



Diversity, Morphological Characteristics and Role of Arbuscular Mycorrhiza fungi (AMF) in the Natural Ecosystem

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ARTICLE INFO

Article history:

Received: 23 September 2014;

Received in revised form:
19 February 2015;

Accepted: 28 February 2015;

Keywords

Mutualism, Soil fertility,
Rhizosphere, Bioprotectant.

ABSTRACT

Microbial diversity contributes to the sustainability in agriculture, horticulture, forestry and range of environment. The mycorrhizal symbiotic association appears to have evolved with plants since as a survival mechanism for fungi and higher plants. Arbuscular mycorrhizae are the most important microbial symbioses for the majority of plants thus allowing each to survive in the existing environment of low temperature, low soil fertility, periodic drought, diseases, extreme environments, P-limitation, plant community development, nutrient uptake, water relations and above-ground productivity. They also act as bioprotectants against pathogens and toxic stresses. This review gives a brief account on AMF which is necessary for the agricultural improvement and soil fertility.

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Introduction

Living things have a complex and multilateral connection with one another where this connection creates a complex ecological system (Wang and Gui, 2006). These types of connections have an effective role in maintaining the natural ecosystem. Therefore, if two living things live, one another and maintain very close connection. This becomes possible or better for them and they will be considered as symbiotic or a sort of coexistence (“participating in life”). Coexistence is a close relationship which exists between most living things in nature; neither plants nor animals (Alizadeh *et al.*, 2007).

The stimulation of microorganisms by the plant root system has now become attracted the researchers attention towards exploration of microbial diversity and their specific functions. Microbial activity in the rhizosphere is a major factor that determines the availability of nutrients to plants and has a significant influence on plant health and productivity. An understanding of the basic principles of rhizosphere microbial ecology, including the function and diversity of the microorganisms, is necessary before soil microbial technologies can be applied (Bolton *et al.*, 1992). In this context, it is important to use a broad definition of the rhizosphere to include the rhizosphere soil, the volume of soil adjacent to and influenced by the root, the root surface or rhizoplane, and the root itself, which includes the cells of the root cortex where invasion and colonisation by endophytic microorganisms has occurred. Soil–plant–microbe interactions are complex and there are many ways in which the outcomes can influence plant health and productivity (Kennedy, 1998). There are several groups of beneficial rhizosphere microorganisms engaged in well-developed symbiotic interactions in which particular organs are formed, such as mycorrhizas and root nodules. A series of developmental events programmed as a result of molecular cross-talk between plant roots and their respective symbionts. The interaction between rhizobial bacteria and the roots of leguminous plants has been well studied (Brockwell *et al.*, 1995), but for the mycorrhizal relationship it has only recently become a significant topic of research (Smith and Read, 1997).

In terms of ubiquity and partnerships throughout the plant kingdom, mycorrhizal relationships are the most significant in plant–microbe symbiosis. There are several types of symbiosis between algae and fungi in the state of lichens, plant and fungi in the state of mycorrhiza. Fungi is a special type of creature which it has no chlorophyll and thus it is unable to synthesize many of its critical living compounds. Therefore, the fungus must obtain the material that they cannot synthesize, from other sources. Arbuscular mycorrhiza (AM) fungi are the most common and abundant coexistent fungi in soil and can coexist with more than 90 percent of plant species to establish a symbiotic relationship (Smith and Read, 2008).

Many thousands of fungi can form the symbiotic relationships, in contrast to the restricted range of plant species that are involved. Even more specific are the unique mycorrhizal relationships formed by the arbutoid, specific orchid and ericoid plant families. The arbuscular mycorrhizal fungi which form the most ancient and widespread mycorrhizal relationship. More than 80% of plant species can form arbuscular mycorrhizas (AM), yet relatively few fungal species (~120) from a restricted taxon, the Glomales, are involved. Both fossil (Remy *et al.*, 1994) and molecular phylogenetic (Simon *et al.*, 1993) evidence that supports the hypothesis that terrestrial plants evolved with the aid of existing arbuscular mycorrhizal relationships. Thus many plants have co-evolved with this symbiosis – a significant factor in explaining the dependency and stability of this relationship. The mycorrhizal symbiosis is a keystone to the productivity and diversity of natural plant ecosystems and it is rare to find a situation where AM do not have a significant ecological presence. This reflects the evolutionary history of the relationship.

Arbuscular mycorrhiza (AM) is an ecologically important and uniformly in the diverse ecosystem through their specific symbiotic association in the plants. Some of them may be predominant in certain areas with broad ecological range (Bostrom, 2001).

AM fungi like other soil fungi occur in the top 15-30 cm. of soil and their number decreases with increasing depth (Redhead, 1977). Geographically, AM fungi are ubiquitous and establish

mutualistic relationship over 90% of vascular plant species (Smith and Read, 1997).

The community of AMF determines the plant community structure by the response of individual plant species to colonization by single or multiple species of AM fungi. Diversity of AM fungi is a major factor in the maintenance of plant biodiversity and to ecosystem stability and function. AMF can enter the roots of many plant species in the same community resulting in simultaneous colonization by several species of AM fungi which result in interconnection of plants through extra radical mycelium (Heijden *et al.*, 1998).

AM fungi are obligate biotrophs and it is believed to reproduce clonally via spores, vesicles and hyphae. When the conditions are favorable, the spore of Glomeromycota starts to germinate, form appressoria on host roots and establish a new mycorrhizal symbiosis where the plants are thought to release some exudates which stimulate the germination of spores. After entering into the roots, AM fungi penetrate into the cortical cells and ultimately form structures like arbuscules and vesicles which are involved in the nutrient and carbohydrate transfer (Saito, 2000).

Arbuscular mycorrhizal fungi are key components of the soil microbiota and obviously interact with other microorganisms in the rhizosphere (Bowen and Rovira, 1999). This, in turn, affects colonization patterns of this region by soil microorganisms and results in mycorrhizosphere effect (Gryndler, 2000). Arbuscular mycorrhizal fungi thus interact with natural and introduced microorganisms in the mycorrhizosphere, hence affecting soil properties and quality.

Microbial populations in the rhizosphere can either interfere with or benefit establishment of AM (Vosatka and Gryndler, 1999). Deleterious rhizosphere bacteria (Nehl *et al.*, 1996) and mycoparasitic relationships (Jeffries, 1997) have been found to interfere with AM development, while many microorganisms can stimulate AM formation and/or functioning (Gryndler, 2000 & Barea *et al.*, 2002). Soil microorganisms can produce compounds that increase root cell permeability, thereby increasing the rates of root exudation. This, in turn, stimulates the growth of hyphae of AMF in the rhizosphere and facilitates root penetration by the fungus.

Rhizosphere microorganisms are also known to affect the pre-symbiotic stages of AM development (Giovannetti, 2000), such as spore germination and germ tube growth (Azcon-Aguilar and Barea, 1992, 1995). Biologically active substances such as amino acids, plant hormones, vitamins, other organic compounds and volatile substances (CO₂), produced by soil microorganisms, can stimulate the growth rates of AMF (Azcon-Aguilar and Barea, 1995; Barea 1997, 2000). Detrimental effects of soil microorganisms on spore germination and hyphal growth in soil have also been reported (Linderman 1992; Azcon-Aguilar and Barea, 1992).

Among the soil microbiota the rhizobacteria behaved as mycorrhiza-helper bacteria, promoting AM establishment while AM formation supports the increased size of the PSB population. Thus the rhizosphere/mycorrhizosphere interactions contributed to the biogeochemical cycling of P and leads to plant health (Barea *et al.*, 2002).

The well-known activities of dinitrogen-fixing bacteria and phosphate-solubilising microorganisms in improving the bioavailability of the major plant nutrients viz., N and P. This nutrient availability contribute to the AM role in nutrient acquisition (Barea *et al.*, 2002).

It is known that certain rhizobial strains improve the processes involved in AM formation by *Glomus mosseae* through spore germination, mycelial growth from the mycorrhizal propagules and “entry point” formation on the developing root system of the common host legume plant (Barea *et al.*, 1996).

Systematic classification of AM fungi:

In the present scenario, the major thrust area of research is the scientific classification of AM fungi. Taxonomy is entering a new phase and many researchers have attempted to propose a suitable classification for AM fungi on the basis of morphological, biochemical and molecular genetics techniques. The vesicular arbuscular mycorrhiza forming fungi were classified as the member of Zygomycota and were placed under the order Glomales (Mortan and Benny, 1990). But, the gene encoding analysis of the small subunit (18S) ribosomal RNA show the AM fungi are not related to Zygomycota and probably share common ancestry with Ascomycota and Basidiomycota. So, they have been assigned to a new monophyletic group, Glomeromycota (Schussler *et al.*, 2001). Based on data from molecular, morphological and biochemical investigations, two new families in the order Glomales i.e. Archaeosporaceae and Paraglomaceae with two new genera *Archaeospora* and *Paraglomus* respectively were created by Mortan and Redecker (2001). The ordinal name ‘Glomales’ has now been changed to Glomerales under the phylum Glomeromycota which is further divided has been divided into four orders i.e. Glomerales, Paraglomerales, Diversisporales and Archaeosporales (Schussler *et al.*, 2001). Several taxonomic and phylogenetic relationships of AM fungi based on molecular characterization have also been reviewed by Reddy *et al.*, (2005). As the number of AM species is increasing day by day, it is quite pertinent to revise the classification of these fungi.

AM fungi diversity and distribution

The genera, which form AM fungal association are *Acaulospora*, *Ambispora*, *Archaeospora*, *Diversispora*, *Entrophospora*, *Gigaspora*, *Glomus*, *Intraspora*, *Kuklospora*, *Otospora*, *Pacispora*, *Paraglomus*, *Sclerocystis* and *Scutellospora* (Schussler *et al.*, 2001; Mortan and Benny, 1990; Oehl and Sieverding, 2004, 2006; Walker *et al.*, 2007 and Palenzuela *et al.*, 2008).

The term Mycorrhizae was used for the first time in the year 1885 by Frank with a biological relationship with their benefits. So the potential of mycorrhizal connection with plant is more than their total potential in singular mode. Mycorrhizal fungi are divided into two general categories endomycorrhiza and ectomycorrhiza. The recent batch establishes a symbiotic relationship with plants, especially tree crops mainly needle leaf forests and eucalyptus trees. Mycorrhizal fungi have two types of mycelium systems: external and internal mycelium; the external Mycelium grow and spread inside the soil, and are able to ease into the tiny pores of the soil where plant roots are normally out of reach, to recruit penetration and nourishment (Ramanankierana, 2007; Smith and Read 2008). Whereas internal myceliums grow in between and inside the parenchyma cells of the host plant roots and create many branches within the plant root cells. This connection of branches in each cell is named as arbuscule and it is believed that the exchange of nutrients between fungus and plant is done through the arbuscule.

Harley, (1961) divided the mycorrhizal symbiosis into two category as Endotheraphic and Ectotheraphic, but since then used two words such as Endomycorrhiza and Ectomycorrhiza.

Although currently the classification of mycorrhizal is based on the type of relationship between fungi and plant to the state of communication between root cells with fungus mycelium, and respectively the three groups of Endomycorrhiza, Ectendomycorrhiza and Ectomycorrhiza are characterized. The three groups are differed based on fungal penetration into the host cell and create various fungal states and its' structures in host cells.

Widespread distribution both in terms of habitats and host species, symbiotic relationships, host growth promotiveness and protection, non specificity for host, positive interaction with other rhizosphere microbes and several other characteristics of AM fungi have obviously forced to find out their practical aspects.

The distribution of species of AM fungi is affected by climatic and edaphic conditions e.g. *Glomus* is found in acidic soil, *Gigaspora* and *Scutellospora* in tropical soils and *Acaulospora* in the soil with pH below 5. Regarding the dispersal of AM fungi, it occurs through AM propagules, like mycelia and spores, which can be moved by biotic and abiotic agents. Dispersal of AM spores over greater distances is dependent upon passive dispersal by wind and water, while animal dispersal of AM spores occurs through ingestion and egestion. Reynolds *et al.*, (2003) reported that this plant microorganism interaction is highly dependent upon the soil environment such as; pH, moisture availability, nutrient availability and presence or absence of other microbes.

Among the different types of mycorrhiza, (AM) are the important beneficial micro-organisms of the soil edaphon in most agro-ecosystems. AM and the mother of plant root endosymbiosis, is a wide spread mutualistic symbiosis between land plants and fungi of the phylum Glomeromycota. Kilronomos and Kendrick, (1993), emphasizes the greater diversity of AM.

Arbuscular mycorrhizal associations occur in a wide spectrum of agricultural crops, most shrubs, tropical tree species and some temperate tree species. It has been found in some gymnosperms, pteridophytes, bryophytes and in some floating and submerged aquatic plants. A recent analysis of phylogenetic distribution of mycorrhizal occurrence among different species of land plants shows that the AM is the predominant and ancestral type of mycorrhiza. Its occurrence in early divergent lineages of liverworts suggests that the origin of AM probably coincided with origin of land plants (Wang and Qui, 2006).

Families, not forming AM include Betulaceae, Fumariaceae, Commelinaceae and Ericaceae. Families that rarely form AM include the Brassicaceae, Chenopodiaceae, Polygonaceae, Orchidaceae and Cyperaceae. Although AM is confined to the roots, they have been reported in diverse structures such as the modified leaves of water fern, *Salvinia cucullata*, fruiting peg of peanut and modified scale like leaves and rhizomes of ginger and canna (Sumbali and Mehrotra, 2009).

The presence or absence of a host plant has an important role to complete the life cycle of these fungi which show host preference to grow. In the absence of hosts, they are present as multinucleate spore with thick wall and subtending hyphae. All AM fungi have been described to date reproduce only by asexual mean (Schussler *et al.*, 2001). Hence, these fungi are incapable of saprophytic survival and can only be grown with a host plant (Douds, *et al.*, 2000; Smith, *et al.*, (2001) and Nair, 2007).

Morphological characteristics of AM fungi:

Morphological characters that are stable and discrete are used to identify and classify the arbuscular mycorrhizal fungi (AMF). The different morphological characters considered in this microbial interaction are described below:-

Colony

A colony refers to hyphal colonization of a root resulting from the same external hyphae and are referred to infection units.

Hyphal Characters

Based on their function, the vegetative hyphae have been differentiated into infective, absorptive and runner hyphae. Fungal hyphae are filamentous network, which tends to form various shapes such as H- shaped parallel connections in *Glomus*, constricted hyphae near branch points as in *Acaulospora* and *Enterophospora* and coiled, swollen and irregularly projections or knobs as in *Gigaspora* and *Scutellospora* (Mortan, and Bentivenga, 1994).

Appresoria

Appresoria are hyphal swellings between two adjacent root epidermal cells. These are the sites where hyphae first penetrate into the root cells by exerting pressure or by enzymatic activity.

Arbuscules

All the Glomalean fungal species form arbuscules which are small tree like, hyphal filled, invaginations of cortical cells that provide intimate contact between the plasmalemma of two symbiotic partners and are, presumably, the point of material exchange between host and fungus. Abrupt narrowing off of branch hyphae reduction in hyphal width forms arbuscules in *Gigaspora* and *Glomus*. At the later stage, arbuscules are digested by host cells where tips are eroded first and then entire arbuscules are dissolved and digested (Brundrett and Kendrick, 1990).

Vesicles

Vesicles are spherical to ovoid, sac like globular to elongated terminal swellings of the hyphae or are intercalary aseptate structures develop after the development of arbuscules. They have fat granules that serve as storage organs of the fungus. Vesicles in Glomaceae are sub- globose to elliptical, where as in Acaulosporaceae they are pleomorphic and knobby. Vesicles are produced in enormous number later in the seasons as the plant mature (Abbott, 1982).

Auxillary Cells

Auxillary cells are cluster of thin walled cells. They differ in shape, size and surface ornamentations. These are only restricted to the sub-order Gigasporaceae. Functionally, they act as a temporary storage structures of carbon compounds (Morton, 1990)

Subtending Hyphae

Besides arbuscules and vesicles, an another morphological feature of AM fungi is the stalk of the spore known as subtending hyphae or sporophore which has importance in identification. Subtending hyphae may be absent as in *Acaulospora*, simple, straight or curved (*Glomus*), swollen and straight, but often appear sessile due to detachment from saccule and two scars present on either side of the spore (*Enterophospora*) and sporophore bulbous as in *Gigaspora* and *Scutellospora* (Manoharachary *et al.*, 2009).

Spore, Sporocarps and Sub-cellular structures

AM fungal spores may be azygospores or chlamydo spores and formed singly or aggregated in sporocarps. Spores are variable in size and ranging from 10-1000µm. The color of the spores varies from hyaline, yellow, reddish-brown, orange,

brown and black. The different shape of the spores may be globose, sub-globose, ovoid, pea shaped, ellipsoid, obovoid, reniform or irregularly elongated. Seven kinds of wall layers have been described in AM spores, namely evanescent, unit, laminated, membranous, coriaceous, amorphous and expanding. The cytoplasm in the spores may be reticulate or vacuolated (Manoharachary *et al.*, 2009).

Role of AM fungi

The relationship between fungi and plants is peaceful, because on one side fungus provides the plants with nourishment, and on the other side it receives the necessary carbohydrates and energy from the host plant. A symbiotic system is formed when a fungus is able to infect the cortex primal cells of the root (Linderman, 1988; Smith and Read, 2003; Wang and Gui, 2006).

Usually coexistence method had a big problem of nutrient absorption for plants but the mycorrhiza fungus can increase the capacity for absorption of nutrient into the host plants (Dalpe and Monreal, 2004). In addition, fungus has the ability to produce and secrete growth hormones and provide a better water absorption and protection against plant pathogens (Heijden *et al.*, 2006).

The AMF using a triple interaction of soil, fungi and plants are able to provide other benefits to host plants that their most important are: Increase plant resistance to diseases, increased biological nitrogen fixation, increasing plant resistance to drought, increased photosynthesis rates, lower concentrations of elements such as cadmium and arsenic in plant tissues and improve soil physical properties (Lindermann, 1988; Ramanankierana, 2007 and Heijden *et al.*, 2006).

The tremendous advances in research on mycorrhizal physiology and ecology over past few years have led to a greater understanding of the multiple roles of mycorrhizal fungi in ecosystem. Some of the benefits of mycorrhizal fungi are described as following:

Uptake and Transfer of mineral nutrients

The major role of AM fungi on host plant is to enhance nutrient mobilization. AM fungi colonize plant roots and ramify into the surrounding bulk soil extending the root depletion zone around the root system which transports water and mineral nutrients from the soil to the plant. AM fungi are well known to improve the absorption of all the nutrients required by plants for their growth such as P, K, Zn, Cu, Mg, Mn and Fe. Hyphae of the AM fungi can also take up amino acids and orthophosphate (Govindarajulu *et al.*, 2005 and Li, *et al.*, 2006). The enhanced effect of AM fungi on the uptake of water and nitrogen mineralization from organic residue has been well documented (Bohra *et al.*, 2007 and Atul-Nayyar *et al.*, 2009).

Phosphorus Uptake

AM fungi play a greater role in order to supply infected plant roots with phosphorus because P is an extremely immobile element in soil. As AM fungi increases the surface area of plant roots and resulted in more proliferation of fibrous roots and hence increase uptake of more phosphorus (Prakash *et al.*, 2009). Alkaline phosphatase activity is related to phosphate metabolism as it is present in the fungal vacuole where polyphosphate granules are present. In the fine branches of arbuscules, these granules are broken down by activity of enzymes and release inorganic phosphorus in the cytoplasm. An increase in phosphorus uptake in mycorrhizal plants than non-mycorrhizal plants has been documented by several workers (Mali *et al.*, 2009; Karthikeyan *et al.*, 2008 and Ojha *et al.*, 2008).

Nitrate uptake

Nitrate can be mobilized from soils and transferred to the root cells by AM external hyphae, improving the inflow of nitrogen to the mycorrhizal plant (Johansen *et al.*, 1993; Tobar *et al.*, 1994 and Azcon *et al.*, 1996). Most of the evidence concerning the effect of AM fungi on nitrate acquisition has been attributed to an indirect P-mediated mechanism since the enzymatic system for nitrate reduction requires phosphate (Hoff *et al.*, 1992).

Nitrate reductase (NR) has been proposed as an index for assaying the effectiveness of AM fungi-host plant combinations for mitigation of water deficit stress (Caravaca *et al.*, 2003, 2005). This enzyme is responsible for nitrate assimilation which is highly sensitive to metabolic and physiological plant status and it is induced by high nitrate supply (Kandlbinder *et al.*, 2000).

The process is highly energy-demanding and hence frequently limited by P availability and hence increase in NR of mycorrhizal plants with respect to nonmycorrhizal ones can be related to the phosphate requirements of this enzyme (Ruíz-Lozano and Azcón, 1996).

Increased Nitrogen Fixation

The tripartite interaction between nodulating legumes, AM fungi and nitrogen fixing *Rhizobium* frequently result in increased level of nodulation and nitrogen fixation as the result of improved P nutrition in infertile or P fixing soils (Dodd, 1990).

Induction of phytohormones

The possible higher N assimilation in AM plants (Toussaint *et al.*, 2004) might have contributed to the production of amino acids such as tyrosine and phenylalanine which are the precursors for the production of Rosmarinic and Caffeic Acids (RA and CA) (Peterson and Simmonds, 2003), subsequently to higher production of the phenylalanine ammonia-lyase a one of the main enzymes involved in the production of CA and RA. Another possible mechanisms could reside in the potential of AM i.e., inducing changes in phytohormone levels in the host plant, such as cytokinins for gibberellin (Allen *et al.*, 1982).

Roots colonized by AM fungi have often much branched and Such changes in morphology are expected to be under phytohormonal control (Selvaraj, 1998). Abscisic acid (ABA) was found to be considerably enhanced in mycorrhizal plants than non-mycorrhizal plant (Danneberg *et al.*, 1992). The production of growth hormones by mycorrhizal fungi such as IAA (Indole Acetic Acid), gibberellin, cytokinin, auxin and growth regulators like Vitamin B have been well documented by many researchers (Manoharachary, *et al.*, 2009; Selvaraj, 1998 and Barea and Azcon-Anguilar, 1982).

Soil aggregation and Stability

Soil aggregation is essential to maintain soil physical properties and facilitate biochemical cycling. (Borie *et al.*, 2006). Hyphae of AM fungi are considered to be primarily soil aggregators and there is a positively correlation between AM fungal hyphae and aggregate stability in natural systems (Borie *et al.*, 2006 and Dodd, 2000).

The important role of the mycorrhizal fungal mycelium in the formation of water-stable soil aggregates is well documented (Andrade *et al.*, 1998; Bethlenfalvay *et al.*, 1999; Miller and Jastrow, 2000). Indeed, AMF produce a very stable hydrophobic glycoprotein, glomalin, which is deposited on the outer hyphal walls of the extraradical mycelium and on adjacent soil particles, and which appears to act as a long-term soil binding agent (Wright and Upadhyaya, 1998, 1999). As a consequence,

the extraradical hyphae, together with the fibrous roots, can form a “sticky-string bag that contributes to the entanglement and enmeshment of soil particles to form macroaggregates” (Miller and Jastrow, 2000), a basic building block of soil structure.

Aggregate stability of soil is an important criterion of a healthy, managed ecosystem (Miller *et al.*, 1992). AMF are essential components of ecosystems and that their use could be crucial, not only for revegetation of spoiled lands, but more importantly for maintaining soil structure in agricultural soils. Many biotic and abiotic interactions around roots are probably mediated by AMF (Bethlenfalvay and Lindermann, 1992). The mechanisms involved in aggregate stabilization are based on the enmeshment of soil particles by hyphae and roots, and on the exudation of polysaccharides (Bearden and Petersen, 2000). The binding effect of roots and hyphae is long-lived, while that of polysaccharides is transient because they are decomposed rapidly by microbes.

Increased resistance to root pathogens

AM fungi are recognized as high potential agents in plant protection and pest management. Mycorrhizal colonization provides a bioprotective effect against a broad range of soil borne fungi and nematodes (Singh *et al.*, 2000; Hol and Cook, 2005 and Elsen *et al.*, 2008). In several cases direct biocontrol potential has been demonstrated, especially for plant disease caused by *Phytophthora*, *Rhizoctonia*, *Pythium*, *Alternaria* and *Fusarium* pathogens (Vyas and Shukla 2005; Rani *et al.*, 2001; Aggarwal *et al.*, 1999 and Boby and Bagyaraj, 2003). Several studies have confirmed synergism between AMF and biocontrol agents such as *Burkholderia cepacia* and *Trichoderma viride* (Ravnskov *et al.*, 2002 and Sharma *et al.*, 2008). AM fungi are known to increase the resistance of plants to pathogens by cell wall modification, production of antimicrobial compounds and altered rhizosphere microflora. The AM fungi might affect plant and soil microbial activity by stimulating the production of root exudates, phytoalexins and phenolic compounds (Morandi, 1996 and Norman and Hooker, 2000).

Phytoremediation

Ecosystems have been contaminated with heavy metals due to various human and natural activities. The use of AM fungi in ecological restoration has been shown to enable host plant establishment on degraded soil and improve soil quality and health (Jeffries *et al.*, 2003).

Arbuscular mycorrhizal (AM) fungi occur in the soil of most ecosystems, including polluted soils. By acquiring phosphate, micronutrients and water, they enhance the nutritional state of their hosts. In some cases mycorrhizal plants can show enhanced heavy metal uptake and root-to-shoot transport (phytoextraction) while in other cases AM fungi contribute to heavy metal immobilization within the soil (phytostabilization). The result of mycorrhizal colonization on clean-up of contaminated soils depends on the plant–fungus–heavy metal combination and is influenced by soil conditions.

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