



REVIEW ARTICLE

Contribution of arbuscular mycorrhizal symbiosis to plant growth under different types of soil stress

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ABSTRACT

The development of symbioses between soil fungi, arbuscular mycorrhizae (AM), and most terrestrial plants can be very beneficial to both partners and hence to the ecosystem. Among such beneficial effects, the alleviation of soil stresses by AM is of especial significance. It has been found that AM fungi can alleviate the unfavourable effects on plant growth of stresses such as heavy metals, soil compaction, salinity and drought. In this article, such mechanisms are reviewed, in the hope that this may result in more efficient use of AM under different stress conditions.

INTRODUCTION

There are several soil fungi, arbuscular mycorrhiza fungi (AMF), in the phylum *Glomeromycota*, order Glomerales, that develop, in most cases, non-specific symbioses with most terrestrial plants. In this obligate association, fungal spores perceive the presence of the host plant through biochemical communication between the two partners and, after approaching the plant roots, AM produce fungal hyphae that grow into the apoplastic space of the host root cortical cells. Highly branched tissues (arbuscules), which are the exchange interface for nutrients and carbon between AM and the host plant, and storage tissues (vesicles) are then formed. It is known that AM fungi can enhance plant growth and production under different conditions, including various soil stresses (Rillig 2004; Hildebrandt *et al.* 2007; Miransari *et al.* 2007, 2008, 2009a,b; Daei *et al.* 2009).

Soil stresses such as heavy metals, compaction, salinity and drought can decrease plant growth and hence production. AM can significantly increase plant growth and production under stress due to the formation of extensive hyphal networks and production of biochemicals like glomalin. Such abilities can result in enhanced water and nutrient uptake and improved soil structure. However, it should be mentioned that high levels of stress may turn the symbiosis between the two partners into a parasitic relationship, as unfavourable conditions may adversely influence AM performance (Rillig 2004; Hildebrandt *et al.* 2007; Miransari *et al.*

2007, 2008, 2009a,b). The adverse effects of AM on plant growth under stress conditions can be through unfavourable effects of the stress on AM functioning and development. These effects include decreased colonisation rate and spore germination, as well as decreased fungal hyphal growth (Jahromi *et al.* 2008; Evelin *et al.* 2009). Accordingly, with respect to the important roles of AM in the ecosystem, some important details regarding such mechanisms are now reviewed.

AM AND HEAVY METALS

There are only a limited number of plants (the metallophytes) that can grow under heavy metals stress, including *Minuartia verna* subsp. *hercynica*, *Arabidopsis* (*Cardaminopsis*) *halleri*, *Thlaspi caerulescens*, and the specific zinc-tolerant species *Viola calaminaria* and *V. gvestphalica* (Tonin *et al.* 2001; Siuta *et al.* 2005; Hildebrandt *et al.* 2006). In addition to the development of some special physiological processes, symbiosis with AM also enables metallophytes to grow under heavy metal stress by substantially reducing plant uptake of the heavy metals (Berreck & Haselwandter 2001). Most metallophytes belong to the families Brassicaceae and Caryophyllaceae, which are known non-mycorrhizal plants (de Mars & Boerner 1996). However, some species in these families, e.g., *Biscutella laevigata* and *Thlaspi* spp., are able to develop symbioses with AM species such as *Glomus intraradices* (Hildebrandt *et al.* 2007). It is interesting to examine how

such species develop mycorrhizal symbiosis and how this ability can be improved under conditions including heavy metal stress.

AM symbiosis with plants has been observed in soils containing heavy metals (Chaudhry *et al.* 1999; Khan *et al.* 2000). Most plants that are tolerant to heavy metal stress, intensify their symbiosis (higher root colonisation) with AM at the stage of high-nutrient demand, *e.g.*, at the reproductive stage. The AM symbiosis of *Thlaspi praecox* results in enhanced phosphate (P) uptake and decreased zinc (Zn) and cadmium (Cd) uptake compared with non-mycorrhizal treatments, indicating the great importance of even low levels of symbiosis under heavy metal stress (Hildebrandt *et al.* 2007). The alleviating potential of AM on heavy metal stress is determined by different factors: type and concentration of heavy metal, plant specification and growth conditions (Hildebrandt *et al.* 1999; Turnau & Mesjasz-Przybylowicz 2003). Molecular analyses have indicated mechanisms involved in heavy metal tolerance of AM.

Root AM colonisation of plants under heavy metal stress results in expression of specific genes responsible for production of proteins (including metallothioneins) that increase the tolerance of plants to stress (Rivera-Becerril *et al.* 2005). Metallothioneins are metal-binding proteins produced in many different organisms when exposed to high concentrations of heavy metals such as copper (Cu), Zn and Cd. There are many AM and plant genes involved in this tolerance to heavy metal stress, including metal transporter genes, which are expressed at different levels, and AM symbiosis can regulate the transcription of such genes (Lanfranco *et al.* 2002; González-Guerrero *et al.* 2005; Hildebrandt *et al.* 2007).

AM can both positively and adversely affect the uptake of heavy metals by plants. Similar to stresses such as soil compaction (Miransari *et al.* 2007, 2008, 2009a,b) and salinity (Tian *et al.* 2004; Subramanian *et al.* 2006), the alleviating effects of AM on plant growth may intensify with increasing heavy metal concentration (Hildebrandt *et al.* 1999; Audet & Charest 2006), indicating a significant interaction between AM and stress level, and, interestingly, the probable reasons for this remain to be investigated. Different species of AM, including *Glomus intraradices*, are able to enhance tolerance of plants such as tomato, corn and *Medicago truncatula* to heavy metal stress (Wulf *et al.* 2003; Hildebrandt *et al.* 2007).

Under heavy metals stress, the diversity of AM spores decreases compared with stress-free conditions. Hence, a limited number of spores are usually found in the rhizosphere of *e.g.*, Zn-tolerant plant species (Pawlowska *et al.* 1996; del Val *et al.* 1999; González-Guerrero *et al.* 2008). When approaching the inner part of the root, heavy metals are located in parenchyma cells, and for most AM structures, in hyphae, arbuscules and vesicles. While the fungal cytoplasm remains free of Zn, Cu or Cd accumulation, the cell wall and electron-dense granules contain high amounts of these elements (González-Guerrero *et al.* 2005, 2008). Heavy metals may also be stored in vesicles (Weiersbye *et al.* 1999). It has also been found that AM hyphae are able to produce insoluble glycoprotein, called glomalalin, which binds to heavy metals. Accordingly, it can be stated that AM are able to keep heavy metals out of plants or reduce concentrations in plants (Hildebrandt *et al.* 2007).

Under heavy metal stress, the unfavourable oxidative effects adversely influence plant growth. However, AM are able to enhance production of antioxidant enzymes, which can alleviate the stress of heavy metals (Avery 2001; Ruiz-Lozano 2003). The gene products can stabilise and rearrange the structure of proteins that are denatured due to the oxidative stress of heavy metals. The enhanced tolerance of AM plants is related to the simultaneous regulation of AM stress genes and plant tolerance genes (Ruiz-Lozano 2003; Hildebrandt *et al.* 2007).

Different enzymes in AM, including glutathione S-transferase, superoxide dismutase, cytochrome P450 and thioredoxin, are involved in alleviating the stress of reactive oxygen species (ROS), thus decreasing the oxidative stress of heavy metals on plants (Hildebrandt *et al.* 2007). Due to the catalysing effects of glutathione S-transferases on conjugating glutathione and hydrophilic products, oxidative stress may be alleviated (Moons 2003; Smith *et al.* 2004).

Although AM are able to enhance iron (Fe) and manganese (Mn) uptake in plants (Marschner & Dell 1994; Miransari *et al.* 2006), they are also able to alleviate the unfavourable effects of aluminium (Al), Mn and Fe (Nogueira *et al.* 2004; Davies *et al.* 2005; Cardoso & Kuyper 2006; Miransari *et al.* 2006) on plant growth, especially at high concentrations. AM are able to decrease the availability of Mn in shoots and hold Fe in roots. AM hyphae can absorb high amounts of nutrients including heavy metals from the soil and transfer them to the shoots in specific plants, resulting in decreased concentrations of heavy metals in the soil. The rate of uptake is very much dependent on AM species and plant genotype (Marschner 1995; Sudova *et al.* 2008).

The role of AM in enhancing plant tolerance to heavy metals is very important and differs between different plant and AM species, depending on the metal species in the soil. For example, according to Joner & Leyval (1997), because of uptake and immobilisation of Cd by extraradical hyphae of *Glomus mosseae*, Cd transfer to the plant decreases. Khan *et al.* (2000) observed similar results for Zn, and stated that Zn absorbed by AM hyphae is crystallised in these hyphae and cortical cells of mycorrhizal roots. The large specific surface area of AM hyphae allows the fungus to absorb high levels of nutrients, even beyond the growing zone of the plant roots. This process is called phytostabilisation, by which AM increase plant ability to immobilise heavy metals in the soil through absorbing such metals in their hyphae and consequently decreasing translocation from plant roots to shoots (Leyval *et al.* 2002). Using plants with the ability to absorb high amounts of heavy metals and in symbiosis with AM provides a favourable environment for reduction of heavy metal concentration in soils. Such ability is very important for phytoextraction of heavy metals from the soil, producing a more favourable environment for plant growth and crop production. The combination of these abilities can contribute highly to establishment of a healthy and productive soil (Pawlowska *et al.* 2000; Christie *et al.* 2004).

Plants produce organic root exudates such as malic and citric acids and/or acid phosphatase when P is deficient, resulting in enhancement of nutrient uptake (Marschner 1998; Khan *et al.* 2000). In addition, the interactive effects of plant roots and microbial populations in the rhizosphere increase root exudation of organic products and hence activ-

ity of soil microorganisms, and eventual plant nutrient uptake (Meharg 1994; Burleigh & Harrison 1997; Khan *et al.* 2000). There are many microorganisms in the soil that can enhance the solubility of different P sources (such as rock phosphate) by producing organic acids, including AM, *Aspergillus* sp., *Bacillus* sp., *Enterobacter* sp., *Pseudomonas* sp. Accordingly, in addition to enhancement of nutrient availability, addition of soil microorganisms including AM can also decrease heavy metals concentration in the soil (Khan *et al.* 2000).

The combined effects of soil bacteria and AM can enhance plant tolerance to heavy metals through promoting plant growth, *e.g.*, by production of the phytohormone, IAA, and increasing AM activity in soils containing heavy metals (Vivas *et al.* 2003). In addition, other researchers have also indicated the positive effects of co-inoculation with AM fungi and soil bacteria on removal of heavy metals from soils (Barea *et al.* 2002, 2005; Azcón *et al.* 2009).

AM AND SOIL COMPACTION

Another important role of AM is improving soil structure (Ryan & Graham 2002). Soil properties, root architecture and agricultural practices determine the stability of the soil structure. For example, unsuitable agricultural practices can adversely influence soil structure by decreasing aggregation stability and hence movement of soil particles, particularly clay particles, resulting in reduction of macropores and a partial increase of micropores. These factors are the main reason for increasing soil bulk density (Cardoso & Kuyper 2006; Miransari *et al.* 2007, 2008, 2009a,b) when soil is compacted under heavy traffic, especially at unfavourable levels of fertiliser and moisture. AM fungi affect soil structure through: (i) binding soil particles on extraradical hyphae, (ii) entanglement of microaggregates by hyphae into macroaggregates, and (iii) providing a C source for plants and microorganisms after AM degradation in the soil (Jastrow *et al.* 1998; Cardoso & Kuyper 2006). Additionally, production of the glycoprotein, glomalin, by AM hyphae, quantified by measuring soil-related proteins, can greatly contribute to enhancement of soil structure (Rillig 2004).

Glomalin affects soil stability more than AM hyphae alone, because its persistence in the soil is higher (6 to more than 40 years) than AM hyphae (from a few days to a few months) (Rillig *et al.* 2001). According to Steinberg & Rillig (2003), 40–75% of AM hyphae and glomalin can, respectively, be detected in soil 150 day after the onset of symbiosis. High amounts of glomalin are available in the soil, ranging from 12 to 60 mg·cm⁻³ in different soils, including forest soils (Rillig *et al.* 2001).

Between 3% and 5% of total soil C and N in rain forest soils (Cardoso & Kuyper 2006) and 5% and 4% of soil C and N stock, respectively, were found in the form of glomalin (Rillig *et al.* 2001). Also, AM hyphae and glomalin account for 15% of soil organic C in grassland (Cardoso & Kuyper 2006). Because glomalin is hydrophobic, it is able to coat the AM hyphae and related soil particles, resulting in enhanced AM tolerance at gas–water interfaces and reduce disruption of macro-aggregates during wetting and drying cycles in the soil (Rillig 2004). Moreover, production of glomalin in the soil increases C storage and affects aggregate stability and,

hence, soil structure (Cardoso & Kuyper 2006). Wright *et al.* (1999) found that the concentration of glomalin was positively correlated with soil structural stability after replacement of conventional tillage with a no-tillage system under corn production. Glomalin production can also affect the soil microbial population as it provides a source of C available to microorganisms (Bai *et al.* 2009).

Crop rotation can also influence glomalin production and soil structural stability (Wright & Anderson 2000). Hence, consideration of tillage practices affecting production and protection of hyphae and glomalin can be of great significance for soil structural stability and, thus, reduced soil erosion. AM have been found to increase plant growth under compaction stress through the enhancement of root growth and nutrient uptake (Miransari *et al.* 2007, 2008, 2009a,b).

AM AND SALINITY

Agricultural soils that are salty or subject to salinity limit crop production and account for more than 7% of all agricultural soils worldwide (Jain *et al.* 1989). The existence of AM in salt-laden crop soils is very common (Juniper & Abbott 1993). AM are able to biologically enhance plant growth and crop production in such salty soils (Al-Karaki *et al.* 2001; Daei *et al.* 2009). The different interactions between AM and host plants under different conditions has received much attention for selection of the most efficient isolates, especially when AM and host plants are subjected to different stresses, and also for evaluation of AM functionality and ecology (Johnson *et al.* 1997; Ruiz-Lozano & Azcón 2000). Different species of AM differ in their tolerance to stress. For example, although under stress there are fewer species, those that are more tolerant to the stress can survive and enhance plant ability to grow more efficiently (Tian *et al.* 2004; Daei *et al.* 2009).

The adverse effects of salinity on AM symbiosis are caused by inhibition of spore germination (Hirrel 1981; Juniper & Abbott 2006) and hyphal growth and development (McMillen *et al.* 1998), as well as reduced production of arbuscules (Pfeiffer & Bloss 1988). Although increased salinity reduces AM colonisation of plant roots, the dependency of plants on AM symbiosis is increased, indicating the significance of AM to alleviate salinity stress on plant growth (Tian *et al.* 2004). When subjected to salinity stress, plants absorb less P (Munns 1993), but plants can alleviate this stress using different mechanisms (Al-Karaki 2000, 2006; Al-Karaki *et al.* 2001; Tian *et al.* 2004). Resistant and non-resistant AM species utilise different mechanisms to enhance plant growth and production under salinity stress. Mechanisms of salt tolerance in non-resistant AM species include improvement of nutrient (N and P) uptake by host plants, while resistant AM species cause enhanced leaf respiration and transpiration, which increases the exchange of carbon dioxide and water through stomatal activity and eventually affects water use efficiency of host plants. AM salt-tolerant species can also alleviate salinity stress on plant growth through increasing the concentration of osmolytes, such as carbohydrates and electrolytes in plant roots (Ruiz-Lozano *et al.* 1996; Feng *et al.* 2002; Tian *et al.* 2004; Boomsma & Vyn 2008; Daei *et al.* 2009). Other related mechanisms stimulate root development and enhance nutrient uptake *via* both resistant and

non-resistant AM species, respectively (Ruiz-Lozano & Azcón 2000), as well as enhancing root hydraulic conductivity (Rosendahl & Rosendahl 1991; Giri *et al.* 2003).

Plant morphological changes when subjected to salinity include decreased root and shoot growth, although under different stresses plant allocate more C to their roots (Hause *et al.* 1996; Wang *et al.* 2001; Miransari & Smith 2007, 2008, 2009). The adverse effects of sodium (Na) on leaf chlorophyll content have been attributed to the inhibiting effects of Na on magnesium (Mg) absorption. However, since AM are able to increase Mg uptake (Marschner & Dell 1994; Giri *et al.* 2003; Giri & Mukerji 2004; Miransari *et al.* 2009a,b), which is necessary for chlorophyll formation, they can alleviate the adverse effects of Na on photosynthesis in addition to the other beneficial effects of AM on photosynthesis (see above). Adjustment of the K/Na ratio is another interesting effect of AM on plant growth under salinity conditions as a result of increased K uptake (Giri *et al.* 2003; Daei *et al.* 2009).

AM AND WATER STRESS

Under arid and semi-arid conditions, drought or water deficiency states constitute one of the most common stresses affecting plant growth and yield (Kramer & Boyer 1997; Feng *et al.* 2002). Similar to salinity stress, drought also affects plant growth through affecting osmotic potential (Ruiz-Lozano 2003). To alleviate osmotic stress, plants respond using anatomical, physiological and cellular mechanisms (Bray 1997). Mycorrhizal plants are able to grow much better under such conditions compared with non-mycorrhizal plants (Auge 2001; Subramanian *et al.* 2006). Drought tolerance of plants, including corn (Sylvia *et al.* 1993; Subramanian *et al.* 1995), soybean (Bethlenfalvay *et al.* 1988) wheat, onion, lettuce (Subramanian *et al.* 2006) and other species of agricultural interest (Auge 2001), increases in symbioses with AM.

In addition to higher nutrient uptake of mycorrhizal plants under stress, the substantial enhancement of root surface area and dense growth of roots also improve tolerance of mycorrhizal plants under stress (Auge *et al.* 1994; Subramanian *et al.* 2006). Under drought stress, AM affect water movement into the plant, influencing plant hydration and physiological processes (Auge 2001). Hence, mycorrhizal plants are able to have higher water potential (higher water use efficiency) and can enhance growth at a faster rate when irrigation is restored.

Moreover, under water stress, mycorrhizal plants can absorb forms of N that are unavailable to non-mycorrhizal plants, resulting in higher growth under stress (Subramanian *et al.* 2006). Adjustment of osmotic potential by AM is probably one of the most important reasons for the improved ability of the host plant to grow under water stress. Through the higher accumulation of organic products, *e.g.*, proline, glycine betaine, carbohydrates such as sucrose and mannitol and non-organic ions including K and Cl, mycorrhizal plants can enhance biomass production under stress relative to non-mycorrhizal plants (Azcón *et al.* 1996; Goicoechea *et al.* 1998; Ruiz-Lozano 2003; Ruiz-Lozano *et al.* 2006). It is also noteworthy that AM can influence plant growth under water stress through affecting soil structure. AM hyphae can enhance soil structure by binding soil particles and through

production of glomalin, which affect soil moisture retention (Auge 2001; Ruiz-Lozano 2003; Auge *et al.* 2004; Rillig 2004).

AM symbiosis enhances plant tolerance to drought stress through altering plant physiology and gene expression (Ruiz-Lozano *et al.* 2006; Aroca *et al.* 2008; Boomsma & Vyn 2008). In addition, production of antioxidant enzymes by mycorrhizal plants when subjected to drought stress is another important reason for the enhanced growth of the host plant under such stress (Ruiz-Lozano 2003).

CONCLUSION

This review indicates the important roles of symbiotic AM in the soil, especially when soil is subjected to some kind of stress. The effects of AM can improve the overall efficiency of an ecosystem and may also result in development of new ideas for the more productive and efficient agricultural strategies.

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