Current developments in arbuscular mycorrhizal fungi research and its role in salinity stress alleviation: a biotechnological perspective

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Abstract

Arbuscular mycorrhizal fungi (AMF) form widespread symbiotic associations with 80% of known land plants. They play a major role in plant nutrition, growth, water absorption, nutrient cycling and protection from pathogens, and as a result, contribute to ecosystem processes. Salinity stress conditions undoubtedly limit plant productivity and, therefore, the role of AMF as a biological tool for improving plant salinity stress tolerance, is gaining economic importance worldwide. However, this approach requires a better understanding of how plants and AMF intimately interact with each other in saline environments and how this interaction leads to physiological changes in plants. This knowledge is important to develop sustainable strategies for successful utilization of AMF to improve plant health under a variety of stress conditions. Recent advances in the field of molecular biology, “omics” technology and advanced microscopy can provide new insight about these mechanisms of interaction between AMF and plants, as well as other microbes. This review mainly discusses the effect of salinity on AMF and plants, and role of AMF in alleviation of salinity stress including insight on methods for AMF identification. The focus remains on latest advancements in mycorrhizal research that can potentially offer an integrative understanding of the role of AMF in salinity tolerance and sustainable crop production.

Keywords

Antioxidants, arbuscular mycorrhiza, Myc factor, salinity, strigolactones

Introduction

Salinity is one of the most prevalent agricultural problems in the arid and semiarid regions of the world, affecting approximately 1 billion ha of land (Abdel Latef & Chaoxing, 2010). Estimations indicate that increased salinization of arable land will result in 30% land loss within the next 25 years, and up to 50% within the next 40 years (Porcel et al., 2012; Wang et al., 2003). Besides having deleterious effects on the physicochemical properties of soil and its microbiological processes, increased salinity also seriously affects plant growth and productivity. Presence of excessive salts in soil results in stunted growth and limited productivity of plants by reducing water uptake, inhibiting metabolic processes, affecting nutrient composition, osmotic balance and hydraulic conductivity (Huang et al., 2010). Many reactive oxygen species (ROS) are also generated in response to salt stress, which causes oxidative damage to lipids, proteins and nucleic acids thereby changing the selective permeability of the cell membranes, eventually causing them to leak (Abdel Latef & Chaoxing, 2010; Huang et al., 2010). A significant research effort has been focused on developing salt-tolerant crops; however, there has been limited success as only a few genetic traits of salt tolerance have been identified (Schubert et al., 2009). Besides the use of salt tolerant crops or their development through genetic engineering, an alternative strategy is to apply biofertilizers that seems to be a more environment friendly and economically viable option (Evelin et al., 2009).

Arbuscular mycorrhizal fungi (AMF) are among the most abundant organisms on earth; a very conservative estimate suggests that they represent 5–10% of global soil microbial biomass (Lanfranco & Young, 2012). These symbiotic associations are commonly described as the result of co-evolution events between fungi and plants and also considered as a plant strategy for growth under a variety of stress conditions (Bandou et al., 2006; Bonfante & Genre, 2008). AMF associate with the roots of higher plants and are found in >80% of plant species (Parniske, 2008). They establish an intimate association with the roots of most land plants (Gutjahr & Paszkowski, 2013), with the fungi supplying mineral nutrients from the soil while acquiring carbon compounds from the photosynthetic host (Lanfranco & Young, 2012). In this association, both partners profit from...
the relationship; AMF improve the host plants nutrient status, influencing mineral nutrition, water uptake, growth and disease resistance, whereas in exchange, the host plant provides organic carbon and the substrate necessary for fungal growth and reproduction (Smith & Read, 2008). AMF play an important part in nutrient cycling with the help of their mycelium in absorbing soil nutrients and providing them to the plant, although their role in carbon flux is less well defined. Recent work by different workers has established that AMF can effect plant fitness (Hoffmann et al., 2011; Wilson et al., 2009), productivity and biodiversity (Wilson et al. 2009). Pellegrino & Bedini (2014) reported that the application of foreign AMF Funneliformis mosseae and Rhizophagus irregularis showed great potential in bio fertilization of crops and bio fertilization of foods. Two review articles published previously (Evelin et al., 2009; Porcel et al., 2012) have explored the physiological mechanisms by which AMF improve plant salinity tolerance. Therefore, in this article, we summarize the most important mechanisms by which mycorrhizal colonization in salt-affect ed plants alleviates salt stress and also lists the latest significant contributions by researchers on the role of AMF in improving different crop performance under salt stress. We also discuss the method of detection of AMF, latest developments in AMF research and focus on approaches that can provide an integrative understanding of the role of AMF in salinity tolerance and sustainable crop production in detail.

Mechanism of AMF root colonization and methods for detection of AMF is given in Supplementary material.

Salinity stress: impact on crop plants

The percentage of agriculture land affected by salinity is continuously increasing, owing to both natural causes and agricultural practices such as irrigation (Munns & Tester, 2008). Of the total 14 billion ha of land available on earth, about 1 billion ha are natural saline soils. It is estimated that more than 50% of global arable land could be salinized by the year 2050 (Ashraf & Akram, 2009).

Salinity reduces crop yield by inhibiting seed germination and also by altering the physiology and anatomy of the plants (Karan & Subudhi, 2012). Salt stress inhibits plant growth and development through different means, including perturbation of various metabolic activities and triggering programmed cell death, leading to reduced crop yield or total crop failure.

Most of the crops, commonly used for food production are sensitive to salinity stress (Flowers & Colmer, 2008) and vary in their response to salt stress tolerance. Among cereals, rice (Oryza sativa) is the most sensitive, while barley (Hordeum vulgare) is regarded as the most tolerant. Bread wheat (Triticum aestivum) is comparatively more tolerant than durum wheat (Triticum turgidum ssp. durum). The dicotyledonous species are more tolerant than monocotyledonous species. Cereal crop plants (rice, wheat and barley) are the most extensively studied for understanding the physiological and molecular basis of salt tolerance (Karan & Subudhi, 2012).

Recently, a large number of investigations have been conducted to elucidate the degree of salt tolerance and the related mechanisms in different crops, for example, sugar beet (Ghoulam et al., 2002), cotton (Meloni et al., 2003), wheat (Raza et al., 2007), cucumber (Shi & Zhu, 2008), radish (Noreen & Ashraf, 2009b), pea (Ahmad et al., 2008; Noreen & Ashraf, 2009a), sunflower (Saeed Akram et al., 2009), turnip (Noreen et al., 2010), maize (Nawaz & Ashraf, 2009), eggplant (Abbas et al., 2010), proso millet (Sabir et al., 2009) and mustard (Ahmad et al., 2012a). These studies revealed that plant salt tolerance is a complex phenomenon and depends on a number of inter-related factors (Ahmad et al., 2012b, 2012c; Ashraf, 2004, 2010; Dash & Panda, 2001).

Plants respond to salinity stress through the complex interactions of many genes, proteins and metabolite/signaling pathways (Ashraf, 2009; Jamil et al., 2011). Plants deal with these stresses by adapting different strategies (Galvan-Ampudia & Testerink, 2011; Kumar et al., 2012); for example, reducing salt uptake or increasing salt exclusion, enhanced K+/Na+ ratio, tissue tolerance, closure of stomata, synthesis of osmolytes, water use efficiency (WUE), up-regulation of antioxidant system for protection against ROS, early flowering and vigorous growth to dilute the salt concentration in plant tissue (Colmer et al., 2006; Türkan & Demiral, 2009). Salinity stress also causes hyper-osmolarity that triggers the mitogen activated protein kinase cascade (Kiegerl et al., 2000), that results in induction of transcription factors followed by increased synthesis of osmolytes, osmoprotectants and detoxifying enzymes (Vinocur & Altman, 2005).

Recently, the use of AMF to alleviate soil stresses on plant growth has received increased attention (Daei et al., 2009; Kumar et al., 2009, 2010; Miransari, 2010) and their role is discussed in the following section.

Impact of salinity on AMF

Arbuscular mycorrhizal colonization in plant roots is influenced by various factors when plants grow under salinity stress conditions. Many researchers reported reduction in colonization under salinity in several plant species such as tomato (Hajiboland et al., 2010), lotus (Sannazzaro et al., 2006), acacia (Giri et al., 2003, 2007) and Jatropha curcas (Kumar et al., 2010). This decline in colonization could be due to the negative effect of salinity on the germination of spores (Hirrel, 1981), inhibited growth of hyphae and hyphal proliferation in soil (McMillen et al., 1998) and reducing the number of arbuscules (Pfetffer & Bloss, 2006), or alternatively, indirectly by the effect on host plants.

Studies on effect of soil salinity on spore production by AMF are rare and need more detailed investigation. Spore formation and germination in saline soils might depend on complex physiological and ecological parameters and also on the genotypes of the plants and AMF. The presence of relatively high spore numbers (mean of 100/10 g soil) in the severely saline soils (EC ~162 dS m⁻¹) have been reported previously (Aliasgharzadeh et al., 2001; Bhaskaran & Selvaraj, 1997) and contrasted with other studies where the average density of spores in saline areas (EC > 45 dS m⁻¹) was reported to be low (Barrow & Aaltonen, 2001; Hirrel, 1981; Kim & Weber, 1985). In some cases, higher spore production may be due to induction of sporulation by salinity stress. If soil salinity affects spore germination, hyphal growth and colonization, then total spore production is likely to be
reduced in saline soil relative to non-saline soils. Aliasgharzadeh et al. (2001) reported that inhibition of spore germination may also cause spore accumulation in saline soil. Asghari & Cavagnaro (2010) reported detrimental effects of soil salinity on spore germination and hyphal growth, and have been identified as being the most important reason for the absence of colonization in halophytes. It is extremely difficult to distinguish between direct and plant-mediated effects on AMF biology because of their obligate biotrophic life style. Previous studies on the effects of salinity stress on spore germination indicated inhibition of spore germination under NaCl concentrations (Hirrel, 1981; Juniper & Abbott, 2006). However, other studies showed that low water potentials delayed germination rather than preventing germination (Hirrel, 1981) and germ tube length was reported to be reduced by decreased water potential (Koske & Halvorson, 1981). Juniper & Abbott (2006) revealed that propagules of different AMF from saline and non-saline soils differ in their ability to germinate and grow in the presence of NaCl in soil solution. Several studies indicated that the formation of AMF colonization may be reduced by increasing soil salinity (Giri et al., 2007; Hajiboland et al., 2010; Huang et al., 2010; Juniper & Abbott, 2006; Sheng et al., 2008). Mechanism of AM root colonization is presented in Fig. 1.

**AMF: salinity stress alleviation**

Plants can respond to salinity stress by modifying themselves at morphological, anatomical and cellular levels, which allow the plant to avoid the stress or to increase its tolerance. These modifications are of vital significance for some plant species, but are not found as a common response in all plants (Jamil et al., 2011). Plants, in addition to the inherent adaptation against these stresses, also show association with many rhizospheric soil microorganisms that can alleviate the stress effect. Salinity affects plant growth and survival by disrupting several physiological mechanisms such as photosynthetic efficiency, membrane integrity and water status (Evelin et al., 2009). There is evidence that AMF, besides using the above-mentioned mechanisms, can alleviate salt stress by improving the physiological processes in plants. However, salinity not only adversely affects the host plant but also the growth of AMF by hampering colonization, spore germination and hyphal elongation as discussed previously (Kumar et al., 2010; Porcel et al., 2012; Sheng et al., 2008). Contrary to some reports, increase in sporulation and colonization has also been observed (Aliasgharzadeh et al., 2001). Mycorrhizal association with the plants have been shown to increase plant growth and yield, water status, enhance accumulation of nutrients, influence plants hormones and affect various physiological and biochemical properties of plants in saline and alkaline soil conditions (Abdel Latef & Chaoxing, 2010; Bandou et al., 2006; Evelin et al., 2009; Kashyap et al., 2004; Kumar et al., 2010; Murkute et al., 2006). Several mechanisms have been proposed to explain the protection of plants from the adverse effect of salt stress. Improvement in the nutrient status of colonized plants can be attributed not only to the uptake of nutrients via the mycorrhizal pathway, but also to indirect effects carried out by morphological and physiological changes in roots due to colonization. Improved salt tolerance of mycorrhizal plants can be mainly related to the changes in physiological processes, for example, increased carbon dioxide exchangeable rate, transpiration, stomatal conductance and WUE, enhanced uptake of nutrients with low mobility, such as P, Zn and Cu (Giri & Mukerji, 2004; Giri et al., 2007; Ruiz-Lozano et al., 2002).

Several studies reveal that arbuscular mycorrhizal inoculated plants maintained a relatively higher water content compared with non-inoculated plants (Colla et al., 2008; Evelin et al., 2009; Jahromi et al., 2008; Sheng et al., 2008), which is facilitated by the improved hydraulic conductivity of the root at low water potential (Kapoor et al., 2008). This improved root conductance is associated with changes in the morphogenetic characters of roots. AMF decrease the meristem activity of root apices and thus lead to an increase in the formation of adventitious roots and these AMF-mediated modifications in root morphology may assist in maintaining nutrient uptake and water balance in the host plant under salinity stress. Sukumar et al. (2013) recently reviewed that changes in root systems in response to AM leading to an increased root branching and root system volume. Giri et al. (2003) reported increased water uptake per unit root length in colonized plants under stress conditions. All these parameters, improved by mycorrhizal colonization, enable host plants to use water more efficiently and allow them to maintain a lower intercellular carbon dioxide concentration. As a consequence, the gas exchange capacity increases in the mycorrhizal plants (Evelin et al., 2009).

Several examples of salinity stress alleviation by AMF have been reported, and these are briefly summarized in Table 1. To some extent, these fungi have also been considered as bio-ameliorators of saline soils (Giri et al., 2007). The following subsections, will discuss the role of AMF during salt stress on growth and biochemical response in plants.

**Dry matter accumulation**

Giri et al. (2007) reported that soil salinity decreased root and shoot dry weights in Acacia and there was a significant positive effect of mycorrhizal inoculation on plant growth regardless of salt concentrations. Inoculating olive plantlets with Glomus mosseae, Glomus intraradices or Glomus claroideum increased plant growth and the ability to acquire N, P and K from non-saline as well as saline media (Porras-Soriano et al., 2009). Abdel Latef & Chaoxing (2010) reported that tomato in salinity stress reduced the dry matter of roots, stems, leaves, leaf area and total biomass significantly in comparison with the control treatment. They also reported accumulation of dry matter in shoots, over root biomass, which might be due to the allocation of a greater proportion of carbohydrates to the shoot than root tissues in mycorrhizal plants (Abdel Latef and Chaoxing, 2010; Shokri & Maadi, 2009). In another study, AMF-inoculated citrus plants showed significant improvement in growth parameters over non-AMF inoculated control plants particularly under higher salinity (Khalil et al., 2011). Borde et al. (2011)
| AM Fungus sps. | Salt stress applied | Host plant used | Impact on plants | References |
|---------------|---------------------|----------------|------------------|------------|
| AMF           | 0–0.5% Na₂SO₄       | Jatropha curcas | AMF increased salt tolerance | Kumar et al. (2013) |
| EndoRoots® (spores of *Glomus* spp.) | EC level 6 dS m⁻¹ using NaCl | “Maxifort” and “Beaufort” hybrid tomato rootstocks | Mycorrhizal fungi increased the total and marketable yield of Maxifort along with vitamin C content and titrable acidity decreased. Salinity tolerance improved in grafted plant with AM inoculation | Oztekin et al. (2013) |
| *Glomus etunicatum* and *Glomus intraradices* | 2, 4, 6 and 8 dS m⁻¹ as NaCl | Citrus jambhiri rootstock | Mycorrhizal citrus seedlings exhibited greater tolerance to salt stress than non-mycorrhizal seedlings | Zarei & Paymaneh (2013) |
| *Glomus etunicatum*, *G. mosseae*, and *G. intraradices* | EC of 13.87 dS m⁻¹ | Wheat genotypes | *G. etunicatum* inoculation resulted in 3.53 fold increase in plant activity or plant total P-uptake over control. | Ardakani et al. (2013) |
| *Glomus deserticola* | Various stress levels of NaCl, zinc and cadmium | *Solanum melongena* L. and *Sorghum sudanense* Staph. | Mycorrhizal seedlings exhibited greater growth response than non-mycorrhizal seedlings | Mohammad & Mittra (2013) |
| AMF           | Salinity stress     | *Astericus maritimus* | Native AMF inoculation plays a key role in the establishment, survival and growth of the plants | Estrada et al. (2013a) |
| Native AMF    | Salinity stress     | Maize plants      | Native AMF help maize plants to overcome the negative effects of salinity stress better than non-AM | Estrada et al. (2013b) |
| *Glomus intraradices* Schenck & Smith | 0, 50, 100 and 200 mM NaCl | Fenugreek [Trigonella foenum-graecum L.] | Salt-induced ultrastructural damage was less in AM plants along with lower lipid peroxidation and electrolyte leakage over non-AM plants | Evelin et al. (2013) |
| *Glomus arenarium*, *G. caledonium*, *G. irregularae*, and *G. mosseae* and root endophyte | Salinity stress | Strawberry cultivars | Fungal symbiosis tended to benefit strawberry plants in their tolerance to salinity | Sinclair et al. (2013) |
| AMF           | 0, 80 and 250 mm NaCl | *Melilotus siculus* (Turra) Vitman ex. B. D Jacks | AM inoculation enhanced P uptake, dry-weight and greater nodulation under salinity stress | Wilson et al. (2012) |
| *Glomus viscosum* H.T. Nicolson strain A6 | 0, 50, 100, 150 and 200 mM NaCl | *Medicago sativa* L. | AMF showed better growth and physiological activities under saline conditions than non-AM plants | Campanelli et al. (2013) |
| *Glomus mosseae* | 400 M L⁻¹ NaCl stress | *C₃ halophyte Suaeda salsa* | AMF increased salt tolerance by increasing SOD and CAT activities and forming SOD and CAT isoforms in *S. salsa* seedlings | Li et al. (2012) |
| *Glomus mosseae* and *G. intraradices* | Salt stress | Pepper plants [Capsicum annuum L. cv. Cumaovasas] | AMF increased relative water content, P, total chlorophyll and carotenoid content | Cekic et al. (2012) |
| *Glomus intraradices* | 0, 1500, 3000 and 4500 ppm of salinity levels | Sour orange [Citrus aurantium L.] and Volkamer lemon [Citrus volkameriana Tan. and Pasq.], | AM plants had significantly higher growth parameters and increased levels of P, K, Mg and Zn compared with the non-inoculated plants | Khalil et al. (2011) |
| *Glomus fasciculatum* | 0, 100, 200 and 300 mM salinity levels | *Bajra* [Pennisetum glaucum] | AMF increased performance under moderate salinity levels by enhancing the antioxidant activity and proline accumulation as compared with non-AM plants | Borde et al. (2011) |
| *Glomus spp.* | Adding a mixture of NaCl, CaCl₂, and MgSO₄ at the molar ratio of 2:2:1 (0.00, 3.13, 6.25 and 9.38 dS m⁻³) | Wheat | AMF colonization mitigate detrimental effect of salinity by improving osmotic adjustment, defense system and antioxidant production | Talaat & Shawky (2011) |
| *Glomus mosseae*, *G. etunicatum* and *G. intraradices* | Salinity stress | Different wheat cultivars | AMF significantly enhanced all nutrients including N, P, Ca, Mg, Mn, Cu, Fe, Zn, Na and Cl | Mardukhi et al. (2011) |
| *Glomus mosseae* & *G. geosporum* | Saline-alkaline soil | *Leymus chinensis* | AMF fungi improved survival, growth and asexual reproduction and could improve the reestablishment of vegetation in bare saline–alkaline soil | Zhang et al. (2011) |
| AMF Species | Salinity Levels | Host Plant | Growth Response |
|-------------|----------------|------------|----------------|
| *Glomus mosseae* | 0, 0.5 and 1.0% NaCl solution | Tomato (*Lycopersicon esculentum*) | AM alleviated the growth limitations imposed by saline conditions |
| *Glomus mosseae*, *Glomus claroideum* & *Glomus intraradices* | 0, 0.14, 0.53 and 0.96 g NaCl kg⁻¹ soil | *Astragalus sinicus* | *G. intraradices* performed better than other two fungi in root colonization and enzyme activity and synergistic interaction between these fungi under NaCl stress also seen |
| *Glomus mosseae* | 0, 0.5 and 1.0 g NaCl kg⁻¹ dry substrate | Maize | AMF symbiosis improves solute accumulation in maize leaves, to mitigate the negative impact of soil salinity |
| *Glomus fasciculatum* | 100 mM and 200 mM conc. of NaCl | *Gmelina arborea* Roxb. | AMF is very effective in strengthening the tolerance of *Gmelina arborea* grown in arid and semi-arid areas |
| *Mycorali* | Saline water (ECs of 1.65 dS m⁻¹) | Cape gooseberry (*Physalis peruviana* L.) | Plant growth enhanced with increased unit leaf rate and leaf area ratio. |
| *Glomus mosseae* | 0-100 mM NaCl | *Lathyrus sativus* | Growth, leaf area, chlorophyll content, fruit fresh weight and yield enhanced in AMF tomato plants |
| *Glomus mosseae* and/or the rhizobium, *Mesorhizobium mediterraneum* | 0, 1%, 2%, 3% and 4% Na₂SO₄ (weight : weight) | *Lettuce* | Dual-inoculation reduced the harmful influence of sulfate salinity |
| *Glomus mosseae* & *Paraglomus occultum* AMF consortia | 100 mM NaCl | *Citrus* (*Citrus tangerine* Hort. ex Tanaka) | Salt tolerance of citrus seedlings could be enhanced by associated AM |
| *Glomus deserticola* | Saline water (ECw=2.6 dS m⁻¹) | *Parwal* (*Trichosanthes dioica* Roxb.) | AMF lessen the deleterious effect of salt stress on seedling growth parameters under salt levels up to 0.5% NaCl |
| *Glomus mosseae* (Nicol & Gerd) and PGPR (*Pseudomonas mendocina* Palleroni) | Two concentrations (2 g and 4 g NaCl kg⁻¹ soil) of saline solution | *Lactuca sativa* L. | AMF improved yield and can help alleviate deleterious effects of salt |
| *Glomus clarum* | 0, 50 and 100 mM NaCl | Pepper (*Capsicum annuum* cv. 11B) | AMF and/or a PGPR alleviating salinity stress in lettuce plants could be limited by their detrimental effect on soil structural stability |
| *Glomus mosseae*, *Glomus intraradices* or *Glomus claroideum* AMF consortia | 6 g NaCl kg⁻¹ | Olive trees | AMF inoculation improved pepper growth under salt or salt-less conditions and reduced cell membrane leakage |
| *Glomus etunicatum*, *G. mosseae* and *G. intraradices* AMF | Soil salinity of 7.41 dS/m | Wheat genotypes | AMF increased plant growth and the ability to acquire nitrogen, phosphorus, and potassium from non-saline as well as saline media |
| *Glomus mosseae* | 1.3 dS/m, 8 dS/m or 15 dS/m salt solution | Tamarix | Selection of the right combination of AMF species, improve wheat cultivation under salinity stress |
| *Glomus mosseae* | Three levels of salt (4, 6 and 8 dS m⁻¹) | *Cajanus cajan* (L.) Millsp. (pigeonpea) | No clear evidence that mycorrhizae increased salinity tolerance, but some species showed dependence on AMF, that they grew poorly at all salinity levels |
| *Glomus mosseae* | 0, 0.5, 1.0, 1.5 and 2.0 g/kg dry substrate | Maize | AMF inoculation increased solute accumulation to maintain osmotic balance and antioxidant enzyme activity in salt stress |
| *Glomus intraradices* | 0-100 mM NaCl | *Lettuce* | AMF alleviated the deleterious effect of salt stress on plant growth, through improving plant water status, chlorophyll concentration, and photosynthetic capacity |
| *Glomus intraradices* | Shoot dry weight, shoot water content and transpiration rate decreased | *Jatropha curcas* L. | Sheng et al. (2008) |

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observed that pearl millet inoculated with AMF showed a significant increase in leaf number, shoot and root length at a moderate level of salinity stress.

**Solute accumulation**

The main impact of NaCl stress on plant tissues is marked in terms of loss of intracellular water and osmotic damage. Osmotic stresses are associated with inhibition of cell growth by restricting wall extension and cellular expansion, leading to reduced plant growth. Production of free amino acids is important osmolytes contributing to osmotic adjustment in plants (Hajlaoui et al., 2010). Osmotic adjustment enables plants to maintain higher turgor pressure under salinity stress (Munns & Tester, 2008). Some studies showed that increasing external salt concentration induces free amino acids accumulation in the leaves and roots (Hajlaoui et al., 2010; Neto et al., 2009; Sheng et al., 2008) but to a lesser extent in arbuscular mycorrhizal plants (Sheng et al., 2011). Root colonization by AMF can induce major changes in the relative abundance of the major groups of organic solutes (Sheng et al., 2011), such as modifying the composition of carbohydrates (Augé et al., 1987) and inducing accumulation of specific osmolytes such as proline (Ruiz-Lozano et al., 1995), thus facilitating osmotic adjustment. Mycorrhizal colonization in plants raised the leaf concentrations of soluble sugars, reducing sugars, soluble protein, total organic acids, fumaric acid, acetic acid, oxalic acid, malic acid and citric acid, and decreased the concentrations of total free amino acids, proline, formic acid and succinic acid. These results suggest that the symbiosis affects the metabolic regulation of organic acids under saline conditions, involving enzymes from the tricarboxylic acid cycle, glyoxylate cycle or glycolysis, thus improving the energetic status of the plant and helping to mitigate the stress (Sheng et al., 2011).

Proline is an osmoprotectant that is synthesized by plants in response to stress, and thereby helps in maintaining the osmotic balance of the cell to alleviate the abiotic stress effect. It also plays key role in scavenging free radicals, stabilizing subcellular structures and buffering cellular redox potential under stresses (Ashraf, 2009). Previous studies have reported a higher proline concentration in arbuscular mycorrhizal plants in comparison with non-AMF plants at different salinity levels (Dudhane et al., 2011; Kumar et al., 2010; Talaat & Shawky, 2011). In contrast, other studies have reported that AMF plants accumulated significantly lower proline than non-AMF plants at various salinity levels (Borde et al., 2010; Jahromi et al., 2008; Rabie & Almadini, 2005; Sheng et al., 2011). Another important solute, glycine betaine \((N,N,N\text{-trimethylglycine betaine})\), also stabilizes the structure and activity of enzymes and protein complexes and maintains the integrity of membranes against the damaging effects of excessive salt (Rhodes et al., 2004). Increased accumulation of betaines in AMF-inoculated plants has been reported (Duke et al., 1986).

Soluble sugar accumulation for lowering osmotic potential is a common physiological response during salt stress. Al-Garni (2006) reported higher concentrations of sugars in *Phragmites australis* plants colonized by *Glomus fasciculatum*, than the non-inoculated plants. The concentration of soluble and reducing sugars decreased when salinity increased in both AMF-inoculated or non-inoculated maize plants, but at the same NaCl level, the AMF symbiosis favored sugar accumulation (Sheng et al., 2011). Many authors have reported the positive correlation between sugar accumulation and mycorrhization (Evelin et al., 2009; Feng et al., 2002; Ocon et al., 2007). The accumulation of high levels of sugars in AMF plants may be the result of an increase in photosynthetic capacity (Sheng et al., 2008; Wu et al., 2010). Accumulation of soluble sugars to adjust the osmotic potential of plants during salt stress constitutes an important plant protection mechanism (Evelin et al., 2009). Increased total carbohydrate content was positively correlated with mycorrhization of *P. australis* plants colonized by *G. fasciculatum* (Al-Garni, 2006), soybean plants colonized by *G. intraradices* (Porcel & Ruiz-Lozano, 2004) and *J. curcas* by AMF consortia (Kumar et al., 2010).

The regulation of organic acid metabolism in plants also plays a key role in salinity tolerance (Guo et al., 2009). AMF inoculation increases the accumulation of organic acids in maize leaves (Sheng et al., 2011). However, the effect of AMF symbiosis was different depending on organic acids. Concentrations of oxalic, acetic, fumaric, malic and citric acids increased, while formic and succinic acid levels decreased although lactic acid concentration was not significantly affected (Sheng et al., 2011). Furthermore, leakage of organic acids into the rhizosphere of AMF plants resulted in a decrease in soil pH, soil EC, organic carbon, and an increase in soil availability of N, P and K (Usha et al., 2004).

Other than organic acids, involvement of three main polyamines from plants such as putrescine, spermidine and spermine are supposed to play a role in plant responses to a variety of environmental stresses such as salinity, high osmolarity, hypoxia and oxidative stress.

Beneficial effects of AMF symbiosis under salinity may be due to alterations in basal energetic metabolism (Giri & Mukerji, 2004; Rabie & Almadini, 2005). Thus, changes in plant metabolism have also been reported in mycorrhizal (*G. mosseae*) maize plants grown at different salt levels (Sheng et al., 2011). Evelin et al. (2009) reported that maintenance of the photosynthetic apparatus via the accumulation of protective molecules and osmolytes and/or the upregulation of antioxidant metabolism by AMF suggests interesting biotechnological opportunities for improving agricultural productivity (Choudhary et al., 2011).

**Chlorophyll concentration**

Salinity stress decreases photosynthesis, often through affecting photosynthetic enzymes, chlorophyll, carotenoids and chloroplast structure (Chaves et al., 2009; Sheng et al., 2008). Reduction of chlorophyll content in leaves is common in response to increased salt stress. This may also be due to the synthesis of nitrogen compounds, such as proline, during stress, which consumes large amounts of nitrogen (Ashraf & Akram, 2009), suppression of specific enzymes that are responsible for the synthesis of photosynthetic pigments, reduction in the uptake of minerals (e.g., Mg) needed for chlorophyll biosynthesis (Evelin et al., 2009), and also increased activity of cell degrading chlorophyllase (Younis et al., 2008). The increase of photosynthetic ability
in mycorrhizal seedlings under salt stress could result from a lower intercellular CO₂ concentration (Sheng et al., 2008). In the presence of AMF, the antagonistic effect of Na on Mg uptake is counterbalanced and suppressed (Giri et al., 2003). Huang et al. (2011) showed higher chlorophyll contents in the leaves of mycorrhizal plants, confirming that the symbiosis plays a key role in modifying photosynthetic and metabolic activities. Campanelli et al. (2012) confirmed that the photosynthetic rate and chlorophyll content were higher in mycorrhizal plants than in non-mycorrhizal plants, and similar observations were also recorded in previous studies (Abdel Latef & Chaoxing, 2010; Borde et al., 2010; Busquets et al., 2010).

Several previous reports showed higher chlorophyll content in leaves of AMF plants under saline conditions (Abdel Latef & Chaoxing, 2010; Colla et al., 2008; Kaya et al., 2009). Wu et al. (2010) demonstrated a significant reduction in the net assimilation rate, transpiration and stomatal conductance in both AMF and non-AMF citrus plants under salt-stress. However, AMF alleviated the salt stress effect in citrus plants by maintaining higher net assimilation rate, transpiration and stomatal conductance than the non-AMF seedlings. AMF-inoculated plants under salt stress reached levels of photosynthetic capacity higher than those of non-stressed plants, showing that in this respect, mycorrhization is capable of fully counterbalancing stress (Zuccarini & Okurowska, 2008).

**Mineral nutrition**

The cycling of macro and micronutrients in an ecosystem is influenced by multiple interactions involving soil microbial populations (Barea et al., 2005; Dames & Ridsdale, 2012). AMF have the potential to improve the sustainability of agroecosystems through their fundamental roles in the efficiency of both nutrient cycling and soil aggregation processes. Mycorrhizas increase the uptake of the nutrients to plant roots mainly by diffusion, particularly in dry soil when diffusion rates are most limited (Marschner et al., 1997). Phosphate is one of the important elements driving the symbiosis (Maeda et al., 2006). Plant roots acquire P as inorganic orthophosphate (Pi) through different pathways, presence of Pi transporters in plants can be the major routes for P uptake (Balzergue et al., 2011). Because of phosphate’s low mobility and reduced availability in soil (Schachtman et al., 1998), plants have developed a variety of ways to cope with phosphate limitation. The most common one is the formation of symbiosis with AMF (Karandashov & Bucher, 2005). AMF colonized plants rely exclusively on the symbiotic route for phosphate acquisition (Smith et al., 2003). Plant phosphate status and AMF development are known to be linked, because high phosphate levels in the soil reduce fungal colonization within the root (Breuillìn et al., 2010), as well as carbon transfer toward the AMF (Olsson et al., 2010). Importantly, inactivation of the symbiotic plant phosphate transporters leads to fungal growth arrest (Javot et al., 2007; Maeda et al., 2006). In this regard, Kiers et al. (2011) have recently shown that more cooperative fungi, in terms of plant growth responses, cost of carbon per unit of P transferred, and resource hoarding strategies, are allocated more carbon.

Helber et al. (2011) reported high-affinity Monosaccharide Transporter2 (MST2) from *Glomus* sp. that functions at several symbiotic root locations. Sugars in plant cell wall can efficiently outcompete the Glc uptake capacity of MST2, proposing that they can serve as alternative carbon sources. The expression of MST2 closely correlates with that of the mycorrhiza-specific Phosphate Transporter4 (PT4). These outcomes highlight the symbiotic role of MST2 and support the hypothesis that the exchange of carbon for phosphate is tightly linked (Helber et al., 2011). The improvement of plant P uptake by AMF has been reported and was considered one of the main explanations for amelioration of stress in salt-affected AMF-colonized plants (Ruiz-Lozano et al., 2012).

Several mechanisms have been suggested by which the AMF plant can enhance growth and nutrient uptake (Miransari, 2010). The extra-radical hyphae assist plant roots to connect to the surrounding soil and increase the soil volume exploited by host plants and also enable plants to survive in nutrient- and/or water-depleted zones (Marschner et al., 1997). Thus, in low-nutrient conditions, AMF-colonized roots may have a greater uptake of relatively immobile macro and micronutrients (Azcón et al., 2003). Additionally, AMF roots often have not only increased length but also modified root architecture. Improved growth of AMF plants has been largely attributed to mycorrhizal-mediated P acquisition, since the addition of P fertilizer has similar effects in the absence of AMF. P has lowest mobility in soil, and thus often limits plant growth, particularly when soil water potential and P diffusion rate is lowered in dry or saline soils. It also tends to be precipitated by ions like Ca²⁺, Mg²⁺ and Zn²⁺ (Abdel Latef & Chaoxing, 2010; Evelin et al., 2009; Giri et al., 2007; Plenchette & Duponnois, 2005).

Saline conditions modify the uptake of mineral nutrients and nutrient balance (Giri et al., 2007). Na and Cl concentrations were lower in mycorrhizal plants than that in non-mycorrhizal plants. Some researchers have hypothesized that lower Na and Cl concentrations in plant tissues may be due to the capacity of the fungus to retain these ions in intra-radical fungal hyphae or to compartmentalize them in the root cell vacuoles (Al-Karaki, 2006). In *Acacia nilotica* plants, total accumulation of P, Zn and Cu was higher in AMF than in non-AMF plants under both control and medium salt stress conditions (Giri et al., 2007). AMF enhance the uptake of various nutrients in plants during salinity stress (Table 2).

Salinity interferes with nitrogen (N) acquisition and utilization by influencing different stages of N metabolism, such as, NO₃⁻ uptake, reduction and protein synthesis (Evelin et al., 2009). AMF enhance better assimilation of N by the host plants. However, the exact mechanism behind N uptake and its transfer from the fungus to the host plant is still not very clear (Evelin et al., 2009; Govindaraju et al., 2005). Hajiboland et al. (2010) observed lower calcium uptake in salt-affected non-AMF tomato plants, although AMF colonization significantly increased Ca uptake and the Ca:Na ratio of both leaves and roots.

Hammer et al. (2011) reported that *G. intraradices* can selectively take up elements such as K⁺, Mg²⁺ and Ca²⁺ while avoiding Na⁺ to keep internal K⁺:Na⁺ and Ca²⁺:Na⁺ ratios within narrow limits, despite concentration changes
Table 2. AMF-enhanced uptake of various nutrients in plants during salinity stress.

| Nutrients uptake improved | Host | AMF | References |
|---------------------------|------|-----|------------|
| K                         | Medicago sativa L. | Glomus viscosum H.T. Nicolson strain A6 | Campanelli et al. (2013) |
| P, K, Mg and Zn           | Sour orange (Citrus aurantium, L.) and Volkamer lemon (Citrus volkameriana Tan. and Pasq.) | Glomus intraradices | Khalil et al. (2011) |
| N, P, K, Ca and Mg        | Wheat | Glomus spp. | Talaat & Shawky (2011) |
| N, P, K⁺ and Ca²⁺         | Leymus chinesis | Glomus mosseae & G. geosporum | Zhang et al. (2011) |
| Enhanced P and K levels   | Lycopersicon esculentum | Glomus mosseae | Latef & Chaoxing (2010) |
| K⁺ and Mg²⁺               | Citrus tangerine Hort. ex Tanaka | Glomus mosseae | Wu et al. (2010) |
| P, K, Zn, Cu and Fe       | Parwal (Trichosanthes dioica Roxb.) | Glomus deserticola | Mathur et al. (2010) |
| P, Ca and K               | Solanum lycopersicum L. cultivars Behta and Piazar | Glomus intraradices | Hajiboland et al. (2010) |
| P, K and N                | Pepper (Capsicum annum cv. 11B 14) | Glomus clarum | Kaya et al. (2009) |
| N and P                   | Cajanus cajan (L.) Millsp. (pigeonpea) | Glomus mosseae | Garg & Manchanda, (2009) |
| K                         | Olive trees | Glomus mosseae, Glomus intraradices or Glomus claroideum | Porras-Soriano et al. (2009) |
| Enhanced K but low Na levels | Cucurbita pepo | Glomus intraradices | Colla et al. (2008) |
| Enhanced P, K, Zn and Cu  | Acacia nilotica | Glomus fasciculatum | Giri et al. (2007) |
| Enhanced P, K and Zn      | Glycine max (soybean) | Glomus etunicatum | Sharifi et al. (2007) |

Table 3. AMF-enhanced antioxidants production in crop plants under salinity stress conditions.

| Antioxidants activity enhanced | AMF | Host plants | References |
|-------------------------------|-----|-------------|------------|
| Leaf isoenzymes of SOD (Fe-SOD, Cu/Zn-SOD1, and Cu/Zn-SOD2) and CAT (CAT1 & CAT2) | Glomus mosseae | Suada salsa | Li et al. (2012) |
| SOD, CAT, POD and APX         | Glomus mosseae | Lycopersicon esculentum | Latef & Chaoxing, (2010) |
| CAT, SOD and root POD         | Glomus fasciculatum | Pennisetum glaucum | Borde et al. (2011). |
| CAT and POX                   | Glomus spp. | Wheat | Talaat & Shawky, (2011). |
| POD, CAT and SOD              | Glomus fasciculatum | Gmelina arborea Roxb. | Dudhane et al. (2011). |
| SOD, POD, ASA-POD, and CAT    | Glomus mosseae | Lycopersicon esculentum L. | Huang et al. (2010). |
| APX, CAT and SOD              | Glomus intraradices | Solanum lycopersicum L. cultivars | Hajiboland et al. (2010). |
| SOD, CAT and POX              | Glomus mosseae | Cajanus cajan (L.) Millsp. (pigeonpea) | Garg & Manchanda, (2009) |
| SOD, POD and APX              | Glomus mosseae | Lycopersicon esculentum | He et al. (2007) |

of several orders of magnitude in the growth environment. These selective mechanisms for ion uptake could partially alleviate salinity stress in host plants by improving their nutrition (Hammer et al., 2011). Campanelli et al. (2012) showed that AMF-mediated growth could be the result of an improvement in nitrogen status, as suggested by the SPAD (Chlorophyll Meter) values monitored during a glasshouse trial. The SPAD values were closely linked to leaf chlorophyll content and leaf N content (Esfahani et al., 2008; Netto et al., 2005). Mycorrhizal fungi had a positive influence in helping to maintain the potassium content at all salinity exposure levels (Campanelli et al., 2012). Potassium is important for water regulation, stomatal behavior and cell expansion (Evelin et al., 2009; Kaya et al., 2009); it also activates a range of enzymes, and Na cannot substitute it in this role (Giri et al., 2007). The positive influence of AMF on maintaining nutrient status and growth of plants grown under salt stress conditions could be regarded as a strategy for salinity tolerance in plants, particularly in nutrient poor soils.

Antioxidants production

Salinity stress induces oxidative stress in plants and resulted in generation of ROS such as superoxide radical (O₂⁻), hydrogen peroxide (H₂O₂), hydroxyl radical (·OH) and singlet oxygen (¹O₂). The activated oxygen species thus generated can cause damage to plant cell structure and function if not controlled by protective mechanisms. Plant cells use several mechanisms to minimize the oxidative damage caused by ROS (Ahmad et al., 2010; Ashraf, 2009; Jamil et al., 2011). The induction of ROS-scavenging enzymes, such as superoxide dismutase (SOD), catalase (CAT), peroxidase (POD) and ascorbate peroxidase (APX) is the most common mechanism for detoxifying the ROS generated during stress conditions. Apart from the salinity-induced antioxidative response, AMF per se could also induce activation of antioxidant defense enzymes. It has been shown by various authors that AMF symbiosis might enhance the activity of such antioxidant enzymes (CAT, POD, APX and SOD) and thus protect the plant from oxidative damage during salt stress (Evelin et al., 2009; Hajiboland et al., 2010; He et al., 2007). Table 3 shows the changes in the activity of various antioxidants by AMF-inoculation during salt stress. Borde et al. (2011) reported enhanced SOD activity in AMF-inoculated pearl millet grown under salinity, as compared with non-AMF plants, supporting the view that increased antioxidative enzyme production could be involved in the beneficial effects of AMF colonization on the
performance of plants grown under salt stress conditions. In tomato plants cultivated in soil with 0, 50 and 100 mM NaCl, AMF-alleviated salt induced reduction of growth and fruit yield (Abdel Latef & Chaoxing, 2010), and was accompanied by an enhancement of activity of SOD, CAT, POD and APX in leaves of both salt-affected and control plants. Similar results have been obtained previously by many other authors (Hajiboland et al., 2010; He et al., 2007; Huang et al., 2010; Kohler et al., 2010).

**Phyto-hormone signaling**

Phyto-hormones including cytokinins, ethylene, abscisic acid (ABA), auxin, jasmonic acid and salicylic acid can also act as signal molecules during the process of AMF symbiosis (Gutjahr & Paszkowski, 2009; Miransari et al., 2012). Understanding of such signaling and communicating molecules between AMF and the host plant can be useful for a more precise characterization of the AMF–plant symbiosis. Miransari et al. (2012) reviewed some of the most recent findings regarding the signaling effects of plant hormones on mycorrhizal fungal symbiosis. It is suggested that enhanced P uptake by AMF plants can increase cytokinins production in the roots. Increased concentrations of cytokinins may enhance shoot growth and root growth (Hause et al., 2007; Miransari et al., 2012). Plant hormones affect P uptake by changing root growth and sugar signaling (Rouached et al., 2010). This may indicate that plant hormones can affect the uptake of nutrients by altering plant physiology and morphology. The response of plants to P deficiency is regulated by soil P levels and mycorrhizal symbiosis through alteration in the expression of the related genes. The binding of transcription factors to the promotion of the P responsive genes can affect the plant’s response to P stress. Such effects are influenced by the related P pathways, allocation and homeostasis regulation in plant cells (Sobkowiak et al., 2012). This may also further elucidate the role of cytokinins during P stress in plant. Mukherjee & Ané (2011) investigated the effects of exudates produced by the germinating spores of *G. intraradices* and ethylene on the process of symbiosis in monocots and eudicots. The exudates induced morphological and physiological (activation of symbiotic genes) changes in the host plant roots. However, ethylene inhibits the process of mycorrhizal symbiosis by adversely affecting the effects of the exudates on the activation of symbiotic association (Miransari et al., 2012).

Strigolactones, released by plant roots, can regulate auxin transport in the plant by affecting auxin carriers (Koltai et al., 2010) or by affecting the secondary messengers, which are active in auxin signaling (Brewer et al., 2009; Ferguson & Beveridge, 2009). This suggests that auxin may indirectly affect the symbiotic level as it is influenced by strigolactones. Hence, the role of Indole Acetic Acid (IAA) in mycorrhizal symbiosis has been suggested (Ludwig-Müller, 2010, 2011). The role of jasmonic acid and salicylic acid to improve plant systematic acquired resistance is also well documented. The level of jasmonates increased in the mycorrhizal roots of plants including *Cucumis sativus* (Vierheilig & Piche, 2002), *Medicago truncatula* (Stumpe et al., 2005) and *Glycine max* (Meixner et al., 2005). Research has also indicated that AMF roots contain high amounts of jasmonic acid in comparison with non-AMF roots (Hause et al., 2007; Meixner et al., 2005). Shekoofeh et al. (2012) evaluated the role of AMF (*G. mosseae* and *G. intraradices*) and salicylic acid (0.2 mM)
in improving the salinity tolerance of green basil (Ocimum basilicum L.). They observed that mycorrhization and salicylic acid improved plant tolerance to salinity by decreasing lipid peroxidation and increasing proline, proteins, reduced sugars and K in aerial parts of basil.

Dodd & Pérez-Alfocea (2012), in their recent review, mentioned the role of soil microbes in improving the crop salt tolerance by altering phyto-hormonal root–shoot signaling. Production of ABA is essential for AM colonization in plant roots and it controls the formation of arbuscules. In contrast, some mycorrhizal fungi accumulate substantial quantities of ABA (Esch et al., 1994), which may be responsible for increased root ABA concentrations of some mycorrhizal plants (Danneberg et al., 1993; Jahromi et al., 2008). Martín-Rodríguez et al. (2011) concluded that ABA had a direct promotive role in arbuscule formation, while ethylene negatively regulated fungal development. Studies demonstrated that different plant hormones can also act as signal molecules and positively or adversely affect AMF symbiosis (Miransari et al., 2012). Plant hormones may control the level and hence specificity of mycorrhizal symbiosis but detailed investigation is required to unravel this mechanism.

Latest development in AM fungal research

The advancement of metagenomics and next generation sequencing technologies has characterized all-known AMF into a single clade, the phylum Glomeromycota, a sister group of Ascomycota and Basidiomycota on the basis of ribosomal RNA phylogeny (Krüger et al., 2012; Lanfranco & Young, 2012). However, phylogenetic reconstruction based on mitochondrial or protein coding nuclear sequence placed the phylum near to Mucorales. Furthermore, ribosomal RNA gene analysis has resulted in changes of AM fungal nomenclature. For example, the frequently studied gene analysis has resulted in changes of AM fungal nomenclature near to Mucorales. Furthermore, ribosomal RNA phylogeny (Kru¨ger et al., 2012; Lanfranco & Young, 2012). Plant hormones may control the level and hence specificity of mycorrhizal symbiosis but detailed investigation is required to unravel this mechanism.

**Conclusions**

In this review, we have shown that AMF play a key role in salinity tolerance by increasing host plant nutrition, and also by improving osmotic adjustment. Successful commercialization of AMF to improve crop growth and yield in saline soil needs further detailed investigation, particularly participation of cation proton antiporters, cyclic nucleotide-gated channels and the isolation of AM fungal salt-tolerant strains for development of a salt-tolerant inoculum. In recent years, our knowledge has improved considerably due to application of genomic technologies. However, several key questions still remain, specifically regarding how AMF invade plant tissues, suppress host defense, exchange nutrients, affect plant hormone signaling and the ecology of AMF in natural environments. Another desirable future goal will be to enhance the potential of AM fungal technology for sustainable agricultural and environmental management by identifying the key molecular players that are required for AM development and function.

**Declaration of interest**

The authors report no conflicts of interest. The authors alone are responsible for the content and writing of this article. Ashwani Kumar acknowledges the Claude Leon Foundation and National Research Foundation (NRF), South Africa, for providing financial support.

**References**

Abbas W, Ashraf M, Akram NA. (2010). Alleviation of salt-induced adverse effects in eggplant (Solanum melongena L.) by glycinebetaine and sugarbeet extracts. Sci Hortic, 125, 188–95.

Abdel Latef AAH, Chaoxing H. (2010). Effect of arbuscular mycorrhizal fungi on growth, mineral nutrition, antioxidant enzymes activity and fruit yield of tomato grown under salinity stress. Sci Hortic, 127, 228–33.

Ahmad P, Ijoh R, Sarwat M, Umar S. (2008). Responses of proline, lipid peroxidation and antioxidative enzymes in two varieties of Pisum sativum L. under salt stress. Int J Plant Production, 2, 353–66.

Ahmad P, Jaleel CA, Salem MA, et al. (2010). Roles of enzymatic and nonenzymatic antioxidants in plants during abiotic stress. Crit Rev Biotechnol, 30, 161–75.
Ahmad P, Hakim RK, Kumar A, et al. (2012a). Salt-induced changes in photosynthetic activity and oxidative defense system of three cultivars of mustard (Brassica juncea L.). Afr J Biotechnol, 11, 2694–703.

Ahmad P, Ashraf M, Younis M, et al. (2012b). Role of transgenic plants in agriculture and biopharming. Biotechnol Adv, 30, 524–40.

Ahmad P, Kumar A, Gupta A, et al. (2012c). Polyamines: role in plants under abiotic stress. In crop production for agricultural improvement. 491–512, Springer Netherlands.

Al-Garni SMS. (2006). Increasing NaCl-salt tolerance of a halophytic plant Phragmites australis by mycorrhizal symbiosis. Am-Euras J Agric Environ Sci, 1, 119–26.

Al-Karaki GN. (2006). Nursery inoculation of tomato with arbuscular mycorrhizal fungi and its role in alleviating salt stress in Medicago sativa L. var. icon. Symbiosis, 59, 1–12.

Alam M, Siddiqui S, Khan SM, et al. (2006). Induced drought tolerance in plants: recent advances. Biotechnol Lett, 28, 169–83.

Alam M, Akram NA. (2009). Improving salinity tolerance of plants through conventional breeding and genetic engineering: an analytical comparison. Biotechnol Adv, 27, 744–52.

Augé R, Schekel K, Wample R. (1987). Rose leaf elasticity changes in response to mycorrhizal colonization and drought acclimation. Physiol Plant, 70, 175–82.

Azcón R, Ambrosano E, Charést C. (2003). Nutrient acquisition in arbuscular mycorrhizal fungi and the influence of host physiological activity. Mycorrhiza, 11, 199–205.

Barde M, Dudhane MP, Jite PK. (2011). Effect of arbuscular mycorrhizal fungus Glomus intraradices strain on wheat yield, yield components, and nutrient uptake using arbuscular mycorrhizal fungi under field conditions. J Plant Physiol, 166, 617–25.

Barnes J, Ridgside C. (2012). What we know about arbuscular mycorrhizal fungi and associated soil bacteria. Afr J Biotechnol, 11, 13 753–60.

Banneberg G, Latus C, Zimmer W, et al. (2008). Improvement of vesicular-arbuscular mycorrhiza on phytohormone balances in maize (Zea mays L.). J Plant Physiol, 141, 33–9.

Bashir M, Panda S. (2001). Salt stress induced changes in growth and enzyme activities in germinating Phaseolus mungo seeds. Biol Plant, 44, 587–9.

Boddie J, Pérez-Alfocea F. (2012). Microbial amelioration of crop salinity stress. J Exp Bot, 63, 3415–28.

Borah J, Aaltonen R. (2001). Evaluation of the internal colonization of Allirixus canescens (Parsh) Nutt. roots by dark septate fungi and the influence of host physiological activity. Mycorrhiza, 11, 199–205.

Beauchamp VB, Walz C, Shafroth PB. (2009). Salinity tolerance and mycorrhizal responsiveness of native xeroriparian plants in semi-arid western USA. Appl Soil Ecol 43, 175–184.

Bhraskar C, Selvaraj T. (1997). Seasonal incidence and distribution of VA-mycorrhizal fungi in native saline soils. J Environ Biol, 18, 209–12.

Bonfante P, Genre A. (2008). Plants and arbuscular mycorrhizal fungi: an evolutionary-developmental perspective. Trends Plant Sci, 13, 492–8.

Borde M, Dudhane M, Jite PK. (2010). AM Fungi Influences the Photosynthetic Activity, Growth and Antioxidant Enzymes in Allium sativum L. under Salinity Condition. Notulae Scien Biolog, 2, 64–71.

Borde M, Dudhane M, Jite P. (2011). Growth photosynthetic activity and antioxidant responses of mycorrhizal and non-mycorrhizal bajra (Pennisetum glaucum) crop under salinity stress condition. Crop Prot, 30, 265–71.

Breuilin F, Schramm J, Hajirezaei M, et al. (2010). Phosphate systemically inhibits development of arbuscular mycorrhiza in Petunia hybrida and represses genes involved in mycorrhizal functioning. Plant J, 64, 1002–17.

Brewer PB, Dun EA, Ferguson BJ, et al. (2009). Strigolactone acts downstream of auxin to regulate bud outgrowth in pea and Arabidopsis. Plant Physiol, 150, 482–93.

Busquets M, Calvet C, Campubri A, Estuín V. (2010). Differential effects of two species of arbuscular mycorrhiza on the growth and water relations of Sparsodium junceum and Anthyllis cytisoides. Symbiosis, 52, 95–101.

Campanelli A, Rutta C, De Mastro G, Morone-Fortunato I. (2012). The role of arbuscular mycorrhizal fungi in alleviating salt stress in Medicago sativa L. var. icon. Symbiosis, 59, 1–12.

Campanelli A, Rutta C, De Mastro G, Morone-Fortunato I. (2013). The role of arbuscular mycorrhizal fungi in alleviating salt stress in Medicago sativa L. var. icon. Symbiosis, 59, 65–76.

Cekic FÖ, Ünyayar S, Ortas I. (2012). Effects of arbuscular mycorrhizal inoculation on biochemical parameters in Capsicum annuum grown under long term salt stress. Turkish J Botany, 36, 63–72.

Chaves M, Flexas J, Pinheiro C. (2009). Photosynthesis under drought and salt stress: regulation mechanisms from whole plant to cell. Ann Bot, 103, 551–60.

Choudhary D, Sharma K, Gaur R. (2011). Biotechnological perspectives of microbes in agro-ecosystems. Biotechnol Lett, 33, 1905–10.

Colla G, Roupheyl E, Cardarelli M, et al. (2008). Alleviation of salinity stress by arbuscular mycorrhizal in zucchini plants grown at low and high phosphorus concentration. Biol Fertil Soils, 44, 501–9.

Colmer T, Munns R, Flowers T. (2006). Improving salt tolerance of wheat and barley: future prospects. Animal Prod Sci, 45, 1425–43.

Daei G, Ardekani M, Rejali F, et al. (2009). Alleviation of salinity stress on wheat yield, yield components, and nutrient uptake using arbuscular mycorrhizal fungi under field conditions. J Plant Physiol, 166, 617–25.

Darius J, Ridsdale C. (2012). What we know about arbuscular mycorrhizal fungi and associated soil bacteria. Afr J Biotechnol, 11, 13 753–60.

Danneberg G, Latus C, Zimmer W, et al. (1993). Influence of vesicular-arbuscular mycorrhiza on phytohormone balances in maize (Zea mays L.). J Plant Physiol, 141, 33–9.

Dash M, Panda S. (2001). Salt stress induced changes in growth and enzyme activities in germinating Phaseolus mungo seeds. Biol Plant, 44, 587–9.

Dodd JC, Pérez-Alfocea F. (2012). Microbial amelioration of crop salinity stress. J Exp Bot, 63, 3415–28.

Dudhane MP, Borde MY, Jite PK. (2011). Effect of arbuscular mycorrhizal fungi on growth and antioxidant activity in Gmelina arborea Roxb. under salt stress condition. Notulae Sci Biolog, 3, 71–8.

Duke E, Johnson C, Koch K. (1986). Accumulation of phosphorus, dry matter and betaine during nacl stress of split root citrus seedlings colonized with vesicular arbuscular mycorrhizal fungi on zero, one or two halves. New Phytol, 104, 583–90.

Ercolfin F, Reinhardt D. (2011). Successful joint ventures of plants: arbuscular mycorrhiza and beyond. Trends Plant Sci, 16, 356–62.

Esch H, Hundeshagen B, Schneider-Poetsch H, Bothe H. (1994). Demonstration of abscisic acid in spores and hyphae of the arbuscular-mycorrhizal fungus Glomus and in the N₂-fixing cyanobacterium Anabaena variabilis. Plant Sci, 99, 9–16.

Esfahani M, Abbasi HRA, Rabiei B, Kavousi M. (2008). Improvement of nitrogen management in rice paddy fields using chlorophyll meter (SPAD). Paddy Water Environ, 6, 181–8.

Estrada B, Aroca R, Azcoñ-Aguilar C, et al. (2013a). Importance of native arbuscular mycorrhizal inoculation in the halophyte for successful establishment and growth under saline conditions. Plant Soil, 370, 175–85.

Estrada B, Aroca R, Maathuis FJ, et al. (2013b). Arbuscular mycorrhizal fungi native from a Mediterranean saline area enhance maize tolerance to salinity through improved ion homeostasis. Plant Cell Environ, 36, 1771–82.

Evelin H, Girì B, Kapoor R. (2013). Ultrastructural evidence for AMF mediated salt stress mitigation in Trigonella foenum-graecum. Mycorrhiza, 23, 71–86.

Evelin H, Kapoor R, Girì B. (2009). Arbuscular mycorrhizal fungi in alleviation of salt stress: a review. Ann Bot, 104, 1263–80.
Feng G, Zhang F, Li X, et al. (2002). Improved tolerance of maize plants to salt stress by arbuscular mycorrhiza is related to higher accumulation of soluble sugars in roots. Mycorrhiza, 12, 185–90.

Ferguson BJ, Beveridge CA. (2009). Roles for auxin, cytokinin, and strigolactone in regulating shoot branching. Plant Physiol, 149, 1929–44.

Fitter A, Helgason T, Hodge A. (2011). Nutritional exchanges in the arbuscular mycorrhizal symbiosis: implications for sustainable agriculture. Fungal Biol Rev, 25, 68–72.

Flowers TJ, Colmer TD. (2008). Salinity tolerance in halophytes. New Phytol, 179, 945–63.

Galvan-Ampudia CS, Testerink C. (2011). Salt stress signals shape the roots. Environ Exp Bot, 72, 39–50.

Giri B, Mukerji K. (2004). Mycorrhizal inoculant alleviates salt stress in Sesbania acactivitya and Sesbania grandiflora under field conditions: evidence for reduced sodium and improved magnesium uptake. Mycorrhiza, 14, 307–12.

Giri B, Kapoor R, Mukerji K. (2003). Influence of arbuscular mycorrhizal fungi and salinity on growth, biomass, and mineral nutrition of Acacia auriculiformis. Biol Fertil Soils, 38, 170–5.

Giri B, Kapoor R, Mukerji KG. (2007). Improved tolerance of Acacia nilotica to salt stress by arbuscular mycorrhiza. Glomus fasciculatum may be partly related to elevated K/Na ratios in root and shoot tissues. Microb Ecol, 54, 753–60.

Govindaraju M, Pfeffer PE, Jin H, et al. (2005). Nitrogen transfer in the arbuscular mycorrhizal symbiosis. Nature, 435, 819–23.

Guo L, Shi D, Wang D. (2009). The key physiological response to alkali stress by the alkali resistant halophyte Puccinellia tenuiflora is the accumulation of large quantities of organic acids and into the rhyzosphere. J Agron Crop Sci, 196, 123–35.

Gutjahr C, Paszkowski U. (2009). Weights in the balance: jasmonic acid and salicylic acid signaling in root–biotroph interactions. Mol Plant Microbe Interact, 22, 763–72.

Gutjahr C, Paszkowski U. (2013). Multiple control levels of root system remodeling in arbuscular mycorrhizal symbiosis. Frontiers in plant science, 4.

Hajboland R, Aliasgharzadeh N, Laeigh SF, Poschenrieder C. (2010). Colonization with arbuscular mycorrhizal fungi improves salinity tolerance of tomato (Solanum lycopersicum L.) plants. Plant Soil, 331, 313–27.

Hajlauh J, Aye NE, Garret JP, Denden M. (2010). Differential effects of salt stress, osmotic adjustment and solutes allocation on the basis of root and leaf tissue senescence of two silage maize (Zea mays L.) varieties. Ind Crops Prod, 31, 122–30.

Hammer EC, Nasr H, Pallon J, et al. (2011). Elemental composition of arbuscular mycorrhizal fungi at high salinity. Mycorrhiza, 21, 117–29.

Hause B, Mrozek S, Isayenkov S, Strack D. (2007). Jasmonates in arbuscular mycorrhizal interactions. Phytochemistry, 68, 101–10.

He ZQ, He CX, Zhang ZB, et al. (2007). Changes of antioxidative enzymes and cell membrane osmosis in tomato colonized by arbuscular mycorrhiza under NaCl stress. Colloids Surf B, 59, 128–33.

Helber N, Wippel K, Sauer N, et al. (2011). A versatile monosaccharide transporter that operates in the arbuscular mycorrhizal fungus Glomus sp. is crucial for the symbiotic relationship with plants. The Plant Cell Online, 23, 3812–23.

Hirrel MC. (1981). The effect of sodium and chloride salts on the germination of Gigaspora margarita. Mycologia, 610–7.

Hoffmann D, Veerheilig H, Schausberger P. (2011). Mycorrhiza-induced trophic cascade enhances fitness and population growth of an acarine predator. Oecologia, 166, 141–9.

Huang Z, He CX, He ZQ, et al. (2010). The effects of arbuscular mycorrhizal fungi on reactive oxdyrdal scavenging system of tomato under salt tolerance. Agric Sci China, 9, 1150–9.

Huang Z, Zou Z, He C, et al. (2011). Physiological and photosynthetic responses of melon (Cucumis melo L.) seedlings to three Glomus species under water deficit. Plant Soil, 339, 391–9.

Jahromi F, Aroca R, Porcel R, Ruiz-Lozano JM. (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. Microb Ecol, 55, 45–53.

Jamal A, Riaz S, Ashraf M, Foolad MR. (2011). Gene expression profiling of plants under salt stress. Crit Rev Plant Sci, 30, 435–58.

Javot H, Pennemta RV, Terzaghi N, et al. (2007). A Medicago truncatula phosphate transporter indispensable for the arbuscular mycorrhizal symbiosis. Proc Natl Acad Sci USA, 104, 1720–5.

Jin L, Sun X, Wang X, et al. (2010). Synergistic interactions of arbuscular mycorrhizal fungi and rhizobia promoted the growth of Lathyrus sativus under sulphate salt stress. Symbiosis, 50, 157–64.

Juniper S, Abbott L. (2006). Soil salinity delays germination and limits growth of hyphae from propagules of arbuscular mycorrhizal fungi. Mycorrhiza, 16, 371–9.

Kapoor R, Sharma D, Bhatnagar A. (2008). Arbuscular mycorrhizae in micropropagation systems and their potential applications. Sci Hortic, 116, 227–39.

Karan R, Subudhi PK. (2012). Approaches to increasing salt tolerance in crop plants. In: Abiotic stress responses in plants New York: Springer, 63–88.

Kanindson V, Buccher M. (2005). Symbiotic phosphate transport in arbuscular mycorrhizas. Trends Plant Sci, 10, 22–9.

Kashyap S, Sharma S, Vasudevan P. (2004). Role of bioinoculants in development of salt-resistant saplings of Morus alba (var. sujanpur) in vivo. Sci Hortic, 100, 291–307.

Kaya C, Ashraf M, Sonmez O, et al. (2009). The influence of arbuscular mycorrhizal colonisation on key growth parameters and fruit yield of pepper plants grown at high salinity. Sci Hortic, 121, 1–6.

Khalil HA, El-Shazly SM, Aboul Nasr AM. (2011). Improved growth of salinity-stressed citrus after inoculation with mycorrhizal fungi. Sci Hortic, 130, 624–32.

Kiegerl S, Cardinale F, Siligan C, et al. (2000). SIMKK, a mitogen-activated protein kinase (MAPK) kinase, is a specific activator of the salt stress-induced MAPK, SIMK. Plant Cell (Online), 12, 2247–58.

Kiers ET, Duhamel M, Beesetty Y, et al. (2011). Reciprocal rewards stabilize cooperation in the mycorrhizal symbiosis. Science, 333, 880–2.

Kim CK, Weber DJ. (1985). Distribution of VA mycorrhiza on halophytes on inland salt playas. Plant Soil, 83, 207–14.

Kohler J, Caravaca F, Roldán A. (2010). An AM fungus and a PGPR intensify the adverse effects of salinity on the stability of rhizosphere soil aggregates of Lactuca sativa. Soil Biol Biochem, 42, 429–34.

Koltai H, Dor E, Hershenhorn J, et al. (2010). Strigolactones’ effect on root growth and root-hair elongation may be mediated by auxin-efflux carriers. J Plant Growth Regul, 29, 129–36.

Koske R, Halvorson W. (1981). Ecological studies of vesicular–arbuscular mycorrhizae in a barrier sand dune. Canad J Bot, 59, 1413–22.

Kosuta S, Chabaud M, Lougnon G, et al. (2003). A diffusable factor from arbuscular mycorrhizal fungi induces symbiosis-specific MeENOD11 expression in roots of Medicago truncatula. Plant Physiol, 131, 952–62.

Krüger M, Krüger C, Walker C, et al. (2012). Phylogenetic reference data for systematics and phytoanatomy of arbuscular mycorrhizal fungi from phylum to species level. New Phytol, 193, 970–84.

Kumar A, Sharma S, Mishra S. (2009). Effect of alkalinity on growth performance of Jatropha curcas inoculated with PGPR and AM fungi. J Phytopathol, 1, 177–84.

Kumar A, Sharma S, Mishra S. (2010). Influence of arbuscular mycorrhizal (AM) fungi and salinity on seedling growth, solute accumulation, and mycorrhizal dependency of Jatropha curcas L. J Plant Growth Regul, 29, 297–306.

Kumar A, Gupta A, Azoou MM, et al. (2012). Genetic approaches to improve salinity tolerance in plants. In: Parvaiz Ahmad MA, Prasad MNV, eds. Salt stress in plants: signalling, omics and adaptations. NewYork: Springer, 63–78.

Kumar A, Sharma S, Mishra S, Dames JF. (2013). Arbuscular mycorrhizal inoculation improves growth and antioxidative response of Jatropha curcas (L.) under Na2SO4 salt stress. Plant Biosys, 1–10. [Epub ahead of print].

Lanfranco L, Young JPW. (2012). Genetic and genomic glimpses of the elusive arbuscular mycorrhizal fungi. Curr Opin Plant Biol, 15, 454–61.
Lee J, Young JPW. (2009). The mitochondrial genome sequence of the arbuscular mycorrhizal fungus *Glomus intraradices* isolate 494 and implications for the phylogenetic placement of *Glomus*. New Phytol, 183, 200–11.

Li T, Liu RJ, He XH, Wang BS. (2012). Enhancement of superoxide dismutase and catalase activities and salt tolerance of *Eulalophyta Suadae salsa* L. by mycorrhizal fungus *Glomus mosseae*. Pedosphere, 22, 217–24.

Ludwig-Müller J. (2010). Hormonal responses in host plants triggered by arbuscular mycorrhizal fungi. *Arbuscular mycorrhizas: physiology and function*. Netherlands: Springer, 169–90.

Ludwig-Müller J. (2011). Auxin conjugates: their role for plant development and in the evolution of land plants. *J Exp Bot*, 62, 1757–73.

Maeda D, Ashida K, Iguchi K, et al. (2006). Knockdown of an arbuscular mycorrhiza-inducible phosphate transporter gene of *Lotus japonicus* suppresses mutalistic symbiosis. *Plant Cell Physiol*, 47, 807–17.

Maillet F, Poinset V, André O, et al. (2011). Fungal lipo-choitoiligo-saccharide symbiotic signals in arbuscular mycorrhiza. *Nature*, 469, 58–63.

Marandi B, Rejali F, Daei G, et al. (2011). Arbuscular mycorrhizas enhance nutrient uptake in different wheat genotypes at high salinity levels under field and greenhouse conditions. *Comptes Rendus Biologies*, 334, 564–71.

Marschner P, Crowley DE, Higashi RM. (1997). Root exudation and physiological status of a root-colonizing fluorescent pseudomonad in mycorrhizal and non-mycorrhizal pepper (*Capsicum annuum* L.). *Plant Soil*, 189, 11–20.

Martin-Rodríguez JA, León-Morcillo R, Vierheilig H, et al. (2011). Ethylene dependent/ethylene independent ABA regulation of tomato plants colonized by arbuscular mycorrhiza fungi. *New Phytol*, 190, 193–205.

Mathur N, Singh J, Bohra S, et al. (2010). Arbuscular mycorrhizal fungi alleviate salt stress of *Trichosanthes dioica* Roxb. *Soil Plant Sci*, 60, 510–16.

McMillen BG, Juniper S, Abbott L. (1998). Inhibition of hyphal growth of a vesicular-arbuscular mycorrhizal fungus in soil containing sodium chloride limits the spread of infection from spores. *Soil Biol Biochem*, 30, 1639–46.

Meixner C, Ludwig-Müller J, Miersch O, et al. (2005). Lack of mycorrhizal autoregulation and phytohormonal changes in the super-nodulating soybean mutant *nfs*1007. *Planta*, 222, 709–15.

Meloni DA, Oliva MA, Martínez CA, Cambraia J. (2003). Photosynthesis and activity of superoxide dismutase, peroxidase and glutathione reductase in cucumber under salt stress. *Environ Exp Bot*, 49, 69–76.

Miranda D, Ulrichs C, Fischer G. (2010). Imbibition and percentage of germination of cape gooseberry (*Physalis peruviana* L.) seeds under NaCl stress. *Agronomia Colombiana*, 28, 29–35.

Miransari M. (2010). Contribution of arbuscular mycorrhizal symbiosis to plant growth under different types of soil stress. *Plant Biol*, 12, 563–9.

Miransari M, Abrishamchi A, Khoshbakhht K, Niknam V. (2012). Plant physiological status of a root-colonizing fluorescent pseudomonad in arbuscular mycorrhiza. *Nature*, 469, 564–71.

Murkute A, Sharma S, Singh S. (2006). Studies on salt stress tolerance of citrus rootstock genotypes with arbuscular mycorrhizal fungi. *Hortic Sci*, 33, 70–6.

Nawaz K, Ashraf M. (2009). Exogenous application of glycinebetaine modulates activities of antioxidant in maize plants subjected to salt stress. *J Agron Crop Sci*, 196, 28–37.

Neto ADA, Prisco JT, Gomes-Filho E. (2009). Changes in soluble amino-N, soluble proteins and free amino acids in leaves and roots of salt-stressed maize genotypes. *J Plant Interact*, 4, 137–44.

Netto AT, Campanstrini E, Oliveira JG, Bressan-Smith RE. (2005). Photosynthetic pigments, nitrogen, chlorophyll fluorescence and SPAD-502 readings in coffee leaves. *Sci Hortic*, 104, 199–209.

Noreen Z, Ashraf M. (2009a). Assessment of variation in antioxidative defense system in salt-treated pea (*Pisum sativum*) cultivars and its putative use as salinity tolerance markers. *J Plant Physiol*, 166, 167–74.

Noreen Z, Ashraf M. (2009b). Changes in antioxidant enzymes and some key metabolites in some genetically diverse cultivars of radish (*Raphanus sativus* L.). *Environ Exp Bot*, 67, 395–402.

Noreen Z, Ashraf M, Akram N. (2010). Salt induced regulation of some key antioxidant enzymes and physio-biochemical phenomena in five diverse cultivars of turnip (*Brassica rapa* L.). *J Agron Crop Sci*, 196, 273–85.

Ocón A, Hampp R, Requena N. (2007). Trehalose turnover during abiotic stress in arbuscular mycorrhizal fungi. *New Phytol*, 174, 879–91.

Olsson PA, Rahm J, Alia-shgharazad N. (2010). Carbon dynamics in mycorrhizal symbioses is linked to carbon costs and phosphorus benefits. *FEMS Microbiol Ecol*, 72, 125–31.

Oztekin GB, Tuzel Y, Tuzel IH. (2013). Does mycorrhiza improve salinity tolerance in graped plants? *Sci Hortic*, 149, 55–60.

Parniske M. (2008). *Arbuscular mycorrhiza*: the mother of plant root endosymbioses. *Nat Rev Microbiol*, 6, 763–75.

Pellegrino E, Bedini S. (2014). Enhancing ecosystem services in sustainable agriculture: Biofertilization and biofortification of chick-pea (*Cicer arietinum*) by arbuscular mycorrhizal fungi. * Soil Biol Biochem*, 68, 429–39.

Peng J, Li Y, Shi P, et al. (2011). The differential behavior of arbuscular mycorrhizal fungi in interaction with *Astragalus sinicus* L. under salt stress. *Mycorrhiza*, 21, 27–33.

Pfeiffer C, Bless H. (2006). Growth and nutrition of guayule (*Parthenium argentatum*) in a saline soil as influenced by vesicular-arbuscular mycorrhiza and phosphorus fertilization. *New Phytol*, 108, 215–21.

Plenchette C, Dupponnois R. (2005). Growth response of the saltbush *Atriplex nummularia* L. to inoculation with the arbuscular mycorrhizal fungus *Glomus intraradices*. *J Arid Environ*, 61, 535–40.

Porcel R, Ruiz-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, 1743–50.

Porcel R, Aroca R, Ruiz-Lozano J. (2012). Salinity stress alleviation using arbuscular mycorrhizal fungi. A review. *Agron Sustain Dev*, 32, 181–200.

Porras-Soriano A, Soriano-Martín ML, Porras-Piedra A, Azcoñ R. (2009). Arbuscular mycorrhizal fungi increased growth, nutrient uptake and tolerance to salinity in olive trees under nursery conditions. *J Plant Physiol*, 166, 1350–9.

Rabie G, Almadini A. (2005). Role of bioinoculants in development of salt-tolerance of *Vicia faba* plants under salinity stress. *Afr J Biotechnol*, 4, 210–22.

Raza SH, Athar HR, Ashraf M, Hameed A. (2007). Glycinebetaine-induced modulation of antioxidant enzymes activities and ion accumulation in two wheat cultivars differing in salt tolerance. *Environ Exp Bot*, 60, 368–76.

Rhodes D, Nadolska-Orczyk A, Rich P. (2004). Salinity, osmolytes and compatible solutes. *Salinity: environment-plants-molecules*. 181–204.

Rouached H, Arpat AB, Poirier Y. (2010). Regulation of phosphate starvation responses in plants: signaling players and cross-talks. *Mol Plant*, 3, 288–99.

Ruiz-Lozano J, Azcoñ R, Gomez M. (1995). Effects of arbuscular-mycorrhizal *Glomus* species on drought tolerance: physiological and nutritional plant responses. *Appl Environ Microb*, 61, 456–60.

Ruiz-Lozano JM, Porcel R, Azcoñ C, Aroca R. (2012). Regulation by arbuscular mycorrhizae of the integrated physiological response to salinity in plants: new challenges in physiological and molecular studies. *J Exp Bot*, 63, 4033–44.

Ruiz-Lozano JM, Collados C, Porcel R, et al. (2002). Identification of a cDNA from the arbuscular mycorrhizal fungus *Glomus intraradices* **AMF and its role in salinity stress alleviation** 473
that is expressed during mycorrhizal symbiosis and up-regulated by N fertilization. Mol Plant Microbe Interact, 15, 360–7.

Sabir P, Ashraf M, Hussain M, Jamil A. (2009). Relationship of photosynthetic pigments and water relations with salt tolerance of proso millet (Panicum miliaceum L.) accessions. Pak J Bot, 41, 2957–64.

Saeed Akram M, Ashraf M, Aisha Akram N. (2009). Effectiveness of potassium sulfate in mitigating salt-induced adverse effects on different physio-biochemical attributes in sunflower (Helianthus annuus L.). Flora-Morphol Distrib Funct Ecol Plants, 204, 471–83.

Sannazzaro AI, Ruiz OA, Alberto EO, Menéndez AB. (2006). Alleviation of salt stress in Lotus glaber by Glomus intraradices. Plant Soil, 285, 279–87.

Schachtman DP, Reid RJ, Alying S. (1998). Phosphorus uptake by plants: from soil to cell. Plant Physiol 116, 447–53.

Schubert S, Neubert A, Schierholt A, et al. (2009). Development of salt-resistant maize hybrids: the combination of physiological strategies using conventional breeding methods. Plant Sci, 177, 196–202.

Shekoofeh E, Sepideh H, Roya R. (2012). Role of mycorrhizal fungi and salicylic acid in salinity tolerance of Ocimum basilicum resistance to salinity. Afr J Biotechnol, 11, 2223–35.

Sheng M, Tang M, Zhang F, Huang Y. (2011). Influence of arbuscular mycorrhiza on organic solutes in maize leaves under salt stress. Mycorrhiza, 21, 423–30.

Sheng M, Tang M, Chen H, et al. (2008). Influence of arbuscular mycorrhizae on photosynthesis and water status of maize plants under salt stress. Mycorrhiza, 18, 287–96.

Shi Q, Zhu Z. (2008). Effects of exogenous salicylic acid on manganese toxicity, element contents and antioxidative system in cucumber. Environ Exp Bot, 63, 317–26.

Shokri S, Maadi B. (2009). Effects of arbuscular mycorrhizal fungus on the mineral nutrition and yield of Trifolium alexandrinum plants under salinity stress. J Agron, 8, 79–83.

Sinclair G, Charest C, Dalpé Y, Khanizadeh S. (2013). Influence of arbuscular mycorrhizal fungi and a root endophyte on the biomass and root morphology of selected strawberry cultivars under salt conditions. Canadian J Plant Sci, 93, 997–9.

Smith SE, Read DJ. (2008). Mycorrhizal symbiosis. Academic Press.

Smith SE, Smith FA, Jakobsen L. (2003). Mycorrhizal fungi can dominate phosphate supply to plants irrespective of growth responses. Plant Physiol, 133, 16–20.

Sokkowiak L, Bielewicz D, Malecka EM, et al. (2012). The role of the P1BS element containing promoter-driven genes in Pi transport and homeostasis in plants. Front Plant Sci, 3, 1–5.

Stockinger H, Walker C, Schüßler A. (2009). ‘Glomus intraradices’ DAOM197198’, a model fungus in arbuscular mycorrhiza research, is not Glomus intraradices. New Phytol, 183, 1176–87.

Stumpe M, Carsjens JG, Stenzel I, et al. (2005). Lipid metabolism in arbuscular mycorrhizal roots of Medicago truncatula. Phytochem, 66, 781–91.

Sukumar P, Legue V, Vayssieres A, et al. (2013). Involvement of auxin pathways in modulating root architecture during beneficial plant–microorganism interactions. Plant Cell Environ, 36, 909–19.

Talaat NB, Shawky BT. (2011). Influence of arbuscular mycorrhizae on yield, nutrients, organic solutes, and antioxidant enzymes of two wheat cultivars under salt stress. J Plant Nutr Soil Sci, 174, 283–91.

Tisserant E, Kohler A, Dozolme Seddas P, et al. (2012). The transcriptome of the arbuscular mycorrhizal fungus Glomus intraradices (DAOM197198) reveals functional tradeoffs in an obligate symbiont. New Phytol, 193, 755–69.

Türkan I, Demiral T. (2009). Recent developments in understanding salinity tolerance. Environ Exp Bot, 67, 2–9.

Uska K, Saxena A, Singh B. (2004). Rhizosphere dynamics influenced by arbuscular mycorrhizal fungus (Glomus deserticola) and related changes in leaf nutrient status and yield of Kinnon mandarin [King (Citrus nobilis) x Willow Leaf (Citrus deliciosa)]. Crop Pasture Sci, 55, 571–6.

Vierheilig H, Piche Y. (2002). Signalling in arbuscular mycorrhiza: facts and hypotheses. Adv Exp Med Biol, 505, 23–9.

Vinocur B, Altman A. (2005). Recent advances in engineering plant tolerance to abiotic stress: achievements and limitations. Curr Opin Biotechnol, 16, 123–32.

Wang W, Vinocur B, Altman A. (2003). Plant responses to drought, salinity and extreme temperatures: towards genetic engineering for stress tolerance. Planta, 218, 1–14.

Wilson GWT, Rice CW, Rillig MC, et al. (2009). Soil aggregation and carbon sequestration are tightly correlated with the abundance of arbuscular mycorrhizal fungi: results from long-term field experiments. Ecol Lett, 12, 452–61.

Wilson B, Ash G, Harper J. (2012). Arbuscular mycorrhizal fungi improve the growth and nodulation of the annual legume messina (Melilotus siculus) under saline and non-saline conditions. Crop Pasture Sci, 63, 164–78.

Wu QS, Zou YN, He XH. (2010). Contributions of arbuscular mycorrhizal fungi to growth, photosynthesis, root morphology and ionic balance of citrus seedlings under salt stress. Acta Physiol Plant, 32, 297–304.

Younis ME, Hasaneen MNA, Ahmed AR, El-Bialy DMA. (2008). Plant growth, metabolism and adaptation in relation to stress conditions. XXI. Reversal of harmful NaCl-effects in lettuce plants by foliar application with urea. Soil Sci Plant Nutr, 2, 83–95.

Zuccarini P, Okurowska P. (2008). Effects of mycorrhizal colonization and fertilization on growth and photosynthesis of sweet basil under salt stress. J Plant Nutr, 31, 497–513.

Zarei M, Paymaneh Z. (2013). Effect of salinity and arbuscular mycorrhizal fungi on growth and some physiological parameters of Citrus jambhiri. Arch Agron Soil Sci, 1–12. [Epub ahead of print].