A Review: Beneficial Effects of the Mycorrhizal Fungi for Plant Growth

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ABSTRACT

The two main types of mycorrhizas are ecto and endomycorrhizas, which differ in their structure and physiological relationships with host plant. Mycorrhizal fungi frequently stimulate plants to reduce root biomass while simultaneously expanding nutrient uptake capacity by extending far beyond root surfaces and proliferating in soil pores that are too small for root hairs to enter. Legume roots are invaded and colonized by rhizobia and also with mycorrhizal fungi. For legumes, arbuscular mycorrhizal (AM) fungi have fundamental effects on the eco-physiology, on the biota of the surrounding soil and on associated non-legumes. AM-fungi are known to be effective in increasing nutrient uptake, particularly phosphorus and biomass accumulation of many crops in low phosphorus soil. AM-fungi have an important role in promotion of biological and chemical properties of plants under stressed environment. Most reports note a positive effect of mycorrhizal inoculation on growth of plants in metal-contaminated soils.
KEY WORDS: Arbuscular mycorrhizal, Ectomycorrhizas, Legume, Rhizosphere, Symbiosis.
Abbreviates: AM: Arbuscular mycorrhizal.

INTRODUCTION

Roots of most terrestrial plants form symbiotic associations with fungi. These ubiquitous symbioses, called mycorrhizas, function as conduits for the flow of energy and matter between plants and soils [7]. Although the term mycorrhiza implies the association of fungi with roots, relationships called mycorrhizal associations, which are involved in the absorption of nutrients from soil, are found between hyphal fungi and the underground organs of the gametophytes of many bryophytes and pteridophytes, as well as the roots of seed plants and the sporophytes of most pteridophytes. The two main types of mycorrhizas are ecto and endomycorrhizas, which differ considerably in their structure and physiological relationships with symbionts.

The term "mycorrhizosphere" was coined to describe the unique properties of the rhizosphere surrounding and influenced by mycorrhizas [20]. Figure 1 illustrates pine seedlings with and without mycorrhizas to highlight some of these properties. Mycorrhizal fungi frequently stimulate plants to reduce root biomass while simultaneously expanding nutrient uptake capacity by extending far beyond root surfaces and proliferating in soil pores that are too small for root hairs to enter. Mycelial networks of mycorrhizal fungi often connect plant root systems over broad areas. These fungi frequently comprise the largest portion of soil microbial biomass [26].
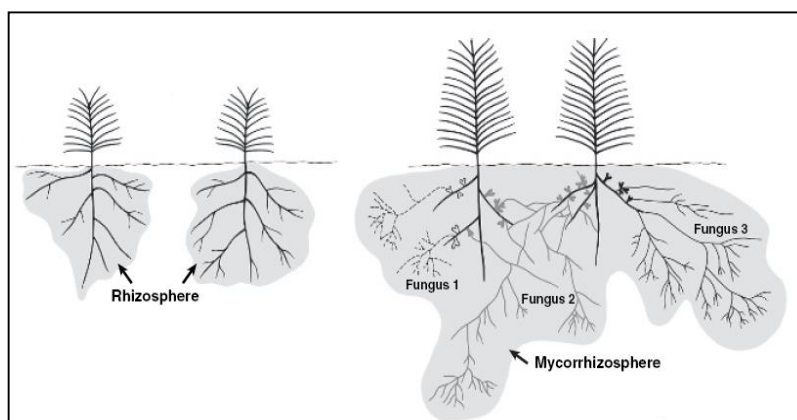

Fig. 1. Drawing of rhizosphere versus mycorrhizosphere. The rhizosphere (left) and mycorrhizosphere (right) of ectomycorrhizal (EM) pine seedlings differ dramatically from one another in plant and soil attributes adapted from Cardon and Whitbeck, 2007.

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Thus, mycorrhizal symbioses physically and chemically structure the rhizosphere, and they impact communities and ecosystems [7]. Arbuscular mycorrhiza (AM) are zygomycetes belonging to the order Glomales. According to both fossil discoveries and DNA sequences, the appearance of both AM and plants is almost 400 million years old. One of the unique characteristics of AM, when in symbiotic relationship with plant roots, is the significant increase in surface area due to the production of extensive hypha helping plants grow under relatively harsh conditions, such as drought stress and nutrient deficiency conditions. AM are the most common mycorrhizal type. The name 'arbuscular' is derived from characteristic structures, the arbuscules (Fig. 2) which occur within the cortical cells of many plant roots and also some mycothalli colonized by AM fungi [32]. Together with storage vesicles located within or between the cells, these structures have been considered diagnostic for AM symbioses. They are formed by bryophytes, pteridophytes, gymnosperms, and angiosperms, and are ubiquitous in most temperate and tropical ecosystems including agricultural systems. The fungal partners in AM associations are remarkably abundant, accounting from 5 to 50 percent of the microbial biomass in agricultural soils [26, 32].
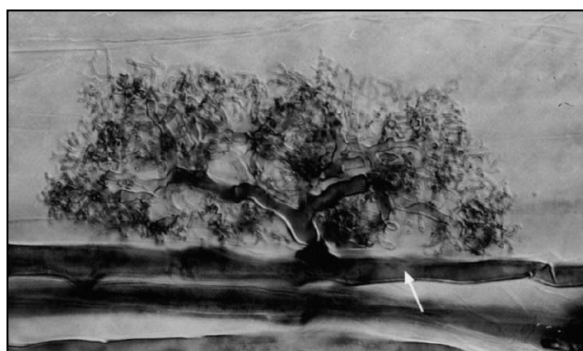

Fig. 2. A mature Arum-type arbuscule of *Glomus mosseae* within a cortical cell of *Allium porrum* (leek). The arbuscule has grown from a well-developed intercellular hypha, adapted from Smith and Read, 2008.

These fungi are members of the Glomeromycota, a monophyletic phylum containing 150-160 described species. Arbuscular mycorrhizas are sometimes called "endomycorrhizas" because the fungal partner forms intraradical structures (i.e., inside plant roots). In AM associations, the interface between plant and fungal tissues that facilitates exchange of materials between plant and fungal symbionts takes the form of arbuscules or coils. Arbuscules and coils are modified fungal hyphae that provide a large surface area for resource exchange. Several genera of AM fungi also form intraradical vesicles that function as fungal storage organs. The extraradical hyphae of AM fungi lack regular cross walls allowing materials, including nuclei, to flow relatively freely within the mycelium. These hyphae can be very abundant; one gram of grassland soil may contain as much as 100m of AM hyphae. The taxonomy of AM fungi is based upon the morphology of large asexual spores produced in the soil or within roots. Beneficial plant–microbe interactions in the rhizosphere are primary determinants of plant health and soil fertility. Arbuscular mycorrhizas, which forms symbioses with majority of plants, influence plant community development, nutrient uptake, water relations, and above-ground productivity. Arbuscular mycorrhizas also act as bioprotectants against pathogens and toxic stresses [37]. However, in order to maximize their benefits, it is essential to ensure that management practices include minimum tillage, reduced use of chemical fertilizer, adopt appropriate crop rotations with minimal fallow, and rationalized pesticide use.

Ectomycorrhizas occur in certain families of woody gymnosperms (e.g., *Pinaceae*) and angiosperms (e.g., Dipterocarpaceae, Betulaceae) and are extremely important in many temperate and boreal forests. The fungal partners in ectomycorrhizal (EM) associations account for an estimated 30 percent of the microbial biomass in forest soils. These fungi are a diverse assemblage of at least 6000 species of basidiomycetes, ascomycetes, and zygomycetes. The oldest fossils providing clear evidence of EM associations date back 50 million years, yet the association is hypothesized to have evolved 130 million years ago. In ectomycorrhizas, the fungus forms a structure called the mantle (or sheath) which encloses the rootlet. From it hyphae or rhizomorphs radiate outwards into the substrate. Hyphae also penetrate inwards between the cells of the root to form a complex intercellular system, which appears as a network of hyphae in section, called the Hartig net. There is little or no intracellular penetration. In a few plants, the development of the Hartig net is slight or absent and, in these, it is particularly important for experiments to confirm that these associations behave in a typically mycorrhizal manner, as for example in *Pisonia*.

In ectendomycorrhizas, the sheath may be reduced or absent; the Hartig net is usually well developed, but the hyphae penetrate into the cells of the plant. As already mentioned, the same species of fungus may form ectomycorrhizas on one species of plant and ectendomycorrhizas on others. Arbutoid mycorrhizas possess sheath, external hyphae and usually a well-developed Hartig net. In addition, there is extensive intracellular development of hyphal coils in the plant cells. In the Orchidaceae, the plants are partially or wholly achlorophyllous for some part of their life. They form mycorrhizas with basidiomycetes of various affinities. The division between orchids that are green for part of their lives and those that are wholly achlorophyllous is mirrored by the identities of their fungal associates. Whereas the fungal symbionts of green orchids are highly effective saprophytes broadly belonging to the form-genus *Rhizoctonia*, those of achlorophyllous orchids are more likely to be able to form ectomycorrhizas on autotrophic plants. For the green orchids, there is new evidence that the adult plants have some capability to provide the fungal symbionts with recent photosynthate for part of the life of the symbiosis, thus apparently reversing the direction of C flow between the partners. The mechanisms behind such bidirectional transfer of organic C have not yet been revealed, but it appears that, contrary to previous suppositions, there is the potential for mutualism [32].

About 3% of vascular plants, mainly forest trees (*Fagaceae*, *Betulaceae*, *Pinaceae*, Eucalyptus, and some woody legumes) form ectomycorrhizas. In spite of the relatively low number of plant species forming ectomycorrhizas, these mycorrhizal associations and the tree species involved play a key role in forest ecosystems and are widely distributed. The fungi involved are mostly Basidiomycota and Ascomycota. In endomycorrhizas, no sheath is formed and the fungi colonize the root cortex both intercellularly and intracellularly.

The number of species of present-day plants forming arbuscular mycorrhizas is very large and their diversity is considerable, not only in taxonomic position but also in life form and geographical distribution. Nearly all herbaceous plants, shrubs and trees of temperate and tropical habitats can form arbuscular mycorrhizas. Whereas most fungi are generalists, associating with a wide range of plants, there is increasing evidence for specificity or selectivity of some plant species for particular fungal symbionts. This is an important area which, together with increasing appreciation of functional diversity among plant–fungus combinations, has significant implications for roles of AM fungi in plant communities. Non-mycorrhizal plants and plants which form more than one type of mycorrhiza are found in a number of families, supporting the idea that loss of AM status or gain of another type of mycorrhiza has evolved many times, probably as a result of different selection pressures and based on different mechanisms [32]. Mycorrhizas involve plant exchange of photosynthates in return for fungal exchange of mineral nutrients. The convergence of so many unrelated forms of mycorrhizas is a testament for the mutual benefits of these trading partnerships. Most mycorrhizal fungi depend heavily on plant photosynthate to meet their energy requirements; AM fungi are obligate biotrophs while EM and ericoid fungi are biotrophs with some saprotrophic abilities. The carbon cost of mycorrhizas is difficult to accurately estimate, but field and laboratory studies suggest that plants allocate 10-20 percent of net primary production to their fungal associates [7]. Several environmental factors, seasonality being one of them, may cause differences in AM colonization. Such variations may depend upon the specific structural, developmental and physiological characteristics of the plant-AM combination. AM colonization, registered as %CRL in *T. plumosus*, was higher in the Entisol and Vertisol during the dry season, but not in the Ultisol [21]. (Fig. 3).
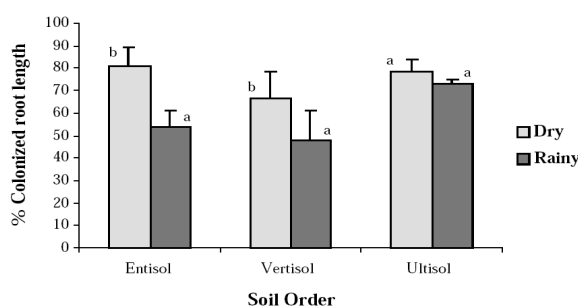

Fig. 3. Changes in AM colonization of *T. plumosus* in three acid savanna soils, adapted from López-Gutiérrez et al., 2004.

Legume responses to arbuscular mycorrhizal

It is believed that the N-fixing capability of *Rhizobium* may enhance if the host plant is also in symbiosis with AM. Under such a situation and with regard to enhancing the colonization rate, uptake of inorganic nutrients and plant growth, *Rhizobium* and AM are synergistic. The extent of plant accommodation for the intracellular settlement of endosymbionts including AM and bacteria has yet to be recognized. Accordingly, there are some differences between the bacteria and AM for the preparation of the symbiosis with their partner. For example, the

weakening strength of the root cell walls for the passage of the bacteria into the roots is not common for AM passage into the roots. Legume roots are invaded and colonized by rhizobia and also with mycorrhizal fungi [13]. As AMF evolved long before legumes, it has been assumed that all legumes have the potential to form symbiosis with AMF. Lupinus is the only known legume genus in which this ability is absent [33]. Legumes may prefer to develop symbiosis with AM species, which are more efficient to supply phosphorus.

This can be very advantageous under the conditions that nutrients are not available at high amounts. Different AM species are able to increase nodulation and N fixation differently. The structure, functioning, and nutritional demand of nodules are different with plant roots. Nodules are produced by cortical cell division, in which rhizobia with high energy and P requirements reside and fix N. The average dry matter of three varieties of common bean was significantly increased to the same extent by inoculation with four individual species of AM [15]. Small but significant difference in the other measured parameters (AM frequency, N uptake, fixed N, P uptake) were measured for the individual inoculants, but the observed trends between inoculants were inconsistent. For legumes, AM-fungi have fundamental effects on the eco-physiology, on the biota of the surrounding soil and on associated non-legumes. For example, Barea and Azcon-Aguilar [5] have demonstrated that AMF are known to be one of the most efficient ecological factors in improving growth and N content in legumes. Hamel and Smith [12] reported that mixture growth of both corn and soybean plants were greatly enhanced when inoculated with mycorrhizal fungi. Although more N appeared to be transferred from soybean to corn when plants were mycorrhizal, growth enhancement was attributed mainly to a better phosphorus uptake by mycorrhizal plants. Jackson and Mason [16] found positive relationships among P availability, VA mycorrhizal infection and pod yield in groundnut (*Arachis hypogaea* L.). Alloush [2] found that chickpea plants inoculated with mycorrhizal fungus *Glomus versiforme* had higher number of nodules, shoot phosphorus content, shoot dry weight and grain yield than un-inoculated chickpea plants.

The effect of mycorrhizas at the plant community level was studied by Requena et al. [29] in a degraded area within the Sierra de los Filabres in Almería. The existing natural vegetation was shrubland, where *Anthyllis cytisoides* L., a drought-tolerant legume able to form symbioses with both rhizobial and mycorrhizal micro-symbionts, was the dominant species. This experiment demonstrated the long term benefits of inoculation not only on plant establishment but also on P acquisition and N_2 fixation by the target legume. The benefits also included increased available P, N and organic matter, and the number of hydro-stable aggregates in the soil supporting the community. Studies using the stable isotope ^{15}N evaluated the amount of N_2 fixed by the shrub legume and showed how this improved N nutrition, via N-transfer to non-N-fixing vegetation grown in association with the inoculated legume. In addition, the mycorrhizal, nodulated Anthyllis plants behaved as a source of mycorrhizal inoculum for the surrounding area, where new seedlings flourished and accelerated the natural succession. This study showed that the introduction of target indigenous plant species, associated with a managed community of microbial symbionts, could be a successful biotechnological tool to aid the integral recovery of degraded ecosystems.

The application of AMF in soils has shown a tremendous improvement in growth and yields of diverse legumes raised. For instance, inoculation with AMF improved growth of chickpea (*Cicer arielinum* L.) and doubled P uptake at low and intermediate levels of P in a pot experiment on sterilized low-P calcareous soil [41]. Inoculation of sterile soil with the fungi significantly improved growth and nutrient uptake by *S. grandiflora*, but the response of the legume was markedly better when soil was inoculated with *G. fasciculatum* than when it was inoculated with *G. mosseae*. Nutrient uptake and growth of *S. grandiflora* in non-sterile soil was also stimulated by inoculation, but the legume did not respond differently to the two endophytes. The natural rock phosphate and AM inoculation facilitated growth parameters and shoot mineral mass of *G. sepium* and *S. sesban* after 4 months of cultivation. More than 200% of weight gains in *S. sesban* were recorded with all AMF when used with 600 or 800 mg natural rock phosphate. For *Gliricidia*, only *G. aggregatum* in the presence of high natural rock phosphate levels showed similar effects. In contrast, *G. fasciculatum* enhanced the height of *Sesbania* by two folds when grown in the presence of 400, 600, and 800 mg natural rock phosphate. Generally, the impact of composite application of AMF and natural rock phosphate on nutritional content was more obvious for *Sesbania* than for *Gliricidia* seedlings. It is interesting that certain legume tribes that cannot form nodules may be colonized by AMF.

Inoculation of both legumes with any of four AMF enhanced nodulation, dry matter yield, and plant N and P contents more than did triple superphosphate. *Gigaspora margarita* and *G. mosseae* were superior to *Gigaspora calospora* and *Acaulospora* species and resulted in more extensive root infection, especially in soyabean. The integration of N_2 fixing trees into stable agroforestry systems in the tropics is being tested because of their ability to produce higher biomass N and P yields, when symbiotically associated with rhizobia and AMF. The tripartite symbiosis between AM, bacteria and legumes is of great significance both for agriculture and for ecology, and scientists have been trying to find the most efficient combination of AM and bacteria.

Improvement of P uptake

VA-fungi are known to assist the plants to absorb mineral nutrients from the soil, particularly low available elements like phosphorus. Improvement of P uptake and plant growth by AM under conditions of low available phosphorus has been well documented. Improved P uptake and plant growth were demonstrated in Andisols following AM inoculation of onion, onion and white clover, and kidney bean. Inoculation increased both spore number and the grain weight of kidney bean at a soil-available P level of 10 mg P kg^{-1}, while these effects were suppressed when soil-available P was 25 mg P kg^{-1}. Indigenous AM fungi predominate over inoculated species in most soils. The effectiveness of using indigenous AM fungi was investigated in several cropping systems. Soils contained more AM spores following cultivation of mycorrhizal crops (e.g., sunflower, maize, soybean, potato kidney bean, adzuki bean, and wheat) than after cultivation of non-mycorrhizal crops (mustard, radish, sugar beet and buckwheat). As a result there was increased growth of succeeding crops following mycorrhizal crops. This effect on maize growth and phosphorus uptake was evident in dry soil conditions and was less pronounced with increasing soil moisture [9]. In white clover (*Trifolium repens* L.), mycorrhizal inoculation doubled the concentration of phosphorus in shoots and roots of infected plants and increased their dry weight [20]. Also Al-Karaki et al. [1] indicated that shoot dry matter, shoot phosphorus and root dry matter were higher for mycorrhizal infected wheat (*Triticum aestivum* L.) plants than for non infected plants.

Under conditions of low P availability, which occur in many soils, the AMF mediated transfer of nutrients has been reported from the host plant to another plant. Hyphae of mycorrhizas may spread from one infected plant and enter the roots of one or more other plants [14]. It has been shown that assimilates may be transported from one plant to another through AM hyphal connections. In a study, transfer of ^{14}C photosynthate from one plant to another was found primarily through AM hyphae rather than leakage from the roots of the donor plants. Similar results were obtained in a ^{32}P experiment, where hyphal linkage between plants was the dominant factor for transferring P [8]. Uptake of P and Zn were significantly and positively affected by the mycorrhizae treatments. An examination of the P concentrations in the plant material showed some variation among mycorrhizal species at each inoculation time but little consistency was present between mycorrhizal species and inoculation times due to a dilution effect of plant growth. As P uptake is an integration of P concentration for mycorrhizal inoculation achievement, P concentration is an important indication. In general, mycorrhizae inoculated plants had higher % P concentration than non-inoculated plants for both inoculation times in three experiments [27].

The AMF, however, differs in their capacity to supply plant nutrients such as P [39] suggesting mass production of the suitable strains for sustainable inoculums development. Although the technology for the production of rhizobial and free living PGPR is commercially available, the production of AM-fungi inocula and the development of inoculation techniques have limited the manipulation of AM-fungi. An appropriate management of selected AM-fungi is now available for exploiting the benefits of these microorganisms in agriculture, horticulture, and in revegetation of degraded ecosystems, and large quantities of AMF inoculums can be produced by pot culture technique. The traditional and most widely used approach has been to grow the fungus with suitable host plants in solid growth medium individually or in combination on the solid growth media [36]. However, current biotechnology practices now allow the production of efficient AM-fungal inoculants to mass propagate them for large scale production systems.

Ganry et al. [11] conducted an experiment to investigate the effect of P fertilization on AM colonization and BNF, and based on the results of a preliminary pot study, selected a field site with a low colonization potential. In the absence of P fertilizer or in the presence of insoluble rock phosphate, there were no significant differences in AM colonization between -AM and +AM treatments, but when soluble superphosphate fertilizer was applied, AM colonization of inoculated roots at 26 days was greater than for the -AM treatment. These early differences disappeared by day 40 with AM frequencies 490% in all treatments.

Mehdi et al. [25] reported that the effects of AM fungi (*G. mosseae* and *G. intraradices*), rhizobial (*R. leguminosarum* bv. viciae) strains, and P (superphosphate and phosphate rock) fertilizers considerably increased the dry biomass of shoots and seeds, P and N contents (shoots and seeds) of lentil cv. "Ziba" plants and percent of root colonized by AM fungus. The rhizobial strain possessing P-solubilizing ability showed a more beneficial effect on plant growth and nutrient uptake than the strain without this activity, although both strains had similar N$_2$-fixing efficiency. Moreover, the P-uptake efficiency was increased when P fertilizers were applied along with AM-fungi and/or P-solubilizing rhizobial strains emphasizing the remarkable importance of dual inoculation in the improvement of plant growth responses as also reported by Zarei et al. [43] for rhizobium-mycorrhizas inoculated lentil plants.

As mentioned, the most prominent effect of AMF is to improve P nutrition of the host plant in soils with low P levels due to the large surface area of their hyphae and their high affinity P uptake mechanisms. To substantiate this concept of plant growth promotion by AMF, several studies have shown that AM fungi contribute

to up to 90% of plant P demand [38]. For instance, the P depletion zone around a non-mycorrhizal roots extends to only 1-2 mm, nearly the length of a root hair whereas extra radical hyphae of AMF extends 8 cm or more beyond the root making the P in this greater volume of soil available to the host (Fig. 4).

There are reports of production of organic acids by AMF that could solubilize the insoluble mineral P, an added advantage in terms of improvement of P uptake by host plants. The rate of P fertilizer application may also affect the response of legumes to AM inoculation. For example, alfalfa dry matter, N uptake, fixed N and P uptake all increased with increasing amounts of superphosphate (0, 1.8, 3.6 g P m^{-2}), with the +AM treatment generally superior for most variables compared with the -AM treatment at each rate of P application [5]. The impact of management systems is of great practical significance to the contribution of AM to crop nutrition and growth and to the environment.
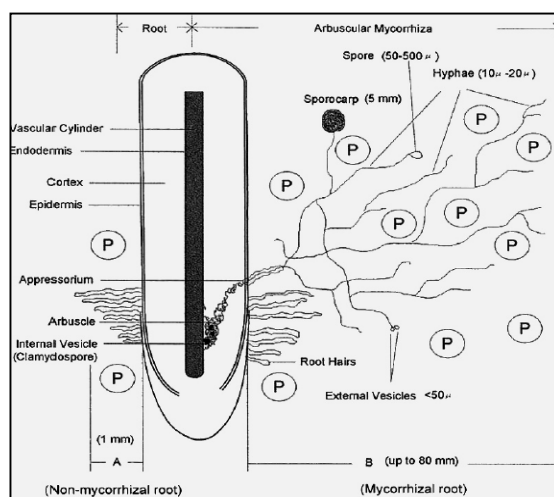

Fig. 4. Root colonized by endomycorrhizal fungus. Note the zone of P (or other nutrient) absorption by a non-mycorrhizal root (A) and by a mycorrhizal root (B) P phosphate ion, adapted from Saghir Khan et al., 2010.

As an example, the management benefit, i.e., the increase in AM contribution by omitting the annual P fertilization of 45 kg ha^{-1} for 20 years for flax was 30% of seed dry weight and 35% of seed P content and of total P uptake at harvest while the P emissions to waters were reduced till 11-19% [18]. The synergistic effects of AM and soil solubilizing P bacteria has been indicated by different researches. Under limited availability of soil P, the interaction effects between P solubilizing bacteria and AM result in the enhanced plant colonization by the host plant and the increased bacterial population in the rhizosphere. The coinoculation of AM and P solubilizing bacteria increased plant N and P uptake, relative to control plants.

Alleviation of environmental stresses

Soils rarely provide ideal conditions for growth and survival of plants and soil microorganisms. Since soil conditions are constantly changing, the soil environment may favor development of arbuscular mycorrhizas at one point in time, and inhibit them at another time. AM-fungi have an important role in promotion of biological and chemical properties of plants under stressed environment. AM help plants to adapt to and resist a wide range of biotic and abiotic stresses they encounter in the environment. Adequate soil moisture and temperature may favor development of arbuscular mycorrhizas. However, when soil moisture or temperature becomes too high or low, mycorrhizal formation may be inhibited.

AMF may alter the metal concentration in plants by metal immobilization in intra- or extra-radical hyphal cell wall components, metal chelation by fungally secreted compounds, such as glomalin, or by metal compartmentalization inside fungal cells. Thus, these AMF act as metal sinks, reducing local concentrations in soils and creating a more suitable environment for plants growing in soils with high metal contents. At themolecular level, some reports show that the expression of plant genes related to metal tolerance was altered by mycorrhizal colonization [3].

Arbuscular mycorrhizal fungi may affect host plant function and productivity under both high and low moisture conditions. In growth chamber studies, Subramanian and Charest [34], found that plant moisture deficits of -1.5 to -2.0 MPa did not affect mycorrhizal colonization or phosphorus uptake by *Triticum aestivum*, *Hippophae rhamnodies* or *Zea mays*. In greenhouse studies, drought-stressed maize infected with *Glomus mosseae* had higher

concentrations of glucose, fructose and total amino acids in leaves and roots than non-mycorrhizal plants [31]. After applying periods of drought stress of varying length and severity, arbuscular mycorrhizal colonization increased leaf area, total plant and root biomass, number of tillers, and grain yield of wheat.

The arbuscular mycorrhizal symbiosis may alleviate plant responses to moderate moisture deficit by several mechanisms including increased water uptake from the soil by hyphae, altered hormonal levels, causing changes in stomatal conductance, increased turgor by lowering leaf osmotic potential, improved nutrition of the host, and improved plant recovery after drought by maintaining the soil-root continuum [10]. AM fungi can enhance plant growth under salinity stress, especially in soils with low level of P and are able to enhance plant tolerance under salinity through altering plant physiology and increasing water and nutrient uptake. For example, mycorrhizal plants absorbed less amounts of Na^+ and Cl^- or inhibit their transfer to the shoots resulting in the increased dry weight of cotton by 68% under the salinity of 3 g/kg [35]. In *Vicia faba*, inoculated with *Glomus clarum* at the salinity of NaCl were accumulated in the roots and were not transferred to the shoots. AM fungi influenced the transfer of K^+, Ca^{2+} and H^+ pump and enhanced the transfer of Ca^{2+} in the apoplast and cell organelles.

It is well documented under pot condition that AMF colonization can affect plant behavior exposed to temperature stress [44]. At high temperatures (32.1-38.0 ∘C), pepper growth with the *Glomus intraradices* isolate and the *Glomus* isolate mixture was enhanced relative to non-AM controls [22]. However, another experiment indicated that at 8 ∘C, *G. claroideum* inoculation reduced the N concentration of *Gnaphalium norvegicum* without clear growth increments. These dissociable results seem to be difficult to explain mycorrhizal function under the conditions of temperature stress [42].

Alleviation of heavy metals stress

Heavy metal uptake and tolerance depend on both plants and soil factors including soil microbes, therefore information on interactions between plant roots and their symbionts such as AM fungi is required in order to understand heavy metal effects. Only few plants (the metallophytes) can cope with the adverse conditions on heavy metal soils. Availability and toxicity of metals to plants and mycorrhizal fungi varies, depending on the actual concentrations and oxidation states of the metals; soil and rhizosphere pH; and soil cation exchange capacity, CEC , texture, organic matter content, and redox potential. In roots, metals such as aluminum can impair cell division, increase cell wall rigidity, alter root respiration, precipitate nucleic acids, and interfere with the uptake and transport of Ca, Mg, P, and Fe. Fungal hyphae sequester metals, which may serve to reduce movement into and toxicity to, the host stress tolerance. Detoxification mechanisms enable the plant and fungus to avoid toxic effects [10]. Most reports note a positive effect of mycorrhizal inoculation on growth of plants in metal-contaminated soils. This protective benefit may be related to the adsorptive or binding capability for metals of the relatively large fungal biomass associated with host plant roots, which may physically minimize or exclude the entry of metals into host plants. Protective responses of arbuscular mycorrhizal fungi to metal toxicity among arbuscular mycorrhizal plants have been variable, but generally existent, depending on host plant and fungal isolate sources.

Several biological and physical mechanisms have been proposed to explain the generally lower metal toxicity to plants colonized by arbuscular mycorrhizal fungi. These include adsorption onto plant or fungal cell walls present on and in plant tissues or onto or into extraradical mycelium in soil [17, 24] chelation by such compounds as siderophores and metallothionens released by fungi or other rhizosphere microbes, and sequestration by plant-derived compounds like phytochelatins or phytates. Other possible metal tolerance mechanisms include dilution by increased root or shoot growth, exclusion by precipitation onto polyphosphate granules, and compartmentalization into plastids or other membrane-rich organelles [10].

Metallophytes have developed various different physiological adaptations which enable them to compete successfully with the harsh conditions in heavy metal soils. In addition, protection by AMF that colonize plant roots and considerably reduce the uptake of heavy metals into plant cells may be one of the means that allow metallophytes to thrive on heavy metal-polluted sites [28, 40]. For example, both zinc violets are strongly colonized by AMF and leaves of *Viola lutea* ssp. *calaminaria* collected from a heavy metal site were earlier found to contain low amounts of heavy metals in ranges similar to those detected in non-metallophytes. This correlation is not likely to be coincidental, since mycorrhizal colonization of the roots increases with increasing heavy metal content of the soil.

Copper and cadmium concentrations in shoots of mycorrhizal plants were higher than those of non-mycorrhizal plants under various Cu and Cd concentrations in solution, especially at low Cu concentrations (Fig. 5). Thus mycorrhizae may improve the transport of heavy metals from the roots to the shoots. As to *A. laevis*, copper concentrations in roots and shoots of host plants were higher than those of non-mycorrhizal plants in all copper treatments, and inoculation of *A. laevis* would increase heavy metal toxicity to plants [19]. Since under adverse conditions AM might be more important for plant metal resistance and under the optimized conditions of normal agricultural practice, however, AM colonization even could increase plant absorption from polluted soil, and

cleansed polluted sites by removing above ground parts. It is suggested that metal-tolerant mycorrhizal inoculants might be considered for soil reclamation, thus *G. caledonium* might be a promising mycorrhizal fungus for bioremediation of heavy metal contaminated soil.

Influence of the plant species on the structure of AM

The influence of the plant species on production of mycorrhizal propagules has been investigated. For example, Azcón- Aguilar et al. [4] studied typical shrubs from semi-arid areas of Murcia and found that *Olea europaea* var. *sylvestris* (Mill.) Lehr and *Retama sphaerocarpa* (L.) Boiss, have a higher capacity to enhance the development of AM propagules in their rhizospheres than *Pistacia lentiscus* L. or *Rhamnus lycioides* L. Further studies [30] analysed the genetic diversity of the AM fungal community that colonized the roots in a shrub land species community (*Genista cinerea* (Vill) DC. in Lam. & DC*., Lavandula latifolia* Medicus, *Thymus mastichina* L., *Rosmarinus officialis* L. and *Thymus zygis* L.). The different co-occurring plant species were colonized by AM fungal communities of different composition. These findings support the earlier contention that there is some level of specificity in mycorrhizal associations.
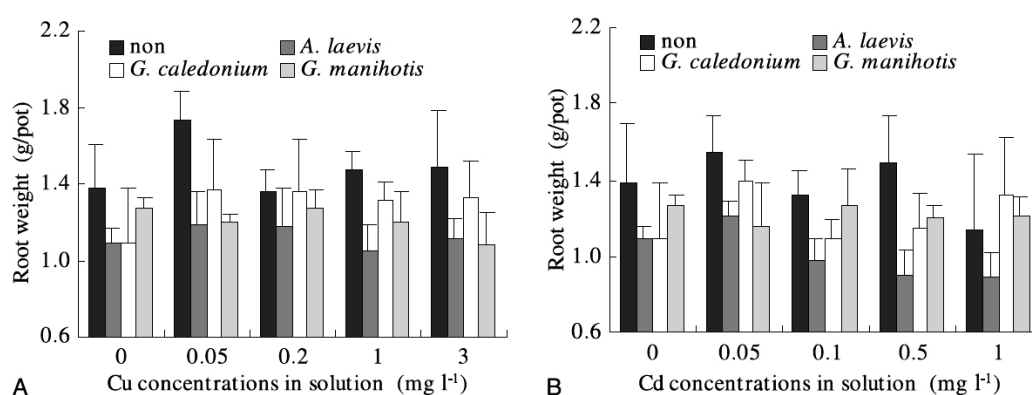

Fig. 5. Influence of Cu and Cd concentrations on root weights under inoculation and non-inoculation conditions, adapted from Liao et al., 2003.

The genetic diversity of AM fungi colonizing the root, the rhizosphere soil and the root-free soil was investigated [23]. Differences in AM fungal communities were found in soils under shrubs and in gaps among them, whereas no differences were detected among AM fungal communities colonizing roots. Soil nutrient content drove most of the spatial variations and genetic diversity in the AM fungal community. Consequently, it was suggested that different shrub species generate resource islands, which differ in nutrient content and, therefore, support different AM fungal communities, at least in their associated rhizosphere soil. Using the same genetic approach Martínez-García et al. [23] characterized the AM fungal community colonizing roots of two plant species, *Ballota hirsuta* Bentham and *Lobularia maritime* (L.) Desv., growing under shrubs and in open areas. Differences between AM fungal genetic diversity of the communities associated with the two species were found. These data represent new information on the specificity of AM fungus-plant interactions in patchy environments, and suggest a control of AM fungi on plant population and community dynamics in arid ecosystems [6].

Conclusion

Arbuscular mycorrhizas have the ability to alleviate many anthropogenic stresses, including effects of metals and polychlorinated aliphatic and phenolic pollutants. Remediation of soils contaminated with toxic pollutants using specific combinations of plants and species or strains of mycorrhizal fungi deserves increased emphasis. In several studies evidence was adduced that the benefit of AM was due to improved P acquisition by the legume, particularly during seedling development. Indeed, P uptake for each of the three varieties of common bean was highly correlated with the % root colonization by AM [15]. Positive responses to AM inoculation can occur in unfertilized soil, but are more likely to occur in soils where low available P status has been corrected by superphosphate application. The use of different extractants for available P in the studies reviewed did not permit an assessment of the relationship between available P status of soils and response to AM inoculation, but this is one area in which further research is warranted. Similarly, there is presently little or no quantitative data on the role of

AM in improving legume symbiotic performance through acquisition of other immobile nutrients or through attenuation of water stress under drought conditions.

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