gene expression but it is also able to induce post-transcriptional modification of fungal proteins (Requena et al., 2007). Transcript profiling of AM fungi during appressorium formation showed that plant contact induces the activation of genes from different categories, including several components related to Ca^{2+}-signaling, including a putative P-type Ca^{2+}-ATPase, a calmodulin, a leucine zipper EF-protein, and a Ca^{2+}-induced Ras inactivator (CAPRI) (Breuninger and Requena, 2004). This suggests the involvement of Ca^{2+} as a second messenger in the transmission of plant-derived signals, leading to appressorium formation in the AM symbiosis (Requena et al., 2007). Thus, upon detection of a host root there is vigorous investment in the production of fungal hyphae, which can then rapidly make contact with essential carbon sources. A major breakthrough in the molecular interactions between both the partners was the identification of the host branching factor 5-deoxy-strigol, which induces the so-called presymbiotic stage characterized by continued hyphal growth, increased physiological activity and profuse branching of hyphae, and the gene, GmGin1, which plays a role in the development of appressoria during AM symbiosis in the plants.

2.2.1.2. Plant responses to fungus-derived signals

The plant responds to the microbial profile of the rhizosphere in different ways depending upon the type of organism present. Detection of pathogen-derived elicitors triggers plant signaling cascades that lead to a defense response (Glazebrook, 2005). On the other hand, plant defense responses are either not mounted at all or mounted only transiently before being suppressed during AM symbiosis (Harrison, 2005). Extensive forward genetic approaches were used to dissect the components of the signal perception and transduction pathways in the AM symbiosis in legume species. These approaches led to the identification of several symbiosis genes, the corresponding plant mutants of which are generally unable to support infection by AM fungi. Yet the nature and function of mycorrhization (Myc) factors are still an enigma. Myc factors are likely to be soluble, fungus-derived

compounds that trigger expression of mycorrhizal-responsive genes (Kosuta et al., 2003) and structural changes in host roots (Olah et al., 2005).

GUS reporter expression [*EARLY NODULATION11 (ENOD11)*-promoter: β-glucuronidase], which is responsive to both AM fungi and a rhizobial Nod-factor, before contact was monitored in root sections adjacent to intensely branching hyphae. The intensity and distribution of GUS expression indicated the detection by the plant of a compound released by the fungus (Kosuta et al., 2003). Interestingly, when contact and penetration were permitted, GUS expression was restricted to infected and associated cells (Chabaud et al., 2002; Genre et al., 2005), indicating the induction of a suppressor activity in non-colonized neighboring cells (Parniske, 2004). When contact is made and a precise area of penetration and colonization is established, gene expression is restricted to cells in direct contact with the penetrating fungus. Similarly, during preinfection and infection stages in the interaction of *Medicago truncatula* with nitrogen-fixing *Rhizobia*, GUS expression was found in the rhizodermis of the larger root section before contact and upon subsequent bacterial entrance into the root tissue became confined to the area of infection, namely the infection site and the invaded nodule (Journet et al., 2001). This resemblance in expression patterns between the two types of root symbiosis suggests that the responses are a part of a rather general symbiont 'anticipation' program (Paszkowski, 2006). To conclude, the infected cells in the plant roots upon perceiving Myc factors trigger the expression of SYM genes (*ENOD11*-promoter GUS reporter gene), common to both bacterial and fungal root endosymbioses, providing a glimpse of conservation and specialization of signaling cascades essential for nodulation and mycorrhiza development.

2.2.2. Early symbiotic phase

2.2.2.1. Appressorium development

The onset of the symbiosis is marked morphologically by the formation of appressoria, the cell-to-cell contact between the fungus and plant and the site of fungal ingress into the host root. The formation of appressoria is one of the first morphological signs that recognition between the plant and the fungus has occurred (Garcio-Garrido and Ocampo, 2002). The development of appressoria can be considered to be the result of successful presymbiotic recognition events when fungal and plant partners are committed to an interaction (Giovannetti et al., 1993a). Structurally, appressoria differ from hyphae by being flattened, elliptical hyphal tips that adhere by unknown means to the surface of host rhizodermal cells. This morphological switch is reflected by changes in fungal gene transcription (Breuninger and Requena, 2004). While physical and chemical rhizodermal cell wall features are required and are sufficient to elicit appressorium formation, penetration needs the support of intact cells whose coordinated, matching response accommodates the fungus (Paszkowski, 2006). Therefore, the discovery that the plant cell actively prepares the intracellular environment for AM fungal hyphae elicited its role during the infection process, and emphasized the significance and indispensable participation of plant processes in the coordinated invasion (Genre et al., 2005, 2008).

2.2.2.2. Arbuscular mycorrhizal (AM) fungi penetration

Actual penetration of the host by AM fungi is by means of a penetration hyphae or infection peg from the appressorium that penetrates either by force or by production of cell wall-dissolving enzymes (Linderman, 1994). Specific plant-regulated processes associated with penetration have been delineated. In *Lotus japonius*, for example, an epidermal cleft opens between two adjacent rhizodermal cells through which the fungus enters. From here, invasion of the rhizodermal cells is initiated and the fungus trespasses through the underlying exodermal cells (Parniske, 2004). In addition to entering through a rhizodermal cleft, the fungus can also traverse rhizodermal cells directly, as shown in detail for *Gigaspora gigantea* penetrating roots of *Medicago truncatula* (Genre et al., 2005). Hence, infection only occurs after preparatory activities in the plant cell. These cytological studies illustrate nicely the extensive complementary contribution made by host cell activity to fungal penetration. This emphasizes the significance and indispensable participation of plant processes in the coordinated invasion (Genre et al., 2005, 2008).

The infection process by arbuscular mycorrhizal fungi is also characterized by a low and regulated production of cell wall-degrading enzymes by the fungus. The production of exo- and endoglucanases, cellulases, xyloglucanases and pectolytic enzymes including polygalacturonase has been demonstrated in various investigations (Garcia-Garrido and Ocampo, 2002). In conclusion, AM fungi seem to colonize the root tissues of host plant by means of a combination of mechanical and enzymatic mechanisms and the coordinated participation of host cell machinery, which aids in the easier penetration of the mycorrhizal fungi into the root cortex (Bonfante and Perotto, 1992).

2.2.3. Mature symbiotic phase: process and signaling

2.2.3.1. Arbuscule development

There are two main morphological types (*Paris* and *Arum*) of AM symbioses with structurally different interfaces. *Paris*-type AM are characterized by intracellular fungal coils that grow directly from cell to cell with little or no intercellular phase, whereas in *Arum*-type AM, a highly branched intracellular tree-like fungal structure known as the arbuscule is formed, subtended by intercellular hyphae (Dickson et al., 2007). Arbuscules are the key feature of the AM symbiosis as they represent an extreme form of intimacy and compatibility and are thought to be the site of nutrient transfer from the fungus to the host plant (Hughes et al., 2008). Following colonization of the host cell by the arbuscule, the architecture of the host cell undergoes remarkable changes. Despite the intense activity of both the partners leading towards arbusculated cells, arbuscules collapse after 2–4 days, leaving an

intact cortical cell that is then able to host another arbuscule (Paszkowski, 2006; Pumplin and Harrison, 2009).

It is not known what triggers fungal entrance into the host cell but the perception of a radical sugar gradient between the vascular tissue and the outer cell layers may be involved in induction of arbuscule formation (Blee and Anderson, 1998). Alternatively, the initiation of arbuscule collapse may be caused by endogenous fungal signaling or coordinated signaling cross-talk. Development of arbuscules is at least partially under the control of the host genetic program. In addition, proteins of the SYM pathway are either required for arbuscule development, such as *LjCASTOR*, *LjSYM15* and likely *LjSYm6*, or contribute to arbuscule formation, such as *LjPOLLUX*, *LjNup 133* and *LjSYM* 24 (Kistner et al., 2005). Global gene expression profiling has been undertaken to identify AM-regulated genes (Guimil et al., 2005, Hojnec et al., 2005). In many cases gene expression was monitored at the stage of a mature symbiosis and long lists of induced and suppressed genes have been created. The list of genes probably includes those essential for signaling during the initiation and formation of arbuscules (Paszkowski, 2006). Hence, formation of arbuscules within host cells is associated with dramatic morphological and physiological alterations in both the symbiotic partners. The molecular basis underlying arbuscule formation has elucidated the role of numerous genes that encode proteins, directly or indirectly involved in a signal transduction network that is required for the development of intracellular accommodation structures for symbiotic fungi by the host cell (Parniske, 2008).

2.2.3.2. The symbiotic interface and nutrient transfer

In root symbiosis, the symbiosome is the cellular environment hosting the microbial partner where the mutual exchange of nutrients and metabolites occurs. In AM, this is the cortical cell lumen harboring hyphal coils or arbuscules surrounded by the perihyphal or periarbuscular plasma membrane, respectively. The periarbuscular membrane, continuous with the plasma membrane of the cortical cell, is a key interface in the symbiosis; however, little is known of its lipid or protein composition or the mechanisms of its development (Pumplin and Harrison, 2009). Both the microbe- and the plant-derived symbiosome membranes tightly regulate the exchange of compounds, which is generally facilitated by membrane-integral transport proteins such as phosphate transport and the P-type H^+-ATPase (Bucher, 2007). Recently, live-cell imaging with fluorescently-tagged proteins has revealed the spatial and temporal information about the protein composition of the periarbuscular membrane. The study indicates that the periarbuscular membrane is composed of at least two distinct domains; an 'arbuscule branch domain' that contains the symbiosis-specific phosphate transporter, MtPT4, and an 'arbuscule trunk domain', that contains the blue copper-binding protein, MtBcp1 (Pumplin and Harrison, 2009).

Extensive transcript profiling has revealed numerous genes that are reported to be upregulated or repressed in mycorrhizae (Liu et al., 2003; Guimil et al., 2005; Hojnec et al., 2005; Kistner et al., 2005). Experimental evidence also exists for cell-specific localization of either transcripts or promoter activity of several genes involved in arbuscule function (i.e. P nutrition) and development. These include genes encoding P-type H^+-ATPases (Krajinski et al., 2002) and P_i transporter genes from tomato and potato (Nagy et al., 2005), *Medicago truncatula* (Harrison et al., 2002), *Lotus japonicus* (Maeda et al., 2006), and the cereals barley, wheat and maize (Glassop et al., 2005). *Medicago truncatula* serine carboxypeptidase (*MtSCP1*), a gene sharing identity with Ser carboxypeptidase II proteins from barley, wheat and *Arabidopsis thaliana*, and *MtCell*, a gene coding a membrane-anchored endo-1,4-β-D-glucanase-like protein, have been shown to be upregulated in the root cortex upon colonization of *M. truncatula* with *Glomus versiforme* (Liu et al., 2003). A mycorrhiza-specific class III chitinase gene is similarly regulated in cells containing developing or mature arbuscules (Bonanomi et al., 2001). The availability of expressed sequence tags (EST) of the model legume *M. truncatula*, and AM fungus, *Glomus intraradices*, permits identification of genes required for development of symbiotic interfaces. Candidate genes have been characterized and genes encoding one plant arabinogalactan protein (AGP) and three AGP-like (AGL) proteins have been identified. AGL proteins encoded by two AGL genes from *G. intraradices* (GiAGLs) represent a new class of AGPs not found in non-AM plants (Schultz and Harrison, 2008). Interestingly, several genes have been identified that are induced both in mycorrhized cortical cells and during rhizobial root colonization in legume species; for example, the early nodulin genes *ENOD2*, *ENOD40* (van Rhijn et al., 1997) and *ENOD11* (Chabaud et al., 2002), the *Vicia faba* leghemoglobin gene *VFLb29* (Vieweg et al., 2004), and the gene calcium-binding protein 1 (*Cbp1*), which encodes a protein sharing similarities with calcium-binding proteins (Kistner et al., 2005). This supports the model outlined for the common symbiotic pathway in AM and rhizobium-induced nodule development using signal transduction based on conserved mechanisms (Paszkowski, 2006; Bucher, 2007). Therefore, the transporters that mediate metabolite exchange at the interface between the plant and the fungus are of biotechnological interest, and some candidate genes encoding mycorrhiza-specific plant phosphate transporters have been cloned and sequenced (Parniske, 2008). These findings provide good support for the hypothesis that in infection processes in the symbioses between plant roots and two different microorganisms, i.e. AM fungi and rhizobial bacteria, similar signal perception and transduction cascades initiate mycorrhization and nodulation (Parniske, 2004; Manchanda and Garg, 2007).

3. MYCORRHIZAE AND THEIR DIVERSE ROLES

Mycorrhizae are the rule in nature, not the exceptions. In this association the fungus takes over the role of the plant's root hair and acts as an extension of the root system (Muchovej, 2004). The beneficial effects of AM fungi result from one or several of the mechanisms. With mycorrhizal colonization in the roots, there is increased absorption surface

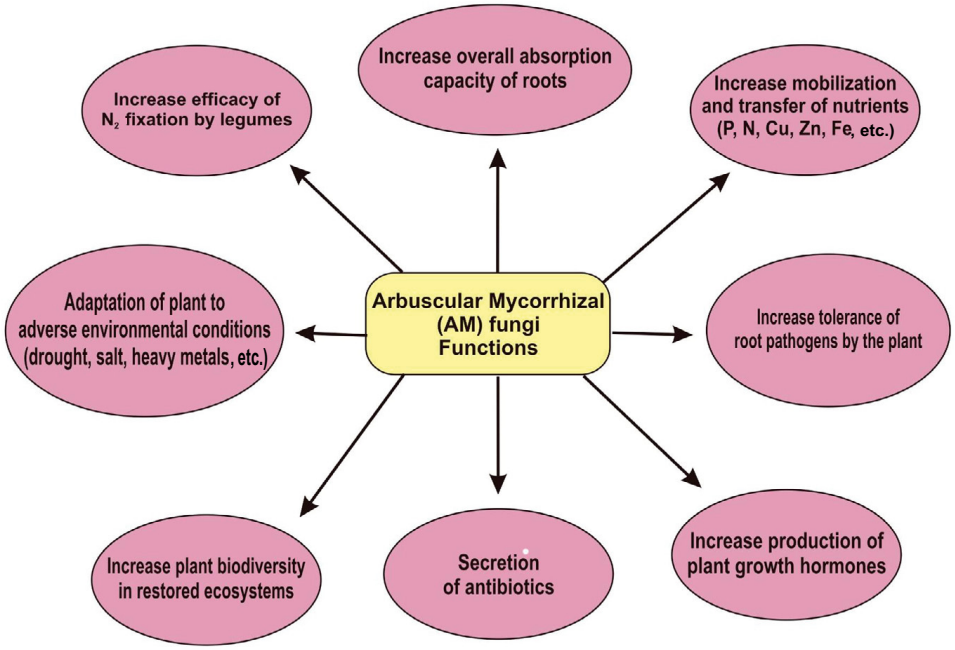

Figure 2. Functional diversity of arbuscular mycorrhizal (AM) symbiosis in terrestrial ecosystems: An overview.

area, greater soil area exposed, greater longevity of absorbing roots, better utilization of low-availability nutrients and better retention of soluble nutrients, thus reducing reaction with soil colloids or leaching losses (Muchovej, 2004; Selvaraj and Chellappan, 2006). AM increase establishment, nodulation and atmospheric nitrogen fixation capacity in legumes (Turk et al., 2008). Mycorrhizae influence the colonization of roots by other microorganisms, and reduce the susceptibility of roots to soil-borne pathogens such as nematodes or phytopathogenic fungi (Selvaraj and Chellappan, 2006). AM also modify soil-plant-water relations, thus promoting better adaptation of plants to adverse conditions, such as drought, salinity or heat stress (Fig. 2). At elevated heavy metal concentrations in soils, mycorrhizal fungi have been shown to detoxify the environment for plant growth (Muchovej, 2004). The real significance of mycorrhizal fungi is that they connect the primary producers of ecosystems, plants, to the heterogeneously distributed nutrients required for their growth, enabling the flow of energy-rich compounds required for nutrient mobilization whilst simultaneously providing conduits for the translocation of mobilized products back to their hosts. Hence, understanding of the ecology and functioning of the AM symbiosis in the natural or agricultural ecosystem is essential for the improvement of plant growth and productivity.

3.1. Mycorrhizal symbiosis and mineral nutrition

Obligately depending on plant photosynthates as energy sources, the extensive mycelial systems (the vegetative parts of the fungus) effectively explore soil substrates and acquire soil inorganic nutrients including the major macro-nutrients N, P and K and some micro-nutrients, Cu, Fe and Zn, with some capacity for acquiring organic nitrogen and phosphorus. These soil-derived nutrients are not only essential for AM development but are also partly transferred to the host plant (Smith and Read, 1997; Leake et al., 2004).

3.1.1. Phosphate uptake assisted by the AM symbiosis

The major role of AM fungi is to supply infected plant roots with phosphorus, which is an extremely immobile element in soils (Bucher, 2007). Even if phosphorus is added to soil in soluble form it soon becomes immobilized as organic phosphorus, calcium phosphates or other fixed forms (Wetterauer and Killon, 1996). AM fungi are known to be effective in increasing nutrient uptake, particularly phosphorus and biomass accumulation of many crops in low phosphorus soil (Osonubi et al., 1991).

3.1.1.1. The route of symbiotic P_i uptake

AM fungi improve plant acquisition of phosphate (P_i). It was recently shown that, depending on the particular plant-fungus combination, symbiotic phosphate uptake may partially participate or even dominate over all P_i acquisition (Smith et al., 2003). Strongly reduced mobility of P_i in the soil and rapid P_i uptake into the root lead to the development of a P_i depletion zone around the root hair cylinder and a rapid decline in P_i acquisition over time (Marschner, 1995;

Roose and Fowler, 2004). The extraradical mycelium of AM fungus grows far beyond the depletion zone, reaching a new pool of soluble phosphate (Smith and Read, 1997). Whereas in non-mycorrhizal roots the extension of the P_i depletion zone is closely related to root hair length (Marschner and Dell, 1994), in mycorrhizal roots the depletion zone of P_i greatly exceeds the root hair cylinder. This indicates that P_i, which is not directly available to the plant, is delivered by the fungal hyphae. Thus, the presence of the P_i depletion zone in the rhizosphere is a major factor contributing to the advantage of plants forming mycorrhizal associations. Strictly speaking, a mycorrhized plant does not constitute a rhizosphere but rather a 'mycorrhizosphere', composed of the rhizosphere and the hydrosphere. In this symbiotic system, the fungus bridges the mycorrhizosphere and P_i is transported, in the form of polyphosphates, from the AM fungus soil interface to the intraradical symbiotic interface (Bucher, 2007).

The proposed metabolic route of symbiotic P_i acquisition starts with the assimilation of inorganic P_i at the hyphal-soil interface by fungal high-affinity transporters (Harrison and van Buuren, 1995; Maldonado-Mendoza et al., 2001; Benedetto et al., 2005). Inside the fungus, inorganic P_i is translocated in the form of polyphosphate from fungal structures outside of the root to those inside (Solaiman et al., 1999; Ohtomo and Saito, 2005). Before release into the periarbuscular interface, phosphate becomes depolymerized into inorganic P_i (Ohtomo and Saito, 2005). P_i is acquired from the interface by plant-encoded phosphate transporters. Such transporters have been identified from several plant backgrounds and were shown to be transcriptionally induced during the development of the AM symbiosis (Harrison et al., 2002; Paszkowski et al., 2002; Glassop et al., 2005; Nagy et al., 2005; Bucher, 2007; Javot et al., 2007; Pumplin and Harrison, 2009). Further, it has been demonstrated that the mycorrhizal P_i uptake pathway could dominate P_i supply to plants irrespective of whether colonized plants exhibited improved growth and total P uptake (Smith et al., 2003, 2004). The fact that the AM fungal contribution to plant P_i uptake is greater in a root-hairless mutant than its wild type indicates that fine tuning of both uptake pathways is required to meet the needs of the plants for this important nutrient (Jakobsen et al., 2005). To conclude, activation of the 'mycorrhizal' uptake pathway is therefore characterized by the induction of mycorrhiza-specific phosphate transporters and (partial) downregulation of the 'direct' uptake pathway phosphate transporters. Given that most phosphorus can be taken up via the 'mycorrhizal' uptake pathway, it can be hypothesized that mycorrhiza-upregulated plant phosphate transporters play a pivotal role in plant productivity and fitness in most natural and agricultural ecosystems.

3.1.1.2. Pht1 genes involved in the AM symbiosis

Legumes such as *M. truncatula* and *L. japonicus* (Young et al., 2003) and solanaceous plants establish mutualistic AM symbiosis under natural conditions (Barker et al., 1998) and can thus be used as experimental systems for molecular-genetic work in mycorrhizae. Interestingly, a H^+-ATPase gene exhibited arbuscule-specific expression in mycorrhizal tissue of *M. truncatula* (Krajinski et al., 2002), and a H^+-ATPase protein was localized in the plant membrane around arbuscule hyphae in a tobacco mycorrhizal plant, which clarified the existence of nutrient transport activities at the interface between the two symbiotic organisms (Gianinazzi-Pearson et al., 2000). The identification of the potato P_i transporter gene *StPT3*, which is expressed in cortical cells colonized by AM fungi, represented a starting point for a detailed analysis of P_i transport at the AM symbiotic interface in solanaceous species. *StPT3* has been clearly identified as a high-affinity transporter. To date, one mycorrhizal-induced P_i transporter coding gene has been identified from *M. truncatula* (*MtPT4*; Harrison et al., 2002; Javot et al., 2007), three have been found in solanaceous species (*StPT3/LePT3*; *StPT4/LePT4* and *StPT5/LePT5*; Karandashov and Bucher, 2005; Nagy et al., 2005), two in rice (*OsPT11* and *OsPT13*; Paszkowski et al., 2002; Guimil et al., 2005) and one in maize, barley and wheat (Glassop et al., 2005).

Despite the large number of mycorrhizal-inducible P_i transporters identified to date, the functional genomics of P_i transport at the symbiotic interface between AM fungi and host plants is not well understood. To date, the most intriguing study on the functional role of mycorrhizal-specific P_i transporters originates from work on *StPT3*-like *LjPT3* from *Lotus japonicus* (Maeda et al., 2006). Knockdown of the *LjPT3* gene resulted in reduced growth of plants carrying transformed roots which were colonized by a mycorrhizal fungus, reduced allocation of radiotracer P_i in the shoot, and decreased fungal colonization of mycorrhizae (Bucher, 2007). The identification of mycorrhiza – specific P_i transporters indicate the presence of a mycorrhiza-specific P_i uptake system in vascular plants. Moreover, it is tempting to speculate that mycorrhizal P_i transporters are involved in self/non-self recognition in mycorrhizae.

3.1.2. Nitrogen transfer at the mycorrhizal interface

As well as benefiting plants by aiding phosphorus uptake from soil (Harrison and van Buuren, 1995), AM fungi can take up and transfer significant amounts of inorganic nitrogen (NH_4^+ or NO_3^-) to their host plants (He et al., 2003). The availability of nitrogen frequently limits plant growth, and depending on soil conditions, nitrogen transfer by mycorrhizal fungi can represent a significant route of uptake by the plant (He et al., 2003). AM fungi have been strongly implicated in the transfer of nitrogen from one plant to another (He et al., 2003), can increase the utilization of different forms of nitrogen by plants (Hodge et al., 2001) and have been shown to take up nitrogen directly and transfer it to host roots (He et al., 2003). Experimental observations have indicated that arginine is usually the principal nitrogenous product accumulated during periods of ammonium feeding at the uptake site, providing support for the importance of this amino acid in N transfer between fungal and plant cells.

The extraradical hyphae of AM fungi are able to take up and assimilate ammonium (NH_4^+) (Johansen et al., 1992,

1993, 1996), nitrate (NO_3^-) (Bago et al., 1996; Johansen et al., 1996) and amino acids (Hawkins et al., 2000; Hodge et al., 2001) from their surroundings and translocate N from diverse sources to the plant (Hawkins et al., 2000; Azcon et al., 2001; Vazquez et al., 2001). Assimilation of NH_4^+ is a principal means of N absorption in AM fungal systems (Hawkins et al., 2000; Toussaint et al., 2004). N uptake and incorporation into amino acids via the glutamine synthetase/glutamate synthase (GS/GOGAT) cycle has been found in AM fungi (Smith et al., 1985). Stable isotope labeling has now suggested that inorganic nitrogen is taken up by the extraradical mycelium, incorporated into amino acids, translocated from extra- to intraradical fungal structures as arginine and then transported as ammonium to the plant (Govindarajulu et al., 2005; Jin et al., 2005). Further support for this uptake route comes from the finding that transcript abundance of key enzymes of nitrogen assimilation and arginine breakdown preferentially accumulate in extra- and intraradical mycelia, respectively (Govindarajulu et al., 2005). A decline in the levels of the major amino acids present together with a decrease in the activity of fungal enzymes involved in the nitrogen assimilation during the mycorrhizal colonization process is seen (Blaudez et al., 1998). The extrusion of ammonia from fungal cells follows other pathways than those mediated by Amt proteins (ammonia transporter), either by passive efflux of the deprotonated form or by protein-mediated mechanisms. Thus, fungal cells are able to maintain a low cytoplasmic ammonia concentration, thus retaining a constant assimilatory capacity and in turn allow for sustained export into the plant root cells (Chalot et al., 2006). Therefore, the operation of a metabolic route assists the AM fungi in N uptake, transport and assimilation.

Various models have been proposed by Jin et al. (2005), Govindarajulu et al. (2005) and Chalot et al. (2006) which involve a number of steps for direct transfer of ammonia from fungal to plant cells (i) AM fungi take up inorganic N (NH_4^+, NO_3^-); (ii) absorbed N is mostly incorporated and stored in arginine; (iii) AM fungi assimilate the N through GS/GOGAT, asparagine synthase and the urea cycle; (iv) stored arginine can be co-transported with PolyP intact to the intraradical mycelium form the extraradical mycelium of AM fungi, and arginine is also bi-directionally transported within the extraradical mycelium; and (v) N released from transported arginine is transferred to the host as NH_4^+ and can be incorporated into other free amino acids in mycorrhizal roots, while carbon (C) not transferred to the host is recycled back to the extraradical mycelium. In analogy to the path of symbiotic P_i uptake, the arbuscule may be the site of symbiotic nitrogen uptake involving plant encoded nitrogen transporters located within the periarbuscular plant membrane (Paszkowski, 2006). Apart from the role of AM fungi in facilitating the uptake of inorganic N by plants, AM fungi also give their host plant the ability to use organic matter as a source of N (Hodge et al., 2001). A key role of the AM symbiosis in linking the process of N mineralization to plant N demand in soil, where the AM symbiosis regulates the recycling of plant residue into living plant biomass, thus impacting the structure of the soil microbial community, has been verified (Leigh et al., 2009; Nayyar et al., 2008). The mechanisms involved in the fungal delivery of N are a matter of considerable interest because, depending on N availability and mobility and given the near-ubiquity of the AM symbiosis, these processes may represent a significant nutritional benefit to the plant. The existence of this pathway and the high flux of nitrogen through it indicate that the arbuscular mycorrhizal symbiosis can effectively transfer large amounts of nitrogen from the soil to plant roots (Jackson et al., 2008).

3.2. Alleviation of salt stress by arbuscular mycorrhizal (AM) fungi

Soil salinization is an ever-increasing threat to the cultivation of crop plants around the globe, with this problem being serious in arid and semi-arid areas. The arbuscular mycorrhizal (AM) symbiosis is a mutually beneficial interaction and is an important integral component of the natural ecosystem. AM fungi occur naturally in saline environments (Garcia and Mendoza, 2007) and have been shown to increase plant yield in saline soils. In saline and sodic soils, drainage is poor and salt accumulates on the surface of the soil, thus adversely affecting plant growth. Salinity affects the formation and function of mycorrhizal symbiosis (Giri et al., 2003; Juniper and Abbott, 2006). However, several studies have demonstrated that inoculation with mycorrhizal fungi improves growth and productivity of plants under a variety of salt stress conditions (Giri and Mukerji, 2004; Giri et al., 2007). Recently, many researchers reported that AM fungi could enhance the ability of plants to cope with salt stress (Yano-Melo et al., 2003; Rabie, 2005; Cho et al., 2006; Ghazi and Al-Karaki, 2006; Sannazzaro et al., 2006) by improving uptake of plant nutrients such as P, N, Zn, Cu and Fe (Cantrell and Linderman, 2001; Asghari et al., 2005; Ghazi and Al-Karaki, 2006). The improvement in the plant P status has been suggested as the most important strategy of salinity stress tolerance in AM colonized plants (Giri et al., 2003). However, other studies have shown that salt stress tolerance of AM plants is not always related to improved P status (Feng et al., 2002), and other physiological processes help in

AM plant growth improvement under such conditions. AM fungi can play an important role in increasing the carbon dioxide exchange rate, transpiration and stomatal conductance (Feng et al., 2002), improving ion imbalance (Zandavalli et al., 2004; Giri et al., 2007), protecting enzyme activity (Giri and Mukerji, 2004; Rabie and Almadini, 2005), facilitating water uptake (Feng et al., 2002; Sheng et al., 2008; Colla et al., 2008), and favorably adjusting the osmotic balance and composition of carbohydrates (Ruiz-Lozano, 2003).

Thus, these microorganisms play an important role in soil productivity and plant nutrition under a variety of salt stress conditions. Owing to the importance of AM fungi under salt stress conditions, they have been considered as bioameliorators of saline soils. Mycorrhizal colonization can improve the physiological performance of stressed plants, leading to higher yields and quality. The induction of resistance is provided through a discriminated absorption of the ions

present in the circulating solution, through better balance of mineral nutrient uptake, by influencing the hormonal balance of the host plant or by increasing water uptake.

3.3. Plant water relationship

Although most of the work done with AM fungi has concentrated on their effects in plant mineral nutrition, there is also increasing interest in drought resistance of mycorrhizal plants (Allen and Boosalis, 1983). AM fungi are important in sustainable agriculture because they improve plant water relations and thus increase the drought resistance of host plants (Allen and Allen, 1986; Nelsen, 1987). Improved plant water status and changes in water relations have been attributed to a wide variety of mechanisms, including some mechanisms not directly related to phosphorus nutrition or water uptake (Davies et al., 1992). The abilities of specific fungus-plant associations to tolerate drought are of great interest (Ruiz-Lozano et al., 1995). AM fungi infection has been reported to increase nutrient uptake in water-stressed plants (Buse and Ellis, 1985), enabling plants to use water more efficiently and to increase root hydraulic conductivity (Graham and Syversen, 1984). Root water uptake depends on root hydraulic conductance, which is ultimately governed by aquaporins (Luu and Maurel, 2005). Aquaporins are membrane intrinsic proteins that form a pore in all cell membranes of living organisms, facilitating the passive water flow through membranes following an osmotic gradient (Kruse et al., 2006). Plasma membrane intrinsic proteins (PIPs) regulate all water transport through plant tissues. The plants over-expressing or lacking one or more PIP genes have more or less root water uptake capacity, respectively (Aharon et al., 2003; Javot et al., 2003). In fact, AM plants are frequently more tolerant to drought and salt stresses than non-AM plants (Rosendahl and Rosendahl, 1991; Khalvati et al., 2005; Al-Karaki, 2006; Porcel et al., 2006; Aroca et al., 2007). AM plants are able to take up more water from the soil than non-AM plants under water-deficient conditions (Marulanda et al., 2003; Khalvati et al., 2005). However, this capacity depends on the fungal species, *Glomus intraradices* being one of the most efficient AM fungi in enhancing plant water uptake from the soil among six fungi tested (Marulanda et al., 2003).

Aroca et al. (2007) evaluated how AM symbiosis influences root hydraulic properties, aquaporin expression and abundance in roots of *Phaseolus vulgaris* L. plants under drought, cold or salinity conditions. They reported that colonization of *P. vulgaris* roots by the AM fungus *Glomus intraradices* prevented leaf dehydration caused by drought and salinity treatments as revealed by the higher relative water content (RWC) of AM leaves compared with non-AM leaves. These results confirm the beneficial effect of AM fungi in host plant water status under these two stresses (Rosendahl and Rosendahl, 1991; Porcel et al., 2006). The protection of mycorrhizal plants against water stress is related to the effects that the endophytes have on increasing leaf conductance and transpiration as well as P and K uptake. Potassium plays a key role in plant water stress and has been found to be the cationic solute which is responsible for stomatal movement in response to changes in bulk leaf water status (Ruiz-Lozano et al., 1995). Thus, AM symbiosis regulates root hydraulic properties and enhances root hydraulic conductance tolerance to drought, cold and salinity stresses (Aroca et al., 2007). Amelioration of drought stress by different AM fungal species can be ascribed to specific physiological (CO_2 fixation, transpiration, water-use efficiency) and nutritional (P and K) mechanisms according to the fungus involved in the symbiotic association. Suitably adapted AM fungal isolates are potentially important for maintaining and restoring the plant-soil equilibrium in sustainable agriculture situations (Ruiz-Lozano et al., 1995). The role played by AM fungi in alleviating water stress of plants has been investigated and it appears that drought resistance is enhanced. The precise mechanisms underpinning this are still in doubt but it could be an indirect effect of the extraradical mycelium improving nutrient absorption. The alleviation of water stress is not only limited to arid or semi-arid zones of the planet, but also where short-term droughts occur; an increased reliance on AM fungi for nutrient uptake can be frequently detected.

3.4. Protection of host roots from pathogens

Multitrophic interactions are powerful forces shaping the structure of living communities. Plants encounter a great diversity of organisms in their environment: some of these interactions are beneficial, e.g. symbiotic fungi and insect pollinators, while some are detrimental, e.g. herbivore insects and pathogenic microorganisms. These interactions between below-ground and above-ground organisms are receiving increasing attention because they may influence plant defenses against biotic and abiotic stresses (van Dam et al., 2000). AM symbiosis is mutualistic interaction between plant roots and soil fungi that is considered beneficial to the plant because of the increased uptake of phosphorus and other scarcely mobile nutrients by mycorrhizal plants. Several investigations have demonstrated their positive impact on nutrient uptake and growth of banana (Jaizme-Vega and Azcon, 1995; Yano-Melo et al., 1999), improved resistance to abiotic stresses (Rufyikiri et al., 2000; Ruiz-Lozano, 2003) and biotic stresses caused by nematodes (Jaizme-Vega et al., 1997; Elsen et al., 2001) and *Fusarium oxysporum* f. sp *cubense*, the causal agent of panama disease (Jaizme-Vega et al., 1998).

Most studies on the interactions between AM fungi and plant parasitic nematodes reported that root colonization by AM fungi increases tolerance of the host to *Meloidogyne* species, such as that of tomato and white cover to *Meloidogyne hapla* (Cooper and Grandison, 1986); peanut to *M. arenaria* (Carling et al., 1996); banana to *M. incognita* (Jazme et al., 1997) and *Prunus* root stocks to *M. javanica* (Calvet et al., 2001). Colonization by AM fungi induces resistance or tolerance to a variety of pathogens in tomato and in other plants (Trotta et al., 1996; Lingua et al., 2002). These changes are mediated by a variety of mechanisms, including the upregulation and downregulation of specific genes (Tahiri-Alaoui and Antoniw, 1996), that result in localized and systemic responses

by the plant. These responses include the synthesis of new isoforms of chitinases and glucanases and the thickening of the cell walls (Azcon-Aguilar et al., 2002; Pozo et al., 2002), that may affect herbivore colonization. Declerck et al. (2002) carried out investigations on the interaction between four AM fungi, *Glomus* sp., *Glomus proliferum*, *G. intraradices* and *G. versiforme*, and the root-rot fungus *Cylindrocladium spathiphylli*. Pre-inoculation of plants with AM fungi attenuated the detrimental effect of the pathogen. These results corroborate previous studies involving other plants grown in the presence of root pathogenic fungi, as these plants were less affected when colonized with AM fungi (Jaizme et al., 1998; Abdalla and Abdel Fattah, 2000). The development of root-rot symptoms on bananas was considerably affected by the presence of AM fungi. The lower disease severity observed in mycorrhizal banana plants was associated with improved growth of the plants. Therefore, AM fungal symbiosis mainly affected the host-pathogen relationship by improving P nutrition, leading to greater resistance to root-infecting fungi. More recently, the effects of different species of AM fungi on parasitism rates have been reported (Gange et al., 2003) but this study did not demonstrate a direct link between AM and attraction of insect parasitoids.

Guerrieri et al. (2004) tested the hypothesis that an AM symbiosis makes tomato plants significantly more attractive towards the aphid parasitoid, *Aphidius ervi* (Haliday), which is well known for its efficiency against the potato aphid pest. The positive effect of mycorrhizal colonization on the attraction of the parasitic wasp, *A. ervi*, to its host plants and a negative effect on insect pest populations observed in this study have important implications for understanding of insect population dynamics and predicting the plant defense mechanisms. Castillo et al. (2006) investigated the effects of single and joint inoculation of olive planting stocks cvs. Arbequina and Picual with the AM fungi, *G. intraradices*, *G. mosseae* or *G. viscosum*, and the root knot nematodes *M. incognita* and *M. javanica* on plant performance and nematode infection. They concluded that prior inoculation of olive plants with AM fungi contributed to improved health status and vigor and reduced the severity of root galling by root-knot nematode. In conclusion, these results demonstrate the positive impact of AM fungi on P nutrition and plant growth under root pathogen pressure. However, this does not imply that better P nutrition alone accounts for increased resistance against phytopathogens. In the past decade, some authors have suggested that other mechanisms could be involved: proposed mechanisms include activation of the plant defense system and disease resistance (Benhamou et al., 1994; St. Arnaud et al., 1994); direct or indirect competition in the rhizosphere (St. Arnaud et al., 1994); biochemical changes in the plant and anatomical changes in the roots (Benhamou et al., 1994; Hooker et al., 1994); and competition for host resources in root tissues (Hooker et al., 1994). Hence, AM fungi have been shown to increase resistance to root-infecting pathogenic fungi and root-invading nematodes. The reasons for increased resistance to pathogens are not well understood, but a well-established AM infection is a prerequisite for protection. This is an intriguing area of research and bioprotection may be the primary role for AM fungi in some natural ecosystems rather than nutrient acquisition. The current emphasis on low input-based agrotechnology for crop production systems has stimulated the use of AM fungi as bioprotectors, phytostimulators or biofertilizers against plant diseases caused by soil-borne pathogens.

3.5. Mycorrhizoremediation

Biosphere pollution by heavy metals and nucleotides has been accelerated dramatically during the last few decades due to mining, smelting, manufacturing, treatment of agricultural soils with agro-chemicals and soil sludge, etc. (He et al., 2005). Heavy metals such as lead (Pb), arsenic (As), cadmium (Cd) and mercury (Hg), being added to our soils through industrial, agricultural and domestic effluents, persist in soils and can either be adsorbed in soil particles or leached into groundwater. Phytoremediation (such as phytoextraction, phytostabilization and rhizofiltration) of soils contaminated by heavy metals has been widely accepted as a cost-effective and environmentally friendly clean-up technology. However, the progress in this field is hindered by lack of understanding of complex interactions in the rhizosphere and plant-based mechanisms which allow metal translocation and accumulation in plants (Yu et al., 2004). Complex interactions between roots, microorganisms and fauna in the rhizosphere have a fundamental effect on metal uptake and plant growth. Some AM fungi are adapted to adverse conditions so they can benefit plants under a variety of environmental stresses. AM fungi are involved in plant interactions with soil toxic metals, either by alleviating metal toxicity to the host or by accentuating it (Meharg, 2003; Pawlowska and Charvat, 2002). Despite the significant role that AM fungi play in plant interactions with soil toxic metals and the ubiquity of AM fungi in the soil environment, only recently has progress been made towards understanding the cellular mechanisms utilized by AM fungi to metabolize heavy metals and alleviate their cytotoxicity (Lanfranco et al., 2002). Numerous studies have revealed that AM fungi confer upon plants tolerance against heavy metal stress (Davies et al., 2001; Levyal et al., 2002; Liao et al., 2003). Plant associations with AM fungi are suggested as a potential biological solution to ameliorate plant resistance to metal toxicity and restore fertility of soils polluted by heavy metals such as Cd (Vivas et al., 2005). A well-developed mycorrhizal symbiosis may enhance the survival of plants in polluted areas by better nutrient acquisition (P, N, Zn, Cu, Fe, etc.), water relations, pathogenic resistance, phytohormone production, contribution to soil aggregation, amelioration of soil structure, and thus improved success of all kinds of bioremediation (Jeffries et al., 2003; Gaur and Adholeya, 2004). Immobilization of metals in the fungal biomass is proposed as a mechanism by which these fungi may increase plant tolerance to heavy metals. Mycorrhizal roots may act as a barrier against metal transport, reducing transfer and enhancing root/shoot Cd ratios (Andrade and Silveira, 2008). This effect is attributed to metal adsorption on hyphal walls, since chitin has an important metal-binding capacity (Joner et al., 2000; Bi et al., 2003; Christie et al., 2004). Recently,

it has been suggested that glomalin, a glycoprotein produced by AM fungi, may have a metal chelating function, diminishing metal availability for plants (Zhu, 2001; Gonzalez-Chavez et al., 2004; Khan et al., 2006; Saleh and Saleh, 2006). Another possible mechanism of metal tolerance includes dilution of metal concentration in plant tissues due to the promotion of plant growth by AM fungi (Andarde and Silveira, 2008), uptake exclusion by precipitation or chelation in the rhizosphere (Kaldorf et al., 1999), and P-mediated effects on the host plant (Wang et al., 2005). The AM fungi associated with metal-tolerant plants may contribute to the accumulation of heavy metals in roots in a non-toxic form inside hyphal cell walls or complexed into phosphate materials inside the cells (Galli et al., 1995). However, the effect of AM fungi on the uptake of metals by plants is not yet totally clear, with reports finding increased uptake of metals (Tonin et al., 2001; Liao et al., 2003; Whitefield et al., 2004; Citterio et al., 2005), decreased uptake (Weissenhorn et al., 1995, Chen et al., 2003) or no uptake effects (Trotta et al., 2006; Wu et al., 2007). Factors such as the metal element and its availability, plant species, fungal species or strain and differences in mycorrhizal and non-mycorrhizal plant size and P content in experiments may account for different results (Levyal and Joner, 2000).

AM fungi, therefore, play a significant ecological role in the phytostabilization of potentially toxic trace element-polluted soils by sequestration and, in turn, help mycorrhizal plants to survive in polluted soils. They can alter plant productivity, because AM fungi can act as biofertilizers, bioprotectants or biodegraders (Xavier and Boyetchko, 2002). Their potential role in phytoremediation of heavy metal-contaminated soils and water is also becoming evident (Khan, 2001; Jamal et al., 2002; Hayes et al., 2003). Thus, the benefits of mycorrhizae may be associated with metal tolerance and also with metal plant nutrition. Therefore, in degraded and contaminated soils, that are often poor in nutrients and with low water-holding capacities, mycorrhizae formation would be of great importance. In conclusion, a biotechnological goal is to use a combined inoculation of selected rhizosphere microorganisms to minimize toxic effects of pollutants and to maximize plant growth and nutrition (Saleh and Saleh, 2006). The ecological complexity and diversity of plant-microbe-soil combinations and the role that AM play in phytorestoration of heavy metal-contaminated soils, i.e. mycorrhizoremediation, thus need to be taken into consideration to restore the fertility of heavy metal soil (Khan, 2006). Ecosystem restoration of heavy metal-contaminated soil practices need to incorporate microbial biotechnology research and development. Since AM fungi are reported to be present on the roots of plants growing on heavy metal-contaminated soils, isolation of indigenous stress-adapted AM fungi can be a potential biotechnological tool for inoculation of plants in disturbed ecosystems.

3.6. Miscellaneous roles of arbuscular mycorrhizal (AM) fungi

Roots colonized by AM fungi are often thicker and carry fewer root hairs. Such changes in morphology are expected to be under phytohormonal control (Selvaraj, 1998). Abscisic acid (ABA) was found to be considerably enhanced in both roots and shoots of AM plants as compared with non-mycorrhizal control (Danneberg, 1992). Also, an increase in Indole Acetic Acid (IAA), gibberellin and cytokinin level was observed in *G. fasciculatum*-inoculated *P. juliflora* recorded by Selvaraj (1998), showed the influence of the AM fungi, *G. fasciculatum*, on increased level of growth hormones. Barea and Azcon-Aguilar (1982) also noted that in axenic experiments, mycorrhizal fungi produced auxin-, gibberellin- and cytokinin-like substances and stimulated plant growth.

The mycorrhizal plants also showed increased production of certain enzymes. Increased peroxidase is one of the most widespread biochemical activities in diseased and injured plant tissues. Spanu and Bonfante-Fasolo (1998) measured the cell wall-bound peroxidase in *Allium porrum* during root growth and development of *G. versiforme*. Pacovsky et al. (1990) studied peroxidase activity in *Phaseolus vulgaris* infected by *G. etunicatum* and found that peroxidase activity increased in the mycorrhizal plants. Phosphatases of the mycorrhizae are both specifically induced in the presence of *Glomus* spores and are sensitive to the level of phosphate in the environment (Pacovsky, 1991). Selvaraj (1998) found that due to inoculation of AM fungi, *G. fasciculatum* acid phosphatase activity was increased in leaves and roots of *P. juliflora*. Tisserant et al. (1993) observed that histochemical tests revealed the presence of alkaline phosphatase in *Glomus*-infected roots of *A. porrum* and *Platamus acerifolia.* The presence of AM specific alkaline phosphatase activity in *A. cepa* and *P. accindentalis* plants inoculated with *G. mosseae* has been reported (Gianinazzi-Pearson and Gianinazzi, 1976). Mycorrhizae also enable plants to survive in disturbed and endangered ecosystems, as those are polluted by radioactive elements. In an atomic power station, products of nuclear fission reactions such as cesium, ^{137}Cs, and strontium, ^{90}Sr, are regularly released into the environment as a result of weapons testing, nuclear power production and nuclear fuel reprocessing (Haury and Schikarski, 1997). Plants absorb the Cs and Sr less efficiently than their nutrient analogues potassium and calcium, respectively (Zhu and Smolders, 2000). Both Cs and Sr are taken up from soil solution by plants as K^+ and Ca^{2+}, as they are similar to those cations in chemical properties (White and Bradley, 2000). AM fungi are beneficial for the uptake of nutrients and also for plants to survive, even from a disturbed soil after radionuclide deposition (Ahiabor and Hirata, 1994). Selvaraj et al. (2004) studied the effect of AM spores, *G. fasciculatum*, on two plants, *Phyllanthus niruri* and *Eclip-tica alba*, and revealed that AM fungi was more beneficial for plant growth. It was noticed that in spite of growth disturbance, AM fungi-inoculated plants were efficient in tolerating the endangered ecosystems. The two experimental host plants showed more uptake of K^+ and Ca^{2+} in the roots of AM-inoculated plants as compared with the uninoculated plants. Thus, through the help of AM fungi and the soil's nature to hold the radionuclide to prevent the expression of radioactivity, chances are greater for the vegetation to survive in the disturbed ecosystems in a better way. There is very strong circumstantial evidence therefore that AM fungi would enhance

uptake and recycling of radionuclides, particularly ^{137}Cs and strontium, ^{90}Sr (Selvaraj et al., 2004). Thus, plants receive support from AM fungi, with the help of its symbiotic association, in the aspect of uptake of phosphorus and other nutrients, enhancement of growth hormones, increase in protein content, increased tolerance to drought and heavy metals, increase in salinity tolerance and resistance to root-borne pathogens. Also, AM fungi can help in uptake of radionuclides in a disturbed ecosystem with radioactive elements (Selvaraj and Chellappan, 2006).

So, not only do the activities of AM fungi have multiple functions that enhance plant performance and productivity, but they also play crucial roles in the development of soil properties and the health of the entire ecosystem. Thus, with important nutrient uptake functions of AM fungi being appropriately managed, mycorrhizae can potentially offer a more effective and sustainable element biofortification to curb human malnutrition.

4. CONCLUSION

The increasing consumer demands for organic or sustainably-produced food requires the incorporation of natural roles of microorganisms, such as arbuscular mycorrhizal (AM) fungi. It is clearly revealed from the preceding discussion that mycorrhizal symbiosis plays fundamental roles in shaping terrestrial ecosystems and must be considered as an essential factor for soil fertility and for promoting plant health and productivity. Over the past few years, a novel and unexpected developmental capacity of plant cells has been discovered that is essential for the intracellular uptake of AM fungi. Recent progress in the molecular and genetic analysis of mycorrhizal development has provided novel insights into the evolution of this symbiosis. Elucidation of molecular events associated with signaling and nutrient acquisition processes has moved rapidly forward. Several genes (GmGin1, *Lj POLLUX*, *Lj Nup 133, Lj SYM 24,* AM-specific Pht1-encoding genes and plant encoded nitrogen transporters) and signaling cascades have been identified which play a role in the establishment of mycorrhizal symbiosis. Collectively, these fungal symbionts confer tolerance to drought, heat, salinity, osmotic stress, disease and herbivory, and thus promote growth and nutrient acquisition. AM symbiosis occurs in almost all habitats, including disturbed soils contaminated with heavy metals, and plays an important role in metal tolerance. Thus, we can conclude that some plants are unable to endure habitat-imposed abiotic and biotic stresses in the absence of fungal endophytes. The use of stress-tolerant mycorrhizal fungi may be a promising strategy to develop tools for soil reclamation and amelioration.

Despite the identification of genes, proteins and enzymes involved in fungal and plant perception, and P and N transport and assimilation, very little is known about how these elements are transferred to the hosts. Thus, the understanding of molecular mechanisms and signaling pathways coupled to AM symbiosis needs further refinement and there is a need to unravel the complexity of the biology of AM symbiosis.

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