



Role of arbuscular mycorrhizal fungi and nitrogen fixing bacteria on legume growth under various environmental stresses

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Key words: AMF, Rhizobium, Interaction, Biotic, Abiotic stress, Symbiosis.

<http://dx.doi.org/10.12692/ijb/7.4.31-46>

Article published on October 10, 2015

Abstract

Arbuscular mycorrhizal fungi and rhizobia are two important plant symbionts. Rhizobia are known for fixing nitrogen inside legume root nodules while Arbuscular mycorrhizal (AM) fungi provide plants with nutrients and other benefits. AM fungi are ubiquitous soil microorganisms and establish a symbiotic relationship with more than 80% of plant species of natural ecosystems while rhizobia association is more specific and involved almost leguminous plants. The symbiosis between legumes-Rhizobium and arbuscular mycorrhizal fungi (AMF) improves plant growth and tolerance against biotic and abiotic stress. This suggests that it is possible to use rhizobia and mycorrhizal to mitigate detrimental impacts of these stresses on terrestrial ecosystem health and agricultural productivity. This will lead to accelerate the natural process of re-vegetation in decertified semiarid ecosystem. AMF and rhizobia interactions in legumes host are complex and our understanding of their impact on plant growth is far from complete. In fact Legumes can host AMF and N₂-fixing bacteria at the same time. However the two symbioses are rarely studied together because of the obligate biotrophy of arbuscular mycorrhizal fungi. In this review, we look into the behavior of three symbiotic associations under stress conditions: drought, salt, pathogens, low minerals and polluted soils with heavy metals. Mutualistic symbioses confer host fitness benefits that can result in stress-tolerance. Based on the analyzed documents, mineral nutrient improvement seems to be the common mechanism under all environmental stresses. The trends of this thematic area will be outlined, from genetically modified microorganisms in order to improve classical screening to found efficient symbiotic micro organisms.

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Introduction

Arbuscular mycorrhizal fungi (AMF) and *Rhizobium* spp. form an intimate association with leguminous plants. AMF colonize the root cortex and rhizobia are located in root nodules. Tripartite symbiotic associations improve plant performance (growth, yield and nutrient content) under different environmental conditions. Arbuscular Mycorrhizal fungi are found in many soils around the world, and they form association with 80% of all terrestrial plant. Mycorrhiza benefits the host through mobilization of phosphorus from non labile sources (Scheublin and Van der Heijden, 2006) whereas rhizobia fixes N₂ and enrich both plants and soil with nitrogen (Hindumathi and Reddy, 2012). It is estimated that 175×10⁶ tones of nitrogen have been acquired worldwide on an annual basis in this way (FAO, 1983), such a contribution reduces the dependence on chemical fertilizers and achieve sustainable agriculture and agroforestry. In addition to the beneficial nutritional effect of the symbiosis on plants and the positive impact on hydric status, soil aggregation and mineral enrichment, AM fungi and rhizobia act as biofertilizer and can reduce the incidence and importance of root diseases through biological process (Hindumathi and Reddy, 2012; Gao *et al.*, 2012). They also, have been successfully used to remove heavy metals from soils in phytoremediation technology. Lots of plant species are completely dependent on microbial symbionts for growth and survival (Van der Heijden *et al.*, 2008) especially legumes.

Legumes are primarily known for their ability to fix nitrogen with the help of root nodule bacterium. Currently, 98 species of legumes-nodulating bacteria belonging to 13 bacterial genera and 13000 legumes species 700 genera are identified (Rajwar *et al.*, 2013). They are very important both ecologically and agriculturally because they are responsible for a substantial part of the global flux of nitrogen. They also provide protein source for human and animal nutrition. In agriculture, legumes are widely used as green manure to improve soil quality by increasing its organic matter content (Zahran, 1999). However, legume growth is reduced by several environmental

factors which cause great yield losses, especially in arid and semi arid areas where salt stress, drought, minerals deficient, pathogens and polluted soils are recurrent. Therefore, legumes grown in these areas not only need to deal with diseases but also need to face the nutrient deficiency problems (Abdel-Fattah *et al.*, 2010) and abiotic stresses. Some researches showed that synergic interaction with AMF and rhizobia help them to deal with these problems. The development of a symbiotic association is a beneficial and also costly process but plant evolved auto regulation to limit the costs of the establishment of symbiosis (Caetano-Anollés and Gresshoff, 1991).

Although, there are many studies on the interactions between AM and bacteria, the underlying mechanisms behind these associations are not yet fully understood especially for legumes in stress conditions. That's why we write this synthesis bibliography to bring more light on this thematic.

-So, this review is aimed to analyze the work done on advantage of rhizobia and AM used as inoculants under various environmental stresses. The review will also provide a clear understanding of this tripartite association and its impact on nodule formation, AM colonization, nitrogen fixation and plant growth under nutrient-poor ecosystems and environmental stress and disease. The main conclusions and future trends for research in this area will then be presented.

Advantage of synergic interaction on salt stress

Salinization of soil is a serious problem and is increasing steadily in many parts of the world, in particular in arid and semi-arid tropics. Soil salinity restricts legumes cultivation and productivity in the world. In fact, salt alters a wide array of metabolic processes, culminating in stunted growth, and reduced enzyme activities and biochemical constituents. High level of salt causes both hyperionic and hyperosmotic stresses, disrupt the structure of enzymes and other macromolecules, damage cell organelles and plasma membrane, disrupt photosynthesis and respiration (Feng *et al.*, 2002).

All these physiological disorders can lead to plant death.

Plants develop a plethora of biochemical and molecular mechanisms to cope with salt stress. Synergic interaction between Arbuscular mycorrhizal (AM) fungi and rhizobium reinforce these mechanisms and help to maintain plant growth and production under salt stress (Fig. 1). Mycorrhizal and nodule symbioses often act synergistically on infection rate, mineral nutrition and plant growth (Biró *et al.*, 2000; Patreze and Cordiro, 2004) which support both needs of nitrogen and phosphorus and increase the tolerance of legumes plants to salinity stress. Rabie *et al.* (2005) showed that the main mechanism for enhanced salinity tolerance in AM plant was the improvement of phosphorus nutrition. Rhizobia occur simultaneously and synergically by providing nitrogen to plant and the fungi (Rabie and Almadini, 2005). It was also well documented that AMF colonization and rhizobia nodulation can alleviate damage of host plants caused by soil salini-

zation through osmotic adjustment (Evelin *et al.*, 2009) (Fig. 1). In fact, the excess of salt cause osmotic stress by way of the decrease of soil water potential, thus disturbing plant water relation. An increase in intracellular inorganic solutes (K^+ , Ca^{2+} , Mg^{2+}), can maintain turgor and reduce the deleterious effects of salt stress on plants (Hajlaoui *et al.*, 2010). Rabie and Almadini (2005) showed that AM faba plants contained significant higher levels of K^+ , Mg^{2+} and Ca^{2+} ions, particularly in the presence of nitrogen-fixing bacterium. They conclude that the greater salt tolerance of AM plants may be the result of the plant inorganic nutrition improvement under salinity stress. The crucial role plays by K in turgor regulation within the guard cells during stomatal movement have been demonstrated (Marschner, 2005). Many studies have demonstrated that AM fungi improves plants protection against salt stress not only via better access to nutritional status (Zandavalli *et al.*, 2004) but also by modifying plant physiology i.e. osmotic modifications (Rao and Tak, 2002) and photosynthesis (Table 1).

Table 1. Selected examples of low mineral stress alleviation in legumes plant by rhizobia and AM inoculants.

Mechanisms	Combinated Fungus/Rhizobia	Legumes	Effects	References
Increase Phosphorus uptake	<i>VA mycorrhizal endophytes / Bradyrhizobium strains</i>	chickpea (<i>Cicer arietinum</i>)	Increase development	Ruiz-Lozano and Azcón, (1993)
Increased Nitrogen phosphorus uptake	et <i>G. mosseae and Acaulospora laevis/ Bradyrhizobium japonicum</i>	<i>Vigna radiata</i>	Increase development	Kadian <i>et al.</i> (2014)
Increased Nitrogen phosphorus uptake	et <i>Glomus intraradices Shen&Shimith/ and Mesorhizobium ciceri</i>	Chickpea	Increases yield and yield components	Erman <i>et al.</i> (2011)
K^+ , Mg^{2+} and Ca^{2+}	<i>Glomus clarum</i>	<i>Vicia faba</i>	Increase growth	Rabie and Almadini (2005)
K^+ , Mg^{2+} and Ca^{2+}	<i>Glomus mosseae</i> and <i>G. versiforme</i>	Trifoliolate Orange (<i>Poncirus trifoliata</i>)	Reduce the deleterious effects of salt stress	Zou and Wu (2011)
Osmotic adjustment	<i>Glomus mosseae</i> and <i>G. versiforme</i>	Trifoliolate Orange (<i>Poncirus trifoliata</i>)	Increase growth	Zou and Wu (2011)
Proline accumulation	<i>Bradyrhizobium Aust 13c/ intraradices/Pisolithus albus</i>	<i>Glomus Acacia maungium</i>	Increase growth	Diouf <i>et al.</i> (2005)
Increased chlorophyll, nitrogen and phosphorus contents.	<i>Glomus fasciculatum /Rhizobium</i>	<i>Cajanus cajan</i>	Increase	Bhattacharjee and Sharma (2012)
Reduction in Na uptake	<i>Bradyrhizobium CAN-11 and mosseae BAS-I</i>	<i>G. Vigna radiata</i> cv.	Increased the yield of	Singh <i>et al.</i> (2011)
Increased uptake of P, N and Mg				
High chlorophyll content				

Some researchers showed that mycorrhization increase nontoxic and osmolyte protective accumulation under saline conditions. Different type of osmolyte (proline, glycine betaine, free amino acids, sugars, polyamines, polyphenols, etc.) was highlighted with different plants. Proline is most common osmolyte in plants under stress conditions

and act as a mediator of osmotic adjustment (Ashraf and Foolad, 2007). Zou and Wu (2011) showed an increasing of proline activity in mycorrhizal plants as compared to nonmycorrhizal plants of Trifoliolate Orange (*Poncirus trifoliata*) significantly by raising salinity. Similarly, Garg and Manchanda (2009), reported that the quantum of an increase in synthesis

and accumulation of proline was higher in mycorrhizal than in non-mycorrhizal *Cajanus cajan* plants subjected to salt stress. The potential role of mycorrhiza in alleviating salt stress to their host plant can be done by reducing salt (especially Na^+) uptake into the host plant. Singh *et al.* (2011) suggested that the beneficial effects of dual inoculation (*Bradyrhizobium* and *Glomus mosseae*) on the growth of *Vigna radiata* L. might be due to reduction in Na^+ . In fact, the enzymes that require K^+ as a cofactor are particularly sensitive to high concentrations of Na^+ or high ratios of Na^+ / K^+ . In contrast to positive effects, some studies, although small, show depressive effects of symbiosis on the growth and yield. For example, some publications showed that high soil salinity limit legume productivity by adversely affecting symbiosis establishment with AM Fungi and Rhizobia and/or efficiency (Manga 2007 Ph.D. thesis, unpublished; Soumare *et al.*, 2007; Kadian *et al.*, 2014). Salinity affect negatively spores germination of AM fungi and rhizobia-plant symbiosis in several processes: growth and survival, root colonization, infection and nodule development and functioning (Juniper and Abbott, 1993).

The reasons that can be used to explain the varied and sometimes contradictory results are the different yield species and strains of Arbuscular Mycorrhizal and rhizobia in saline conditions.

It is therefore of great importance to combine selected plants with specific AM fungal isolates adapted to high concentrations of salt in future research programs.

Advantage of synergic interaction on drought stress

Legumes responses to water and salt stress are considered mostly identical (Munns, 2002). Drought and salinity share a physiological water deficit. However salinity is more destructive because of phytotoxicity of ions such as Na^+ and Cl^- . In a drying soil, the soil water potential decreases and so does the soil hydraulic conductivity. Thus it is more difficult for plants to extract water and, as a consequence, the

plant water potential tends to decrease. This decrease diffusion, uptake by root and transport of nutrients from roots to shoots and may directly affect the physical aspects of some physiological processes (Sardans *et al.*, 2008). Shortage of assimilates at the roots decrease root growth and these roots may be less able to utilize all the soil's reserves of water. In general, legume plants are highly dependent on mycorrhiza to achieve their maximum growth. AM fungi helps in water regulation of plants by extending their hyphae towards the available moisture zone for continuous water absorption and translocating them to plants (Fig. 2) In fact, AM fungi hyphae can transport water by itself from soil reservoirs not accessible to plant roots (Ruiz-Lozano and Azcon, 1995). AMF may also increase drought resistance of plants by lowering leaf osmotic potential for greater turgor maintenance, by regulating stomatal conductance (Augé *et al.*, 1986) or photosynthesis. Few years after, Augé and Duan (1991) found that mycorrhizal symbiosis can alter non hydraulic root-to-shoot signaling in drying soil. AM plants are not only able to take up more water under drought conditions (Marulanda *et al.*, 2003), but also to use water more efficiently. Moreover, additive and sometimes synergistic effects on legume performance are frequently seen when both rhizobia and AMF are present (Goss and de Varennes, 2002). Previous study of Ruiz-Lozano and Azcón (1993) on chickpea (*Cicer arietinum*) plants showed that the symbiotic efficiency was dependent on the particular combination of the *Rhizobium* strain and *Glomus* species. AM symbiosis protect roots nodules in legume plant against premature nodule senescence induced by drought stress. According to Porcel and Ruiz-Lozano *al.* (2004), this could be cause by a higher activity of the of the antioxidant enzyme of glutathione reductase in nodules of AM colonized roots. In recent work, Fan and Liu (2011) provided the molecular mechanisms involved in AM inoculated plants "trifoliate orange" response to DS through regulatory and functional sets of genes. According their works *G. mosseae* inoculation under drought stress significantly increased the mRNA abundance of four genes encoding different antioxidant enzymes

like, oxi-doreductase, lactoylglutathione lyase, and flavonoid biosynthase (Fig 2).

Advantage of synergic interaction on plant disease

Plant pathogens are responsible for tremendous annual crop and revenue losses throughout the world. Biocontrol approach should be a better alternative to solve these problems. It is therefore important to understand how symbiotic microorganisms reduce infection and proliferation of phytopathogens. Since soil borne pathogens, as well as symbionts share common habitat and show differential influence on the growth of the host plant, major interest has been focused on the relevance of AMF and rhizobia in the control of soil borne pathogens (Dar *et al.*, 1997;

Singh *et al.*, 2010). Aysan and Demir (2009) showed that the suitable combination of AM and Rhizobia may increase the plant growth and resistance to pathogens. Previous research of Dar *et al.* (1997) on the interaction between AMF *Glomus mosseae* (Gm), root nodulating symbiont *Rhizobium leguminosarum*, and root rot pathogen *Fusarium solani* on the common bean (*Phaseolus vulgaris*) indicate that Gm has a vital role in inhibiting the root pathogen from invasion, more so in the presence of *R. leguminosarum*.

The mechanisms are varied and depend on environmental situation, the host plant and symbiont in presence (Table 2).

Table 2. Selected examples to pathogenic attacks alleviation in legumes plant by dual symbioses AMF and Rhizobia Dual symbioses AMF and Rhizobia effects on legume host subject to pathogenic attacks.

Mechanisms	Pathogens	Fungus/Rhizobia species	Legumes	Effects	References
Accumulation of phytoalexins	<i>Furasium</i> , <i>Oxysporum</i>	<i>G. fasciculatum</i>	Faba bean (<i>Vigna unguiculata</i>)	Increase the plant growth and resistance	Sundaresan <i>et al.</i> (1993)
Inhibiting the root pathogen	<i>Fusarium solani</i>	<i>Glomus mosseae</i> / <i>Rhizobium leguminosarum</i>	Common bean (<i>Phaseolus vulgaris</i>)	Increase the plant growth and resistance	Dar <i>et al.</i> (1997);
*-Growth and reproduction, inhibition	<i>Cylindrocladium parasiticum</i>	<i>Glomus mosseae</i> / <i>Bradyrhizobium sp.</i>	Peanut and soybean	Decreased severity and incidence at low P	Gao <i>et al.</i> (2012)
*Activation of plant defense system					
Competition for nutrients and space	<i>Cylindrocladium parasiticum</i>	<i>Glomus mosseae</i> / <i>Bradyrhizobium sp.</i>	Common bean (<i>Phaseolus vulgaris</i>)	Increase the plant growth and resistance	Gao <i>et al.</i> (2012)

Since parasites reduce the mass of the root system and its ability to absorb nutrients, endomycorrhizal colonization allows the remaining roots to be more effective and to partially offset the reduction in biomass caused by the parasite. According Gao *et al.* (2012), rhizobia and AMF might compete for the colonizing sites of plant roots with pathogens, and thus protect plants out of pathogen infection as the roles of most biocontrol. Another well accepted mechanism of biocontrol agents was proposed by Compant *et al.* (2005). Based on these results, it was postulated that rhizobium and AMF produce toxic metabolites which prevent growth and proliferation of phytopathogens. For example, exudates of rhizobitoxine have been well documented as the main mechanisms underlying the inhibition of soil-borne pathogens by rhizobium and AMF. Gao *et al.* (2012),

suggest that the mechanisms of resistance to pathogens are through an increase of phenolic acids in root exudates. They found that phenolic acids (ferulic acid, cinnamic acid and salicylic acid) in the root exudates were coincidentally enhanced by rhizobia and/or AMF inoculation.

Selvaraj and chellappan (2006) showed that an increase of phenols in roots of *Arachis hypogea* colonized by *G. fasciculatum*. This increase level of orthodihydric phenol was also correlated with resistance to pathogen. The increase in phenols in AM inoculated plants could be attributed to triggering of pathways of aromatic biosynthesis. According Benhamou *et al.* (1994) the deposited phenols may act as a barrier to pathogen. Other natural defenses as phytoalexins compounds are involved in reducing the

incidence of disease. Sundaresan *et al.* (1993) showed that *G. fasciculatum* reduced the severity of disease caused by *Furasium oxysporum* on Faba bean (*Vigna unguiculata*) through the accumulation of phytoalexins. Mycorrhiza may act indirectly on pathogens. In fact, it is well established that mycorrhizae induce significant physiological changes in their host plant, one of which is to alter the

quantity and quality of root exudates (Graham, 1981). So, by creating a new environment in the mycosphere, AM fungi might contribute to the proliferation of specific microorganisms, some of them interacting with pathogens through a range of mechanisms such as antibiosis, competition for resources and parasitism (Filion *et al.*, 1999).

Table 3. Selected examples of heavy metal stress alleviation in legumes plant by dual symbioses AMF and Rhizobia.

Mechanisms	Pollutant	Fungus/Rhizobia	Legumes	Effect	References
Better nutrient acquisition enhanced the photosynthetic capacity	Mn and Cr	<i>Glomus mosseae</i> , <i>Gigaspora</i> sp. and <i>Acaulospora</i> sp. <i>leguminosarum</i> <i>bv. viceae</i> ,	<i>Vicia faba</i> / <i>R.</i>	Increase the plant growth and resistance	Ismail 2014
N, P uptake/ metals uptake.	by affecting Nickel availability and uptake.	<i>R. leguminosarum trifoli/Glomus mosseae</i>	<i>bv Trifolium Repens</i>	Increase the plant growth and resistance	Vivas <i>et al.</i> (2006)
Exclusion strategy	Zn (0–1,000 mg/kg dry soil) and Cd	species not specified	cowpea (<i>Vigna sinensis</i>)	Increase dry weight, root: shoot ratio, leaf number and area, plant length, leaf pigments, total carbohydrates, N and P content	Al-Garni (2006)
Exclusion strategy	Pb	<i>Bradyrhizobium/ macrocarpum Tul/</i>	<i>Glomus</i> Soybean	Number of pod, Nodule dry weights of mycorrhizal roots decrease	Andrade <i>et al.</i> (2004)

Linderman (1992) showed that, in general, when AM are formed, there is an increase in the number and proportion of bacteria from the mycorrhizosphere soil that can inhibit specific pathogens *in vitro*, compared to those from rhizosphere soil from non-mycorrhizal plants.

Furthermore, it has been well documented that inoculation with rhizobia and/or AMF had potential impacts to the disease occurrence and development (Aysan and Demir, 2009), which probably due to the increase of plant growth and nutrient status after roots colonized by rhizobia and AMF (Siddiqui and Singh, 2004). Barea and Azcon-Aguilar (1983) suggested that an increase in P status of the host as a result of AMF association can increase host immunity to infections which can limit pathogen infection. In contrast in these studies, few works from Gao *et al.*

(2012), found that mycorrhization and nodulation of roots were significantly inhibited by *C. parasiticum* infection in a field experiment. This was explaining as results of competition between by indigenous rhizobia, AMF and pathogen (Table 2).

Advantage of synergic interaction on Low mineral area

It is widely recognized that nitrogen and phosphorus constitute the most limited nutrient factors for vegetative growth. This deficiency of macro and micronutrients has become major constraint to productivity, stability and sustainability of soils (Bell and Dell, 2008). That why these major nutrients required for plant growth are supplied by fertilizers or manures. However, an improper use of chemical fertilizer / pesticides leads to disastrous consequences of environmental quality. Biofertilizers are the

alternative sources to meet the nutrient requirement of plant under poor soil. Bhattacharjee and Sharma (2012), found that the increase in pigeon pea (*Cajanus cajan L.*) productivity after co-inoculation with *G. fasciculatum* and *Rhizobium* was associated with increased N, P and chlorophyll content. This indicates that AMF + Rhizobia treatments enhance nutrients uptake (Fig 2). The mechanisms of stress tolerance may involve promotion of root extension, improved mineral nutrition and water uptake (Ruiz-Lozano *et al.*, 1995) (Fig. 2). According to Cardoso and Kuyper (2006); Medina *et al.* (2007), mycorrhizal colonization improves P acquisition by plants because the extraradical mycelium grows beyond the nutrient depletion zone of the root system. In the same way, Xavier and Germida (2002) showed that *Glomus clarum* and *Rhizobium leguminosarum* increased lentil (*Lens culinaris L.*) productivity (shoot + seeds)

in soil with low N and P available by increasing N and P uptake. However the symbiotic efficiency is dependent on the particular combination of the AM species, rhizobia strain, the host cultivar (Xavier and Germida, 2002) and the limiting mineral (Pelaez *et al.*, 2010). For example, Saxena *et al.* (1997) reported that the nodulation and growth of *Vigna radiata* inoculated with a *Bradyrhizobium sp.* varied significantly depending upon the co-inoculated AMF species. Inoculation of *R. leguminosarum bv phaseoli* strain in combination with arbuscular mycorrhizal fungi *Scutellospora heterogama* and *Entrophospora colombiana* decreased growth, nodulation and chlorophyll concentrations in black bean grown low manganese (Mn) contents (Pelaez *et al.*, 2010). It mean that the tripartite symbiosis is not a random occurrence, but on that is regulate by legume host as already suggested by Bradbury *et al.* (1991).

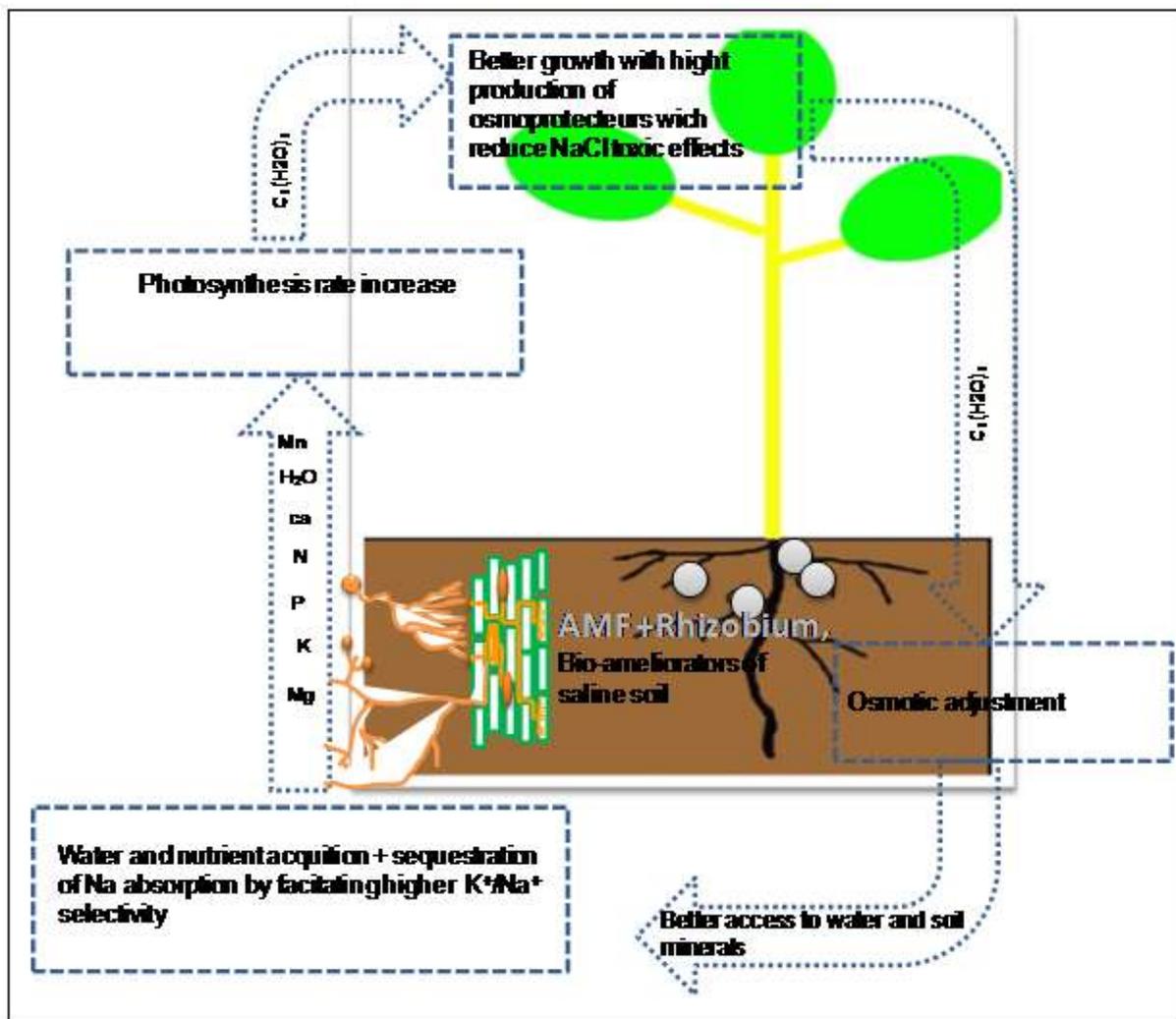


Fig. 1. Summary of protection mechanism against salinity by the tripartite symbiosis.

Advantage of synergic interaction on polluted soils (heavy metals)

Water and soil pollution are a very important environmental problem and have been drawing considerable public attention because metals are very toxic and remain persistent in soils. The quantity and diversity of toxic and hazardous wastes have been increased with the increase in quick industrial development and urbanization (Ismail, 2014). The most common heavy metal contaminants are cadmium (Cd), copper (Cu), mercury (Hg), lead (Pb), zinc (Zn), and nickel (Ni). Heavy metals ions taken up by plants from contaminated soil and water operate as stress factors causing physiological constraints leading to impaired metabolism and reduced growth (Bingham *et al.*, 1986). Heavy metals absorbed by roots and translocated to shoot have also negative

impact on human health as they can enter the food chain via agricultural products or contaminated drinking water. In roots, metals can impair cell division, increase cell wall rigidity, alter root respiration, and precipitate nucleic acids. They also disturb the balance between oxidants and antioxidants in the cell (Khan *et al.*, 2010). In fact, high concentration of heavy metals (HM) inactivates enzymic antioxidant defense system in plants resulting into increased Reactive oxygen species (ROS) signaling generally leading to death of plants (Khan *et al.*, 2010). Unfortunately, metals cannot be biodegraded. However microorganisms can interact with these contaminants and transform them from one chemical form to another by changing their oxidation state (Tabak *et al.*, 2005).

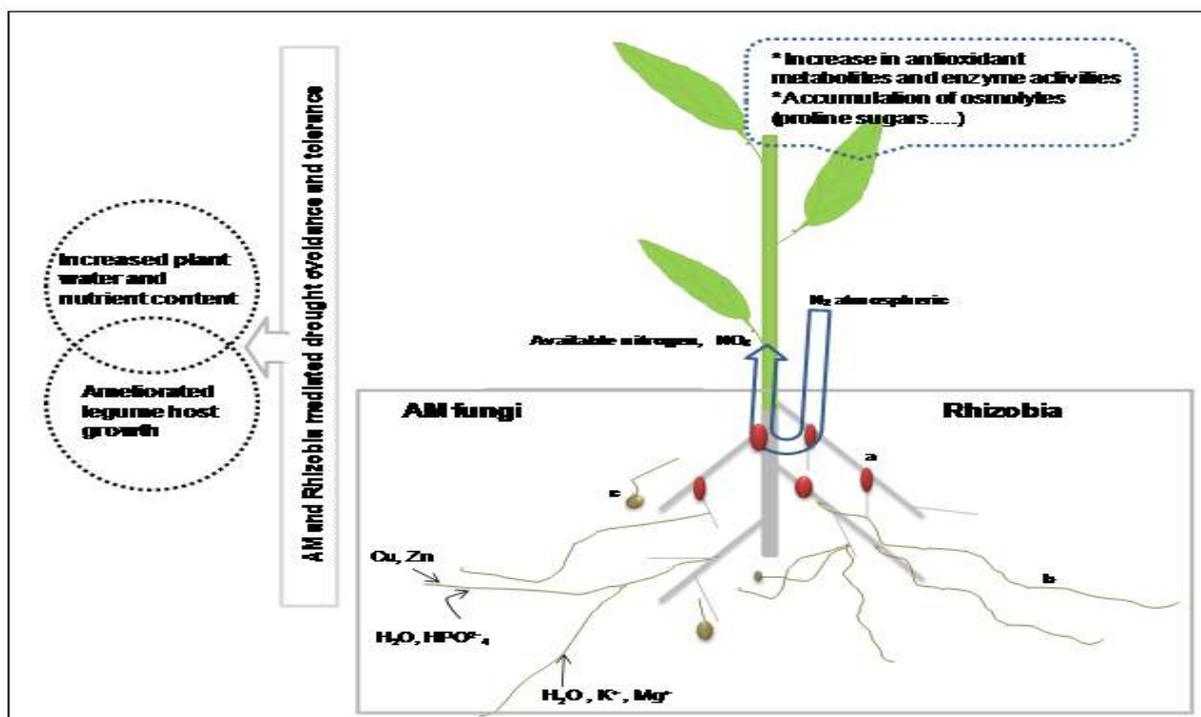


Fig. 2. Simplified model for improved plant nutrient use efficiency with AMF and Rhizobia inoculants under drought or salt stress (adapted from Rapparini and Peñuelas 2014). a) nodule, b) hyphae, c) spore.

Microbial inoculation using strains adapted to high heavy metals concentrations can restore the plant biomass value. AM fungi and rhizobia symbioses interactions to improve legume development in soils subjected to heavy metal stress has been reported by several works as an important component of phytoremediation technology (Jing *et al.*, 2007). For

instance, Biró *et al.* (2000) showed a synergistic effect and significantly increased plant tolerance to heavy metals when inoculated with dual symbiosis AM-fungi and N₂-fixing rhizobia. According Burd *et al.* (2000), AM inoculums and/or bacteria confer tolerance to Ni by modifying specific plant physiological processes and/or by affecting metals

availability and uptake. In fact, changes in root exudates, pH and physico-chemical properties of the soil (Grichko *et al.*, 2000) may be involved and such changes could reduce metal root uptake or translocation from root to shoot tissue. Most of the reports on this topic concluded that AM colonized plants translocate less HMs to their shoots than the corresponding nonmycorrhizal plants, as shown for herbaceous (Redon *et al.*, 2009) or tree (Lin *et al.*, 2007) legumes. Fungal hyphae sequester metals, which may serve to reduce movement into and toxicity to the host stress tolerance. Al-Garni (2006) provided a mechanistic explanation for the observation that AM fungal and rhizobia can promote cowpea (*Vigna sinensis*) under soil polluted with Zn and Cd. They showed that these metals were accumulated in roots suggesting that an exclusion strategy for metal tolerance exists in such organisms. Yet in other study (Joner and Leyval, 1997) demonstrated that AM fungi and rhizobia can also act as a filtration barrier against transfer of heavy metals to plant shoots. According to Rivera- Becerril *et al.*, (2002), AM can provide mycorrhizal buffer to stress imposed by Cd (Rivera- Becerril *et al.*, 2002) or Cd tolerance by changing its polyamine metabolism, thus, stabilizing Cd in the root system of colonized plants. However, effect of heavy metals depends upon duration of exposure, dose and type of metal used (Giller *et al.*, 1989). Prolonged exposure to heavy metals may lead to a reduced growth rate or to the loss of several beneficial properties, such as the nitrogen-fixing ability in the case of rhizobia. A delay in the mycorrhizal colonization in plants growing in contaminated soils was also reported by Koomen *et al.* (1990). In recent work, Ismaiel *et al.* (2014) showed that the co-inoculation with R+AMF in faba bean plants had a negative effect on nodulation number compared to the single inoculation with R only which showed the highest number of nodules in faba bean (*Vicia faba*) plants irrigated with heavy metal polluted water. Table 3 summarizes published works on effect of fungi and rhizobia symbiosis on legume growth under heavy metal stress. Overall, tripartite symbiosis offers some protection against metal toxicity. However, the diversity of AMF and

rhizobia in metal soil polluted must be examined to identify the suitable species that are effective in remediation processes.

Mechanisms of Mutualistic Benefits

Arbuscular mycorrhizal fungi (AMF) usually enhance nodulation and nitrogen fixation in legumes. Several authors have shown that the increase in the availability of phosphorus essential for the establishment of nodulation and efficiency of nitrogen fixation (Abd-Alla *et al.*, 2014; Tajini *et al.*, 2012; Sakamoto *et al.*, 2013). It has been demonstrated for increased N₂ fixation in mycorrhizal plants that when both nitrogen and phosphorus are limiting, AM fungi can improve phosphorus uptake by the plant which in turn would result in more energy available for nitrogen fixation by rhizobia (Mortimer *et al.*, 2008). For Smith (2002), plant-rhizobium system benefits from the presence of AM fungi because the mycorrhizae ameliorate not only P deficiency but also any other nutrient deficiencies that might be limiting to rhizobium. For example, AM fungi increase Ca²⁺ uptake which in turn increases nod-gene induction and expression, and concurrently affects the attachment of rhizobia to root hairs and nodule development (Smith *et al.*, 1992).

Increase mineral nutrient levels in the plants would also lead to increased photosynthesis, making a greater proportion of photosynthates available to the rhizobium nodules (Mortimer *et al.*, 2008). Previous studies of Ruiz-lozano *et al.*, (2001) showed that under drought condition, AM fungi protect soybean plants against the detrimental effects of drought and helped them cope with the premature nodule senescence induced by drought stress. According Muller *et al.* (2001); Ocón *et al.*, (2007), AM fungi synthesizes trehalose in the extraradical mycelium, which serves as the main storage carbohydrate and also as an abiotic-stress protectant in plants colonized by AM fungi and nitrogen fixing micro-organisms.

All these relationships are indirect, but according Bayne and Bethlenfalvay (1987) arbuscular mycorrhizas may directly and preferentially stimulate

nodule function. For example, higher leghaemoglobin content and nitrogenase activity was observed in mycorrhizal plants (Manchanda and Garg, 2011).

It is well established that mycorrhizal colonization generally has a positive effect on nodulation but much less is known about the impact of rhizobial colonization on AMF activity. Using *G.mosseae*, as a representative AM fungus, Barea *et al.* (1996) and Tobar *et al.* (1996) demonstrated that genetically modified *Rhizobium meliloti* increased AM colonization and nutrient acquisition by *Medicago sativa* compared to the wild type. Early studies of Mosse (1962) reported inoculation with different bacteria increased branching and led to better AMF colonization of the root. Moreover, negative effect of nodulation on AMF colonization was reported by several authors. Thus, Sakamoto *et al.* (2013), found that an established nodulation in the roots of alfalfa and soybean respectively suppressed AM fungal colonization, suggesting that rhizobial nodulation systemically suppresses AM fungal colonization. Therefore, symbiotic efficiency of the association was dependent on the particular combination of AMF and *Rhizobium* strain indicating that not all AMF interact equally well with all rhizobia. Incompatibility between AMF and rhizobia in the tripartite association can be manifested as yield depressions (Bethlenfalvay *et al.*, 1985). These yield depressions may be the result of competition between the host and the endophytes for nutrients such as P, or competition between the endophytes for carbohydrates (Bethlenfalvay *et al.*, 1985). According to Stamford *et al.* (1997), the inability of the endophytes to supply adequate levels of N or P to the host could lead to poor plant growth and yield.

Conclusion and future trends

This review has focused on recent research concerning interaction between AM fungi, rhizobia and legumes under different abiotic stresses. A large number of differing types of interaction operating through a variety of modes have been identified. However, mineral nutrient improvement appears to be the common mechanism under all environmental

stresses. The review reported shows also, that it is not possible to generalize on microbial interactions, because each microbial partner needs a specific study. The diversity of AMF and rhizobia in each stress must be examined to identify the suitable species that are effective in remediation processes (in helping plant deal with stress). Therefore, besides the classical screening in order to found efficient symbiotic couple, scientists would be also in the process of engineering plants genetically using different genes. New biotechnological approaches with genetically modified microorganisms which enhance the availability and success of microorganisms as inoculants in agriculture would be extremely helpful in this way. With the scarcity of fresh water in the world (about 97% of earth water is seawater) and salinization, efficient symbiotic microorganism may help to reclaim salinized areas, but also because it would allow us to use brackish water for irrigation in agriculture. Keeping this in view, the development of microbial inoculum for an improved remediation of disturbed soils should focus on potential of symbiotic microorganisms and plant species

References

- Abdel-Fattah GM, El-Dohlob SM, El-Haddad SA, Hafez EE, Rashad YM.** 2010. An ecological view of arbuscular mycorrhizal status in some Egyptian plants. *J Environ Sci.* **37**, 123–136.
- Al-Garni SMS.** 2006. Increased heavy metal tolerance of cowpea plants by dual inoculation of an arbuscular mycorrhizal fungi and nitrogen-fixer *Rhizobium* bacterium. *Afr J Biotech.* **5(2)**, 133-142.
- Andrade SAL, Abreu CA, de Abreu MF, Silveira APD.** 2004. Influence of lead additions on arbuscular mycorrhiza and *Rhizobium* symbioses under soybean plants. *Appl Soil Ecol* **26**, 123–131. <http://dx.doi.org/10.1016/j.apsoil.2003.11.002>
- Arfaoui A, Sifi B, El Hassni M, El Hadrami I, Boudabous A.** 2005. Biochemical analysis of chickpea protection against *Fusarium* wilt afforded by two *Rhizobium* isolates. *Plant Pathol J* **4**, 35–42.

- Ashraf M, Foolad MR.** 2007. Roles of glycine betaine and Proline in improving plant abiotic stress resistance. *Envir and Exp Bot* **59(2)**, 206-216. <http://dx.doi.org/10.1016/j.envexpbot.2005.12.006>
- Augé RM, Duan X.** 1991. Mycorrhizal fungi and nonhydraulic root signals of soil drying. *Plant Physiol* **97**, 821-824.
- Augé RM, Schekel KA, Wample RL.** 1986. Osmotic adjustment in leaves of VA mycorrhizal nonmycorrhizal rose plants in re-sponse to drought stress. *Plant Physiol* **82**, 765-770. <http://dx.doi.org/10.1104/pp.82.3.765>
- Aysa E, Demir S.** 2009. Using arbuscular mycorrhizal fungi and *Rhizobium leguminosarum* biovar phaseoli against *Sclerotinia sclerotiorum* (Lib.) de bary in the common bean (*Phaseolus vulgaris* L.). *Plant Pathol J* **8**, 74-78.
- Azcón-Aguilar C, Barea JM.** 1996. Arbuscular mycorrhizas and biological control of soil-borne plant pathogens. An overview of the mechanisms involved. *Mycorrhiza* **6**, 457-464. <http://dx.doi.org/10.1007/s005720050147>
- Barea JM, AzcoÂn-Aguilar C.** 1983. Mycorrhizas and their significance in nodulating nitrogen-fixing plants. *Adv Agron* **36**, 1-54.
- Barea JM, Tobar RM, Azcon-Aguilar C.** 1996. Effects of a genetically modified *Rhizobium meliloti* inoculant on the development of arbuscular mycorrhizas, root morphology, nutrient uptake and biomass accumulation in *Medicago sativa*. *New Phytologist* **134**, 361-369. <http://dx.doi.org/10.1111/j.1469-8137.1996.tb04641.x>
- Bayne HG, Bethlenfalvay GJ.** 1987. The Glycine-Glomus-Rhizobium symbiosis. IV. Interaction between the mycorrhizal and nitrogen-fixing endophytes. *Plant Cell Environ.* **10**, 607-612.
- Bell RW, Dell B.** 2008. Micronutrients for Sustainable Food, Feed, Fibre and Bioenergy Production. First edition, IFA, Paris, France (www.fertilizer.org)
- Benhamou N, Fortin JA, Hamel C, St-Arnaud M, Shatilla A.** 1994. Resistance responses of mycorrhizal Ri T-DNA-transformed carrot roots to infection by *Fusarium oxysporum* f. sp. *chrysanthemi* *Phytopathology* **84**, 958-968.
- Bethlenfalvay GJ, Brown MS, Stafford AE.** 1985. Glycine-Glomus Rhizobium symbiosis. II. antagonistic effects between mycorrhizal colonization and nodulation. *Plant Physiol* **79**, 1054-1058. <http://dx.doi.org/10.1104/pp.79.4.1054>
- Bhattacharjee S, Sharma GD.** 2012. Effect of Dual Inoculation of Arbuscular Mycorrhiza and *Rhizobium* on the Chlorophyll, Nitrogen and Phosphorus Contents of Pigeon Pea (*Cajanus cajan* L.). *Advances in Microbiology* **2**, 561-564. <http://dx.doi.org/10.4236/aim.2012.24072>
- Bingham FT, Pereyca FJ, Jarrell WM.** 1986. Metal toxicity to agricultural crops. *Met Ions Biol Syst* **20**, 119-156.
- Biró B, Köves-Péchy K, Vörös I, Takács T, Eggenberger P, Strasser RJ.** 2000. Interrelations between *Azospirillum* and *Rhizobium* nitrogen-fixers and arbuscular mycorrhizal fungi in the rhizosphere of alfalfa in sterile, AMF-free or normal soil conditions. *Appl. Soil Ecol.* **15**, 159-168. [http://dx.doi.org/10.1016/S0929-1393\(00\)00092-5](http://dx.doi.org/10.1016/S0929-1393(00)00092-5)
- Bradbury SM, Peterson RL, Bowley SR.** 1991. Interactions between three alfalfa nodulation genotypes and two Glomus species. *New p* **119**, 115-120.
- Burd IG, Dixon DG, Glick BR.** 2000. Plant growth promoting bacteria that decrease heavy metal toxicity in plants. *Canadian Journal of Microbiology* **46**, 237-245.

- Caetano-Anollés G, Gresshoff PM.** 1991. Plant genetic control of nodulation. *Ann Rev Microbiol* **45**, 345–382.
- Cardoso IM, Kuyper TW.** 2006. Mycorrhizas and tropical soil fertility. *Agric Ecosyst Environ* **116**, 72–84.
<http://dx.doi.org/10.1016/j.agee.2006.03.011>
- Compant S, Brion D, Jerzy N, Christophe C, Essaïd AB.** 2005. Use of plant growth-promoting bacteria for biocontrol of plant diseases: principles, mechanisms of action, and future prospects. *Appl Environ Microbiol* **71**, 4951–4959.
- Dar GH, Zargar MY, Beigh GM.** 1997. Biocontrol of Fusarium root-rot in the common bean (*Phaseolus vulgaris* L.) by using symbiotic *Glomus mosseae* and *Rhizobium leguminosarum*. *Microb Ecol.* **34**, 74–80.
<http://dx.doi.org/10.1007/s002489900036>
- Diouf D, Duponnois R, Ba AM, Neyra M, Leusueur D.** 2005. Symbiosis of *A. auriculiformis* and *A. mangium* with mycorrhizal fungi and *Bradirhizobium* spp. Improves salt tolerance in greenhouse conditions. *Functional Plant Biology* **32**, 1143–1152.
<http://dx.doi.org/10.1071/FP04069>
- Evelin H, Kapoor R, Giri B.** 2009. Arbuscular mycorrhizal fungi in alleviation of salt stress: a review. *Ann Bot* **104**, 1263–1280.
<http://dx.doi.org/10.1093/aob/mcp251>
- Fan QJ, Liu JH.** 2011. Colonization with arbuscular mycorrhizal fungus affects growth, drought tolerance and expression of stress-responsive genes in *Poncirus trifoliata*. *Acta Physiol. Plant.* **33**, 1533–1542.
<http://dx.doi.org/10.1007/s11738-011-0789-6>
- FAO.** 1983. Technical Handbook on Symbiotic Nitrogen Fixation. Food and Agriculture Organization of the United Nations, Rome.
- Feng G, Zhang FS, Li LX, Tian CY, 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.
<http://dx.doi.org/10.1007/s00572-002-0170-0>
- Filion M, St-arnaud M, Fortin JA.** 1999. Direct interaction between the arbuscular mycorrhizal fungus *Glomus intraradices* and different rhizosphere microorganisms. *New Phytol.* **141**, 525–533.
- Gao X, Lu X, Wu M, Zhang H, Pan R.** 2012. Co-Inoculation with Rhizobia and AMF Inhibited Soybean Red Crown Rot: From Field Study to Plant Defense-Related Gene Expression Analysis. *PLoS ONE* **7(3)**, e33977.
<http://dx.doi.org/10.1371/journal.pone.0033977>
- Garg N, Manchanda G.** 2008. Effect of arbuscular mycorrhizal inoculation of salt-induced nodule senescence in *Cajanus cajan* (pigeonpea). *Journal of Plant Growth Regulators* **27**, 115–124.
<http://dx.doi.org/10.1007/s00344-007-9038-z>
- Giller KE, McGrath SP, Hirsch PR.** 1989. Absence of nitrogen fixation in clover grown on soil subject to long-term contamination with heavy metals is due to survival of only ineffective *Rhizobium*. *Soil Biol. Biochem.* **21**, 841–848.
[http://dx.doi.org/10.1016/0038-0717\(89\)90179-X](http://dx.doi.org/10.1016/0038-0717(89)90179-X)
- Goss MJ, de Varennes A.** 2002. Soil disturbance reduces the efficacy of mycorrhizal associations for early soybean growth and N₂ fixation. *Soil Biol. Biochem.* **34**, 1167–1173.
[http://dx.doi.org/10.1016/S0038-0717\(02\)00053-6](http://dx.doi.org/10.1016/S0038-0717(02)00053-6)
- Graham PH.** 1981. Some problems on nodulation and symbiotic nitrogen fixation in *Phaseolus vulgaris* L.: A review. *Field Crop Res.* **4**, 93–112.
[http://dx.doi.org/10.1016/0378-4290\(81\)90060-5](http://dx.doi.org/10.1016/0378-4290(81)90060-5)
- Grichko VP, Filby B, Glick BR.** 2000. Increased

ability of transgenic plants expressing the bacterial enzyme ACC deaminase to accumulate Cd, Co, Cu, Ni, Pb and Zn. *J. Biotechnol.* **81**, 45–53.

[http://dx.doi.org/10.1016/S0168-1656\(00\)00270-4](http://dx.doi.org/10.1016/S0168-1656(00)00270-4)

Hajlaoui H, El Ayeb N, Garrec JP, Denden M. 2010. Differential effects of salt stress on osmotic adjustment and solutes allocation on the basis of root and leaf tissue senescence of two silage maize (*Zea mays* L.) varieties. *Ind Crop Product* **31**, 122-130.

<http://dx.doi.org/10.1016/j.indcrop.2009.09.007>

Hindumathi A, Reddy BN. 2012. Synergistic effect of arbuscular mycorrhizal fungi and Rhizobium on the growth and charcoal rot of soybean [*Glycine max* (L.) Merr.] *World Journal of science and Technology* **2(7)**, 63-70.

Ismail AA, Hegazy HS, Azb MAP. 2014. Physiological response of *Vicia faba* L. to inoculation with *Rhizobium* and arbuscular mycorrhizal fungi: Comparative study for irrigation with Nile water and wastewater. *AJCS* **8(5)**, 781-790.

Jing Y, He Z, Yang X. 2007. Role of soil rhizobacteria in phytoremediation of heavy metal contaminated soils. *J Zhejiang Univ Sci B* **8**, 192–207.

<http://dx.doi.org/10.1631/jzus.2007.B0192>

Joner EJ, Leyval C. 1997. Uptake of ¹⁰⁹Cd by Roots and Hyphae of a *Glomus mosseae* /*Trifolium subterraneum* Mycorrhiza from Soil Amended with High and Low Concentration of Cadmium, *New Phytol*, **135**, 353-360.

<http://dx.doi.org/10.1046/j.1469-8137.1997.00633.x>

Juniper S, Abbott L. 1993. Vesicular-arbuscular mycorrhizas and soil salinity. *Mycorrhiza* **4**, 45–57.

Kadian N, Yadav K, Aggarwal A. 2014. Application of AM Fungi with *Bradyrhizobium japonicum* in improving growth, nutrient uptake and yield of *Vigna radiata* L. under saline soil. *Journal of Stress Physiology & Biochemistry* **10**, 134-152.

Khan MS, Zaisi A, Musarrat J. 2010. Microbes for Legume Improvement. eds *Microbes for Legumes improvement*, Vienna : springer, 273-271 p.

Koomen I, McGrath SP, Giller K. 1990. Mycorrhizal Infection of Clover is Delayed in Soils Contaminated with Heavy Metals from Past Sewage Sludge Applications, *Soil Biol. Biochem.* **22**, 871-873.

[http://dx.doi.org/10.1016/0038-0717\(90\)90170-5](http://dx.doi.org/10.1016/0038-0717(90)90170-5)

Lin AJ, Zhang XH, Wong MH, Ye ZH, Lou LQ, Wang YS, Zhu YG. 2007. Increase of multimetal tolerance of three leguminous plants by arbuscular mycorrhizal fungi colonization. *Environ Geochem Health* **29**, 473–481.

<http://dx.doi.org/10.1007/s10653-007-9116-y>

Linderman RG. 1992. Vesicular arbuscular mycorrhizae and soil microbial interactions. In: *Mycorrhizae in sustainable agriculture*. ASA Special Publication No. 54, American Society of Agronomy Inc. Madison, Wisconsin, USA, 45–70 p.

Manchanda G, Garg N. 2011. *Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology: Official Journal of the Societa Botanica Italiana.* **145**, 88-97.

Marschner P, Grierson PF, Rengel Z. 2005. Microbial community composition and functioning in the rhizosphere of three *Banksia* species in native woodland in Western Australia. *Applied Soil Ecology* **28**, 191–201.

<http://dx.doi.org/10.1016/j.apsoil.2004.09.001>

Marulanda A, Azcón R, Ruiz-Lozano JM. 2003. Contribution of six arbuscular mycorrhizal fungal isolates to water uptake by *Lactuca sativa* plants under drought stress. *Physiol Plant* **119**, 526–533.

<http://dx.doi.org/10.1046/j.1399-3054.2003.00196.x>

Medina A, Jakobsen I, Vassilev N, Larsen AR. 2007. Fermentation of sugar beet waste by *Aspergillus niger* facilitates growth and P uptake of external mycelium of mixed populations of arbuscular

mycorrhizal fungi. *Soil Biol Biochem* **39**, 485–492.
<http://dx.doi.org/10.1016/j.soilbio.2006.08.019>

Mortimer PE, Pérez-Fernández MA, Valentine AJ. 2008. The role of arbuscular mycorrhizal colonization in the carbon and nutrient economy of the tripartite symbiosis with nodulated *Phaseolus vulgaris*. *Soil Biol Biochem* **40**, 1019–1027.
<http://dx.doi.org/10.1016/j.soilbio.2007.11.014>

Mosse B. 1962. The establishment of vesicular-arbuscular mycorrhiza under aseptic conditions. *J. Gen. Microbiol.* **27**, 509–520.

Muller J, Boller T, Wiemkem A. 2001. Trehalose becomes the most abundant non-structural carbohydrate during senescence of soybean nodules. *J Exp Bot* **52**, 943–947.

Munns R. 2002. Comparative physiology of salt and water stress, *Plant Cell Environ.* **20**, 239–250.
<http://dx.doi.org/10.1046/j.00168025.2001.00808.x>

Ocón A, Hampp R, Requena N. 2007 Trehalose turnover during abiotic stress in arbuscular mycorrhizal fungi. *New Phytol* **174**, 879–891.
<http://dx.doi.org/10.1111/j.1469-8137.2007.02048.x>

Parádi I, Bratek Z, Láng F. 2003. Influence of arbuscular mycorrhiza and phosphorus supply on polyamine content, growth and photosynthesis of *Plantago lanceolata*. *Biol. Plant.* **46**, 563–569.

Patreze CM, Cordeiro L. 2004. Nitrogen-fixing and vesicular-arbuscular mycorrhizal symbioses in some tropical legume trees of tribe Mimoseae, *Forst Ecol. Mangt.* **196**, 275–285.

Pelaez C, Olivares E, Cuenca G, Izaguirre-Mayoral ML. 2010. Manganese modulates the responses of nitrogen-supplied and Rhizobium-nodulated *Phaseolus vulgaris* L. to inoculation with arbuscular mycorrhizal fungi. *Soil Biology & Biochemistry* **42**, 1924–1933.

<http://dx.doi.org/10.1016/j.soilbio.2010.07.001>

Porcel R, Ruíz-Lozano JM. 2004. Arbuscular mycorrhizal influence on leaf water potential, solute accumulation, and oxidative stress in soybean plants subjected to drought stress. *J Exp Bot.* **55**, 1743–1750.

Rabie GH, Almadini AM. 2005. Role of bioinoculants in development of salt-tolerance of *Vicia faba* plants under salinity stress. *Afr J Biotechnol* **4**, 210–222.

Rajwar A, Sahgal M, Johri BN. 2013. Legume-Rhizobia symbiosis and interactions in agrosystems. in : Arora NK(ed) *plant microbe symbiosis : fundamentals and advances*. Springer, New Delhi 233–265 p.
http://dx.doi.org/10.1007/978-81-322-1287-4_9

Rapparini F, Peñuelas J. 2014. Mycorrhizal Fungi to Alleviate Drought Stress on Plant Growth . Use of Microbes for the Alleviation of Soil Stresses Miransari (ed.) 21–42 p.
http://dx.doi.org/10.1007/978-1-4614-9466-9_2.

Rao AV, Tak R. 2002. Growth of different tree species and their nutrient uptake in limestone mine spoil as influenced by arbuscular mycorrhizal (AM) fungi in India arid zone. *J. Arid Environ* **51**, 113–119.
<http://dx.doi.org/10.1006/jare.2001.0930>

Redon PO, Beguiristain T, Leyval C. 2009. Differential effects of AM fungal isolates on *Medicago truncatula* growth and metal uptake in a multimetallic (Cd, Zn, Pb) contaminated agricultural soil. *Mycorrhiza* **19**, 187–195.
<http://dx.doi.org/10.1007/s00572-009-0230-9>

Rivera-Becerril F, Calantzis C, Turnau K, Caussanel JP, Belimov AA, Gianinazzi S, Strasser RJ, Gianinazzi-Pearson V. 2002. Cadmium accumulation and buffering of cadmium-induced stress by arbuscular mycorrhiza in three *Pisum sativum* L. genotypes. *J Exp Bot.* **53**,

1177–1185.

<http://dx.doi.org/10.1093/jexbot/53.371.1177>

Ruiz-Lozano JM, Azcón R. 1993. Specificity and functional compatibility of VA mycorrhizal endophytes in association with *Bradyrhizobium* strains in *Cicer arietinum*. *Symbiosis* **15**, 217–226.

Ruiz-Lozano JM, Azcón R, Gómez M. 1995. Effects of arbuscular- mycorrhizal *Glomus* species on drought tolerance: Physiological and nutritional plant responses. *Applied and Environmental Microbiology* **61**, 456–460.

Ruiz-Lozano JM, Collados C, Barea JM, Azcón R. 2001. Arbuscular mycorrhizal symbiosis can alleviate drought induced nodule senescence in soybean plants. *New Phytologist* **151**, 493–502.
<http://dx.doi.org/10.1046/j.0028-646x.2001.00196.x>

Sakamoto K, Ogiwara N, Kaji T. 2013. Involvement of autoregulation in the interaction between rhizobial nodulation and AM fungal colonization in soybean roots. *Biol Fertil Soils* **49**, 1141–1152.
<http://dx.doi.org/10.1007/s00374-014-0896-9>.

Sardans J, Peñuelas J, Ogaya R. 2008. Drought's impact on Ca, Fe, Mg, Mo and S concentration and accumulation patterns in the plant sand soil of a Mediterranean evergreen *Quercus ilex* forest. *Biogeochemistry* **87**, 49–69.
<http://dx.doi.org/10.1186/1471-2229-10-188>

Saxena AK, Rathi SK, Tilak KBR. 1997. Differential effect of various endomycorrhizal fungi on nodulating ability of green gram by *Bradyrhizobium* sp. (Vigna) strain S24. *Biol Fertil Soils* **24**, 175–178.
<http://dx.doi.org/10.1007/s003740050227>

Scheublin TR, Vander Heijden MGA. 2006. Arbuscular mycorrhizal fungi colonize nonfixing root nodules of several legume species. *New Phytol.* **172**, 732–738.

<http://dx.doi.org/10.1111/j.1469-8137.2006.01858.x>

Selvaraj T, Chellappan P. 2006. Arbuscular Mycorrhizae: A Diverse Personality **7**, 349–358.

Siddiqui ZA, Singh LP. 2004. Effects of soil inoculants on the growth, transpiration and wilt disease of chickpea. *J Plant Dis Protect* **111**, 151–157.

Singh LP, Singh Gill S, Tuteja N. 2011. Unraveling the role of fungal symbionts in plant abiotic stress tolerance. *Plant Signal Behav* **2**, 175–191.
<http://dx.doi.org/10.4161/psb.6.2.14146>

Singh PK, Singh M, Vyas D. 2010. Biocontrol of *Fusarium* Wilt of *Chickpea* using Arbuscular Mycorrhizal Fungi and *Rhizobium leguminosorum* Biovar. *Caryologia* Vol. 63, no. **4**, 349–353.
<http://dx.doi.org/10.1080/00087114.2010.10589745>

Siqueira JO, Saggin-Júnior OJ. 1995 The importance of mycorrhizal association in natural low fertility soils. In: Machado, editor. International symposium on environmental stress: maize in perspective. p. 240–80.

Smith SE. 2002. Soil microbes and plants-raising interest, mutual gains. *New Phytol.* **156**, 142–144.
<http://dx.doi.org/10.1046/j.1469-8137.2002.00514.x>

Smith SE, Robson AD, Abbott LK. 1992. The involvement of mycorrhizas in assessment of genetically dependent efficiency of nutrient uptake and use. *Plant and Soil* **146**, 169–179.
<http://dx.doi.org/10.1007/BF00012010>

Soumare A, Manga A, Thiao M, Ndoye, I, Diop T. 2008. Effect of the inoculation of arbuscular mycorrhizal fungi on the development of *Acacia nilotica* subsp. *Adestringens* subjected to various concentrations of salt. *Université Cheikh Anta Diop Journal des Sciences et Technologie* **7**, 74 – 83.

Stamford NP, Ortega AD, Temprano F, Santos

DR. 1997. Effects of phosphorus fertilization and inoculation of Bradyrhizobium and mycorrhizal fungi on growth of Mimosa caesalpiniaefolia in an acid soil. Soil Biol Biochem **29**, 959–964

[http://dx.doi.org/10.1016/S0038-0717\(96\)00240-4](http://dx.doi.org/10.1016/S0038-0717(96)00240-4)

Sundaresan P, Ubalthouse Raja N, Gunasekaran P. 1993. Induction and accumulation of phytoalexins in cowpea roots infected with a mycorrhizal fungus *Glomus fasciculatum* and their resistance to *Fusarium* wilt disease. J. Biosci. **18(2)**, 291–301.

<http://dx.doi.org/10.1007/BF02703126>

Tabak H, Lens P, van Hullebusch E, Dejonghe W. 2005. Development in bioremediation of soil and sediment polluted with metals and radionuclides- 1. Microbial processes and mechanisms affecting metals contamination and influencing metals toxicity and transport. Rev Environ Sci Biotechnol. **24**, 115–156.

<http://dx.doi.org/10.1007/s11157-005-2169-4>

Tajini F, Trabelsi M, Drevon JJ. 2012. Combined inoculation with *Glomus intraradices* and *Rhizobium tropici* CIAT899 increases phosphorus use efficiency for symbiotic nitrogen fixation in common bean (*Phaseolus vulgaris* L.) Saudi Journal of Biological Sciences **19**, 157–163.

<http://dx.doi.org/10.1016/j.sjbs.2011.11.003>

Tobar RM, Azcón-Aguilar C, Sanjuan J, Barea JM. 1996. Impact of a genetically modified Rhizobium strain with improved nodulation competitiveness on the early stages of arbuscular mycorrhiza formation. Appl Soil Ecol. **4**, 15–21.

[http://dx.doi.org/10.1016/0929-1393\(96\)00104-7](http://dx.doi.org/10.1016/0929-1393(96)00104-7)

van der Heijden MGA, Bardgett RD, Straalen NMV. 2008. The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. Ecol Lett **11(3)**, 296–310.

<http://dx.doi.org/10.1111/j.1461-0248.2007.01139.x>

Van der Heijden MGA, Bardgett RD, van Straalen NM. 2008. The unseen majority: soil

microbes as drivers of plant diversity and productivity in terrestrial ecosystems. Ecol Lett **11**, 296–310.

<http://dx.doi.org/10.1111/j.1461-0248.2007.01139.x>

Vivas A, Biró B, Ruíz-Lozano JM, Barea JM, Azcón R. 2006. Two bacterial strains isolated from a Zn-polluted soil enhance plant growth and mycorrhizal efficiency under Zn toxicity. Chemosphere **62**, 1523–1533.

<http://dx.doi.org/10.1016/j.chemosphere.2005.06.053>

Xavier LJC, Germida JJ. 2002. Response of lentil under controlled conditions to co-inoculation with arbuscular mycorrhizal fungi and rhizobia varying in efficacy. Soil Biol Biochem **34**, 181–188.

[http://dx.doi.org/10.1016/S0038-0717\(01\)00165-1](http://dx.doi.org/10.1016/S0038-0717(01)00165-1)

Yano-Melo AM, Saggin OJ, Maia LC. 2003. Tolerance of mycorrhizal banana (*Musa* sp. cv. Pacovan) plantlets to saline stress. Agric. Ecosystems and Environ. **95** (1), 343–348.

[http://dx.doi.org/10.1016/S0167-8809\(02\)00044-0](http://dx.doi.org/10.1016/S0167-8809(02)00044-0)

Zahrán HH. 1999. *Rhizobium*–legume symbiosis and nitrogen fixation under severe conditions and in an arid climate. Microbiology and Molecular Biology Reviews **63**, 968–989.

Zandavalli RB, Dillenburg LR, Paul, VD. 2004. Growth responses of *Araucaria angustifolia* (Araucariaceae) to inoculation with the mycorrhizal fungus *Glomus clarum*. Appl. Soil Ecol. **25**(3), 245–255.

<http://dx.doi.org/10.1016/j.apsoil.2003.09.009>

Zhang YF, Wang P, Yang YF, Bi Q, Tian SY, Shi XW. 2011. Arbuscular mycorrhizal fungi improve re-establishment of *Leymus chinensis* in bare saline-alkaline soil: implication on vegetation restoration of extremely degraded land. J Arid Environ. **75**, 773–8

<http://dx.doi.org/10.1016/j.jaridenv.2011.04.008>

Zou YN, Wu QS. 2011. Sodium Chloride Stress Induced Changes in Leaf Osmotic Adjustment of Trifoliate Orange (*Poncirus trifoliata*) Seedlings Inoculated with Mycorrhizal Fungi. Not Bot Horti Agrobo **39(2)**, 64–69.