



REVIEW ARTICLE

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

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## Keywords

Arbuscular mycorrhiza; drought; ecosystem efficiency; heavy metals; salinity; soil compaction.

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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. gnestphalica* (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 glomalin, 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<sup>-3</sup> 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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## REFERENCES

- Al-Karaki G.N. (2000) Growth of mycorrhizal tomato and mineral acquisition under salt stress. *Mycorrhiza*, **10**, 51–54.
- Al-Karaki G.N. (2006) Nursery inoculation of tomato with arbuscular mycorrhizal fungi and subsequent performance under irrigation with saline water. *Scientia Horticulturae*, **109**, 1–7.
- Al-Karaki G.N., Hammad R., Rusan M. (2001) Response of two tomato cultivars differing in salt tolerance to inoculation with mycorrhizal fungi under salt stress. *Mycorrhiza*, **11**, 41–47.
- Aroca R., Vernieri P., Ruiz-Lozano J.M. (2008) Mycorrhizal and non-mycorrhizal *Lactuca sativa* plants exhibit contrasting responses to exogenous ABA during drought stress and recovery. *Journal of Experimental Botany*, **8**, 2029–2041.
- Audet P., Charest C. (2006) Effects of AM colonization on “wild tobacco” plants grown in zinc-contaminated soil. *Mycorrhiza*, **16**, 277–283.
- Auge R.M. (2001) Water relations, drought and vesicular arbuscular mycorrhizal symbiosis. *Mycorrhiza*, **11**, 3–42.
- Auge R.M., Duan X., Ebel R.C., Stodola A.J.W. (1994) Nonhydraulic signaling of soil drying in mycorrhizal maize. *Planta*, **193**, 74–82.
- Auge R.M., Sylvia D.M., Park S.J., Bittery B.R., Saxton A.M., Moore J.L., Cho K. (2004) Partitioning mycorrhizal influence on water relations of *Phaseolus vulgaris* into soil and root components. *Canadian Journal of Botany*, **82**, 503–514.
- Avery S.V. (2001) Metal toxicity in yeasts and the role of oxidative stress. *Advances in Applied Microbiology*, **49**, 111–142.
- Azcón R., Gómez M., Tobar R.M. (1996) Physiological and nutritional responses of *Lactuca sativa* to nitrogen sources and mycorrhizal fungi under drought. *Biology and Fertility of Soils*, **22**, 156–161.
- Azcón R., Medina A., Roldán A., Biró B., Vivas A. (2009) Significance of treated agrowaste residue and autochthonous inoculates (Arbuscular mycorrhizal fungi and *Bacillus cereus*) on bacterial



- community structure and phytoextraction to remediate soils contaminated with heavy metals. *Chemosphere*, **75**, 327–334.
- Bai C., He X., Tang H., Shan B., Zhao L. (2009) Spatial distribution of arbuscular mycorrhizal fungi, glomalin and soil enzymes under the canopy of *Astragalus adsurgens* Pall. in the Mu Us sandland, China. *Soil Biology and Biochemistry*, **41**, 941–947.
- Barea J., Azcón R., Azcón-Aguilar C. (2002) Mycorrhizosphere interactions to improve plant fitness and soil quality. *Antonie van Leeuwenhoek*, **81**, 343–351.
- Barea J., Pozo M., Azcón R., Azcón-Aguilar C. (2005) Microbial co-operation in the rhizosphere. *Journal of Experimental Botany*, **56**, 1761–1778.
- Berreck M., Haselwandter K. (2001) Effect of the arbuscular mycorrhizal symbiosis upon uptake of cesium and other cations by plants. *Mycorrhiza*, **10**, 275–280.
- Bethlenfalvay G.J., Brown M.S., Ames R.N., Thomas R.E. (1988) Effects of drought on host and endophyte development in mycorrhizal soybeans in relation to water use and phosphate uptake. *Physiologia Plantarum*, **72**, 565–571.
- Boomsma C., Vyn T. (2008) Maize drought tolerance: potential improvements through arbuscular mycorrhizal symbiosis? *Field Crops Research*, **108**, 14–31.
- Bray E.A. (1997) Plant responses to water deficit. *Trends in Plant Science*, **2**, 48–54.
- Burleigh S.H., Harrison M.J. (1997) A novel gene whose expression in *Medicago truncatula* is suppressed in response to colonization by vesicular-arbuscular mycorrhizal fungi and to phosphate nutrition. *Plant Molecular Biology*, **34**, 199–208.
- Cardoso I.M., Kuyper T.W. (2006) Mycorrhizas and tropical soil fertility. *Agriculture, Ecosystems and Environment*, **116**, 72–84.
- Chaudhry T.M., Hill L., Khan A.G., Kuek C. (1999) Colonization of iron- and zinc-contaminated dumped waste by microbes, plants and associated mycorrhizae. In: Wong M.H., Wong J.W.C., Baker A.J.M. (Eds), *Remediation and management of degraded land*. CRC Press LLC, Boca Raton FL; Chap. 27, pp 275–283.
- Christie P., Li X., Chen B. (2004) Arbuscular mycorrhiza can depress translocation of zinc to shoots of host plants in soils moderately polluted with zinc. *Plant and Soil*, **261**, 209–217.
- Daei G., Ardekani M., Rejali F., Teimuri S., Miransari M. (2009) Alleviation of salinity stress on wheat yield, yield components, and nutrient uptake using arbuscular mycorrhizal fungi under field conditions. *Journal of Plant Physiology*, **166**, 217–225.
- Davies F.T., Jr, Calderon C.M., Huaman Z., Gómez R. (2005) Influence of a flavonoid (formononetin) on mycorrhizal activity and potato crop productivity in the highlands of Peru. *Scientia Horticulturae*, **106**, 318–329.
- Evelin H., Kapoor R., Giri B. (2009) Arbuscular mycorrhizal fungi in alleviation of salt stress: a review. *Annals of Botany*, **104**, 1263–1280.
- Feng G., Zhang F.S., Li X.L., Tian C.Y., Tang C., Rengel Z. (2002) Improved tolerance of maize plants to salt stress by arbuscular mycorrhiza is related to higher accumulation of soluble sugars in roots. *Mycorrhiza*, **12**, 185–190.
- Giri B., Mukerji K.G. (2004) Mycorrhizal inoculant alleviates salt stress in *Sesbania aegyptiaca* and *Sesbania grandiflora* under field conditions: evidence for reduced sodium and improved magnesium uptake. *Mycorrhiza*, **14**, 307–312.
- Giri B., Kapoor R., Mukerji K.G. (2003) Influence of arbuscular mycorrhizal fungi and salinity on growth, biomass, and mineral nutrition of *Acacia auriculiformis*. *Biology and Fertility of Soils*, **38**, 170–175.
- Goicoechea N., Szalai G., Antolin M.C., Sanchez-Diaz M., Paldi E. (1998) Influence of arbuscular mycorrhizae and *Rhizobium* on free polyamines and proline levels in water-stressed alfalfa. *Journal of Plant Physiology*, **153**, 706–711.
- González-Guerrero M., Azcón-Aguilar C., Mooney M., Valderas A., MacDiarmid C.W., Eide D.J., Ferrol N. (2005) Characterization of a *Glomus intraradices* gene encoding a putative Zn transporter of the cation diffusion facilitator family. *Fungal Genetics Biology*, **42**, 130–140.
- González-Guerrero M., Melville L.H., Ferrol N., Lott J., Azcón-Aguilar C., Peterson R.L. (2008) Ultrastructural localization of heavy metals in the extraradical mycelium and spores of the arbuscular mycorrhizal fungus *Glomus intraradices*. *Canadian Journal of Microbiology*, **54**, 103–110.
- Hause B., Demus U., Teichmann C., Parthier B., Wasternack C. (1996) Developmental and tissue-specific expression of JIP-23, a jasmonate-inducible protein of barley. *Plant and Cell Physiology*, **37**, 5641–5649.
- Hildebrandt U., Kaldorf M., Bothe H. (1999) The zinc violet and its colonization by arbuscular mycorrhizal fungi. *Journal of Plant Physiology*, **154**, 709–711.
- Hildebrandt U., Hoef-Emden K., Backhausen S., Bothe H., Bozek M., Siuta A., Kuta E. (2006) The rare, endemic zinc violets of Central Europe originate from *Viola lutea* Huds. *Plant Systematics Evolution*, **257**, 205–222.
- Hildebrandt U., Regvar M., Bothe H. (2007) Arbuscular mycorrhiza and heavy metal tolerance. *Phytochemistry*, **68**, 139–146.
- Hirrel M.C. (1981) The effect of sodium and chloride salts on the germination of *Gigaspora margarita*. *Mycology*, **43**, 610–617.
- Jahromi F., Aroca R., Porcel R., Ruiz-Lozano J.M. (2008) Influence of salinity on the *in vitro* development of *Glomus intraradices* and on the *in vivo* physiological and molecular responses of mycorrhizal lettuce plants. *Microbial Ecology*, **55**, 45–53.
- Jain P.K., Paliwal K., Dixon R.K., Gjerstad D.H. (1989) Improving productivity of multipurpose trees on substandard soil. *Indian Journal of Forestry*, **87**, 38–42.
- Jastrow J.D., Miller R.M., Lussenhop J. (1998) Contributions of interacting biological mechanisms to soil aggregate stabilization in restored prairie. *Soil Biology and Biochemistry*, **30**, 905–916.
- Johnson N.C., Graham J.H., Smith F.A. (1997) Functioning of mycorrhizal associations along the mutualism–parasitism continuum. *New Phytologist*, **135**, 574–586.
- Joner E.J., Leyval C. (1997) Uptake of <sup>109</sup>Cd by roots and hyphae of a *Glomus mosseae*/Trifolium subterraneum mycorrhiza from soil amended with high and low concentration of cadmium. *New Phytologist*, **135**, 353–360.
- Juniper S., Abbott L. (1993) Vesicular–arbuscular mycorrhizas and soil salinity. *Mycorrhiza*, **4**, 45–57.
- Juniper S., Abbott L. (2006) Soil salinity delays germination and limits growth of hyphae from propagules of arbuscular mycorrhizal fungi. *Mycorrhiza*, **16**, 371–379.

- Khan A.G., Kuek C., Chaudhry T.M., Khoo C., Hayes W.J. (2000) Role of plants, mycorrhizae and phytochelators in heavy metal contaminated land remediation. *Chemosphere*, **41**, 197–207.
- Kramer P.J., Boyer J.S. (1997) *Water relations of plants and soils*. Academic Press, San Diego, USA.
- Lanfranco L., Bolchi A., Ros E.C., Ottonello S., Bonfante P. (2002) Differential expression of a metallothionein gene during the pre-symbiotic versus the symbiotic phase of an arbuscular mycorrhizal fungus. *Plant Physiology*, **130**, 58–67.
- Leyval C., Joner E.J., del Val C., Haselwandter K. (2002) Potential of arbuscular mycorrhizal fungi for bioremediation. In: Gianinazzi S., Schuepp J.M., Barea J.M., Haselwandter K. (Eds), *Mycorrhizal technology in agriculture, from genes to bioproducts*. Birkhauser Verlag, Basel, Switzerland, pp 175–186.
- de Mars B.G., Boerner R.E.J. (1996) Vesicular arbuscular mycorrhizal development in the Brassicaceae in relation to plant life span. *Flora*, **191**, 179–189.
- Marschener H. (1998) Role of root growth, arbuscular mycorrhiza and root exudates for the efficiency in nutrient acquisition. *Field Crops Research*, **56**, 203–207.
- Marschner H. (1995) *Mineral nutrition of higher plants*, 2nd edition. Academic Press, London.
- Marschner H., Dell B. (1994) Nutrient uptake in mycorrhizal symbiosis. *Plant and Soil*, **159**, 89–102.
- McMillen B.G., Juniper S., Abbott L.K. (1998) Inhibition of hyphal growth of a vesicular–arbuscular mycorrhizal fungus in soil containing sodium chloride limits the spread of infection from spores. *Soil Biology and Biochemistry*, **30**, 1639–1646.
- Meharg A.A. (1994) Integrated tolerance mechanisms – constitutive and adaptive plant responses to elevated metal concentrations in the environment. *Plant, Cell and Environment*, **17**, 989–993.
- Miransari M., Smith D.L. (2007) Overcoming the stressful effects of salinity and acidity on soybean [*Glycine max* (L.) Merr.] nodulation and yields using signal molecule genistein under field conditions. *Journal of Plant Nutrition*, **30**, 1967–1992.
- Miransari M., Smith D.L. (2008) Using signal molecule genistein to alleviate the stress of suboptimal root zone temperature on soybean–*Bradyrhizobium* symbiosis under different soil textures. *Journal of Plant Interactions*, **3**, 287–295.
- Miransari M., Smith D. (2009) Alleviating salt stress on soybean [*Glycine max* (L.) Merr.]–*Bradyrhizobium japonicum* symbiosis, using signal molecule genistein. *European Journal of Soil Biology*, **4**, 146–152.
- Miransari M., Bahrami H.A., Rejali F., Malakouti M.J. (2006) Evaluating the effects of arbuscular mycorrhizae on corn (*Zea mays* L.) yield and nutrient uptake in compacted soils. *Iranian Soil and Water Journal*, (In Persian, Abstract in English, CAB abstracts) **1**, 106–122.
- Miransari M., Bahrami H.A., Rejali F., Malakouti M.J., Torabi H. (2007) Using arbuscular mycorrhiza to reduce the stressful effects of soil compaction on corn (*Zea mays* L.) growth. *Soil Biology and Biochemistry*, **39**, 2014–2026.
- Miransari M., Bahrami H.A., Rejali F., Malakouti M.J. (2008) Using arbuscular mycorrhiza to reduce the stressful effects of soil compaction on wheat (*Triticum aestivum* L.) growth. *Soil Biology and Biochemistry*, **40**, 1197–1206.
- Miransari M., Rejali F., Bahrami H.A., Malakouti M.J. (2009a) Effects of soil compaction and arbuscular mycorrhiza on corn (*Zea mays* L.) nutrient uptake. *Soil and Tillage Research*, **103**, 282–290.
- Miransari M., Rejali F., Bahrami H.A., Malakouti M.J. (2009b) Effects of arbuscular mycorrhiza, soil sterilization, and soil compaction on wheat (*Triticum aestivum* L.) nutrient uptake. *Soil and Tillage Research*, **104**, 48–55.
- Moons A. (2003) *Osgtu3* and *osgtu4*, encoding tau class glutathione S-transferases, are heavy metal- and hypoxic stress-induced and differentially salt stress-responsive in rice roots. *FEBS Letters*, **553**, 427–432.
- Munns R. (1993) Physiological processes limiting plant growth in saline soils: some dogmas and hypotheses. *Plant, Cell and Environment*, **16**, 15–24.
- Nogueira M.A., Magelhaes G.C., Cardoso E.J.B.N. (2004) Manganese toxicity in mycorrhizal and phosphorus-fertilized soybean plants. *Journal of Plant Nutrition*, **27**, 141–156.
- Pawlowska T.E., Blaszkowski J., Ruhling A. (1996) The mycorrhizal status of plants colonizing a calamine spoil mound in southern Poland. *Mycorrhiza*, **6**, 499–505.
- Pawlowska T.E., Chaney R.L., Chin M., Charvat I. (2000) Effects of metal phytoextraction practices on the indigenous community of arbuscular mycorrhizal fungi at a metal-contaminated landfill. *Applied and Environmental Microbiology*, **66**, 2526–2530.
- Pfeiffer C.M., Bloss H.E. (1988) Growth and nutrition of guayule (*Parthenium argentatum*) in a saline soil as influenced by vesicular–arbuscular mycorrhiza and phosphorus fertilization. *New Phytologist*, **108**, 315–321.
- Rillig M.C. (2004) Arbuscular mycorrhizae and terrestrial ecosystem processes. *Ecological Letters*, **7**, 740–754.
- Rillig M.C., Wright S.F., Nichols K.A., Schmidt W.F., Torn M.S. (2001) Large contribution of arbuscular mycorrhizal fungi to soil carbon pools in tropical forest soils. *Plant and Soil*, **233**, 167–177.
- Rivera-Becerril F., van Tuinen D., Martin-Laurent F., Metwally A., Dietz K.J., Gianinazzi S., Gianinazzi-Pearson V. (2005) Molecular changes in *Pisum sativum* L. roots during arbuscular mycorrhiza buffering of cadmium stress. *Mycorrhiza*, **16**, 51–60.
- Rosendahl C.N., Rosendahl S. (1991) Influence of vesicular arbuscular mycorrhizal fungi (*Glomus* sp.) on the response of cucumber (*Cucumis sativus*) to salt stress. *Environmental and Experimental Botany*, **31**, 313–318.
- Ruiz-Lozano J.M. (2003) Arbuscular mycorrhizal symbiosis and alleviation of osmotic stress. New perspectives for molecular studies. *Mycorrhiza*, **13**, 309–317.
- Ruiz-Lozano J., Azcón R. (2000) Symbiotic efficiency and infectivity of an autochthonous arbuscular mycorrhizal *Glomus* sp. from saline soils and *Glomus deserticola* under salinity. *Mycorrhiza*, **10**, 137–143.
- Ruiz-Lozano J.M., Azcón R., Gómez M. (1996) Alleviation of salt stress by arbuscular-mycorrhizal *Glomus* species in *Lactuca sativa* plants. *Physiologia Plantarum*, **98**, 767–772.
- Ruiz-Lozano J.M., Porcel R., Aroca R. (2006) Does the enhanced tolerance of arbuscular mycorrhizal plants to water deficit involve modulation of drought-induced plant genes? *New Phytologist*, **171**, 693–698.
- Ryan M.H., Graham J.H. (2002) Is there a role for arbuscular mycorrhizal fungi in production agriculture? *Plant and Soil*, **244**, 263–271.

- Siuta A., Bożek M., Jędrzejczyk M., Rostański A., Kuta E. (2005) Is the Blue Zinc Violet (*Viola guestphalica* Nauenb.) a taxon of hybrid origin? Evidence from embryology. *Acta Biologica Cracoviensia Series Botanica*, **47**, 237–245.
- Smith A.P., deRidder B.P., Guo W.J., Seeley E.H., Regnier F.E., Goldsbrough P.B. (2004) Proteomic analysis of *Arabidopsis* glutathione S-transferases from benoxacor- and copper-treated seedlings. *Journal of Biological Chemistry*, **279**, 26098–26104.
- Steinberg P.D., Rillig M.C. (2003) Differential decomposition of arbuscular mycorrhizal fungal hypha and glomalin. *Soil Biology and Biochemistry*, **35**, 191–194.
- Subramanian K., Charest C., Dwyer L.M., Hamilton R.I. (1995) Arbuscular mycorrhizas and water relations in maize under drought stress at tasselling. *New Phytologist*, **129**, 643–650.
- Subramanian K., Santhanakrishnan P., Balasubramanian P. (2006) Responses of field grown tomato plants to arbuscular mycorrhizal fungal colonization under varying intensities of drought stress. *Scientia Horticulturae*, **107**, 245–253.
- Sudova R., Doubkova P., Vosatka M. (2008) Mycorrhizal association of *Agrostis capillaris* and *Glomus intraradices* under heavy metal stress: combination of plant clones and fungal isolates from contaminated and uncontaminated substrates. *Applied Soil Ecology*, **40**, 19–29.
- Sylvia D.M., Hammond L.C., Bennet J.M., Hass J.H., Linda S.B. (1993) Field response of maize to a VAM fungus and water management. *Agronomy Journal*, **85**, 193–198.
- Tian C.Y., Feng G., Li X.L., Zhang F.S. (2004) Different effects of arbuscular mycorrhizal fungal isolates from saline or non-saline soil on salinity tolerance of plants. *Applied Soil Ecology*, **26**, 143–148.
- Tonin C., Vandenkoornhuyse P., Joner E.J., Straczek J., Leyval L. (2001) Assessment of arbuscular mycorrhizal fungi diversity in the rhizosphere of *Viola calaminaria* and effect of these fungi on heavy metal uptake by clover. *Mycorrhiza*, **10**, 161–168.
- Turnau K., Mesjasz-Przybyłowicz J. (2003) Arbuscular mycorrhiza of *Berkheya coddii* and other Ni-hyperaccumulating members of Asteraceae from ultramafic soils in South Africa. *Mycorrhiza*, **13**, 185–190.
- del Val C., Barea J.M., Azcón-Aguilar C. (1999) Diversity of arbuscular mycorrhizal fungus populations in heavy-metal contaminated soils. *Applied and Environmental Microbiology*, **65**, 718–723.
- Vivas A., Azcón R., Biró B., Barea J.M., Ruiz-Lozano J.M. (2003) Influence of bacterial strains isolated from lead-polluted soil and their interactions with arbuscular mycorrhizae on the growth of *Trifolium pratense* L. under lead toxicity. *Canadian Journal of Microbiology*, **49**, 577–588.
- Wang B., Lüttge U., Ratajczak R. (2001) Effects of salt treatment and osmotic stress on V-ATPase and V-PPase in leaves of the halophyte *Suaeda salsa*. *Journal of Experimental Botany*, **52**, 2355–2365.
- Weiersbye I.M., Straker C.J., Przybyłowicz W.J. (1999) Micro-PIXE mapping of elemental distribution in arbuscular mycorrhizal roots of the grass, *Cynodon dactylon*, from gold and uranium mine tailings. *Nuclear Instruments, Methods of Physical Research, Section B*, **158**, 335–343.
- Wright S.F., Anderson R.L. (2000) Aggregate stability and glomalin in alternative crop rotations for the central Great Plains. *Biology and Fertility of Soils*, **31**, 249–253.
- Wright S.F., Starr J.L., Paltineanu I.C. (1999) Changes in aggregate stability and concentration of glomalin during tillage management transition. *Soil Science Society of America Journal*, **63**, 1825–1829.
- Wulf A., Manthey K., Doll J., Perlick A., Franken P., Linke B., Meyer F., Kuster H., Krajinski F. (2003) Transcriptional changes in response to arbuscular mycorrhiza development in the model plant *Medicago truncatula*. *Molecular Plant-Microbe Interactions*, **16**, 306–314.