Chapter 13
Role of Arbuscular Mycorrhiza in Amelioration of Salinity

R. Hajiboland

Abstract Soil salinity is world wide problem because it negatively affect plant productivity and yield of plants particularly in arid and semi-arid regions of the world. Excessive salts decline soil water availability for plants, inhibit plants metabolism and nutrients uptake and is also responsible for osmotic imbalance. All of these changes contribute to stunted growth and less productivity of plants. Exploitation of soil microorganisms for utilizing salt affected soils is of considerable interest to plant and soil scientists. Arbuscular mycorrhizal fungi (AMF) are ubiquitous soil microorganisms inhabiting the rhizosphere and establish a symbiotic relationship with the roots of many plants. Arbuscular mycorrhizal fungi are from integral components of all natural ecosystems and are known to occur in saline soils. Symbiotic association of a plant with AMF results in higher ability for taking up the immobile nutrients in nutrient-poor soils as well as improvement of tolerance to salinity. The possible mechanisms for alleviation of salinity stress by AMF include: (1) improvement of plant nutrient uptake, particularly P, (2) elevation of K:Na ratio, (3) providing higher accumulation of osmosolutes, and (4) maintaining higher antioxidant enzymatic activities. In addition, some aquaporin genes are up-regulated in mycorrhizal plants, causing significant increase in water absorption capacity of salt-affected plants. In contrast, expression of proline biosynthetic enzymes and LEA genes as stress indicators are maintained in mycorrhizal salt stressed plants suggesting that mycorrhizal plants are less susceptible to salinity because of salinity-avoidance mechanisms.

Keywords Antioxidant defense system • Aquaporins • Arbuscular mycorrhizal fungi (AMF) • Ion homeostasis • Halophytes • K:Na ratio • Mineral nutrition • Salinity

R. Hajiboland (✉)
Plant Science Department, University of Tabriz, 51666-14779 Tabriz, Iran
e-mail: ehsan@tabrizu.ac.ir

P. Ahmad et al. (eds.), *Salt Stress in Plants: Signalling, Omics and Adaptations*,
DOI 10.1007/978-1-4614-6108-1_13,

Saline soils occupy nearly 8% of the earth land surface and have been considered a serious limiting factor in crop production (Pitman and Läuchli 2004). Salinity causes primarily ion toxicity because of excessive amounts of Na or Cl and reduction of osmotic potential of the soil solution resulting in reduction of plant-available water (Munns and Tester 2008). Accumulation of Na causes ionic imbalance and/or ion toxicity, leading to serious disturbances in cell metabolism and functions and significant loss of plant productivity and quality (Munns and Tester 2008).

More than 80% of all higher plants are colonized by AMF (Strack et al. 2003). The root colonization by AMF is regulated both by plant and fungus and influenced also by environmental factors (Smith and Smith 1997). Mycorrhizal fungi exploit water and mineral salts from soils more effectively than plant roots and transfer them to host (Augé 2001). Arbuscular mycorrhiza fungi occur in saline soils (Aliasgharzadeh et al. 2001). Although salinity might affect the formation and function of mycorrhizae (Juniper and Abbott 1993), AM colonization has been observed in different species grown in saline soils (Asghari et al. 2005). Many studies have demonstrated that AMF inoculation improves growth of plants under salinity (Giri and Mukerji 2004; Sannazzaro et al. 2006; Hajiboland et al. 2010). Accordingly, AMF have been considered as bio-ameliorators of salt-affected soils (Rao 1998).

The physiological and biochemical mechanisms involving in the improvement of salt tolerance in AM plants are still unknown. Although increased tolerance to salinity in AM plants can be ascribed to improved mineral nutrition, especially that of P (Giri et al. 2003, 2007), it is not the only mechanism by which salt tolerance can be induced by AMF colonization. Improvements in physiological processes such as photosynthesis and water use efficiency have also been evidenced in mycorrhizal plants grown under salinity (Sheng et al. 2008). Thus, AMF mitigate the adverse effects of excess salt in plants in various ways.

In this chapter, the most important mechanisms involved in the alleviating salt stress by AM colonization in plants are discussed. Beside this subject, the effects of soil salinity on the viability and inoculation capability of AMF and the effect of different combinations of plant genotypes and fungi species or isolates on the beneficial effect of AM association under salinity are discussed. Finally, some evidences on the changes in the expression pattern of genes involve in salinity response of plants are presented.

Structure and Function of AM

Arbuscular mycorrhizal symbiosis is formed between vascular plants and members of Glomeromycota. Arbuscular mycorrhizal fungi are obligate symbiotic fungi and their evolution is dated back 460 million years ago suggesting that AMF played a crucial role in initial colonization of terrestrial ecosystems (Smith and Read 2008). The success in the evolution of AMF association has been attributed to the role of fungi in the capture of nutrients from the soil (Bonfante and Perotto 2000).

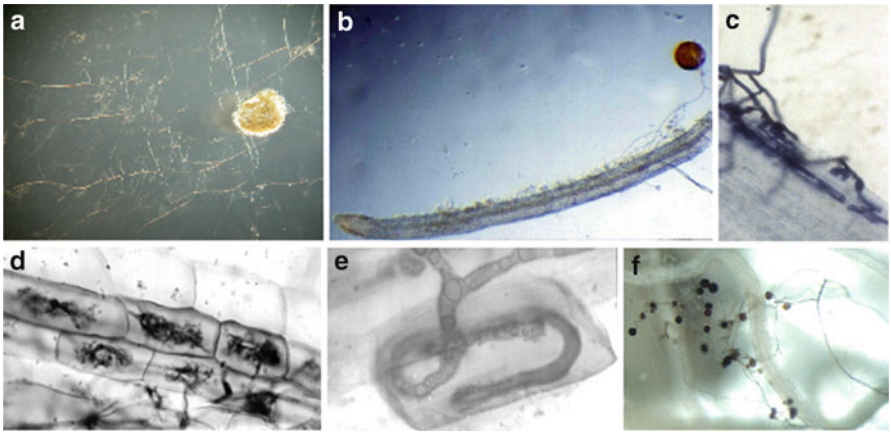

Fig. 13.1 Life cycle of an arbuscular mycorrhizal fungus. (**a**) Spore germination on water-agar. (**b**) Host recognition and pre-symbiotic growth in the proximity of a host root. (**c**) Appressoria formation on the root epidermis and colonization of the first root cortex layer. (**d**) Arbuscules in inner cortical cells. (**e**) Detail of an intracellular hypha, the so-called coil, in a cell of the root cortex. (**f**) Extraradical mycelium exploring the soil and forming the next spore generation (Retrieved from http://www.iab.kit.edu/heisenberg/286.php, 2012, Karlsruhe Institute of Technology, Germany)

Morphology, Life Cycle and Colonization of Roots

An established association between AMF and plant roots have three major components include the plant root that provides carbohydrates to the fungus, fungal structures within cortical cells (arbuscules and vesicles) that are directly interacted with the plant cytoplasm and the extraradical hyphae that are involved in the uptake of water and nutrients (Smith and Read 2008).

Arbuscules are fine and tree-like hyphal structures are separated from plant cell contents by plant plasma membrane and are responsible for the exchange of carbon and nutrients between fungi and the host cell. Vesicles found in some but not all genera of AMF and serve as carbon storage compartments for the fungi (Fig. 13.1). Formation of vesicles depends on environmental conditions (Smith and Read 2008).

Intraradical hyphae, extraradical hyphae and extraradical auxiliary cells are other important structures of AMF. The AM fungi spread its hyphae within root cortical cells by means of intraradical hyphae and form colonization units such as arbuscules and vesicles. Extraradical hyphae include branching hyphae that colonize the rhizosphere and are responsible for nutrients uptake, infective hyphae that run towards and along root surfaces and establish new entry points and reproductive hyphae that develop fertile spores after colonization of roots. Extraradical auxiliary vesicles are lipid storage compartments (Smith and Read 2008).

Under favorable environmental conditions, spores of AMF germinate and based on structural morphogenesis, show a sequence of steps include asymbiotic, presymbiotic and the symbiotic stages (Smith and Read 2008). In the asymbiotic stage, fungal spores are produced by the extraradical hyphae after establishment of symbiotic association with the host plant. In the presymbiotic stage, germinated spores grow toward the host root by production of hyphal branches that occurs before the formation of structures such as appressoria. Appressorium is an enlarged extraradical hyphal tip that attaches to the surface of the host plant root. This stage is influenced by root exudates such as organic acids, amino acids, carbohydrate monomers, phenolics, flavonoids or volatiles compounds. Plant hormones such as auxin also play a crucial role at this stage (Smith and Read 2008). The symbiotic stage refers to the penetration and development of the intraradical hyphae and the formation of arbuscles in the root cortex.

Mycorrhizal Specificity, Infectivity and Plant Responsiveness and Dependency

Arbuscular mycorrhizal fungi species are non-specific root endosymbionts and different fungal species can colonize a range of vascular plants from herbaceous to woody plants. However, these species are considerably different in both specificity and infectivity. Specificity refers to the ability of the fungus to colonize root cells of particular plant species, infectivity is the amount of colonization (Sylvia et al. 1998).

The relative performance of colonized and non-colonized plants is called ‘plant responsiveness’ or ‘fungus effectiveness’. Responsiveness diminishes as nutrients availability becomes saturating in the soil. The inability of a plant to grow in the absence of colonization has been defined as ‘dependence’ and is calculated as the level of nutrient availability below which non-colonized plants cease to grow (Janos 2007).

Difference in responsiveness can be divided into dependence and non-dependence components (Sawers et al. 2008). The essential distinction between responsiveness to mycorrhizas and dependence upon mycorrhizas is that the first is the conjoint property of plant species interacting with an AMF, but the second is a constitutive property of a plant species or genotype and is used to classify plants as facultative or obligately mycotrophic. Dependence is a plant attribute, but responsiveness or effectiveness are emergent properties of the interaction between plant and fungus species (Janos 2007).

Ecological Importance of AMF

Many studies have demonstrated that AM contributes to plant growth via capture of immobile soil nutrients particularly in poor soils. Enhancement of P, Zn, Cu, Mn,

and Fe uptake as well as plants growth improvement in nutrient-poor soils by AMF colonization are well documented (Smith and Read 2008). However, the benefits afforded plants from mycorrhizal symbioses are not confined to improvement of nutrients uptake. Mycorrhizal symbiosis is a key component in the adaptation of plants with adverse environmental conditions such as drought (Augé 2001; Miransari 2010), osmotic stress (Ruiz-Lozano 2003), salinity (Evelin et al. 2009; Porcel et al. 2012; Ruiz-Lozano et al. 2012) and biotic stresses (Pozo and Azcón 2007).

AMF Mediated Amelioration of Salinity Stress in Plants

Arbuscular mycorrhizas have been shown to decrease yield losses of plants in saline soils. This includes not only dry matter production, but also leaf chlorophyll content and photosynthesis rate compared with nonAM plants.

Effect of Soil Salinity on AMF Viability, Infectivity and Establishment of Symbiosis

Colonization of plant roots by AMF is influenced by various factors when plants grow under saline conditions. Reduction in AM colonization upon salinity has been reported in many plant species such as tomato (Zhi et al. 2010; Hajiboland et al. 2010), lotus (Sannazzaro et al. 2006) and acacia (Giri et al. 2003, 2007). Decline in AM colonization could be caused directly by salt-induced inhibition of spore germination (Hirrel 1981), hyphal growth and spreading (McMillen et al. 1998), reduction in the number of arbuscules (Pfeiffer and Bloss 1988); or indirectly by the effect on host plant.

Occurrence, Sporulation and Germination of AMF in Saline Soils

The abundance and distribution of AMF in different ecological regions and their relationship with soil properties have been studied by some researchers (Barrow et al. 1997; Bhardwaj et al. 1997; Cook et al. 1993; Aliasgharzadeh et al. 2001). Arbuscular mycorrhizal fungi occur naturally in saline environments (Allen and Cunningham 1983; Pond et al. 1984; Rozema et al. 1986; Ho 1987; Aliasgharzadeh et al. 2001). The AMF most commonly observed in saline soils are *Glomus* spp. (Allen and Cunningham 1983; Pond et al. 1984; Ho 1987). The occurrence of spores of almost only the *Glomus* spp. in the saline and sodic soils suggests that these fungi are the dominant root colonizers in such soils (Landwehr et al. 2002).

Formation of spores in soils depends on some physiological and ecological parameters (Redecker et al. 2000) and on the genotype of plants and fungi (Clapp et al. 1995). Published reports on the effect of soil salinity on spore production by

AMF are rare. Occurrence of relatively high spore numbers (mean of 100 per 10 g soil) has been reported in the highly saline soils (ECe ~162 dS m^{-1}) (Bhaskaran and Selvaraj 1997; Sengupta and Chaudhuri 1990; Aliasgharzadeh et al. 2001) while in other studies low or even zero spore populations were found in soils with ECe higher than 45 dS m^{-1} (Barrow et al. 1997; Hirrel 1981; Kim and Weber 1985). Stimulation of spore production under salinity as occurs in some Mucorales and *Aspergillus* species (Hirrel 1981; Tressner and Hayes 1971), or inhibition of spore germination (Juniper and Abbott 2006) both may cause accumulation of spores in saline soils. It means that the fungi may produce more spores at lower root colonization levels in severe saline conditions (Juniper and Abbott 1993).

Arbuscular mycorrhizal fungi are obligate biotrophs and it is mainly not possible to differentiate between direct and plant-mediated effects on their biology. Spore germination is the only phase of the AMF life cycle that is independent of the presence of a plant and can be studied in the absence of complex interactions with plant growth (Daniels and Graham 1976; Hepper 1979; Daniels and Trappe 1980). Germination of spores of an AMF consists of four distinct phases: hydration, activation, germ tube emergence and growth of hyphae (Tommerup 1984). The available data on the effects of salinity on germination of AMF spores indicate inhibition of spore germination by increasing concentrations of NaCl (Hirrel 1981; Estaun 1989, 1991; Juniper and Abbott 1993, 2006). It has been also demonstrated that low water potentials delay (i.e. increased the duration of the stages of germination preceding germ tube emergence) rather than prevent germination (Hirrel 1981) and the inhibitory effect of NaCl on spore germination is reversible (Hirrel 1981; Estaun 1989). Root exudates stimulate growth and alter the morphology of germ tubes (Mosse and Hepper 1975). Since root exudation is greatly influenced by soil chemistry and soil moisture availability (Rovira 1969), stimulatory effect on germ tube growth may be altered significantly under saline conditions.

In a recent work Juniper and Abbott (2006) demonstrated that, different isolates and species of AMF differ in the ability to germinate and grow in the presence of NaCl. Two isolates of *Scutellospora calospora* showed the highest germination at 300 mM NaCl, while isolates of *Acaulospora laevis* did not germinate in the presence of NaCl. The specific rate of hyphal extension was reduced by NaCl (Table 13.1). It was found that, spores of *Glomus sp.* Curragh 2 extracted from soil did not germinate at 300 mM NaCl, while intra-root propagules of this fungus germinated under these conditions. This may indicate different ecological roles for the two types of propagule. Authors stated also that overall production of hyphae was reduced in the presence of NaCl because germination was inhibited (Juniper and Abbott 2006). Increased production of the glycoprotein glomalin is related to suboptimal mycelium growth (Hammer and Rillig 2011).

The Effect of Salinity on the Formation of Mycorrhizas and Establishment of Symbiosis

Several works suggest that formation of mycorrhizas is reduced by soil salinity (Hirrel and Gerdemann 1980; Ojala et al. 1983; Poss et al. 1985; Duke et al.

Table 13.1 Percentage of maximum germination of spores of AM fungi, lengths of hyphae produced from spores (mm) and rates of hyphal extension (mm day^{-1}) from spores or pieces of colonized root in various species and isolates of AM fungi

Parameters	Germination			Length of hyphae			Rate of hyphal extension		
NaCl treatment (mM)	0	100	300	0	100	300	0	100	300
Gigaspora decipiens (WUM 6–1)	100[a]	64[b]	6[c]	400[a]	152[b]	0	17.4	5.8	0.1
Scutellospora calospora (WUM 12–2)	97[a]	100[a]	97[a]	405[a]	148[b]	0	19.2	11.5	3.0
Scutellospora calospora (WUM 12–3)	100[a]	85[a]	92[a]	410[a]	205[a]	82[c]	33.1	10.1	0.9
Glomus sp. Curragh 2 (WUM 23–1)	100[a]	80[a]	0	33[a]	18[b]	0	0.8	0.5	0.2

Data of each raw within each parameter followed by the same letter are not significantly different ($P<0.05$). From Juniper S, Abbott LK (1993) Vesicular-arbuscular mycorrhizas and soil salinity. Mycorrhiza 4:45–57, with permission

1986; Rozema et al. 1986; McMillen et al. 1998; Giri et al. 2003, 2007; Sannazzaro et al. 2006; Juniper and Abbott 2006; Sheng et al. 2008; Zhi et al. 2010; Hajiboland et al. 2010). However, other workers observed no inhibitory effect of salinity on the formation of mycorrhizas (Duke et al. 1986; Hartmond et al. 1987; Copeman et al. 1996; Yano-Melo et al. 2003). Although salinity may result in no change in the percentage of mycorrhizal roots, the total length of mycorrhizal root decreases with increasing salinity because of decreased total root growth (Poss et al. 1985). In the study on banana plants (Yano-Melo et al. 2003), salinity did not negatively influence AMF colonization expressed as percentage, but the total length of AMF-colonized roots was reduced because of decline in total root length by salinity. In this work, the increase of soil ECe stimulated root colonization by *G. clarum* and *G. etunicatum* at soil ECe up to ~5 dS m^{-1} and that by *A. scrobiculata*, up to 7.39 dS m^{-1}. Similar results were reported for tomato plants (Copeman et al. 1996).

Apart from the salt-induced changes in the hyphal morphology that affect their infective capacity (Juniper and Abbott 1993, 2006), physiological changes in the host plants caused by soil salinity may directly affect their colonization. In this respect it is important to differentiate between the primary infection, i.e. first entry into the root by the fungus, and secondary infection that occurs after ramnification of fungal hyphae from sites of initial colonization (Wilson 1984). Initial infection is dependent on germination of spores or other fungal propagules, growth of hyphae and entry into the plant root. Each of these stages can be a limiting step in the formation of mycorrhizas (Bowen 1987). Three forms of AMF propagules are responsible for colonization include AMF spores, mycorrhizal roots or root fragments and the mycelia. The relative importance of these propagules depends strongly on the environmental conditions (Juniper and Abbott 2006). Under salinity conditions, loss of viability of these propagules is a critical factor in the survival of AMF (Dixon et al. 1993).

Physiology of the host plant influences strongly the secondary infection, because for the spread of hyphae fungus needs photosynthates translocated from the plant at the arbuscules or via the internal hyphae. Apart from the toxic effects of specific ions such as sodium and chloride and physiological drought, photosynthesis *per se* is influenced negatively by salinity and reduction of the availability of photosynthates affects mycorrhizal development and function. Reduction in root growth with increasing salinity (Hirrel and Gerdemann 1980; Ojala et al. 1983; Poss et al. 1985) may also lower the probability of contact between roots and fungal hyphae and thus decrease colonization levels. Colonization of roots in the earlier growth stages is independent of root density, while after formation of initial mycorrhizas the probability of secondary hyphae encountering and infecting roots is highly dependent on root density (Abbott and Robson 1984).

With increasing concentration of toxic ions in the soil, this factor becomes more important limitation for plant growth but the availability of nutrients such as phosphorus becomes a progressively less important limitation. Under these conditions, allocation of limited photosynthates to maintain mycorrhizal association caused strong growth reduction unless there are non-nutritional benefits of AMF to the plant (Allen et al. 1981).

In some studies salt treatments were applied on plants grown on soil with a native population of AMF and, therefore, the plants were presumably colonized before the imposition of the salt stress. In other works, mycorrhizal seedlings were transplanted into saline soil (Pfeiffer and Bloss 1988). In all these cases, there was sufficient time between inoculation and imposition of salt stress, therefore, the effect of salinity on initial formation of mycorrhizas could not be evaluated. In perennial plants such as orchard trees even the age of association is important determinant on the extent to which mycorrhizal plants are influenced by salinity. This could explain contradictory results obtained by different authors (e.g. by Duke et al. 1986; Hartmond et al. 1987). In the older associations, there is much more opportunity for mycorrhizas to develop in the absence of salinity stress. Even if starting salt treatment retards hyphal growth in soil and thus formation of new entry points, colonization density increases because hyphal growth continues in the intercellular spaces of the root cortex. In addition, various AMF isolates used by different authors differ in their ability to grow under saline conditions (Estaun 1991).

Effect of AMF on Plant Growth and Performance in Saline Soils

Higher dry matter production in mycorrhizal plants under salt stress conditions has been reported by many authors in different plant species.

Plants Dry Matter Production

Root colonization by *G. mosseae* enhanced growth of maize plants irrespective to the level of P with and without NaCl (Feng et al. 2002). In tomato, salt stress

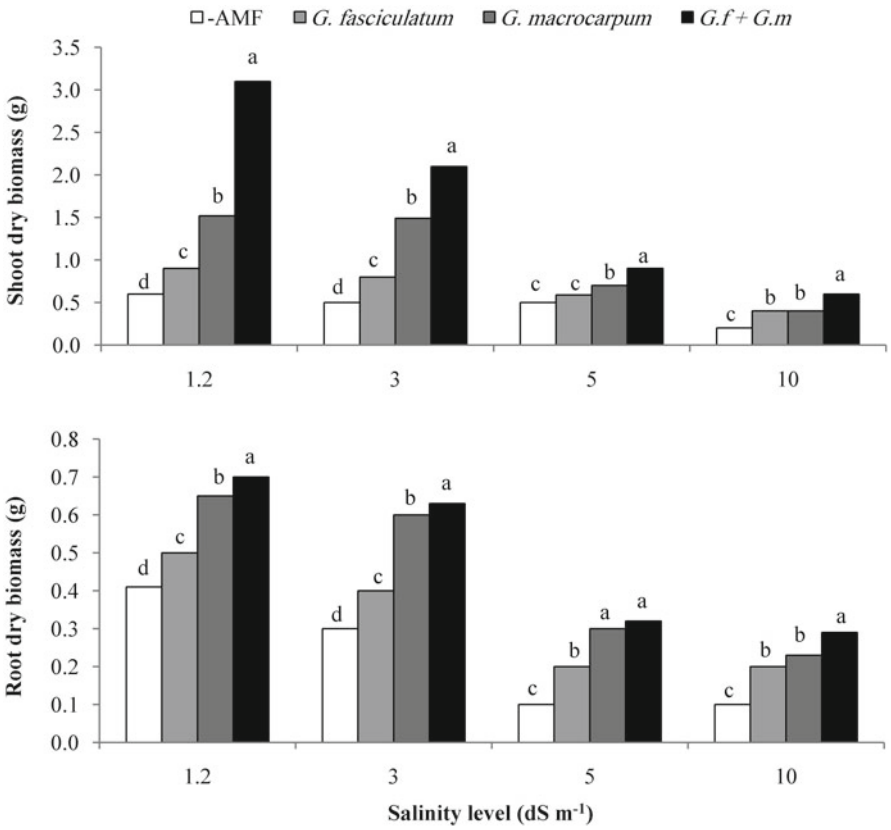

Fig. 13.2 Shoot and root dry biomass production (g) as affected by mycorrhizal colonization and salinity in acacia (*Acacia nilotica*) plants. *Bars* indicated by the same letter within each salinity level are not significantly different ($P < 0.05$) (From Giri B, Kapoor R, Mukerji KG (2003) Influence of arbuscular mycorrhizal fungi and salinity on growth, biomass, and mineral nutrition of *Acacia auriculiformis*. Biol Fertil Soil 38:170–175, with permission)

significantly reduced dry matter of roots, stems, leaves, and total biomass and leaf area compared with the control treatment (Abdel-Latef and Chaoxing 2011). Effect of AMF on dry matter of tomato plants was more pronounced in the biomass of shoot than root likely due to the allocation of greater proportion of carbohydrates to the shoot compared with root in AM plants (Shokri and Maadi 2009; Abdel-Latef and Chaoxing 2011).

In acacia (*Acacia nilotica*) plants, root and shoot dry weights decreased as soil salinity increased and there was a significant influence of AM inoculation on plant growth irrespective to the salinity levels. Although high salinity levels reduced production of root and shoot biomass in both AM and nonAM plants, dry matter production was higher in AM plants (Fig. 13.2) (Giri et al. 2003, 2007). Growth improvement of *Lotus glaber* plants by *G. intraradices* was more obvious under 200 mM NaCl (Sannazzaro et al. 2006) demonstrates the capacity of the AMF to realize its symbiotic activity particularly under stress conditions.

Arbuscular mycorrhizal colonization enhanced salt tolerance of olive plants and improved its growth and nutrient acquisition (Porras-Soriano et al. 2009). Inoculating olive plantlets with *Glomus mosseae*, *Glomus intraradices* or *Glomus claroideum* increased growth and the ability to take up N, P, and K from both saline and non-saline media and improved also survival rate of plantlets after transplantation. Salt stress reduced stem diameter, number and length of shoots and nutrient content of plants, but AMF colonization alleviated all of these negative effects. Inoculation by *G. mosseae* increased shoot and root growth by 163% and 295% in the non-saline medium respectively, while the corresponding values for salinized plants were by 239% and 468% under saline conditions (Porras-Soriano et al. 2009). This finding confirmed again higher effectiveness of AMF under stress compared with non-stress conditions.

Pearl millet (*Pennisetum glaucum*) plants inoculated with AMF had significantly higher leaf number, shoot and root length under moderate level of salinity stress and both plant fresh and dry weight increased significantly in AM plants at all levels of salinity stress (Borde et al. 2011). A significant shoot dry weight increment was observed in *Theobroma cacao* inoculated with AMF (Chulan and Martin 1992). In lettuce plants and at all examined salinity levels, growth was positively influenced by AM colonization (Ruiz-Lozano and Azcón 2000). In citrus plants growth parameters of AM inoculated plants were significantly superior over non-inoculated control particularly under higher salinity level (Khalil et al. 2011).

A field experiment was under taken to study the effect of inoculation with *Glomus macrocarpum* and salinity on growth of *Sesbania aegyptiaca* and *S. grandiflora* (Giri and Mukerji 2004). It was observed that, AM seedlings had significantly higher production of root and shoot biomass compared with nonAM plants when grown under saline conditions. The number of nodules was also significantly higher in AM than nonAM plants (Giri and Mukerji 2004).

Leaf Chlorophyll Concentration

Arbuscular mycorrhizal inoculation influences positively chlorophyll concentration of leaves. Chlorophyll concentrations are usually reduced by salinity because of suppression of specific enzymes responsible for the synthesis of photosynthetic pigments (Murkute et al. 2006). Reduction in the uptake of minerals such as Mg following an antagonistic effect of Na on Mg absorption needed for chlorophyll biosynthesis also reduces the chlorophyll concentration in the leaf (Sheng et al. 2008). In the presence of mycorrhiza, the antagonistic effect of Na on Mg uptake is diminished (Giri et al. 2003) and mycorrhizal plants have shown greater absorption of Mg (Wu et al. 2010).

Mycorrhizal maize plants treated with 100 mM NaCl had 81% higher chlorophyll concentration at low P supply level and 15% at sufficient P supply than non-mycorrhizal plants (Feng et al. 2002). In acacia plants salinity decreased leaf chlorophyll concentration of nonAM plants and chlorophyll content was higher in AM than nonAM plants (Giri et al. 2003). In tomato increasing salinity caused

reduction of chlorophyll content compared with control plants. Mycorrhizal colonization significantly improved chlorophyll concentration in comparison to the nonAM plants under both control and saline conditions (Abdel-Latef and Chaoxing 2011). Higher chlorophyll content in leaves of AM plants under saline conditions has been also observed by other authors (Colla et al. 2008; Kaya et al. 2009; Hajiboland et al. 2010).

Photosynthesis

Chlorophyll a fluorescence analysis reveals salt-induced structural and functional disruption of photosynthetic apparatus and damage to the PSII (Baker 2008). An improvement of photochemical parameters by AMF colonization was observed in salt affected tomato plants (Hajiboland et al. 2010). However, these parameters never were higher than nonAM plants without salt treatment (Fig. 13.3). This implies that the AMF colonization acted only for maintenance of photochemical capacity in stressed leaves and did not increase its potential for energy trapping (Hajiboland et al. 2010).

Photosynthesis is one of the primary processes to be affected by salt stress (Chaves et al. 2009). A significant reduction in the net assimilation rate, transpiration and stomatal conductance in both nonAM and AM citrus was found in salt-stressed plants (Wu et al. 2010). However, AM seedlings had significantly higher net assimilation rate, transpiration and stomatal conductance than the nonAM seedlings under salt stress. Similar results were obtained by Ruiz-Lozano et al. (1996), Sheng et al. (2008) and Hajiboland et al. (2010) under salt stress (Table 13.2). Inoculated plants under salt stress reach levels of photosynthetic capacity even superior to those of non-stressed plants (Zuccarini and Okurowska 2008). Arbuscular mycorrhizal plants have often higher CO_2 assimilation capacity because of elevated stomatal conductance. AM plants have greater sink strength of roots and this has been suggested as a reason for the often observed mycorrhizal promotion of stomatal conductance (Augé 2000). Elevated stomatal conductance due to mycorrhizal colonization of roots caused higher water loss in AM plants, however, water relations are not disrupted (Hajiboland et al. 2010). Higher shoot water potential and lower concentration of ABA in xylem sap observed in AM plants at low soil water potential (Augé et al. 2008) demonstrated an improved water uptake in AM plants because of changes in root morphology and fineness (Wu et al. 2010).

Root Growth

Roots are involved in sensing conditions in the soil environment (Davies and Zhang 1991) and are the site for exchange of carbohydrate and mineral nutrients between AMF and host plant. Root production of growth regulators that influence plant metabolism is reduced under salinity that is likely the main cause of growth inhibition in salinized plants (Amzallag 1997). Colonization by AMF improves not only

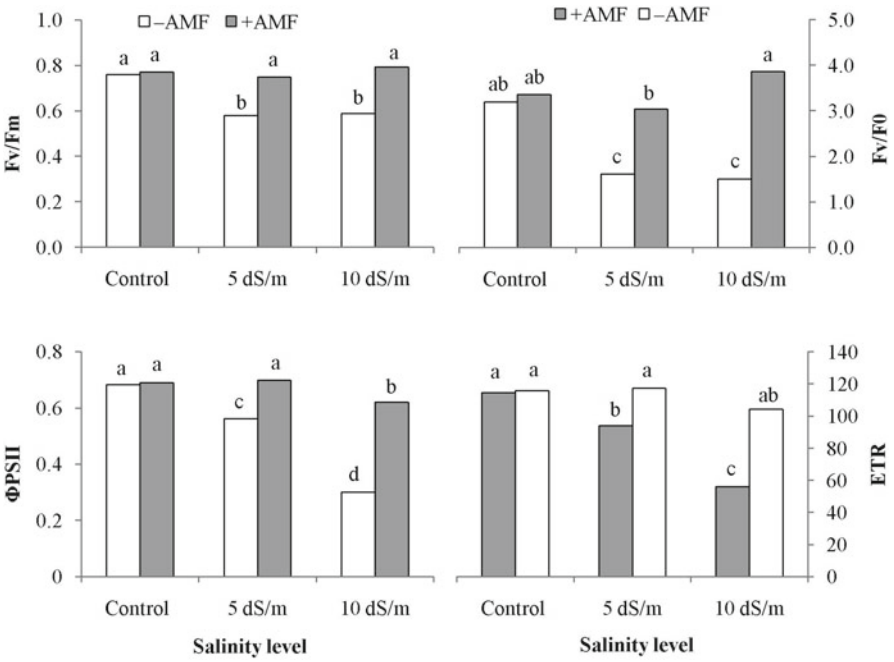

Fig. 13.3 Changes in chlorophyll fluorescence parameters (F_v/F_m: maximum quantum yield of PSII, F_v/F_0: the ratio of variable to maximum fluorescence, Φ_{PSII}: effective quantum yield of PSII and ETR: linear electron transport rate) in the leaves of tomato (*Solanum lycopersicum* cv. Behta) plants grown at different levels of salinity and inoculated with *Glomus intraradices*. *Bars* indicated by the same letter are not statistically different ($P<0.05$) (From Hajiboland R, Aliasgharzadeh N, Laiegh SF, Poschenrieder C (2010) Colonization with arbuscular mycorrhizal fungi improves salinity tolerance of tomato (*Solanum lycopersicum* L.) plants. Plant Soil 331:313–327with permission)

Table 13.2 Changes in gas exchange parameters of the leaves of tomato (*Solanum lycopersicum* cv. Behta) plants grown at different levels of salinity and inoculated with *Glomus intraradices*

		Salinity (dS m^{-1})		
		Control	5	10
Net assimilation rate (μmol m^{-2} s^{-1})	−AMF	6.51^a	4.58^b	2.04^c
	+AMF	6.39^a	6.37^a	3.59^b
Transpiration rate (mmol m^{-2} s^{-1})	−AMF	3.20^b	2.39^c	0.59^e
	+AMF	4.16^a	3.10^b	1.71^d
Stomatal conductance (mmol m^{-2} s^{-1})	−AMF	55^b	33^c	7^e
	+AMF	58^b	49^b	19^d

Data within each parameter indicated by the same letter are not statistically different ($P<0.05$). From Hajiboland R, Aliasgharzadeh N, Laiegh SF, Poschenrieder C (2010) Colonization with arbuscular mycorrhizal fungi improves salinity tolerance of tomato (*Solanum lycopersicum* L.) plants. Plant Soil 331:313–327, with permission

Table 13.3 Effect of inoculation of citrus (*Citrus tangerine*) seedlings with *Glomus mosseaes* on root morphology under control and salinity (100 mM NaCl) treatments

		Root length (cm)	Root projected area (cm^2)	Root surface area (cm^2)	Root average diameter (mm)	Root volume (cm^3)
Control	−AMF	175^{c}	9.59^{b}	30.1^{b}	0.55^{a}	0.41^{b}
	+AMF	221^{a}	12.07^{a}	37.9^{a}	0.55^{a}	0.52^{a}
Salinity	−AMF	125^{d}	6.58^{c}	20.7^{c}	0.54^{a}	0.28^{c}
	+AMF	188^{c}	9.71^{b}	30.5^{b}	0.53^{a}	0.40^{b}

Same letter within each column indicates no significant difference among treatments. From 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, with permission

growth of aerial parts but also affects root growth considerably. Arbuscular mycorrhizal association alters morphology of root in a structural, spatial, quantitative and temporal manner (Kapoor et al. 2008). It was observed that, mycorrhizal citrus seedlings had greater root length, root surface and projected area than the nonAM control seedlings under NaCl stress (Table 13.3) (Wu et al. 2010). Similar results have been observed in grapevine, apple, pepper, maize, zucchini and beach plum (Locatelli et al. 2002; Aguin et al. 2004; Schroeder and Janos 2005; Zai et al. 2007). In addition, mycorrhizal association decreases the meristematic activity of root apices and thus leads to an increase in the number of adventitious roots (Berta et al. 1993). In acacia, the number of lateral roots was significantly greater in AM than nonAM plants (Giri et al. 2003). It was also suggested thatAM colonization prolongs the life of rootlets and stimulates them to branch. This results in production of greater root system and higher total potential absorbing surface (Khalil et al. 2011). The importance of increased root surface area in enhancing nutrient uptake capacity is well known, and can be involved in stimulation of growth in AM plants. The improvement of AM root morphology is often attributed to a modified balance of growth regulators such as cytokinins and gibberellins (Berta et al. 1993). Arbuscular mycorrhizal fungi may also provide the host plant with growth hormones, including auxins, cytokinins, gibberellins and vitamins which also may affect plant growth (Barea and Azcón-Aguilar 1982).

Mycorrhizal Dependency of Plants

Although in many cases AM colonization was reduced with increasing salinity, the dependency of plants on AMF was increased (Giri and Mukerji 2004; Miranda et al. 2011). It indicates that association between AMF and plants was strengthened in saline environment once the association was established. This demonstrates the ecological importance of AM association for plants survival and growth in saline soils. Indeed under salt stress conditions, plants need mycorrhiza for both acclimatization and continued nutrient uptake during progressive growth stages (Giri and Mukerji 2004).

Effect of AMF on Mineral Nutrition of Salinized Plants

It has been widely believed that alleviation of salt stress by AMF is mainly the result of an improvement in plant P nutrition (Hirrel and Gerdemann 1980). Phosphorus concentration in plant tissues is rapidly lowered under saline conditions because phosphate ions precipitate with Ca^{2+} ions in saline soil and become unavailable to plants (Marschner 2012). Decline in plants P concentration at increased salinity levels is the result of both reduced P uptake and transport into shoot (Al-Karaki et al. 2001).

Arbuscular mycorrhizal fungi have been shown to positively influence the composition of mineral nutrients of plants under salt stress conditions (Al-Karaki and Clark 1998; Giri et al. 2003, 2007). Mycorrhizae increase particularly uptake of the nutrients that move to plant roots mainly by diffusion, especially in dry soil when nutrient diffusion rates are most limited (Marschner 2012). The enhancement of plant P uptake by AMF has been frequently reported and considered as one of the main reasons for amelioration of growth in salinized plants colonized by AMF (Al-Karaki 2000; Ruiz-Lozano and Azcón 2000). Enhanced uptake of P by AMF in salt-affected plants may reduce the negative effects of Na and Cl ions by maintaining membrane integrity, thus facilitates selective ion intake as well as compartmentalization within vacuoles and thereby, preventing ions from interference with plant metabolic pathways (Evelin et al. 2009).

The external hyphae of AMF deliver up to 80% of plants P requirement (Marschner and Dell 1994). Mycorrhizal uptake can even replace completely direct uptake by plant transporters possibly following loss of function of the direct uptake pathway in roots colonized by AMF (Smith et al. 2003). The extended network of AMF hyphae allows AM roots to explore more soil volume than nonAM plants. Indeed, AM hyphae extend beyond the depletion zones around roots and acquire nutrients that are several centimeters away from the root surface, and thus suppress the adverse effect of salinity stress (Smith and Read 2008).

In a field experiment conducted to study the effect of colonization with *Glomus macrocarpum* and salinity on growth of *Sesbania aegyptiaca* and *S. grandiflora*, AM seedlings had significantly higher P and N concentration but lower Na concentration than nonAM seedlings. It was stated that reduction in Na uptake in association with a concomitant increase in P and N absorption in AM plants are important salt-alleviating mechanisms for *S. grandiflora* plants growing in saline soil (Giri and Mukerji 2004). In *Acacia nilotica* plants, total accumulation of P, Zn, and Cu was higher in AM than in nonAM plants under both control and medium salt stress conditions (Giri et al. 2007) (Table 13.4).

Mycorrhizal colonization increased Mg uptake in two species of *Sesbania* under salinity (Giri and Mukerji 2004). Greater Mg uptake may be the reason for increasing chlorophyll concentration and hence improving photosynthetic efficiency of mycorrhizal plants. Calcium uptake was significantly lower in salt-affected tomato plants and AMF colonization enhanced significantly Ca uptake and Ca:Na ratio of both leaves and roots (Hajiboland et al. 2010). Similar results were obtained by other authors (Sharifi et al. 2007; Yano-Melo et al. 2003). An improved Ca nutrition caused maintenance of cellular ion homeostasis and improvement of plant growth under salt stress (Cramer 2004).

Table 13.4 Leaf concentration of P, Zn and Cu as affected by salinity and inoculation with *Glomus fasciculatum* in acacia (*Acacia nilotica*) plants

	1.2 dS m^{-1}		4.0 dS m^{-1}		6.5 dS m^{-1}		9.5 dS m^{-1}	
	−AMF	+AMF	−AMF	+AMF	−AMF	+AMF	−AMF	+AMF
P concentration (%)	0.6^{b}	1.2^{a}	0.5^{bc}	1.2^{a}	0.2^{c}	0.9^{b}	0.1^{c}	0.6^{b}
Zn concentration (ppm)	5.0^{c}	14^{a}	5.2^{c}	12^{a}	1.8^{d}	8.2^{b}	0.1^{d}	$3.2^{c,d}$
Cu concentration (ppm)	1.8^{c}	5.5^{a}	1.8^{c}	5.4^{a}	1.4^{c}	4.3^{b}	0.5^{a}	1.2^{c}

Data in each raw followed by the same letter are not statistically different ($P<0.05$). Data from (Giri et al. 2007)

Several mechanisms may be involved in enhancing the nutrients uptake by AMF. Mycorrhizal plants can explore a greater volume of soil beyond the zone of P, K and Zn depletion, lower the threshold concentration for absorption from soil solution, enhance root exudates and alter rhizosphere pH that increase availability of nutrients and solubilize organic P by production of phosphatase (Marschner 2012). These explanations, however, hardly apply to Ca. For this ion the AMF-mediated improvement of membrane integrity and therefore selectivity of ion uptake and transport is more likely the involving mechanism (Cramer 2004).

Activity of phosphatases increased in mycorrhizal pearl millet plants that led to increase in P uptake under saline conditions (Borde et al. 2011). The alkaline phosphatases are involved in hyphal P acquisition and one or several acid phosphatases are responsible for P transfer processes (Ezawa et al. 2002).

In summary, results of these studies indicate that AM plants have greater ability for nutrient uptake (especially P) than nonAM plants at all salinity levels. Positive influence of AMF on the mineral nutrition of plants grown under slat stress conditions could be regarded as a strategy for salt stress tolerance in plants. Moreover, improved plants growth and nutrient acquisition demonstrates the potential of AMF colonization for protecting plants against salt stress in nutrient poor soils.

Effect of AMF on Ion Homeostasis and K:Na Ratio of Salinized Plants

Ionic imbalances occur in plant cells due to salt stress. Salt stress affects mainly plant physiology and metabolism through changes in the status of ions inside the cells (Hasegawa et al. 2000; Munns et al. 2006). Ionic imbalance may be resulted from changes in nutrient availability, competitive uptake, transport or partitioning within plants (Rabie 2005). Thus, plant salt tolerance may be tightly related to its ability for regulation of ionic balance, particularly Na^{+}, K^{+}, Ca^{2+} and Mg^{2+} (Munns et al. 2006).

Elevated Na in soil solution inhibits acquisition of other nutrients by disrupting various transporters in the root plasma membrane, such as K-selective ion channels. Sodium transport is a unidirectional flow and thus results in progressive accumulation of Na in the shoot and leaf tissues with age of the plant. Detrimental effect of Na is due to its ability to compete with K for binding sites essential for various cellular functions. Potassium is one of the most important nutrients and has an important role in water balance, cell extension and solute transport in the xylem. Potassium in the plant cells is required not only for stabilizing pH in the cytoplasm, but also for increasing the osmotic potential in the vacuole (Marschner 2012). High levels of Na, or high Na:K ratios can disrupt various enzymatic processes in the cytoplasm. Maintenance of a high cytosolic K:Na ratio is a key feature of plant salt tolerance and greater K:Na ratio in AM compared with nonAM plants is the important mechanism for enhancement of salt tolerance by AMF colonization (Chinnusamy et al. 2005).

Concentration of Na was reported to be lower in AM than nonAM plants in various species regardless of salinity level (Giri et al. 2003, 2007; Giri and Mukerji 2004). This may be explained by dilution effect because of plant growth enhancement by AMF colonization. In olive plants K content was enhanced by 6.4-fold with *G. mosseae*, 3.4-fold with *G. intraradices*, and 3.7-fold with *G. claroideum* under saline conditions (Porras-Soriano et al. 2009). In *Acacia nilotica*, AM plants had lower concentration of Na in shoot tissues even at high salinity level, while Na concentration increased drastically in nonAM plants at same salinity level. In addition, AM inoculated *A. nilotica* roots accumulated more Na and thus prevented transport of Na to shoot tissues that may be considered another strategy for alleviation of detrimental effect of salinity in AM plants (Giri et al. 2007). Mycorrhizal pearl millet plants accumulated more salt in the root and prevented transport of Na into shoot (Borde et al. 2011). It was suggested that in AM plants, Na may be kept inside root cell vacuoles and intraradical fungal hyphae and by this means is prevented from being transported into the shoots (Cantrell and Linderman 2001). Increased K and Mg concentrations in citrus seedlings by AM colonization under salinity reported by Wu et al. (2010) would help the seedlings to prevent cellular Na accumulation to a toxic level and thus protect host plants against salt injury. In a field experiment, concentration of Na declined while K and Mg concentration increased under salinity when *Sesbania aegyptiaca* and *Sesbania grandiflora* inoculated with AMF (Giri and Mukerji 2004).

These results indicate that inoculation with AMF has marked influence on the acquisition and tissue concentrations of Na and K. The higher K accumulation in AM plants under salt stress conditions results in maintaining a high K:Na ratio, preventing the disruption of metabolic processes and inhibition of protein synthesis. Selective ion uptake, thus, is the main mechanism in AM plants for protection against ion imbalance caused by salinity.

It is noteworthy that reduction of Na concentration in AM plants does not necessarily mean an AM-mediated impairment of Na uptake. Lower Na accumulation in AM plants could be the result of dilution of Na in plant tissues as the consequence of growth improvement of AM compared with nonAM plants. In a pot

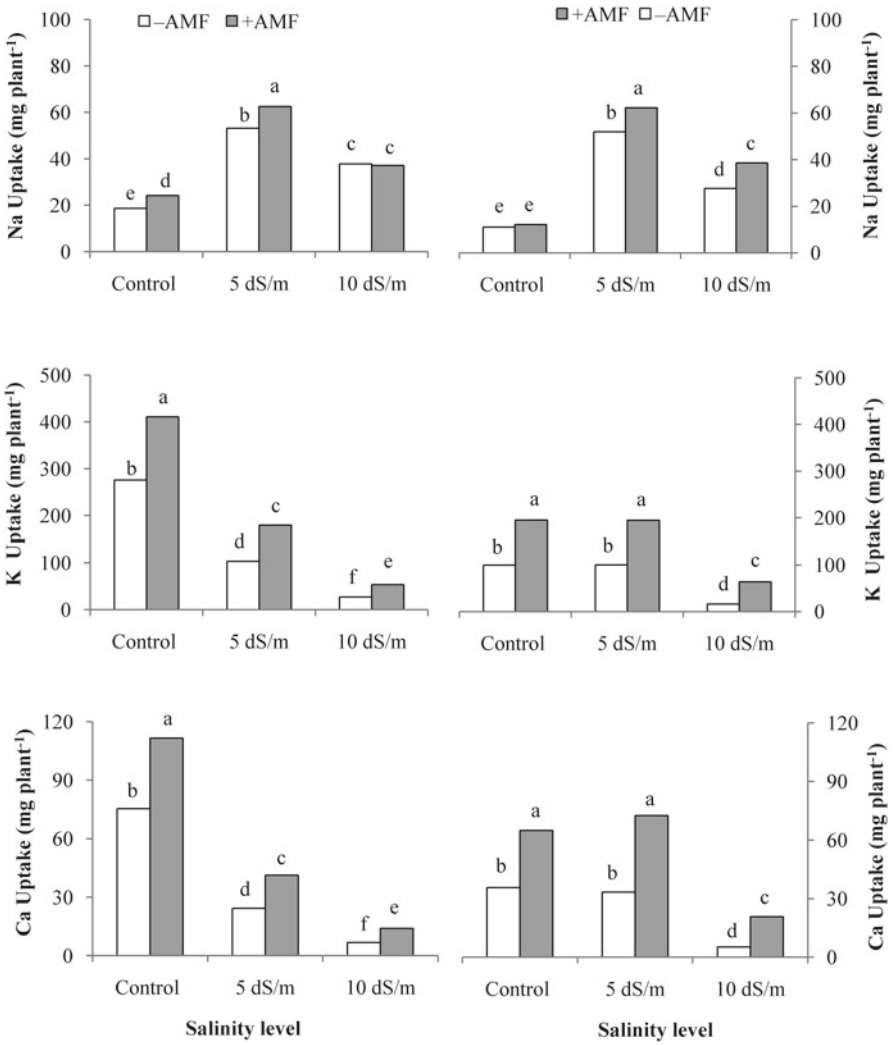

Fig. 13.4 Influence of different salinity levels on uptake of Na, K and Ca by tomato cultivars Behta and Piazar colonized (+AMF) or not (−AMF) with *Glomus intraradices*. *Bars* indicated by the same letter are not significantly different ($P<0.05$) (From Hajiboland R, Aliasgharzadeh N, Laiegh SF, Poschenrieder C (2010) Colonization with arbuscular mycorrhizal fungi improves salinity tolerance of tomato (*Solanum lycopersicum* L.) plants. Plant Soil 331:313–327 with permission)

experiment, mycorrhizal tomato plants grown in saline soil had greater Na uptake than nonAM counterparts (Hajiboland et al. 2010) (Fig. 13.4). Unfortunately, most of the authors have not provided the Na content or uptake (mg plant^{-1}) data and it is not possible to draw a precise conclusion on the influence of mycorrhization on Na uptake in plants.

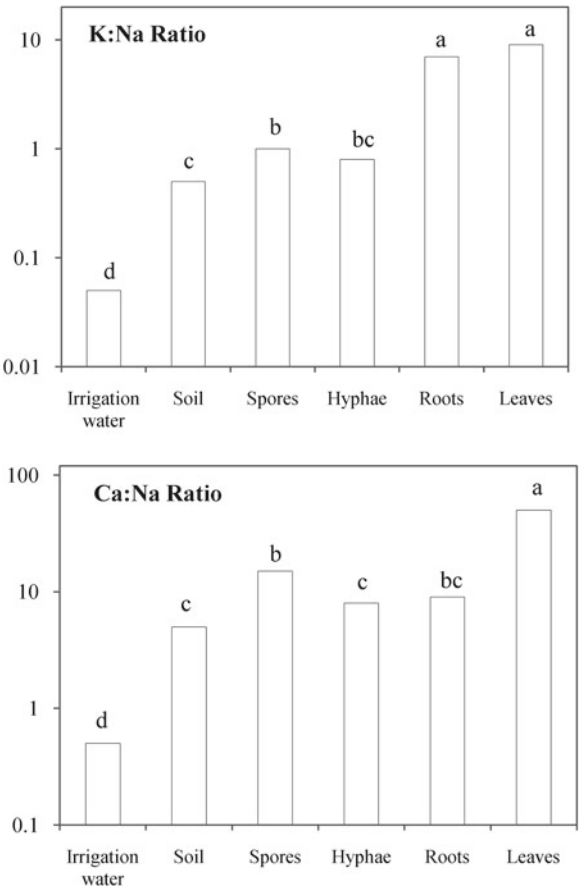

Fig. 13.5 K:Na ratio and Ca:Na ratio of the irrigation water, soil, AMF spores and hyphae and associated plant roots and leaves for samples taken from field. *Bars* indicated by the same letter are not significantly different ($P < 0.05$)

In mycorrhizal plants, ion discrimination could take place during the uptake of nutrients from the soil by fungi or during transfer to the host plant. In general, there are morphological barriers for ion selection in plants including the root hair membrane, the casparian stript and before transfer to the shoot, the xylem membranes (Tester and Davenport 2003). In order to investigate whether AMF can prevent uptake of toxic Na in response to salinity, a pioneer work has been undertaken using proton-induced X-ray emission (PIXE) method (Hammer et al. 2011). Composition of elements in the soil solution, spores and hyphae as well as plant samples were determined in this study (Fig. 13.5). It was shown that Na ions are excluded from entering the AMF cells while K, Ca and Mg concentration were significantly elevated in the spores and hyphae compared with surrounding soil. These results revealed that mycorrhizal fungi act as the first barrier for ion selection and AMF alleviate salt stress in plants by pre-selecting nutrients and preventing toxic salt ions from entering the plant. It was also demonstrated that AMF are able to keep the internal K:Na and Ca:Na ratios within a narrow range in spite of several orders of

magnitude of variation in the environment. If a significant proportion of elements acquisition by plants occurs via the AMF pathway as observed for P (Smith et al. 2003), this pre-selection mechanism in AMF could well explain the often higher K:Na ratios in AM plants (Hammer et al. 2011).

In this report, even higher K:Na and Ca:Na ratio was observed in plant tissues compared with spores and hyphae of AMF. If we consider the mycorrhizal uptake pathway as the dominant pathway for K and Na (and other ions) uptake as shown for P (Smith et al. 2003), we can hypothesize that the periarbuscular membrane is another barrier that provide a selective delivery of various ions to the host plant. Our knowledge on the function of periarbuscular membrane even for P is really limited and detailed works are needed for elucidating the selective transport of ions via periarbuscular membrane.

Effect of AMF on Water Relations and Solute Accumulation in Salinized Plants

One of the main consequences of salinity is loss of intracellular water and osmotic damages. Osmotic effects are associated with inhibited cell wall extension and cellular expansion, leading to growth reduction. Osmotic adjustment enables plants to maintain turgor potential under saline conditions (Rhodes et al. 2004; Munns and Tester 2008).

Accumulation of osmotically active organic solutes e.g. osmolytes, is a well known response to salinity in the majority of glycophytes that results from alterations in intermediary and secondary nitrogen and carbon metabolism (Hasegawa et al. 2000). This response is an important component of salinity tolerance in plants. Low molecular- weight compatible solutes like proline, glycine betaine, free amino acids, organic acids and soluble sugars accumulate to high levels without disturbing intracellular biochemistry and protect sub-cellular structures, mitigate oxidative damage, maintain the osmotic balance and protect enzymes in presence of high cytoplasmic ion concentrations (Hasegawa et al. 2000; Rhodes et al. 2004; Munns and Tester 2008).

Proline and Glycine Betaine

Free amino acids are important osmolytes contributing to osmotic adjustment in plants (Hajlaoui et al. 2010). Increasing external salt concentration causes accumulation of free amino acids in the leaves and roots (Abd-El Baki et al. 2000; Neto et al. 2009; Hajlaoui et al. 2010; Sheng et al. 2011) but this effect is less expressed in AM compared with nonAM plants (Sheng et al. 2011). Glycine betaine (N, N, N-trimethylglycine betaine) stabilizes the structure and activity of enzymes and proteins and maintain membranes integrity despite of damaging effects of excessive salt (Rhodes et al. 2004). Accumulation of betaines under salt stress was found to increase when the plant is colonized by AMF (Duke et al. 1986).

Among free amino acids, proline is much more important in osmotic adjustment of salt-stressed maize plants (Rhodes et al. 2004). Proline is synthesized by plants in response to stresses including salinity and ameliorates the abiotic stress effect. Proline also plays a role in scavenging free radicals, stabilizing subcellular structures and buffering cellular redox potential under stresses (Wang et al. 2009). The salinity stress responsive genes, containing proline responsive elements (ACTCAT) in the promoters, are induced by proline (Chinnusamy et al. 2005). In higher plants, proline is synthesized from glutamic acid via the two enzymes, pyrroline-5-carboxylate synthetase (P5CS) and pyrroline-5-carboxylate reductase (P5CR). In tobacco overexpressing the P5CS gene, proline production increased that caused enhanced salinity and drought tolerance in transgenic plants (Kishor et al. 1995).

Reports on the effect of AM symbiosis on proline accumulation are contradictory. Several authors have reported a higher proline concentration in AM plants than in nonAM plants at different salinity levels (Khaled et al. 2003; Sharifi et al. 2007). Enhanced proline accumulation in cells of AM plants can increase osmotic potential (Hajlaoui et al. 2010), thereby improve the tolerance of AM plants to salinity. On the contrary, other authors reported that AM plants accumulated significantly lower proline than nonAM plants at various salinity levels (Duke et al. 1986; Ruiz-Lozano et al. 1996; Jahromi et al. 2008; Rabie and Almadini 2005; Borde et al. 2011; Sheng et al. 2011). Lower proline content of AM plants under saline conditions compared with nonAM plants may suggest that proline accumulation in plants is an indicator of stress, and lower proline content of AM plants is a reflection of an increased salt resistance in plants upon mycorrhization, i.e. less injury. Species and genotypes with higher salt resistance accumulate lower proline under salinity conditions (Rush and Epstein 1976; Tal et al. 1979; Watad et al. 1983) that supports the view that proline accumulation in response to salt stress is an indicator of stress perception. Accordingly, it was suggested that proline is a symptom of stress in less salt-tolerant species (Wang et al. 2004; Evelin et al. 2009; Porcel et al. 2012). In citrus plants, AM seedlings accumulated less proline than nonAM seedlings under drought conditions (Wu et al. 2007). In soybean plants mycorrhization with either *G. mosseae* or *G. intraradices* did not induce the expression of the p5cs genes analyzed (Porcel et al. 2004). Under drought conditions, the levels of p5cs transcripts in AM plants were considerably lower than that in the corresponding nonAM plants, indicating that the induction of p5cs gene is not a mechanism by which the AM symbiosis protects their host plant against drought stress (Porcel et al. 2004). These results suggest that AM plants are less stressed by drought than nonAM plants due to primary drought-avoidance mechanisms. Similar salinity avoidance mechanisms are likely involved in many of species in the presence of AMF (Table 13.5).

Soluble Sugars

Accumulation of soluble sugars is a mean for lowering osmotic potential during salt stress. In a study on maize plants, concentration of soluble and reducing sugars declined by increasing salinity levels, but at a given NaCl level, sugar concentration

Table 13.5 Relative water content in shoots, proline content in roots and expression of *Lsp5cs* (pyrroline-5-carboxylate synthetase) gene probes from roots of lettuce (*Lactuca sativa*) plants subjected to 0, 50, or 100 mM NaCl and inoculated with *Glomus intraradices*

	Control		50 mM NaCl		100 mM NaCl	
	−AMF	+AMF	−AMF	+AMF	−AMF	+AMF
Relative water content (%)	93^{b}	96^{a}	86^{d}	93^{b}	91^{c}	95^{b}
Proline concentration (μmol g^{-1} FW)	0.1^{d}	0.2^{d}	6^{a}	0.8^{c}	$5^{a,b}$	4.1^{b}
Relative *Lsp5cs* expression	100^{d}	37^{e}	1354^{a}	235^{c}	616^{b}	660^{b}

Data in each raw followed by the same letter are not statistically different ($P<0.05$). Data from (Jahromi et al. 2008)

Table 13.6 Concentration of soluble sugars, reducing sugars, total free amino acids and total organic acids in leaves of maize plants inoculated with *Glomus mosseae* and grown at three NaCl levels

	Control		0.5 g Kg^{-1}		1.0 g Kg^{-1}	
	−AMF	+AMF	−AMF	+AMF	−AMF	+AMF
Soluble sugars (mg g^{-1} DW)	24^{c}	40^{a}	18^{d}	32^{b}	15^{d}	25^{c}
Reducing sugars (mg g^{-1} DW)	16^{d}	38^{a}	13^{c}	30^{b}	8^{f}	20^{c}
Total free amino acids (mg g^{-1} DW)	1^{c}	0.5^{cd}	4^{b}	0.4^{d}	8^{a}	0.2^{d}
Total organic acids (mg g^{-1} DW)	$28^{b,c}$	40^{a}	22^{c}	31^{b}	38^{a}	40^{a}

Data in each raw followed by the same letter are not statistically different ($P<0.05$). Data from (Sheng et al. 2011)

of AM plants was higher than nonAM plants (Table 13.6) (Sheng et al. 2011). Similar results were obtained in mungbean (Rabie 2005) and maize (Feng et al. 2002). Increased sugar concentration in the roots of AM plants was also reported in soybean subjected to drought stress (Porcel and Ruiz-Lozano 2004). However, some authors observed no role of soluble carbohydrates in the responses of AM plants to salinity (Sharifi et al. 2007).

In general, the increase in sugar content is found to be positively correlated with mycorrhization of plants. The high levels of sugars in mycorrhizal plants may be the result of an increase in photosynthetic capacity (Sheng et al. 2008; Wu et al. 2010). Symbiotic interactions in AM associations are based on the exchange of carbohydrates and mineral nutrients between the plant and the fungus. Using AM and nonAM clover plants of comparable plant size and growth rate and with similar N and P contents, it has been demonstrated that AMF colonization stimulates

photosynthesis in order to compensate for the carbon requirement of the fungus and to eliminate growth reduction of plant (Wright et al. 1998).

The consumption of carbon by AMF can be up to 20% of the host photosynthates. Therefore, plant roots become a strong sink for carbohydrates when colonized by AMF and mycorrhizal sink strength influences the whole plant carbon balance. In conclusion, the requirement for carbohydrates by AMF could cause an increased allocation to and accumulation of soluble sugars in the roots (Wright et al. 1998; Lerat et al. 2003). This higher accumulation of soluble sugars in AM plant tissue, especially in roots, could make AM plants more resistant to osmotic stress induced by exposure to salt. Moreover, the increased sugar accumulation may also be due to hydrolysis of starch to sugars in the seedlings inoculated with AMF (Nemec 1981). In conclusion, AM symbiosis competes strongly for root-allocated carbon resulting in an enhanced allocation of carbohydrates to roots for AM growth and development as well as for protection of membranes and proteins.

Trehalose is a non-reducing disaccharide and the main storage carbohydrate in AMF has been found to play an important role as a stress protectant that stabilizes dehydrated enzymes and membranes and protects biological structures from desiccation damage (Paul et al. 2008). It is present in the extraradical mycelium and spores of AMF (Becard et al. 1991) but is rare in higher plants. Induction of trehalose accumulation in the roots after AMF colonization has been reported (Schubert et al. 1992). Although trehalose metabolizing enzymes showed a transient activation at 500 mM NaCl in extraradical hyphae of *Glomus intraradices*, trehalose content did not show any change (Ocón et al. 2007). In contrast, in nodulated pigeonpea plants, salinity led to an increase in trehalose-6-P synthetase and trehalose-6-P phosphatase activities resulting in increased trehalose content in nodules, which was accompanied by inhibition of trehalase activity, the catabolizing enzyme. Arbuscular mycorrhizal pigeonpea plants had lower trehalase activity under both control and saline conditions (Garg and Chandel 2011). More investigations are required for study of the accumulation of trehalose in extraradical hyphae and mycorrhizal roots in order to evaluate the potential of trehalose in protecting AM plants from salt stress.

Organic Acids

The regulation of organic acid metabolism also plays a key role in plant tolerance to saline conditions (Guo et al. 2010). It is well known that organic acids, as metabolically active solutes, play a role in osmotic adjustment, in the balance of cation excess (Hatzig et al. 2010), and in pH homeostasis (Hasegawa et al. 2000; López-Bucio et al. 2000; Yang et al. 2007; Hatzig et al. 2010). They prevent toxic chloride accumulation in cells and are important osmolytes in plant vacuoles (Guo et al. 2010). Under salt stress, increased citric acid concentration in alfalfa roots (Francoise et al. 1991), and increased salicylic acid synthesis in the leaves and roots of maize plants (Szalai and Janda 2009) have been reported. Arbuscular mycorrhizal symbiosis induces accumulation of organic acids in maize leaves (Sheng et al. 2011)

(Table 13.6). However, the effect of AM symbiosis was different depending on organic acids. Concentrations of oxalic, fumaric, acetic, malic, and citric acids increased, formic and succinic acid concentrations decreased while lactic acid concentration did not significantly affect (Sheng et al. 2011). On the other hand, AMF colonization changed the concentration of organic acids in root exudates (Zhang et al. 2003). Release of organic acids into rhizosphere of AM plants caused reduction of soil pH, EC and organic carbon, and an increase in the availability of plants to soil N, P, and K (Usha et al. 2004).

Polyamines

The three main polyamines found in plants putrescine (Put), spermidine (Spd) and spermine (Spm) are thought to play an important role in plant responses to a wide array of environmental stresses such as salinity, high osmolarity, hypoxia and oxidative stress (Bouchereau et al. 1999; Groppa and Benavides 2008). Exogenously added Spd and Spm protect plants from saline stress (Chattopadhyay et al. 2002) whereas transgenic plants overexpressing Spd and Spm biosynthetic enzymes are more tolerant to saline and hyperosmotic stress (Kasukabe et al. 2004). Similar pathways for Put synthesis to those described in plants and bacteria have been found in ectomycorhizae (Fornalé et al. 1999) and in an AM fungus (Sannazzaro et al. 2004). Information regarding polyamines in AMF or in their symbiotic interaction with plants is very limited. Free polyamines have been suggested to play an important role in the initial stages of the infection of pea roots by *Glomus intraradices* (Ghachtouli et al. 1995).

Mycorrhization changes the polyamine balance of salt-affected *Lotus glaber* plants. Colonization by *Glomus intraradices* increased (Spd + Spm)/Put ratio in lotus roots. This increment in salt stressed AM plants was even higher than those produced by salinization or AM symbiosis separately, suggesting an additive effect of both factors on the root (Spd + Spm)/Put ratio (Sannazzaro et al. 2007). It has been proposed that modulation of polyamine pools is one of the mechanisms used by AMF to improve adaptation of plants to saline soils (Sannazzaro et al. 2007).

Effect of AMF on Antioxidant Defense Capacity of Salinized Plants

One of the earliest responses of plants to salinity is the accumulation of reactive oxygen species (ROS) (Hasegawa et al. 2000; Parida and Das 2005). During salt stress, excessive generation of ROS such as superoxide radical ($O_2^{\bullet -}$), hydrogen peroxide (H_2O_2), hydroxyl radical ($^{\bullet}OH$), and singlet oxygen ($^1O_2$) occurs. These cytotoxic activated oxygen species can seriously disrupt normal metabolism through oxidative damage to membranes, proteins and nucleic acids (Apel and Hirt 2004).

Plant cells contain protection mechanisms that can minimize oxidative damage caused by ROS. The induction of ROS-scavenging enzymes, include superoxide dismutase (SOD), catalase (CAT), peroxidase (POD) and ascorbate peroxidase (APX) is the most common mechanism for detoxification of ROS synthesized during stress response. The steady-state levels of ROS in plants cells are determined by the balance between the generation of ROS and activities of scavenging enzymes (Apel and Hirt 2004).

Under salt stress, the activity of antioxidant enzymes becomes higher in order to eliminate more ROS (Parida and Das 2005). A strong correlation between the efficiency of antioxidant defense system and the level of salt tolerance has been reported in many plants (Benavides et al. 2000; Garratt et al. 2002). A constitutively high antioxidant capacity under stress conditions can prevent damages due to ROS formation (Harinasut et al. 2003). There are reports showed a greater SOD activity in salt tolerant compared with salt sensitive plants (Benavides et al. 2000). The increased POD activity in response to salinity (Harinasut et al. 2003) and higher POD activity in tolerant plants was also reported (Sreenivasulu et al. 1999). In *Solanum pennellii*, the wild salt tolerant tomato species, SOD and APX activity was higher than those in the cultivated tomato (Shalata and Tal 1998). Compared with cultivated tomato (*Solanum lycopersicum*), the better protection of *S. pennellii* root plastids from salt induced oxidative stress was correlated with increased activities of SOD, APX and POD (Mittova et al. 2002).

Apart from the salinity-induced antioxidative response, mycorrhization *per se* could also induce activation of antioxidant defense enzymes. In spite of the symbiotic nature of AM association, it represents a massive invasion of plant roots by the fungi. Induction of antioxidant enzymes observed during appressoria formation during the early stage of symbiosis development was attributed to a defense response of plants (Blilou et al. 2000). Oxidative burst and generation of superoxide radicals occur also during development of hypersensitive response in plant–pathogen interactions (Mehdy et al. 1996). Superoxide dismutase which plays a role in detoxification processes by catalyzing the conversion of free $O_2^{\bullet -}$ to O_2 and H_2O_2, very often is associated with plant-pathogen interactions (Davies and Dow 1997). Stimulation of constitutive SODs in different AM symbiosis and induction of specific SOD isoforms has been reported (Arines et al. 1994; Niki et al. 1998). Mycorrhizal clover roots exhibit two additional SOD isoforms as compared to nonAM roots: a myc-CuZn-SOD and a Mn-SOD (Palma et al. 1993). There are reports on general stimulation of CAT, POD, APX and SOD in AM compared to nonAM roots (He et al. 2007; Hajiboland et al. 2010). In bean (*Phaseolus vulgaris*) colonized by *Glomus clarum*, SOD and CAT were induced in roots at late stage of the symbiosis development under low P (Lambais et al. 2003). Cell wall bound peroxidase was measured in *Allium porrum* during root growth and development of *Glomus versiforme* (Spanu and Bonfante-Fasolo 1988). At initial stage of fungal infection, the enzyme activity was maximum and decreased in later stages when roots were highly colonized. In *Phaseolus vulgaris* inoculated with *Glomus etunicatum* peroxidase activity increased in the AM plants (Pacovsky et al. 1991).

Table 13.7 Activity of antioxidant enzymes (U mg^{-1} FW) and concentration of malondialdehyde (MDA, nmol g^{-1} FW) in the leaves of tomato (*Solanum lycopersicum* cv. Zhongzha105) plants inoculated with *Glomus mosseaes* and grown at different levels of salinity

		SOD activity	APX activity	POD activity	CAT activity	MDA content
Control	−AMF	3.2^{c}	$0.20^{d,e}$	1.8^{d}	6.3^{c}	75^{c}
	+AMF	7.1^{a}	0.34^{b}	2.1^{d}	11.3^{a}	60^{d}
50 mM	−AMF	4.0^{bc}	0.29^{d}	2.5^{cd}	9.7^{b}	110^{b}
	+AMF	6.0^{b}	$0.39^{a,b}$	4.2^{a}	11.5^{a}	99^{c}
100 mM	−AMF	1.7^{e}	0.32^{c}	3.0^{c}	4.0^{d}	160^{a}
	+AMF	2.8^{d}	0.42^{a}	3.9^{b}	$5.8^{c,d}$	100^{c}

Same letter within each column indicates no significant difference among treatments. From Abdel-Latef AAH, Chaoxing H (2011) Effect of arbuscular mycorrhizal fungi on growth, mineral nutrition, antioxidant enzymes activity and fruit yield of tomato grown under salinity stress. Sci Hort 127:228–233, with permission

Reports on the response of antioxidant defense system in AM plants under saline conditions are contradictory; increase, no change, or even decrease in the activity of enzymes have been reported in AM plants subjected to salinity. Indeed the response of the individual enzymes varies with respect to the host plant and the fungal species as well as duration and level of salinity treatment. Nevertheless, in many reports higher activity of antioxidant defense enzymes was associated with growth amelioration of AM plants under salinity. In pearl millet plants grown under salinity, enhanced SOD activity in AM plants as compared to nonAM ones supports the view that increased antioxidative enzyme activities could be involved in the beneficial effects of AM colonization on the performance of plants under saline conditions (Borde et al. 2011). In addition, gradual exposure of AMF to salinity that caused salt adaptation in the fungi enhanced its ability to colonize plant roots under saline conditions. This enhancement was correlated with induction of SOD activity in adapted fungi as compared to non adapted fungi (Borde et al. 2011). In tomato plants cultivated in soil with 0, 50 and 100 mM NaCl, AMF colonization alleviated salt induced reduction of growth and fruit yield (Abdel-Latef and Chaoxing 2011), that was accompanied by an enhancement of activity of SOD, CAT, POD and APX in leaves of both salt-affected and control plants. In addition, inoculation with AMF caused reduction in MDA content in comparison to salinized plants, indicating lower oxidative damage in the colonized plants. Similar results have been obtained by many other authors (He et al. 2007; Kohler et al. 2009; Zhi et al. 2010; Hajiboland et al. 2010) confirming that AM symbiosis really influences activity of antioxidant defense system and support the view that AMF can contribute to protect plants against salinity by alleviating the salt induced oxidative stress (Table 13.7). Enhanced antioxidant enzymes activity and lower lipid peroxidation in AM plants may contribute to better maintenance of the photochemical reactions in leaves under salinity. In addition, this mechanism improves salt tolerance via maintaining membrane integrity that would facilitate compartmentalization within vacuole and selective ion uptake. In conclusion, activation of antioxidant capacity of host plant by AMF

symbiosis may be the result of common response to invasion of fungi and may also be because of a complex interaction of AMF, plant and salinity and need molecular analyses.

Effect of Different Plant Genotypes and Fungi Isolates on the Alleviating Effect of AMF in Salinized Plants

Symbiotic association between AMF and their hosts is usually believed to be nonspecific (Smith and Read 2008), however, many studies have confirmed the existence of differences in the physiological characteristics of mycorrhizal association within the species and even within isolates of the AMF (Bethlenfalvay et al. 1989, 1997; Smith and Smith 1997). Differences in fungal behavior or characteristics in interacting with hosts have attracted attention of scientists in recent years in order to improve selection of efficient isolates or to understand functional diversity or ecological plasticity of the fungi (Camprubi and Calvet 1996; Johnson et al. 1997; Douds and Millner 1999).

It has been found that under long term saline stress, although the richness of AM fungal species decreased, some species were still able to survive due to adaptation with these edaphic conditions (Copeman et al. 1996; Camprubi and Calvet 1996; del Val et al. 1999). The AMF species or isolates that are able to survive in stressed edaphic environments are considered as tolerant species/isolates and may have a higher ability to improve growth of host plants than species or isolates from non-stress edaphic condition (Tian et al. 2004).

The host plant species, cultivar and growing conditions can also influence the effectiveness of AM symbiosis in nutrient uptake (Janos 2007). Similarly, alleviation of salt stress by a given AMF species or isolates is dependent on the host plant species or genotype.

Effect of Different AMF Isolates

It has been widely accepted that AMF are able to adapt to specific edaphic conditions (Brundrett 1991; del Val et al. 1999; Copeman et al. 1996). It is expected that an isolate from saline soil would have a higher capacity to promote plant growth under saline stress. Copeman et al. (1996) suggested that differences in fungal behavior and efficiency can be due to the origin of the AMF.

In a study on cotton plants colonized by *Glomus mosseaes* isolated from non-saline soil, growth of plants were promoted under saline stress without affecting Na and Cl concentrations (Tian et al. 2004). Although isolate from saline soil increased Na and Cl concentrations in this species at higher NaCl level, it also significantly increased plant dry weight (Table 13.8) (Tian et al. 2004). This suggests that saline soil AMF isolate had a different mechanism for improving the salinity tolerance of

Table 13.8 Effect of inoculation of cotton (*Gossypium arboreum* L, cv. Xin-lu-zao No. 1) plants with two different isolates of *Glomus mosseaes* on shoot and root dry weight (DW) and concentration of P, Na and Cl under different salinity levels

		Shoot DW (g pot^{-1})	Root DW (g pot^{-1})	Shoot P (mg g^{-1})	Shoot Na (mg g^{-1})	Shoot Cl (mg g^{-1})
Control	−AMF	6.01	1.65	1.02	0.35	5.87
	Isolate from saline soil	6.46	1.51	2.27	0.44	7.06
	Isolate from non-saline soil	6.44	1.56	1.95	0.40	6.46
1 g Kg^{-1} NaCl	−AMF	5.54	1.46	1.20	0.78	9.29
	Isolate from saline soil	5.89	1.33	1.77	1.03	12.06
	Isolate from non-saline soil	6.06	1.49	1.74	0.65	9.39
2 g Kg^{-1} NaCl	−AMF	4.91	1.21	1.45	0.94	10.59
	Isolate from saline soil	4.91	1.07	1.30	2.14	16.36
	Isolate from non-saline soil	5.81	1.54	1.65	0.97	11.15
3 g Kg^{-1} NaCl	−AMF	3.09	0.99	1.54	2.45	19.82
	Isolate from saline soil	4.06	0.77	1.42	3.72	29.08
	Isolate from non-saline soil	5.19	1.21	1.71	2.49	18.95
Inoculation		***	**	***	***	***
Salt		***	***	***	***	***
Inoculation × salt		***	n.s	***	**	***

***Significant at $P<0.001$, **significant at $P<0.01$, n.s no difference
Same letter within each column indicates no significant difference among treatments. From Tian CY, Feng G, Li XL, Zhang FS (2004) Different effects of arbuscular mycorrhizal fungal isolates from saline or non-saline soil on salinity tolerance of plants. Appl Soil Ecol 26:143–148, with permission

cotton plants than the isolate from non-saline soil. Different species of AMF differentially affected growth and yield of wheat genotypes under salinity (van der Heijden et al. 1998a, b; Scheublin et al. 2004; Daei et al. 2009). The efficiency of different AMF species on enhancing plant growth under salinity was observed in the following order: *Glomus etunicatum* > *G. mosseae* > *G. intraradices* (Fig. 13.6). Higher root colonization by *Glomus etunicatum* and *G. mosseae* relative to *G. intraradices* resulted in increased nutrient uptake and less Na and Cl absorption by plant, and hence, increased plant growth under salinity (Daei et al. 2009).

The different behavior of AMF was also evidenced by Ruiz-Lozano et al. (1996) in lettuce plants subjected to salt stress and inoculated with three different AMF. In that study, the effect of *G. mosseae* and *G. fasciculatum* on salt tolerance seemed to be based on increased photosynthetic rate and water use efficiency rather than on

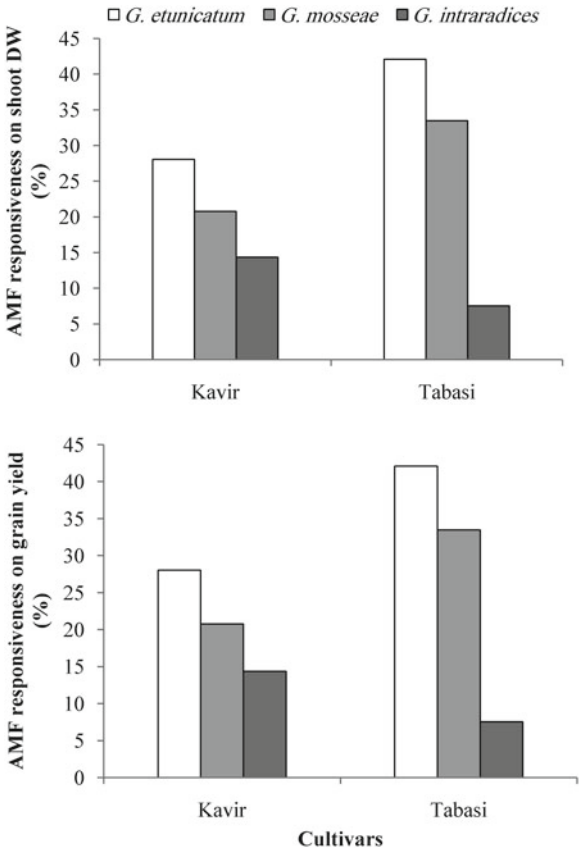

Fig. 13.6 Mycorrhizal responsiveness (%) calculated on the basis of shoot dry weight or grain yield in two cultivars of wheat plants inoculated with three different AMF species (From Daei G, Ardekani MR, Rejali F, Teimuri S, Miransari M (2009) Alleviation of salinity stress on wheat yield, yield components, and nutrient uptake using arbuscular mycorrhizal fungi under field conditions. J Plant Physiol 166:617–625, with permission)

nutrient uptake (N or P). *Glomus deserticola*, in contrast, seemed to protect host plants against salt stress by increasing P uptake, in addition to the above-mentioned physiological processes. In another study on lettuce plants, *Glomus* sp. isolated from saline soils protected the host plant against salinity by stimulating root growth, while in the case of *G. deserticola,* the increase in N and P accumulation was the basis for alleviating effect under salinity (Ruiz-Lozano and Azcón 2000).

Study on *Astragalus sinicus* plants confirmed that AMF species are different in their efficiency for alleviation of salt stress. Tolerance of *A. sinicus* plants to salinity was enhanced by the three AMF species with increasing salinity levels, however, different AMF species varied in their ability to ameliorate the inhibitory effect of salt stress. This difference was reflected in plant growth response, intensity of root colonization and activity of succinate dehydrogenase and alkaline phosphatase in intraradical mycelium (Peng et al. 2011). The symbiosis formed by *G. intraradices* under increasing salinity levels were more efficient compared to that formed by *G. mosseae* or *G. claroideum* (Peng et al. 2011).

In the study on olive plants, *G. mosseae* was the most efficient AM fungus in terms of olive tree performance, and particularly in the protection offered against the detrimental effects of salinity (Porras-Soriano et al. 2009). Arbuscular mycorrhizal fungi differ in their ability to enhance nutrient uptake even when the extent of AM colonization is similar (Ruiz-Lozano and Azcón 2000). Specific mechanisms conferring functional differences among AMF could be expected from changes in fungal characteristics such as length of external mycelium, hyphae distribution, and/or nutrients translocation. In agreement with these ideas, Jakobsen et al. (1992) proposed a consistent relationship between the total length of root colonized by each fungus and the ability to alleviate the nutrient limitation effect caused by salinity.

In a study on soybean plants it was shown that exposure of the AMF to gradually increased concentrations of NaCl prior to salt stress enhanced root colonization, host plant growth, root proline and concentration of some mineral nutrients under salinity (Sharifi et al. 2007). It was hypothesized that pre-treatment of AMF by salt may result in salt acclimation that may in turn enhance the ability of the AMF to infect the roots, induction of root proline accumulation and mineral acquisition (Sharifi et al. 2007).

In contrast, other authors demonstrated that beneficial effect of AMF on host plants under saline conditions is not necessarily related to the level of salinity in the habitat of a given fungal isolate. Similar results were obtained in tomato plants inoculated with saline soil isolates of *G. mosseae* and *G. fasciculatum* (Poss et al. 1985). Copeman et al. (1996) found that an isolate from non-saline soil promoted shoot growth, but tended to increase leaf Cl concentration. Conversely, an isolate from saline soil suppressed plant growth but decreased the concentration of Cl in leaves. They suggested that although AMF originating from saline soil did not promote plant growth, reduction in leaf Cl concentration by these AMF may have beneficial implications for plant survival in saline soil (Copeman et al. 1996).

In lettuce plants, when the mycorrhizal responses were expressed per unit of mycorrhiza formed, *G. deserticola* and a native isolate from saline soil (*Glomus* sp.) differed in their symbiotic efficiency particularly under higher salinity levels (Ruiz-Lozano and Azcón 2000). The total mycorrhizal root length was highest in *Glomus* sp.-colonized plants, but plants colonized by *G. deserticola* responded more pronouncedly to inoculation. The superior ability of *G. deserticola* for improving plant growth and mineral nutrition was due to a higher rate of spread of extraradical mycelium than that of *Glomus* sp. (Ruiz-Lozano and Azcón 2000). These results indicate that specific compatibility relationships exist among symbionts, and AM symbiotic efficiency is dependent on AMF species. It implies also that, the mycorrhizae formed by *G. deserticola* was more efficient in improvement of host plants growth than that formed by *Glomus* sp. and *Glomus* sp. needed to form a higher amount of mycorrhiza than *G. deserticola* to achieve a similar symbiotic effect (Ruiz-Lozano and Azcón 2000). Authors suggested that the selection of the most suitable AMF for a specific plant genotype is of practical interest for improving the effectiveness under particular environmental conditions.

Regarding different ability of AMF to minimize stress effects and to promote plant growth (Daei et al. 2009), it has also been suggested that establishment of mixed communities by different AMF species may be more beneficial to the growth of plants than any of individual species (Koide 2000; Alkan et al. 2006; Peng et al. 2011). Root colonization of *G. mosseae* was enhanced in the presence of the other two fungi in a mix inoculation treatment particularly under high salinity conditions. There was likely a synergistic interaction between different AMF species under salt stress probably as the result of a functional complementation in P acquisition as suggested by Koide (2000). Selection of an AMF species/strain adapted to the local climate and soil conditions is the first step for a successful restoration program (Dodd and Thomson 1994).

Effect of Plant Genotypes

Salinity tolerance varies widely among species or ecotypes of the same species (Beauchamp et al. 2009). Some works also suggest that seeds collected from highly saline soils exhibit often higher establishment and performance in the presence of NaCl than seeds originated from non-saline soils (Hajiboland et al. 2010).

Study on *Lotus glaber* plants showed that *G. intraradices* established a more efficient symbiosis with the salt-tolerant than with the salt-sensitive genotype (Sannazzaro et al. 2006). Saline conditions reduced colonization rate of roots in sensitive but not in tolerant genotype, suggesting that the tolerant genotype offered the fungal partner higher protection and better chances of growth within host tissues than salt sensitive genotype. On the other hand, tolerant genotype inoculated with *G. intraradices* had not only higher root and shoot growth under saline conditions, but they also had higher leaf water and chlorophyll concentration as well as higher shoot:root ratio regardless of salinity level (Sannazzaro et al. 2006).

In tomato plants, the salt-tolerant cultivar showed higher AM colonization than the salt-sensitive cultivar (Al-Karaki et al. 2001). However, the enhancement in P, K, Zn, Cu, and Fe acquisition due to AMF inoculation was more pronounced in salt-sensitive than in salt-tolerant cultivar under saline conditions. These results suggest that although the salt-tolerant cultivar were highly infected with AMF, salt-sensitive cultivars benefited more from AMF colonization than salt-tolerant cultivar under saline soil conditions (Al-Karaki et al. 2001). In contrast, another report on tomato plants demonstrated that though similar root colonization, mycorrhizal responsiveness was greater in salt-tolerant compared with salt-sensitive cultivar likely because of greater photosynthesis rate under salinity in tolerant cultivar that could adequately provide carbohydrates for the fungi partner and result in more benefit of plants from AMF association (Hajiboland et al. 2010).

It has been stated that different wheat cultivars are able to perform differently irrespective of their mycorrhizal symbioses (Hetrick et al. 1984), however, other researchers indicated that the higher root colonization and hence, higher nutrient uptake, are the most important reasons for the greater performance of mycorrhizal tolerant varieties under salinity (Miransari 2011; Mardukhi et al. 2011). In an

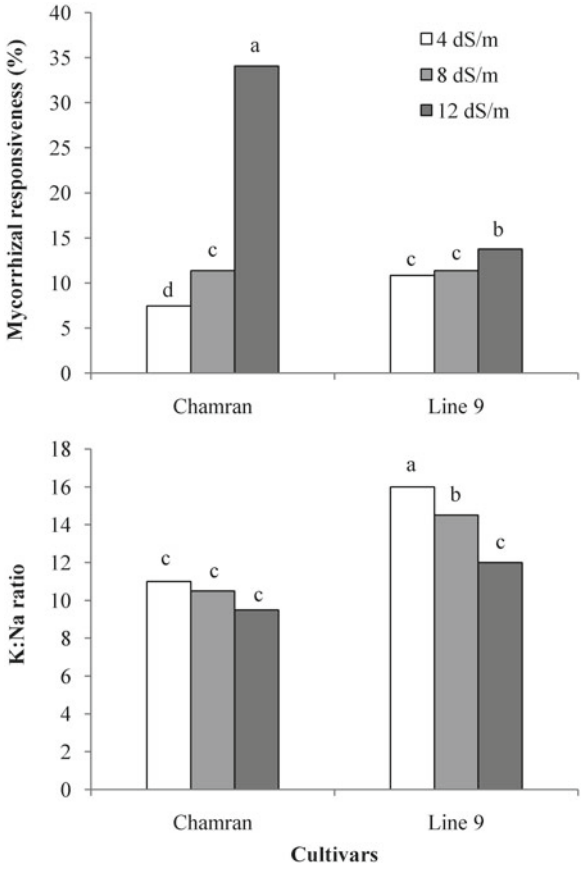

Fig. 13.7 Mycorrhizal responsiveness and K:Na ratio in two cultivars of wheat plants inoculated with AMF. Cultivar 'Chamran' is a semi- resistant and Line 9 is a resistant cultivar to salinity. *Bars* indicated by the same letter are not significantly different ($P<0.05$) (Data from (Mardukhi et al. 2011))

experiment on wheat plants grown under greenhouse conditions, two cultivars with different salinity resistance responded differently to mycorrhization under salinity (Mardukhi et al. 2011). Though a lower colonization in the roots of salinity resistant cultivar, higher nutrient uptake and K:Na ratio were observed in this cultivar. In contrast, regarding dry matter production mycorrhizal responsiveness was higher in less-tolerant cultivar (Fig. 13.7). Higher nutrient uptake in resistant cultivar under salinity despite of lower root colonization demonstrated that AMF association of salt resistant cultivar was more efficient than less-tolerant cultivar (Mardukhi et al. 2011).

Difference in symbiotic efficiency is also reflected in the mycorrhizal dependency index of plants grown under saline conditions. Mycorrhizal dependency in the salt tolerant genotype of lotus plant was similar under saline and non-saline conditions, while it was much greater under saline conditions compared with control in the salt sensitive genotype (Sannazzaro et al. 2006).

In conclusion, results of many studies demonstrated that different combinations of plant species/genotypes and AMF species/isolates can perform differently under salinity stress. Statistically significant interaction between plant genotypes and AMF species (Al-Karaki et al. 2001; Sannazzaro et al. 2006; Hajiboland et al. 2010; Mardukhi et al. 2011) emphasizes the importance of selecting the right combination of AMF species and host plant under salinity stress in order to achieve more efficient alleviation of the stress.

One of the causes for genotypic differences in the AMF responsiveness under salinity is likely different translocation of photosynthates to the roots under stress. Higher photosynthates allocation to the roots results in higher root dry weight and colonization and hence, AM symbiosis in some genotypes (Miransari and Smith 2007, 2008; Miransari et al. 2007, 2008).

On the other hand, non-dependence differences in the mycorrhizal responsiveness such as variation in the ability of genotypes to establish colonization, in the efficiency of water and nutrient uptake and exchange between fungus and host plant under salinity are very important traits for enhancement of profitability of plants-AMF interactions under saline conditions. The right combination of AMF species and host plant can partially or completely alleviate the stress of salinity, thus, knowledge on the relationship between plants and the fungi is important for successful utilization of AMF under particular conditions. Detailed studies are needed on the nature of difference between various combinations of plant species/genotypes and AMF species/isolates.

Changes in Gene Expression Patterns in Salt Stressed Plants upon Mycorrhization

The mechanisms underlying the alleviation of salt stress by AMF have not yet been elucidated at molecular level. Plant salt tolerance itself is a complex trait (Shi et al. 2000) and many different factors contribute in this process include production of compatible solutes, energy supply for the export of Na and Cl, specific transporters for the transfer of Na and Cl into the vacuole or apoplastic spaces, adequate water supply by aquaporins to maintain osmobalance (Hasegawa et al. 2000). Accordingly, any study on the impact of AMF colonization on the expression of genes with products involved in salt tolerance is faced with the multiplicity and complexity of the traits (Ouziad et al. 2006). Among the proteins functioning in salt tolerance of plants, Na/H transporters, aquaporins, proline biosynthetic enzyme and the expression of stress marker *LEA* gene have been investigated so far in AM plants at molecular level.

Na/H Transporters

Prevention of Na entry into the cell and/or sequestration of Na into the vacuole are strategies by which plants cope with high salinity. Sodium transporters contributing

to Na homeostasis include Na/H antiporters in plasmamembrane (SOS1), Na/H antiporters in vacuole (NHX1) and Na uniporter in plasmamembrane (HKT1) (Zhu 2003). The Na/H antiporters mediate the transfer of Na out of the cytoplasm into either vacuole (NHX1) or apoplast (SOS1). There are six fully sequenced members of vacuolar Na/H transporters (Xia et al. 2002). Transgenic plants overexpressing vacuolar Na/H antiporters are more salt tolerant than the controls as shown for *Arabidopsis* (Apse et al. 1999; Gaxiola et al. 1999; Sottosanto et al. 2004), *Oryza sativa* (Fukuda et al. 1999) and *Brassica* (Zhang et al. 2001). Upregulation of tonoplast or plasmamembrane Na/H antiporter genes under salt stress has been reported in *Nicotiana excelsior* (Yamada et al. 1997), *Arabidopsis* (Gaxiola et al. 1999) or *Oryza sativa* (Fukuda et al. 1999), but was not observed in tomato (Ouziad et al. 2006) and in another work with *Arabidopsis* (Apse et al. 1999).

Analyzing expression of two tomato Na/H antiporter genes *LeNHX1* and *LeNHX2* showed no significant change in the expression due to colonization (Fig. 13.8) (Ouziad et al. 2006). This indicates that AMF colonization does not trigger the expression or activity of Na/H antiporter genes.

Aquaporins

Water molecules pass through the channels formed by aquaporins in the plasmalemma or the tonoplast (Maurel et al. 1997; Zeuthen 2001; Hill et al. 2004). Aquaporins belong to the major intrinsic protein (MIP) family of transmembrane channels, which permit selective membrane passage of water but not of H^+ and other ions (Weig et al. 1997; Chen et al. 2001; Hill et al. 2004). Root water uptake depends on root hydraulic conductance, which is ultimately governed by aquaporins (Luu and Maurel 2005). Plants aquaporins are divided in four groups depending on their sequence homology. These four groups are called plasma membrane intrinsic proteins (PIPs), tonoplast intrinsic proteins (TIPs), nodulin like intrinsic proteins (NIPs) and small and basic intrinsic proteins (SIPs).

There is some evidence that PIP proteins could regulate the whole water transport through plant tissues, and plants overexpressing or lacking one or more *PIP* genes have more or less root water uptake capacity, respectively (Aharon et al. 2003; Javot et al. 2003). Aquaporins are controlled at activity or transcriptional levels. As a short-term response to stresses such as drought and salinity, aquaporins activity is regulated by phosphorylation (Johansson et al. 1996; Maurel et al. 1995) while during longer time they are down-regulated by reduction of gene expression.

Overexpression of a *PIP* aquaporin in transgenic tobacco improved plant vigor under favorable growth conditions, but had not beneficial effect under salt stress and influenced even negatively plants growth under drought stress and accelerated plants wilting (Aharon et al. 2003). Similar result has been obtained in *Arabidopsis* and tobacco plants regarding two different *PIP* aquaporin genes (Jang et al. 2007).

During AM formation, the plant plasmamembrane extends to form the periarbuscular membrane. Periarbuscular membrane is closely surrounds the fungal hyphae and results in a three to tenfold increase in plant cell surface (Gianinazzi-Pearson 1996). Upregulation of aquaporins in AM plants under well-watered conditions

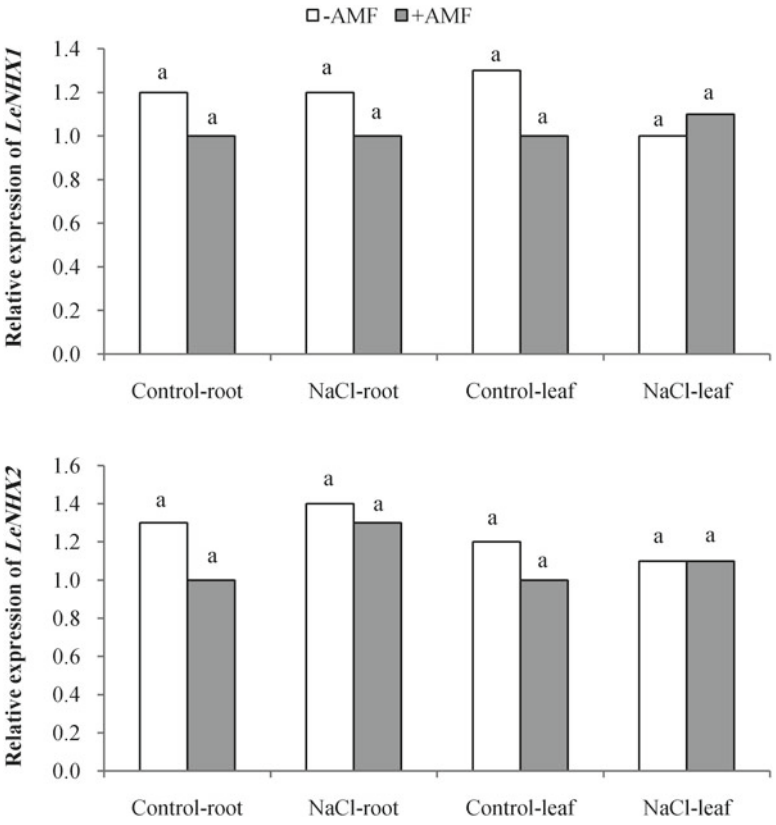

Fig. 13.8 Expression of two Na^+/H^+ antiporters (*LeNHX1* and *LeNHX2*) of tomato (*Solanum lycopersicum* cv. Tmina) plants grown under salinity and colonized with a mixture of *Glomus geosporum* and *Glomus intraradices*. *Bars* indicated by the same letter are not significantly different ($P<0.05$).(Data from (Ouziad et al. 2006))

optimizes nutrients and water exchange between two symbiotic partners (Krajiski et al. 2000).

Arbuscular mycorrhizal plants are able to take up more water from the soil than nonAM plants under water deficit conditions (Marulanda et al. 2003; Khalvati et al. 2005). In lettuce plants, *PIP2* gene expression declined by drought stress while AM inoculation by itself increased expression of the *PIP2* gene under both watering regimes (Alguacil et al. 2009). Porcel et al. (2006), in contrast, observed that under drought conditions, the AM colonization accelerated reduction of a *PIP* gene expression in roots of *Glycine max* plants and decreased the expression of two *PIP* genes in roots of *Lactuca sativa* plants. Aroca et al. (2006) reported also that, nonAM roots have higher expression of *PvPIP1;3* and *PvPIP2;1* compared with AM roots

under drought conditions. In this study, colonization of *Phaseolus vulgaris* roots by AMF resulted in maintaining root hydraulic conductance under drought and prevented leaf dehydration as judged by higher relative water content of AM leaves compared with nonAM ones (Aroca et al. 2006). Lettuce plants colonized by *Glomus mosseae* showed down-regulation of *PIP* gene expression (Porcel et al. 2006). These authors concluded that down-regulation of plant aquaporins by AM symbiosis allows conservation of water in plant tissues under drought and confirms the beneficial effect of AMF in water status of host plants observed under drought conditions (Porcel et al. 2006; Aroca et al. 2006).

In a study on lettuce plants inoculated with *Glomus intraradices* and *Glomus mosseae* it was found that both fungi use different strategies to protect the host plant against drought stress (Marulanda et al. 2003). *Glomus intraradices* showed higher capacity to enhance the root water permeability, rate of root water uptake and movement by maintaining high levels of *PIP* aquaporin gene expression. *Glomus mosseae*, in contrast, protected plants against drought stress by greater conservation of the water existing in the plant and down-regulation of *PIP* genes expression. Down regulation of *PIP* genes has been suggested by other authors as a mechanism for reduction of membrane water permeability and to allow cellular water conservation (Yamada et al. 1995; Smart et al. 2001).

Because of negative water potential in saline soils, plants of saline habitats are faced with drought problem and must maintain their osmotic balance in the cytoplasm. There is a correlation between the expression or activity of aquaporins and the susceptibility to salt stress (Johansson et al. 2000).

The expression of aquaporins was strongly impaired by salt treatment in tomato plants (Ouziad et al. 2006). In ice plants, transcript levels of some aquaporins are down-regulated in the first 30 h after exposure to salt stress and recover when this stress is interrupted (Yamada et al. 1995). Salinity reduced either the activity or abundance of aquaporins in paprika pepper (Carvajal et al. 1999) and melon (Carvajal et al. 2000). Other authors, however, reported an up-regulation of aquaporin mRNA transcripts under salt stress, e.g., in *Nicotiana excelsior* (Yamada et al. 1997), *Arabidopsis thaliana* (Gaxiola et al. 1999), *Oryza sativa* (Fukuda et al. 1999) and *Beta vulgaris* (Xia et al. 2002). Such differences may be a consequence of the mode of the salt stress set, the differences between plant species and the complexity in expression pattern of different members of the large family of aquaporins (Sarda et al. 1999; Ouziad et al. 2006).

In works on *Phaseolus vulgaris* (Aroca et al. 2007) and *Lactuca sativa* (Jahromi et al. 2008), roots of mycorrhizal plants maintained or even decreased the expression of *LsPIP2* gene, whereas the expression of *LsPIP1* gene was up-regulated, particularly at 100 mM NaCl. In tomato plants, in contrast, transcript levels of both a tonoplast (*LeTIP*) and plasmamembrane (*LePIP1*) aquaporin genes in roots were reduced by AMF colonization. In contrast to the roots, in the leaves, AMF colonization resulted in a drastic increase of the mRNA of all three aquaporin genes (*LePIP1, LePIP2* and *LeTIP*) assayed under salt stress (Ouziad et al. 2006).

Inoculation with *Glomus intraradices* in the absence of salinity caused an inhibition of the expression of *LsPIP1* and *LsPIP2* genes (Jahromi et al. 2008) that was in

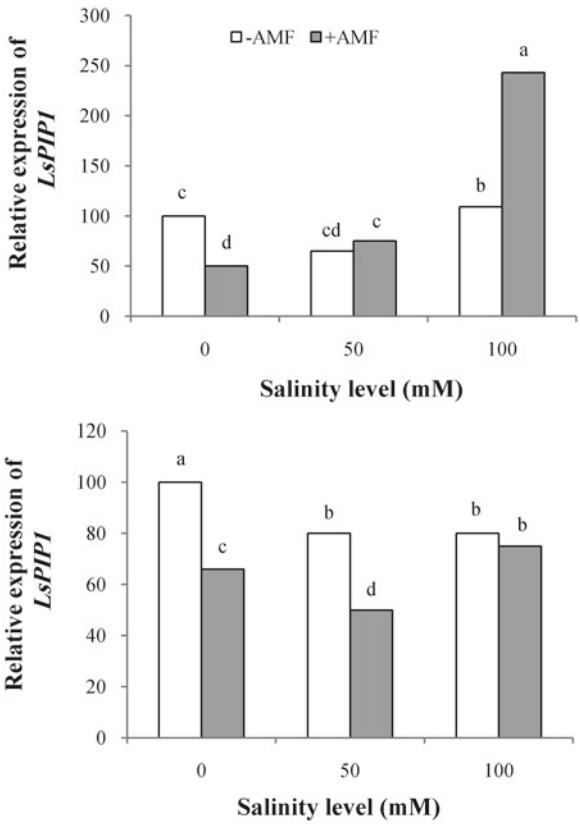

Fig. 13.9 Expression of *LsPIP1* and *LsPIP2* (plasma membrane aquaporins) gene probes from roots of lettuce (*Lactuca sativa*) plants subjected to 0, 50, or 100 mM NaCl and inoculated with Glomus intraradices. *Bars* indicated by the same letter are not significantly different ($P<0.05$) (Data from (Jahromi et al. 2008))

agreement with other authors (Porcel et al. 2006; Aroca et al. 2006). Under salinity conditions, however, the expression of *LsPIP2* gene maintained unaffected while *LsPIP1* gene was up-regulated (Fig. 13.9) (Jahromi et al. 2008). The latter finding was the opposite of that obtained for the same gene (*LsPIP1*) under drought conditions in plants inoculated with *Glomus mosseae* (Porcel et al. 2006). These results demonstrated that the same aquaporin gene responds differently to each AMF and the response depends also on the nature of applied osmotic stress (Ruiz-Lozano and Aroca 2010). Aroca et al. (2007) demonstrated also that, the gene *PvPIP1;2* was inhibited by three applied stresses in AM and nonAM plants in a similar way, while the gene *PvPIP1,3* showed important differences in AM and nonAM plants according to the stress imposed (Aroca et al. 2007).

The *NtAQP1* aquaporin of tobacco has been isolated and characterized as a plasma membrane intrinsic aquaporin (Biela et al. 1999). Effect of an impairment of *NtAQP1* gene expression on the AMF colonization pattern and symbiotic efficiency has been investigated (Fig. 13.10) (Porcel et al. 2005). Data from this study showed that impairment in *NtAQP1* gene expression did not influence AMF colonization ability. However, symbiotic efficiency was affected in *NtAQP1* antisense plants.

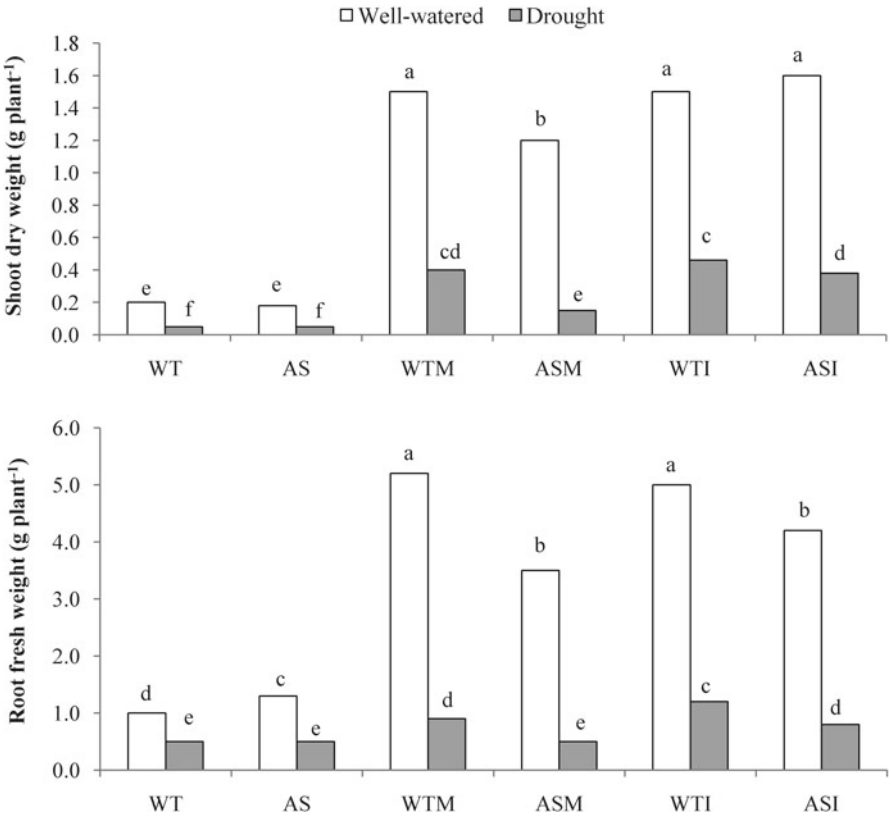

Fig. 13.10 Shoot dry weight and root fresh weight in wildtype (*WT*) or antisense (*AS*) tobacco plants inoculated or not with *Glomus mosseae* (*M*) or *Glomus intraradices* (*I*) and cultivated under well-watered conditions or subjected to drought stress. *Bars* indicated by the same letter are not significantly different ($P < 0.05$) (Data from (Porcel et al. 2005))

Beneficial effect of AMF colonization was similar in wild type and antisense plants under well-watered conditions, while under drought stress mycorrhizal wild type plants grew more than mycorrhizal *NtAQP1* antisense plants. It indicates that the symbiotic efficiency of AMF was greater with wild type than with *NtAQP1* antisense plants (Porcel et al. 2005). Taken together, these results indicate that enhanced symplastic water transport via the plasma membrane aquaporin NtAQP1 is important for the efficiency of AMF symbiosis, at least under drought stress conditions.

AMF in Halophytes

In saline soils both the macrobiota (halophytes) and the microbiota (rhizosphere-constituents) usually adapt to the particular stress conditions (Ruiz-Lozano and

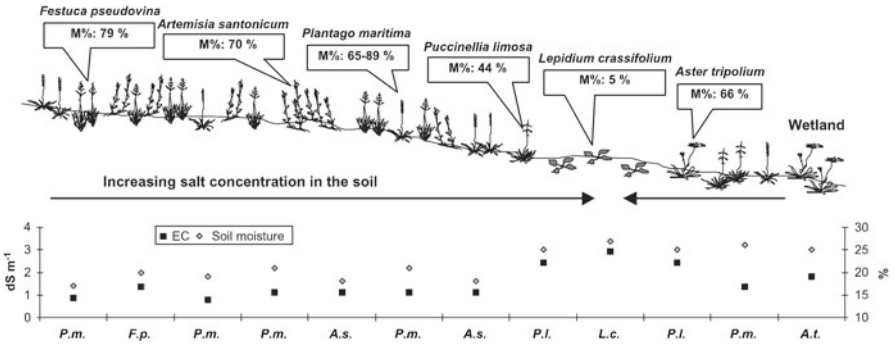

Fig. 13.11 The relative location of halophytes along the toposequence in Puszta at Apaj, Hungary. The percentage of mycorrhizal colonization was demonstrated as M% values. Soil moisture and electric conductivity were determined directly at the site in 10–20 cm soil depth close to the roots of the plants indicated. P.m., *Plantago maritima*; F.p., *Festuca pseudovina*; A.s., *Artemisia santonicum*; P.c., *Puccinellia limosa*; L.c., *Lepidium crassifolium*; A.t., *Aster tripolium* (From Füzy A, Biró B, Tóth T, Hildebrandt U, Bothe H (2008) Drought, but not salinity, determines the apparent effectiveness of halophytes colonized by arbuscular mycorrhizal fungi. J Plant Physiol 165:1181–1192, with permission)

Azcón 2000). It has been stated that high salinity in soils has adverse effects on germination and hyphal growth (Juniper and Abbott 1993, 2006) and colonization of plants by AMF (Juniper and Abbott 1993). However, there are reports from all over the world that plants of saline habitats can be colonized by AMF (Fig. 13.11) (Barrow et al. 1997; Landwehr et al. 2002; Plenchette and Duponnois 2005; Mathur et al. 2007; Asghari et al. 2008; Füzy et al. 2008).

Many halophytes belong to families like Caryophyllaceae, Chenopodiaceae and Plumbaginaceae, which are frequently reported as being nonAM (Harley and Harley 1987; Wang and Qiu 2006). Nevertheless, halophytes like *Aster tripolium* (Asteraceae), *Artemisia maritima* (Asteraceae) and *Plantago maritima* (Plantaginaceae) are intensively colonized by AMF (Harley and Harley 1987; Carvalho et al. 2001; Hildebrandt et al. 2001; Landwehr et al. 2002). Salt marsh plants such as *Spartina patens* and *Distichlis spicata* form also AMF association (Hoefnagels et al. 1993). These AMF associations could protect plants against the detrimental effects of ion toxicity and alleviate salt stress symptoms.

In a study on the biodiversity of halophytes and their mycorrhizal status in Seŏvlje salterns (Slovenia), fungal colonization was detected in the roots of *Salsola soda*, and *Salicornia europaea* and *Suaeda maritima* (Chenopodiaceae) *Plantago cornuti* (Plantaginaceae) and typical AM fungal structures were present in *Artemisia caerulescens*, *Aster tripolium* and *Inula crithmoides* (Asteraceae) and *Plantago cornuti* (Plantaginaceae) (Sonjak et al. 2009). This has been also shown for most of the halophytes collected from different salt marsh environments (Hildebrandt et al. 2001; Landwehr et al. 2002; Füzy et al. 2008), thus showing that AMF might have important roles in these extreme environments.

In a study on several salt marshes from the North and Baltic Sea and of German inland salt habitats, *Aster tripolium* and *Artemisia maritime* (Asteraceae), *Plantago maritima* and *P. coronopus* (Plantaginaceae) and *Oenanthe lachenalii* (Apiaceae) showed a high rate of AMF colonization, and low, though distinct, AMF infection was detected in samples of *Puccinellia maritime* and *P. distans* (Poaceae) and even of *Salicornia europaea* (Chenopodiaceae), at inland salt marshes, whereas other species like *Spartina anglica* (Poaceae), *Juncus gerardii* (Juncaceae), and *Triglochin maritimum* (Juncaginaceae) were nonAM (Hildebrandt et al. 2001). In a study on the two salt affected regions in Hungary, *Aster tripolium*, *Plantago maritime*, *Artemisia santonicum* and *Matricaria chamomilla* were the most heavily colonized plants (Füzy et al. 2008). In other survey on some areas of Turan Biosphere Reserve (TBR) in north east Iran that includes 1.8 million hectares of flat, semi-arid desert plains, halophyte species were studied for their mycorrhizal status (Asghari et al. 2008). Typical structures of AMF with different levels of colonization was observed in *Haloxylon aphyllum*, *Kochia stellaris*, *Halocnemum strobilaceum*, *Seidlitzia rosmarinus, Salsola sp.* (Chenopodiaceae) and *Zygophyllum eurypterum* and *Peganum harmala* (Zygophyllaceae). In this study, different levels of AM colonization were found in the same plant species from different locations but with the same salinity level. In addition, AM colonization in roots of halophytes existed at lower levels of salinity (<45 dSm^{-1}) while it was absent at higher salinity levels (>45–140 dSm^{-1}) (Asghari et al. 2008).

Chenopodiaceae are found in halophytic plant communities worldwide and include more halophytic species than other plant families. Although this family has been generally regarded to be nonAM (Hirrel et al. 1978; Reeves et al. 1979), there are reports on the occurrence of AM colonization in chenopods in the field (Johnson et al. 1995; Aguilera et al. 1998; O'Connor et al. 2001; He et al. 2002). A colonization rate of 60% in *Arthrocnemum indicum* with typical vesicles and arbuscules and of 48% in *Suaeda maritime* with vesicles were found in salt marshes of the Ganges delta in India (Sengupta and Chaudhuri 1990). In later works, the mycorrhizal status of numerous Chenopodiaceae, particularly the genus *Atriplex*, was confirmed (Hildebrandt et al. 2001; Plenchette and Duponnois 2005; Asghari et al. 2005), and inoculation of *Atriplex gardeneri* (Allen 1983), *A. nummularia* (Asghari et al. 2005) and *A. canescens* (Williams et al. 1974) with AMF was proven to enhance efficiently the growth and survival of this Chenopodiaceae.

Atriplex nummularia Lindl. A perennial chenopod was reported to have a relatively high level of AM colonization (10–30%) in spring and summer under field conditions (Asghari et al. 2005). In a glasshouse experiment, however, only low and patchy colonization (1–2%) was detected in inoculated *A. nummularia* plants. Despite low colonization rate, inoculation with AMF increased shoot dry weight, particularly before production of high density roots and depletion of P and other nutrients in the pots (Asghari et al. 2005). Factors characteristics of field conditions e.g. environmental factors, age and phenology of host plant (Wilson and Hartnett 1998), soil properties such as activity of hydrolytic enzymes (Mamatha et al. 2002) may be responsible for the high levels of colonization of *A. nummularia* under field versus glasshouse conditions (Asghari et al. 2005).

Colonization of halophytes is sometimes not accompanied by characteristic structures of AMF. On the other hand, results for a given species from different areas are contradictory. AMF colonization of *Salicornia europaea* (Chenopodiaceae) was reported to be usually very low, if detected (Harley and Harley 1987; Landwehr et al. 2002; Wang and Qiu 2006). No arbuscule was also detected in the roots of *Salicornia europaea* from Sečovlje salterns (Sonjak et al. 2009). In contrast, in the study of halophytes in central European salt marshes, Hildebrandt et al. (2001) demonstrated that colonization of individual specimens of this species is high and arbuscules are also present. This difference in the colonization level is likely the result of the species and subspecies composition of the genus *Salicornia* (Martinčič et al. 2007). Rare arbuscules were detected in the roots of *Arthrocnemum macrostachyum* (Chenopodiaceae) and *Limonium angustifolium* (Plumbaginaceae) and no arbuscules were seen in *Atriplex portulacoides* and *Beta vulgaris* L. subsp. Maritime (Chenopodiaceae) roots (Sonjak et al. 2009). The colonization of other halophytes from the Chenopodiaceae family including *Salicornia europaea*, *Salsola soda* and *Suaeda maritima* and *Spergularia marina* from the Caryophyllaceae family was determined only by the presence of hyphae without any arbuscules (Sonjak et al. 2009).

Indeed, there is no correlation between fungal structures frequency and fungal colonization rate of roots with efficiency of symbiosis and its influence on plant growth (Füzy et al. 2008; Smith and Read 2008; Tonin et al. 2001; Vogel-Mikuš et al. 2005). A high level of colonization is not necessarily associated with an extensive exchange of metabolites between the two symbiotic partners. A few active fungal structures in only a small number of roots may also help plants to cope with stress. On the other hand, results obtained from field sampling should be interpreted carefully because during the course of a year, the number of fungal structures particularly arbuscules (with a short half-life) vary significantly (Smith and Read 2008; Füzy et al. 2008).

Though a low diversity of AMF species, there is a high abundance of spores in inland and coastal habitats (Hildebrandt et al. 2001; Landwehr et al. 2002; Carvalho et al. 2004) indicating that saline soils are the sites where AMF thrive (Füzy et al. 2008). However, distribution of spores of AMF in saline soils and salt marshes is often patchy and highly variable from soil sample to sample (Landwehr et al. 2002).

Negative influence of soil salinity on spore germination and hyphal growth of AMF have been identified as being the most important reason for the absence of AMF colonization in halophytes (Juniper and Abbott 2006). However, in a study on some halophyte species it was shown that reducing soil salinity (0.4 dSm^{-1}) did not improve AM colonization (Asghari and Cavagnaro 2010). On the other hand, despite of low level of AM colonization, halophytes showed a positive growth response to AM inoculation in non-saline soil conditions (Asghari and Cavagnaro 2010). More studies are required to determine factors that influence AM colonization rate and responsiveness in halophytes.

Ecological Considerations and Use of AMF for Restoration of Saline Soils

Millions of hectares of land world-wide are affected by salinity. Restoration of salinized soils is a global concern. Arbuscular mycorrhizal fungi are considered as an important component of riparian ecosystem function (Beauchamp et al. 2009).

In semi-arid environments, stability of soil aggregates is important for supporting plants growth and in turn, protecting the soil against water erosion (Kohler et al. 2010). The AMF association contributes significantly to the stability of soil aggregates (Caravaca et al. 2005). Arbuscular mycorrhizal fungi influence the stability of macroaggregates (>250 mm) via hyphal enmeshment aggregates (Miller and Jastrow 2000), by deposition of organic substances (Bearden and Petersen 2000) and via production of the glycoprotein glomalin, which acts as an insoluble glue to stabilize aggregates (Rillig 2004; Gadkar and Rillig 2006). Arbuscular mycorrhizal colonization improves biochemical properties of rhizosphere and bulk soil, increases activity of catalase, neutral and alkaline phosphatases in soil, increases P solubility and decreases soil EC (Zhang et al. 2011).

The competitiveness of plants in saline soils is mainly determined by the level of salinity and drought, which favor species that can establish, grow to maturity, and reproduce under these conditions (Sonjak et al. 2009). Planting halophytes that have morphological and physiological adaptations to overcome osmotic and ionic stresses is often the only opportunity to produce forage for livestock in saline areas. The yield of such plantations could be enhanced by AM inoculation (Sonjak et al. 2009). Inoculation of sites with AMF is also needed when restoring historic floodplain areas following extended *Tamarix* occupations. *Tamarix* (Beauchamp et al. 2005) similar with some members of the Chenopodiaceae is not associated with AMF (Titus et al. 2002). Colonization rate and spore density of AMF in the rhizosphere soil of some ephemeral plant species such as *Chorispora tenella*, *Ceratocephalus testiculatus*, *Eremopyrum orientale* and *Veronica Campylopoda* growing in an area dominated by *Tamarix spp.* are significantly lower under the shrub canopies than beyond (Shi et al. 2006). During restoration process in areas with extensive and dense *Tamarix* occupation, therefore, AMF inoculation may improve the performance of native species over *Tamarix* sprouts or weeds such as *Kochia spp.* and *Salsola spp.* (Chenopodiaceae) (Johnson 1992).

Conclusion and Future Perspectives

Detailed studies are needed to elucidate biochemical, physiological and molecular mechanisms and signal transduction pathways involving in the salt alleviating effect of AMF symbiosis in plants. Results of many works suggest that AM plants are suffering from the salt stress less than nonAM plants. Higher relative water content, lower proline and ABA content and lower expression of the stress marker *LEA* gene

in AM compared to nonAM plants reported for various plant species suggest that the AMF decreased salt stress injury. These results evidenced that some salt-avoidance mechanisms are likely to be improved due to mycorrhization.

The great gap in our knowledge seems to be the function of ion transporter systems operating in the symbiosis including direct pathways at the soil-root interface and the mycorrhizal pathway and the possible changes in their relative contribution under salinity. On the other hand, information on the properties of ion trafficking at arbuscule-plant cell interface is really limited. Biochemical and molecular study of Na exclusion mechanisms in the roots such as Na/H antiporters and cyclic-nucleotide-gated ion channels as well as mechanisms operating at xylem loading level may elucidate the extent to which AMF act via improvement of plants ability to exclude salts. These studies would allow understanding if the AM symbiosis affects Na uptake, distribution, compartmentation and allocation at the cellular and whole plant level.

Our knowledge of the molecular mechanisms for salt amelioration by AMF in plants is limited to the changes in the expression pattern of only a few genes. Identification of temporal and spatial patterns in the expression of genes involved in production of various antioxidant enzymes and antioxidant metabolites and enzymes controlling synthesis of various osmoregulators will provide further insights into molecular basis of the mechanisms.

Study of temporal and spatial expression patterns of different members of transporters, ion channels as well as aquaporin gene families and their localization in the shoot, root and particularly in the arbuscule-plant cell interfaces may also provide an integrative perspective on the role of specific molecules in the AM-plants interactions under salt stress. In addition of using molecular and fluorescence microscopy approaches, application of imaging techniques for localization of ions in the fungi-plant cell interaction spaces may also provide evidences on the nature of differences among the various combinations of plant genotypes/fungi isolates in the efficiency for allevation of salt stress.

References

Abbott LK, Robson AD (1984) Colonization of the root systems of subterranean clover by three species of vesicular-arbuscular mycorrhizal fungi. New Phytol 96:275–281

Abd-El Baki BGK, Siefritz F, Man HM, Weiner H, Kaldenhoff R, Kaiser WM (2000) Nitrate reductase in *Zea mays* L. under salinity. Plant Cell Environ 23:515–521

Abdel-Latef AAH, Chaoxing H (2011) Effect of arbuscular mycorrhizal fungi on growth, mineral nutrition, antioxidant enzymes activity and fruit yield of tomato grown under salinity stress. Sci Hort 127:228–233

Aguilera LE, Gutierrez JR, Moreno RJ (1998) Vesicular arbuscular mycorrhizae associated with saltbushes *Atriplex spp.* (Chenopodiaceae) in the Chilean arid zone. Rev Chil Hist Nat 71:291–302

Aguin O, Mansilla JP, Vilarino A, Sainz MJ (2004) Effects of mycorrhizal inoculation on root morphology and nursery production of three grapevine rootstocks. Am J Enol Vitic 55:108–111

Aharon R, Shahak Y, Wininger S, Bendov R, Kapulnik Y, Galili G (2003) Overexpression of plasma membrane aquaporins in transgenic tobacco improves plant vigour under favourable growth conditions but not under drought or salt stress. Plant Cell 15:439–447

Alguacil MM, Kohler J, Caravaca F, Roldán A (2009) Differential effects of *Pseudomonas mendocina* and *Glomus intraradices* on lettuce plants physiological response and aquaporin *PIP2* gene expression under elevated atmospheric CO_2 and drought. Microb Ecol 58:942–951

Aliasgharzadeh N, Saleh Rastin N, Towfighi H, Alizadeh A (2001) Occurrence of arbuscular mycorrhizal fungi in saline soils of the Tabriz Plain of Iran in relation to some physical and chemical properties of soil. Mycorrhiza 11:119–122

Alkan N, Gadkar V, Yarden O, Kapulnik Y (2006) Analysis of quantitative interactions between two species of arbuscular mycorrhizal fungi, *Glomus mosseae* and *G. intraradices*, by real-time PCR. Appl Environ Microbiol 72:4192–4199

Al-Karaki GN (2000) Growth of mycorrhizal tomato and mineral acquisition under salt stress. Mycorrhiza 10:51–54

Al-Karaki GN, Clark RB (1998) Growth, mineral acquisition, and water use by mycorrhizal wheat grown under water stress. J Plant Nutr 21:263–276

Al-Karaki GN, Hammad R, Rusan M (2001) Response of two tomato cultivars differing in salt tolerance to inoculation with mycorrhizal fungi under salt stress. Mycorrhiza 11:43–47

Allen MF (1983) Formation of vesicular-arbuscular mycorrhizae in *Atriplex gardneri* (Chenopodiaceae): seasonal response in a cold desert. Mycologia 75:773–776

Allen EB, Cunningham GL (1983) Effects of vesicular-arbuscular mycorrhizae on *Distichlis spicata* under three salinity levels. New Phytol 93:227–236

Allen MF, Smith WK, Moore TS, Christensen M (1981) Comparative water relations and photosynthesis of mycorrhizal and non-mycorrhizal *Bouteloua gracilis* H.B.K. Lag ex Steud. New Phytol 88:683–693

Amzallag GN (1997) Tolerance to salinity in plants: new concept for old problems. In: Jaiwal PK, Singh RP, Gulati A (eds) Strategies for improving salt tolerance in higher plants. Science, Enfield, pp 1–17

Apel K, Hirt H (2004) Reactive oxygen species: metabolism, oxidative stress, and signal transduction. Annu Rev Plant Biol 55:373–399

Apse M, Aharon G, Snedden W, Blumwald E (1999) Salt tolerance conferred by overexpression of a vacuolar Na^+/H^+ antiport in *Arabidopsis*. Science 285:1256–1258

Arines J, Quintela M, Vilarino A, Palma JM (1994) Protein patterns and superoxide dismutase activity in non-mycorrhizal and arbuscular-mycorrhizal *Pisum sativum* L. plants. Plant Soil 166:37–45

Aroca R, Ferrante A, Vernieri P, Chrispeels MJ (2006) Drought, abscisic acid and transpiration rate effects on the regulation of PIP aquaporin gene expression and abundance in *Phaseolus vulgaris* plants. Ann Bot 98:1301–1310

Aroca R, Porcel R, Ruiz-Lozano JM (2007) How does arbuscular mycorrhizal symbiosis regulate root hydraulic properties and plasma membrane aquaporins in *Phaseolus vulgaris* under drought, cold or salinity stresses? New Phytol 173:808–816

Asghari HR, Cavagnaro TR (2010) Mycorrhizal response of halophytes to plant growth in non-saline soil conditions. In proceedings book of the 19th world congress of soil science, soil solutions for a changing world, 1–6 Aug 2010, Brisbane

Asghari HR, Marschner P, Smith SE, Smith FA (2005) Growth response of *Atriplex nummularia* to inoculation with arbuscular mycorrhizal fungi at different salinity levels. Plant Soil 273:245–256

Asghari HR, Amerian M, Gorbani H (2008) Soil salinity affects arbuscular mycorrhizal colonization of halophytes. Pak J Biol Sci 11:1909–1915

Augé RM (2000) Stomatal behavior of arbuscular mycorrhizal plants. In: Kapulnik Y, Douds DD (eds) Arbuscular mycorrhizas: physiology and function. Kluwer, Dordrecht, pp 201–237

Augé RM (2001) Water relations, drought and vesicular-arbuscular mycorrhizal symbiosis. Mycorrhiza 11:3–42

Augé RM, Toler HD, Sams CE, Nasim G (2008) Hydraulic conductance and water potential gradients in squash leaves showing mycorrhiza-induced increases in stomatal conductance. Mycorrhiza 18:115–121

Baker NR (2008) Chlorophyll fluorescence: a probe of photosynthesis *in vivo*. Annu Rev Plant Biol 59:89–113

Barea JM, Azcón-Aguilar C (1982) Production of plant growth-regulating substances by the vesicular-arbuscular mycorrhizal fungus *Glomus mosseae*. Appl Environ Microbiol 43:810–813

Barrow JR, Havstad KM, McCaslin BD (1997) Fungal root endophytes in fourwing saltbush, *Atriplex canescens*, on arid rangelands of southwestern USA. Arid Soil Res Rehabil 1:177–185

Bearden BN, Petersen L (2000) Influence of arbuscular mycorrhizal fungi on soil structure and aggregate stability of vertisols. Plant Soil 218:173–183

Beauchamp VB, Stromberg JC, Stutz JC (2005) Interactions between *Tamarix ramosissima* (saltcedar), *Populus fremontii* (cottonwood), and mycorrhizal fungi: effects on seedling growth and plant species coexistence. Plant Soil 275:221–231

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

Becard G, Doner LW, Rolin DB, Douds DD, Pfeffer PE (1991) Identification and quantification of trehalose in vesicular arbuscular mycorrhizal fungi *in vivo* ^{13}C NMR and HPLC analyses. New Phytol 108:547–552

Benavides MP, Marconi PL, Gallego SM, Comba ME, Tomaro ML (2000) Relationship between antioxidant defence systems and salt tolerance in *Solanum tuberosum*. Austr J Plant Physiol 27:273–278

Bentivenga SP, Bever JD, Morton JB (1997) Genetic variation of morphological characters within a single isolate of the endomycorrhizal fungus *Glomus clarum* (Glomaceae). Am J Bot 84:1211–1216

Berta G, Fusconi A, Trotta A (1993) VA mycorrhizal infection and the morphology and function of root systems. Environ Exp Bot 33:159–173

Bethlenfalvay GJ, Brown MS, Franson RL, Mihara KL (1989) The *glycine-glomus-bradyrhizobium* symbiosis. IX. Nutritional, morphological and physiological response of nodulated soybean to geographic isolates of the mycorrhizal fungus of *Glomus mosseae*. Physiol Plant 76:226–232

Bhardwaj S, Dudeja SS, Khurana AL (1997) Distribution of VAM fungi in the natural ecosystem. Fol Microbiol 42:589–594

Bhaskaran C, Selvaraj T (1997) Seasonal incidence and distribution of VAM fungi in native saline soils. J Environ Biol 18:209–212

Biela A, Grote K, Otto B, Hoth S, Hedrich R, Kaldenho R (1999) The *Nicotiana tabacum* plasma membrane aquaporin *NtAQP1* is mercury-insensitive and permeable for glycerol. Plant J 18:565–570

Blilou I, Ocampo JA, García-Garrido JM (2000) Induction of Ltp (lipid transfer protein) and Pal (phenylalanine ammonia-lyase) gene expression in rice roots colonized by the arbuscular mycorrhizal fungus *Glomus mosseae*. J Exp Bot 51:1969–1977

Bonfante P, Perotto S (2000) Outside and inside the roots: cell to cell interactions among arbuscular mycorrhizal fungi, bacteria and host plant. In: Podila GK, Douds DD (eds) Current advances in mycorrhizae research. The American Phytopathological Society, St. Paul, pp 141–155

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 30:265–271

Bouchereau A, Aziz A, Larher F, Martin-Tanguy T (1999) Polyamines and environmental challenges: recent development. Plant Sci 140:103–125

Bowen G (1987) The biology and physiology of infection and its development. In: Safir GR (ed) Ecophysiology of VA mycorrhizal plants. CRC, Boca Raton, pp 27–57

Brundrett M (1991) Mycorrhizas in natural ecosystems. Adv Ecol Res 21:300–313

Camprubi A, Calvet C (1996) Isolation and screening of mycorrhizal fungi from citrus nurseries and orchards and inoculation studies. Hort Sci 31:363–369

Cantrell IC, Linderman RG (2001) Preinoculation of lettuce and onion with VA mycorrhizal fungi reduces deleterious effects of soil salinity. Plant Soil 233:269–281
Caravaca F, Alguacil MM, Torres P, Roldán A (2005) Plant type mediates rhizospheric microbial activities and soil aggregation in a semiarid Mediterranean salt marsh. Geoderma 124:375–382
Carvajal M, Martínez V, Alcaraz CF (1999) Physiological function of water channels as affected by salinity in roots of paprika pepper. Physiol Plant 105:95–101
Carvajal M, Cerdá A, Martínez V (2000) Does calcium ameliorate the negative effect of NaCl on melon root water transport by regulating aquaporin activity? New Phytol 145:439–447
Carvalho LM, Cacador I, Martins-Loucão MA (2001) Temporal and spatial variation of arbuscular mycorrhizas in salt marsh plants of the Tagus estuary (Portugal). Mycorrhiza 11:303–309
Carvalho LM, Correia PM, Martins-Loucão MA (2004) Arbuscular mycorrhizal fungal propagules in a salt marsh. Mycorrhiza 14:165–170
Chattopadhyay MK, Tiwari BS, Chattopadhyay G, Bose A, Sengupta DN, Ghosh B (2002) Protective role of exogenous polyamines on salinity-stressed rice (*Oryza sativa*) plants. Physiol Plant 116:192–199
Chaves M, Flexas J, Pinheiro C (2009) Photosynthesis under drought and salt stress: regulation mechanisms from whole plant to cell. Ann Bot 103:551–560
Chen G-P, Wilson ID, Kim SH, Grierson D (2001) Inhibiting expression of a tomato ripening-associated membrane protein increases organic acids and reduces sugar levels of fruit. Planta 212:799–807
Chinnusamy V, Jagendorf A, Zhu JK (2005) Understanding and improving salt tolerance in plants. Crop Sci 45:437–448
Chulan HA, Martin K (1992) The vesicular-arbuscular (VA) mycorrhiza and its effects on growth of vegetatively propagated *Theobroma cacao* L. Plant Soil 144:227–233
Clapp JP, Young JPW, Merryweather JW, Fitter AH (1995) Diversity of fungal symbionts in arbuscular mycorrhizas from a natural community. New Phytol 130:259–265
Colla G, Rouphael Y, Cardarelli M, Tullio M, Rivera CM, Rea E (2008) Alleviation of salt stress by arbuscular mycorrhizal in zucchini plants grown at low and high phosphorus concentration. Biol Fert Soils 44:501–509
Cook JC, Butler RH, Madol T (1993) Some observations on the vertical distribution of VAM in roots of salt marsh grasses growing in saturated soils. Mycologia 85:547–550
Copeman RH, Martin CA, Stutz JC (1996) Tomato growth in response to salinity and mycorrhizal fungi from saline or nonsaline soils. Hort Sci 31:341–344
Cramer G (2004) Sodium–calcium interactions under salinity stress. In: Läuchli A, Lüttge S (eds) Salinity: environment–plants–molecules. Springer, Netherlands, pp 205–227
Daei G, Ardekani MR, Rejali F, Teimuri S, Miransari M (2009) Alleviation of salinity stress on wheat yield, yield components, and nutrient uptake using arbuscular mycorrhizal fungi under field conditions. J Plant Physiol 166:617–625
Daniels BA, Graham SO (1976) Effects of nutrition and soil extracts on germination of *Glomus mosseae* spores. Mycologia 68:108–116
Daniels BA, Trappe JM (1980) Factors affecting spore germination of the vesicular-arbuscular mycorrhizal fungus *Glomus epigaeus*. Mycologia 72:457–471
Davies HA, Dow JM (1997) Induction of extracellular matrix glycoproteins in Brassica petioles bywounding and in response to *Xanthomonas campestris*. Mol Plant-Microb Interact 10:812–820
Davies WJ, Zhang J (1991) Root signals and the regulation of growth and development of plants in drying soil. Annu Rev Plant Physiol 42:55–73
del Val C, Barea JM, Azcon-Agular C (1999) Divisity of arbuscular mycorrhizal fungus populations in heavy-metal contaminated soils. Appl Environ Microbiol 65:718–723
Dixon RK, Garg VK, Rao MV (1993) Inoculation of *Leucaena* and *Prosopis* seedlings with *Glomus* and *Rhizobium* species in saline soil: rhizosphere relations and seedling growth. Arid Soil Res Rehabil 7:133–144
Dodd JC, Thomson BD (1994) The screening and selection of inoculant arbuscular-mycorrhizal and ectomycorrhizal fungi. Plant Soil 159:149–158

Douds DD Jr, Millner PD (1999) Biodiversity of arbuscular mycorrhizal fungi in agroecosystems. Agric Ecosyst Environ 74:183–193

Duke ER, Johnson CR, Koch KE (1986) Accumulation of phosphorus, dry matter and betaine during NaC1 stress of split-root citrus seedlings colonized with vesicular-arbuscular mycorrhizal fungi on zero, one or two halves. New Phytol 104:583–590

Estaun MV (1989) Effect of sodium chloride and mannitol on germination and hyphal growth of the vesicular-arbuscular mycorrhizal fungus *Glomus mosseae*. Agric Ecosyst Environ 29:123–129

Estaun MV (1991) Effect of NaC1 and mannitol on the germination of two isolates of the vesicular-arbuscular mycorrhizal fungus *Glomus mosseae.* In: Proceedings book of 3rd European symposium on mycorrhizas. University of Sheffield, Sheffield

Evelin H, Kapoor R, Giri B (2009) Arbuscular mycorrhizal fungi in alleviation of salt stress: a review. Ann Bot 104:1263–1280

Ezawa T, Smith SE, Smith FA (2002) P metabolism and transport in AM fungi. Plant Soil 244:221–230

Feng G, Zhang FS, Li XL, 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

Fornalé S, Sarjala T, Bagni N (1999) Endogenous polyamine content and metabolism in the ectomycorrhizal fungus *Paxillus involutus*. New Phytol 143:581–587

Francoise F, Daniel LR, John G (1991) Effects of salt stress on amino acid, organic acid and carbohydrate composition of root, bacteroids, and cytosol of alfalfa (*Medicago sativa* L.). Plant Physiol 96:1228–1236

Fukuda A, Nakamura A, Tanaka Y (1999) Molecular cloning and expression of the Na^+/H^+ exchanger gene in *Oryza sativa*. Biochim Biophys Acta 1446:149–155

Füzy A, Biró B, Tóth T, Hildebrandt U, Bothe H (2008) Drought, but not salinity, determines the apparent effectiveness of halophytes colonized by arbuscular mycorrhizal fungi. J Plant Physiol 165:1181–1192

Gadkar V, Rillig M (2006) The arbuscular mycorrhizal fungal protein glomalin is a putative homolog of heat shock protein 60. FEMS Microbiol Lett 263:93–101

Garg N, Chandel S (2011) The effects of salinity on nitrogen fixation and trehalose metabolism in mycorrhizal *Cajanus cajan* (L.) Millsp. plants. J Plant Growth Regul 30:490–503

Garratt LC, Janagoudar BS, Lowe KC (2002) Salinity tolerance and antioxidant status in cotton culture. Free Radic Biol Med 33:502–511

Gaxiola RA, Rao R, Sherman A, Grisafi P, Alper SL, Fink GR (1999) The *Arabidopsis thaliana* proton transporters, *AtNhx1* and *Avp1*, can function in cation detoxification in yeast. Proc Natl Acad Sci USA 96:1480–1485

Ghachtouli NE, Paynot M, Morandi D, Martintanguy J, Gianinazzi S (1995) The effect of polyamines on endomycorrhizal infection of wild-type *Pisum sativum*, cv. Frisson (nod + myc+) and 2 mutants (nod– myc + and nod–myc–). Mycorrhiza 5:189–192

Gianinazzi-Pearson V (1996) Plant cell responses to arbuscular mycorrhizal fungi: getting to the roots of the symbiosis. Plant Cell 8:1871–1883

Giri M, Mukerji KG (2004) Mycorrhizal inoculant alleviates salt stress in *Sesbania aegyptiaca* and *Sesbania grandiflora* under field conditions: evidence for reduced sodium and improved magnesium uptake. Mycorrhiza 14:307–312

Giri B, Kapoor R, Mukerji KG (2003) Influence of arbuscular mycorrhizal fungi and salinity on growth, biomass, and mineral nutrition of *Acacia auriculiformis*. Biol Fertil Soil 38:170–175

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. Microbiol Ecol 54:753–760

Groppa MD, Benavides MP (2008) Polyamines and abiotic stress: recent advances. Amino Acids 34:35–45

Guo LQ, Shi DC, Wang DL (2010) 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 rhizosphere. J Agron Crop Sci 196:123–135

Hajiboland R, Aliasgharzadeh N, Laiegh SF, Poschenrieder C (2010) Colonization with arbuscular mycorrhizal fungi improves salinity tolerance of tomato (*Solanum lycopersicum* L.) plants. Plant Soil 331:313–327

Hajlaoui H, Ayeb NE, 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 Crops Prod 31:122–130

Hammer EC, Rillig MC (2011) The influence of different stresses on glomalin levels in an arbuscular mycorrhizal fungus-salinity increases glomalin content. PLoS One 6(12): e28426

Hammer EC, Nasr H, Pallon J, Olsson PA, Wallander H (2011) Elemental composition of arbuscular mycorrhizal fungi at high salinity. Mycorrhiza 21:117–129

Harinasut P, Poonsopa D, Roengmongkol K, Charoensataporn R (2003) Salinity effects on antioxidant enzymes in mulberry cultivar. Sci Asia 29:109–113

Harley JL, Harley EL (1987) A check-list of mycorrhiza in the British flora. New Phytol 10:1–102

Hartmond U, Schaesberg NV, Graham JH, Syvertsen JP (1987) Salinity and flooding stress effects on mycorrhizal and nonmycorrhizal citrus rootstock seedlings. Plant Soil 104:37–43

Hasegawa PM, Bressan RA, Zhu JK, Bohnert HJ (2000) Plant cellular and molecular responses to high salinity. Annu Rev Plant Physiol Plant Mol Biol 51:463–499

Hatzig S, Kumar A, Neubert A, Schubert S (2010) PEP-carboxylase activity: a comparison of its role in a C_4 and a C_3 species under salt stress. J Agron Crop Sci 196:185–192

He XL, Mouratov S, Steinberger Y (2002) Spatial distribution and colonization of arbuscular mycorrhizal fungi under the canopies of desert halophytes. Arid Land Res Manag 16: 149–160

He ZQ, He CX, Zhang ZB, Zou ZR, Wang HS (2007) Changes of antioxidative enzymes and cell membrane osmosis in tomato colonized by arbuscular mycorrhizae under NaCl stress. Colloids Surf B Biointerfaces 59:128–133

Hepper CM (1979) Germination and growth of *Glomus caledonius* spores: the effects of inhibitors and nutrients. Soil Biol Biochem 11:269–277

Hetrick BAD, Bockus WW, Bloom J (1984) The role of vesicular-arbuscular mycorrhizal fungi in the growth of Kansas winter wheat. Can J Bot 62:735–740

Hildebrandt U, Janetta K, Ouziad F, Renne B, Nawrath K, Bothe H (2001) Arbuscular mycorrhizal colonization of halophytes in Central European salt marshes. Mycorrhiza 10:175–183

Hill AE, Shachar-Hill B, Shachar-Hill Y (2004) What are aquaporins for? J Membr Biol 197:1–32

Hirrel MC (1981) The effect of sodium and chloride salts on the germination of *Gigaspora margarita*. Mycologia 73:610–617

Hirrel MC, Gerdemann JW (1980) Improved growth of onion and bell pepper in saline soils by two vesicular–arbuscular mycorrhizal fungi. Soil Sci Soc Am J 44:654–655

Hirrel MC, Mehravaran H, Gerdemann JW (1978) Vesiculararbuscular mycorrhiza in the Chenopodiaceae and Cruciferae: do they occur? Can J Bot 56:2813–2817

Ho I (1987) Vesicular-arbuscular mycorrhizae of halophytic grasses in the Alvard desert of Oregon. Northwest Sci 61:148–151

Hoefnagels MH, Broome SW, Shafer SR (1993) Vesicular-arbuscular mycorrhizae in salt marshes in North Carolina. Estuaries 16:851–858

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. Microbial Ecol 55:45–53

Jakobsen I, Abbott LK, Robson AD (1992) External hyphae of vesicular-mycorrhizal fungi associated with *Trifolium subterraneum* L. New Phytol 120:371–380

Jang JY, Lee SH, Ree JY, Chung GC, Ahn SJ, Kang H (2007) Transgenic *Arabidopsis* and tobacco plants overexpressing and aquaporin respond differently to various abiotic stresses. Plant Mol Biol 64:621–632

Janos DP (2007) Plant responsiveness to mycorrhizas differs from dependence upon mycorrhizas. Mycorrhiza 17:75–91

Javot H, Lauvergeat V, Santoni V, Martin-Laurent F, Guclu J, Vinh J, Heyes J, Franck KI, Schaffner AR, Bouchez D, Maurel C (2003) Role of a single aquaporin isoform in root water uptake. Plant Cell 15:509–522

Johansson I, Larsson C, Ek B, Kjellbom P (1996) The major integral proteins of spinach leaf plasma membranes are putative aquaporins and are phosphorylated in response to Ca^{2+} and apoplastic water potential. Plant Cell 8:1181–1191

Johansson I, Karlsson M, Johanson U, Larsson C, Kjellbom P (2000) The role of aquaporins in cellular and whole plant water balance. Biochim Biophys Acta 1465:324–342

Johnson WC (1992) Dams and riparian forests: case study from the upper Missouri River. Rivers 3:229–242

Johnson GPC, Kenkel NC, Booth T (1995) The distribution and phenology of arbuscular mycorrhizae along an inland salinity gradient. Can J Bot 73:1318–1327

Johnson NC, Graham JH, Smith FA (1997) Functioning of mycorrhizal associations along the mutualism–parasitism continuum. New Phytol 135:574–586

Juniper S, Abbott LK (1993) Vesicular-arbuscular mycorrhizas and soil salinity. Mycorrhiza 4:45–57

Juniper S, Abbott LK (2006) Soil salinity delays germination and limits growth of hyphae from propagules of arbuscular mycorrhizal fungi. Mycorrhiza 16:371–379

Kapoor R, Sharma D, Bhatnagar AK (2008) Arbuscular mycorrhizae in micropropagation systems and their potential applications. Sci Hort 116:227–239

Kasukabe Y, He L, Nada K, Misawa S, Ihara I, Tachibana S (2004) Overexpression of spermidine synthase enhances tolerance to multiple environmental stresses and up-regulates the expression of various stress-regulated genes in transgenic *Arabidopsis thaliana*. Plant Cell Physiol 45:712–722

Kaya C, Ashraf M, Sonmez O, Aydemir S, Tuna LA, Cullu AM (2009) The influence of arbuscular mycorrhizal colonization on key growth parameters and fruit yield of pepper plants grown at high salinity. Sci Hort 12:1–6

Khaled LB, Gõmez AM, Ouarraqi EM, Oihabi A (2003) Physiological and biochemical responses to salt stress of mycorrhized and/or nodulated clover seedlings (*Trifolium alexandrinum* L.). Agronomie 23:571–580

Khalil HA, Eissa AM, El-Shazly SM, Aboul-Nasr AM (2011) Improved growth of salinity-stressed citrus after inoculation with mycorrhizal fungi. Sci Hort 130:624–632

Khalvati MA, Hu Y, Mozafar A, Schmidhalter U (2005) Quantification of water uptake by arbuscular mycorrhizal hyphae and its significance for leaf growth, water relations, and gas exchange of barley subjected to drought stress. Plant Biol 7:706–712

Kim CK, Weber DJ (1985) Distribution of VA mycorrhiza on halophytes on inland salt playas. Plant Soil 83:207–214

Kishor PB, Hong Z, Miao G-H (1995) Overexpression of pyrroline-5- carboxylate synthetase increases proline production and confers osmotolerance in transgenic plants. Plant Physiol 108:1387–1394

Kohler J, Hernández JA, Caravaca F, Roldán A (2009) Induction of antioxidant enzymes is involved in the greater effectiveness of a PGPR versus AM fungi with respect to increasing the tolerance of lettuce to severe salt stress. Environ Exp Bot 65:245–252

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 42:429–434

Koide RT (2000) Functional complementarity in the arbuscular mycorrhizal symbiosis. New Phytol 147:233–235

Krajinski F, Biela A, Schubert D, Gianinazzi-Pearson V, Kaldenhoff R, Franken P (2000) Arbuscular mycorrhiza development regulates the mRNA abundance of Mtaqp1 encoding a mercury-insensitive aquaporin of *Medicago truncatula*. Planta 211:85–90

Lambais MR, Ríos-Ruiz WF, Andrade RM (2003) Antioxidant responses in bean (*Phaseolus vulgaris*) roots colonized by arbuscular mycorrhizal fungi. New Phytol 160:421–428

Landwehr M, Hildebrandt U, Wilde P, Nawrath K, Tóth T, Biró B, Bothe H (2002) The arbuscular mycorrhizal fungus *Glomus geosporum* in European saline, sodic and gypsum soils. Mycorrhiza 12:199–211

Lerat S, Lapointe L, Gutjahr S, Piché Y, Vierheilig H (2003) Carbon partitioning in a split-root system of arbuscular mycorrhizal plants is fungal and plant species dependent. New Phytol 157:589–595

Locatelli LM, Vitovski CA, Lovato PE (2002) Root architecture of apple rootstocks inoculated with arbuscular mycorrhizal fungi. Pesq Agropec Bras 37:1239–1245

López-Bucio J, Nieto-Jacobo MF, Ramírez-Rodríguez V, Herrera-Estrella L (2000) Organic acid metabolism in plants: from adaptive physiology to transgenic varieties for cultivation in extreme soils. Plant Sci 160:1–13

Luu DT, Maurel C (2005) Aquaporins in a challenging environment: molecular gears for adjusting plant water status. Plant Cell Environ 28:85–96

Mamatha G, Bagyaraj DJ, Jaganath S (2002) Inoculation of field-established mulberry and papaya with arbuscular mycorrhizal fungi and a mycorrhiza helper bacterium. Mycorrhiza 12:313–316

Mardukhi B, Rejali F, Daei G, Ardakani MR, Malakouti MJ, Miransari M (2011) Arbuscular mycorrhizas enhance nutrient uptake in different wheat genotypes at high salinity levels under field and greenhouse conditions. Com Rend Biol 334:564–571

Marschner P (2012) Rhizosphere biology. In: Marschner P (ed) Marschner's mineral nutrition of higher plants, 3rd edn. Academic Press, USA, pp 369–388

Marschner H, Dell B (1994) Nutrient uptake in mycorrhizal symbiosis. Plant Soil 159:89–102

Martinčič A, Wraber T, Jogan N, Podobnik A, Turk B, Vreš B, Ravnik V, Frajman B, Strgulc-Krajšek S, Trčak B, Bačič T, Fischer MA, Eler K, Surina B (2007) Mala Flora Slovenije: Ključ Za Določanje Praprotnic in Semenk. Tehniška založba Slovenije, Ljubljana

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

Mathur N, Singh J, Bohra S, Vyas A (2007) Arbuscular mycorrhizal status of medicinal halophytes in saline areas of Indian Thar desert. Int J Soil Sci 2:119–127

Maurel C, Kado RT, Guern J, Chrispeels MJ (1995) Phosphorylation regulates the water channel activity of the seed-specific aquaporin alpha-TIP. EMBO J 14:3028–3035

Maurel C, Chrispeels M, Lurin C, Tacnet F, Geelen D, Ripoche P, Guern J (1997) Function and regulation of seed aquaporins. J Exp Bot 48:421–430

McMillen BG, Juniper S, Abbott LK (1998) Inhibition of hyphal growth of a VA mycorrhizal fungus in soil containing sodium chloride limits the spread of infection from spores. Soil Biol Biochem 30:1639–1646

Mehdy MC, Sharma YK, Sathasivan K, Bays NW (1996) The role of activated oxygen species in plant disease resistance. Physiol Plant 98:365–374

Miller RM, Jastrow JD (2000) Mycorrhizal fungi influence soil structure. In: Kapulnik Y, Douds DD (eds) Arbuscular mycorrhizas: molecular biology and physiology. Kluwer, Dordrecht, pp 3–18

Miranda D, Fischer G, Ulrichs C (2011) The influence of arbuscular mycorrhizal colonization on the growth parameters of cape gooseberry (*Physalis peruviana* L.) plants grown in a saline soil. J Soil Sci Plant Nutr 1:18–30

Miransari M (2010) Contribution of arbuscular mycorrhizal symbiosis to plant growth under different types of soil stress. Plant Biol 1:563–569

Miransari M (2011) Arbuscular mycorrhizal fungi and nitrogen uptake. Arch Microbiol 193:77–81

Miransari M, Smith DL (2007) Overcoming the stressful effects of salinity and acidity on soybean [*Glycine max* (L.) Merr.] nodulation and yields using signal molecule genistein under field conditions. J Plant Nutr 30:1967–1992

Miransari M, Smith DL (2008) Using signal molecule genistein to alleviate the stress of suboptimal root zone temperature on soybean-*Bradyrhizobium* symbiosis under different soil textures. J Plant Interact 3:287–295

Miransari M, Bahrami HA, Rejali F, Malakouti MJ, Torabi H (2007) Using arbuscular mycorrhiza to reduce the stressful effects of soil compaction on corn (*Zea mays* L.) growth. Soil Biol Biochem 39:2014–2026

Miransari M, Bahrami HA, Rejali F, Malakouti MJ (2008) Using arbuscular mycorrhiza to reduce the stressful effects of soil compaction on wheat (*Triticum aestivum* L.) growth. Soil Biol Biochem 40:1197–1206

Mittova V, Tal M, Volokita M, Guy M (2002) Salt stress induces up-regulation of an efficient chloroplast antioxidant system in the salt-tolerant wild tomato species *Lycopersicon pennellii* but not in the cultivated species. Physiol Plant 115:393–400

Mosse B, Hepper C (1975) Vesicular-arbuscular mycorrhizal infections in root organ cultures. Physiol Plant Pathol 5:215–223

Munns R, Tester M (2008) Mechanisms of salinity tolerance. Ann Rev Plant Biol 59:651–681

Munns R, James RA, Läuchli A (2006) Approaches to increasing the salt tolerance of wheat and other cereals. J Exp Bot 57:1025–1043

Murkute AA, Sharma S, Singh SK (2006) Studies on salt stress tolerance of citrus rootstock genotypes with arbuscular mycorrhizal fungi. Hort Sci 33:70–76

Nemec S (1981) Histochemical characterization of *Glomus etunicatum* infection of Citrus limon roots. Can J Bot 59:609–617

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 4:137–144

Niki T, Mitsuhara I, Ohtsubo S, Ohashi Y (1998) Antagonistic effect of salicylic acid and jasmonic acid on the expression of pathogenesis-related (PR) protein genes in wounded mature tobacco leaves. Plant Cell Physiol 39:500–507

O'Connor PJ, Smith SE, Smith FA (2001) Arbuscular mycorrhizal associations in the southern Simpson desert. Aust J Bot 49:493–499

Ocón A, Hampp R, Requena N (2007) Trehalose turnover during abiotic stress in arbuscular mycorrhizal fungi. New Phytol 174:879–891

Ojala JC, Jarrell WM, Menge JA, Johnson ELV (1983) Influence of mycorrhizal fungi on the mineral nutrition and yield of onion in saline soil. Agron J 75:255–259

Ouziad F, Wilde P, Schmelzer E, Hildebrandt U, Bothe H (2006) Analysis of expression of aquaporins and Na^+/H^+ transporters in tomato colonized by arbuscular mycorrhizal fungi and affected by salt stress. Environ Exp Bot 57:177–186

Pacovsky RS, De Silva P, Carvalho MTV, Tsai SM (1991) Growth and nutrient allocation in *Phaseolus vulgaris* L. colonized with endomycorrhizae or *Rhizobium*. Plant Soil 132:127–137

Palma JM, Longa MA, del Rio LA, Arines J (1993) Superoxide dismutase in vesicular-arbuscular red clover plants. Physiol Plant 87:77–83

Parida AK, Das AB (2005) Salt tolerance and salinity effects on plants: a review. Ecotoxicol Environ Saf 60:324–349

Paul MJ, Primavesi LF, Jhurreea D, Zhang Y (2008) Trehalose metabolism and signaling. Annu Rev Plant Biol 59:417–441

Peng J, Li Y, Shi P, Chen X, Lin H, Zhao B (2011) The differential behavior of arbuscular mycorrhizal fungi in interaction with *Astragalus sinicus* L. under salt stress. Mycorrhiza 21:27–33

Pfeiffer CM, Bloss HE (1988) Growth and nutrition of guayule *(Parthenium argentatum)* in a saline soil as influenced by vesicular- arbuscular mycorrhiza and phosphorus fertilization. New Phytol 108:315–321

Pitman M, Läuchli A (2004) Global impact of salinity and agricultural ecosystems. In: Läuchli A, Lüttge S (eds) Salinity: environment–plants–molecules. Springer, Dordrecht, pp 3–20

Plenchette C, Duponnois R (2005) Growth response of the saltbush *Atriplex nummularia* L. to inoculation with the arbuscular mycorrhizal fungus *Glomus intraradices*. J Arid Environ 61:535–540

Pond EC, Menge JA, Jarrell WM (1984) Improved growth of tomato in salinized soil by vesicular-arbuscular mycorrhizal fungi collected from saline soils. Mycologia 76:74–84

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 55:1743–1750

Porcel R, Azcón R, Ruiz-Lozano JM (2004) Evaluation of the role of genes encoding for Δ^1-pyrroline-5-carboxylate synthetase (P5CS) during drought stress in arbuscular mycorrhizal *Glycine max* and *Lactuca sativa* plants. Physiol Mol Plant Pathol 65:211–221

Porcel R, Gómez M, Kaldenhoff R, Ruiz-Lozano JM (2005) Impairment of *NtAQP1* gene expression in tobacco plants does not affect root colonisation pattern by arbuscular mycorrhizal fungi but decreases their symbiotic efficiency under drought. Mycorrhiza 15:417–423

Porcel R, Aroca R, Azcón R, Ruiz-Lozano JM (2006) PIP aquaporin gene expression in arbuscular mycorrhizal Glycine max and *Lactuca sativa* plants in relation to drought stress tolerance. Plant Mol Biol 60:389–404

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

Porras-Soriano A, Soriano-Martín ML, Porras-Piedra A, Azcón R (2009) Arbuscular mycorrhizal fungi increased growth, nutrient uptake and tolerance to salinity in olive trees under nursery conditions. J Plant Physiol 166:1350–1359

Poss JA, Pond E, Menge JA, Harrell WM (1985) Effect of salinity on mycorrhizal onion and tomato in soil with and without additional phosphate. Plant Soil 88:307–319

Pozo MJ, Azcón C (2007) Unravelling mycorrhiza-induced resistance. Curr Opin Plant Biol 10:393–398

Rabie GH (2005) Influence of arbuscular mycorrhizal fungi and kinetin on the response of mungbean plants to irrigation with seawater. Mycorrhiza 15:225–230

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

Rao DLN (1998) Biological amelioration of salt affected soils. In: Microbial interactions in agriculture and forestry, 1st edn. Science, Enfield, pp 21–238

Redecker D, Morton JB, Bruns TD (2000) Ancestral lineages of arbuscular mycorrhizal fungi (Glomales). Mol Phylogenet Evol 14:276–284

Reeves FB, Wagner D, Moorman T, Kiel J (1979) The role of endomycorrhizae in revegetation practices in the semi-arid west. I. A comparison of incidence of mycorrhizae in severely disturbed vs. natural environments. Am J Bot 66:6–13

Rhodes D, Nadolska-Orczyk A, Rich PJ (2004) Salinity, osmolytes and compatible solutes. In: Läuchli A, Lüttge S (eds) Salinity: environment–plants–molecules. Springer, Dordrecht, pp 181–204

Rillig MC (2004) Arbuscular mycorrhizae, glomalin, and soil aggregation. Can J Soil Sci 84:355–363

Rovira AD (1969) Plant root exudates. Bot Rev 35:35–57

Rozema J, Arp W, Van Diggelen J, Van Esbroek M, Broekma R, Punt H (1986) Occurrence and ecological significance of vesicular-arbuscular mycorrhiza in the salt marsh environment. Acta Bot Neerl 35:457–467

Ruiz-Lozano JM (2003) Arbuscular mycorrhizal symbiosis and alleviation of osmotic stress new perspectives for molecular studies. Mycorrhiza 13:309–317

Ruiz-Lozano JM, Aroca R (2010) Modulation of aquaporin genes by the arbuscular mycorrhizal symbiosis in relation to osmotic stress tolerance. In: Seckbach J, Grube M (eds) Symbioses and stress, vol 17, Cellular origin, life in extreme habitats and astrobiology. Springer, Berlin, pp 357–374

Ruiz-Lozano JM, Azcón R (2000) Symbiotic efficiency and infectivity of an autochthonous arbuscular mycorrhizal *Glomus sp.* from saline soils and *Glomus deserticola* under salinity. Mycorrhiza 10:137–143

Ruiz-Lozano JM, Azcón R, Goméz M (1996) Alleviation of salt stress by arbuscular-mycorrhizal Glomus species in *Lactuca sativa* plants. Physiol Plant 98:767–772

Ruiz-Lozano JM, Porcel R, Azcón 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(11):4033–4044

Rush DW, Epstein E (1976) Genotypic responses to salinity: differences between salt-sensitive and salt-tolerant genotypes of tomato. Plant Physiol 57:162–166

Sannazzaro AI, Alvarez CL, Menéndez AB, Pieckenstain FL, Albertó EO, Ruiz OA (2004) Ornithine and arginine decarboxilase activities and effect of some polyamine biosynthesis inhibitors on *Gigaspora rosea* germinating spores. FEMS Microbiol Lett 230:115–121

Sannazzaro AI, Ruíz OA, Alberto EO, Menendez AB (2006) Alleviation of salt stress in *Lotus glaber* by *Glomus intraradices*. Plant Soil 285:279–287

Sannazzaro AI, Echeverría M, Albertó EO, Ruiz OA, Menéndez AB (2007) Modulation of polyamine balance in *Lotus glaber* by salinity and arbuscular mycorrhiza. Plant Physiol Biochem 45:39–46

Sarda X, Tousch D, Ferrare K, Cellier F, Alcon C, Dupuis JM, Casse F, Lamaze T (1999) Characterization of closely related delta- TIP genes encoding aquaporins which are differentially expressed in sunflower upon water deprivation through exposure to air. Plant Mol Biol 40:179–191

Sawers RJ, Gutjahr C, Paszkowski U (2008) Cereal mycorrhiza: an ancient symbiosis in modern agriculture. Trends Plant Sci 13:93–97

Scheublin TR, Ridgway KP, Young PW, van der Heijden MGA (2004) Non legumes, legumes, and root nodules harbor different arbuscular mycorrhizal fungal communities. Appl Environ Microbiol 70:6240–6246

Schroeder MS, Janos DP (2005) Plant growth, phosphorus nutrition, and root morphological responses to arbuscular mycorrhizas, phosphorus fertilization, and intraspecific density. Mycorrhiza 15:203–216

Schubert A, Wyss P, Wiekman A (1992) Occurrence of trehalose in vesicular-arbuscular mycorrhizal fungi and in mycorrhizal roots. J Plant Physiol 140:41–45

Sengupta A, Chaudhuri S (1990) Vesicular-arbuscular mycorrhiza in pioneer salt marsh plants of the Ganges river delta in West Bengal (India). Plant Soil 122:111–113

Shalata A, Tal M (1998) The effect of salt stress on lipid peroxidation and antioxidants in the leaf of the cultivated tomato and its wild salt-tolerant relative *Lycopersicon pennellii*. Physiol Plant 104:169–174

Sharifi M, Ghorbanli M, Ebrahimzadeh H (2007) Improved growth of salinity-stressed soybean after inoculation with salt pre-treated mycorrhizal fungi. J Plant Physiol 164:1144–1151

Sheng M, Tang M, Chen H, Yang BW, Zhang FF, Huang YH (2008) Influence of arbuscular mycorrhizae on photosynthesis and water status of maize plants under salt stress. Mycorrhiza 18:287–296

Sheng M, Tang M, Zhang F, Huang Y (2011) Influence of arbuscular mycorrhiza on organic solutes in maize leaves under salt stress. Mycorrhiza 21:423–430

Shi H, Ishitani M, Kim C, Zhu J-K (2000) The *Arabidopsis thaliana* salt tolerance gene SOS1 encodes a putative Na^+/H^+ antiporter. Proc Natl Acad Sci USA 97:6896–6901

Shi ZY, Zhang L, Feng G, Christie P, Tian CY, Li XL (2006) Diversity of arbuscular mycorrhizal fungi associated with desert ephemerals growing under and beyond the canopies of Tamarisk shrubs. Chinese Sci Bull 51:132–139

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

Smart LB, Moskal WA, Cameron KD, Bennett AB (2001) *MIP* genes are down-regulated under drought stress in *Nicotiana glauca*. Plant Cell Physiol 42:686–693

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

Smith FA, Smith SE (1997) Structural diversity in (vesicular)-arbuscular mycorrhizal symbioses. New Phytol 137:373–388

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

Sonjak S, Udovič M, Wraber T, Likar M, Regvar M (2009) Diversity of halophytes and identification of arbuscular mycorrhizal fungi colonising their roots in an abandoned and sustained part of Sečovlje salterns. Soil Biol Biochem 41:1847–1856

Sottosanto JB, Gell A, Blumwald E (2004) DNA array analyses of *Arabidopsis thaliana* lacking a vacuolar Na^+/H^+ antiporter: impact of *AtNHX1* on gene expression. Plant J 40:752–771

Spanu P, Bonfante-Fasolo P (1988) Cell-wall-bound peroxidase activity in roots of mycorrhizal *Allium porrum*. New Phytol 109:119–124

Sreenivasulu N, Ramanjulu S, Ramachandra-Kini K, Prakash HS, Shekar-Shetty H, Savithri HS, Sudhakar C (1999) Total peroxidase activity and peroxidase isoforms as modified by salt stress in two cultivars of fox-tail millet with differential salt tolerance. Plant Sci 141:1–9

Strack D, Fester T, Hause B, Schliemann W, Walter MH (2003) Arbuscular mycorrhiza: biological, chemical, and molecular aspects. J Chem Ecol 29:1955–1979

Sylvia DM, Fuhrmann JJ, Hartel PG, Zuberer D (1998) Principles and applications of soil microbiology. Prentice, Upper Saddle River

Szalai G, Janda T (2009) Effect of salt stress on the salicylic acid synthesis in young maize (*Zea mays* L.) plants. J Agric Crop Sci 195:165–171

Tal M, Katz A, Heikin H, Dehan K (1979) Salt tolerance in the wild relatives of the cultivated tomato: proline accumulation in *Lycopersicon esculentum* Mill., L., Peruvianum Mill. and *Solanum pennelli* Cor. Treated with NaCl and polyethylene glycol. New Phytol 82:349–355

Tester M, Davenport R (2003) Na tolerance and Na transport in higher plants. Ann Bot 91:503–527

Tian CY, Feng G, Li XL, Zhang FS (2004) Different effects of arbuscular mycorrhizal fungal isolates from saline or non-saline soil on salinity tolerance of plants. Appl Soil Ecol 26:143–148

Titus JH, Titus PJ, Nowak RS, Smith SD (2002) Arbuscular mycorrhizae of Mojave desert plants. West North Am Naturalist 62:327–334

Tommerup IC (1984) Effect of soil water potential on spore germination by vesicular-arbuscular fungi. Trans Br Mycol Soc 83:193–202

Tonin C, Vandenkoornhuyse P, Joner E, Straczek J, Leyval C (2001) Diversity of AM fungi in the rhizosphere of *Viola calaminaria* and effect of these fungi on heavy metal uptake by clover. Mycorrhiza 10:161–168

Tressner HD, Hayes JA (1971) Sodium chloride tolerance of terrestrial fungi. Appl Microbiol 22:210–213

Usha 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 Kinnow mandarin [King (*Citrus nobilis*)×Willow Leaf (*Citrus deliciosa*)]. Aust J Agric Res 55:571–576

van der Heijden MGA, Boller T, Wiemken A, Sanders IR (1998a) Different arbuscular mycorrhizal fungal species are potential determinants of plant community structure. Ecology 79:2082–2091

van Der Heijden MGA, Klironomos JN, Ursic M, Moutoglis P, Streitwolf-Engel R, Boller T, Wiemken A, Sanders IR (1998b) Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Nature 396:69–72

Vogel-Mikuš K, Drobne D, Regvar M (2005) Zn, Cd and Pb accumulation and arbuscular mycorrhizal colonization of pennycress *Thlaspi praecox* Wulf Brassicaceae from the vicinity of a lead mine and smelter in Slovenia. Environ Pollut 133:232–242

Wang B, Qiu Y-L (2006) Phylogenetic distribution and evolution of mycorrhizas in land plants. Mycorrhiza 16:299–363

Wang W, Vinocur B, Shoseyov O, Altman A (2004) Role of plant heat-shock proteins and molecular chaperones in the abiotic stress response. Trends Plant Sci 9:244–252

Wang F, Zeng B, Sun ZX, Zhu C (2009) Relationship between proline and Hg^{2+}-induced oxidative stress in a tolerant rice mutant. Arch Environ Contam Toxicol 56:723–731

Watad AEA, Reinhold L, Lerner HR (1983) Comparison between a stable NaCl-selected Nicotiana cell line and the wild type: K^+, Na^+, and proline pools as a function of salinity. Plant Physiol 73:624–629

Weig A, Deswarte C, Chrispeels MJ (1997) The major intrinsic protein family of *Arabidopsis* has 23 members that form three distinct groups with functional aquaporins in each group. Plant Physiol 114:1347–1357

Williams SE, Wollum AG II, Aldon FE (1974) Growth of *Atriplex canescens* (Pursh.) Nutt. improved by formation of vesicular-arbuscular mycorrhizae. Proc Soil Sci Soc Am 38:962–965

Wilson JM (1984) Comparative development of infection by three vesicular-arbuscular mycorrhizal fungi. New Phytol 97:413–426

Wilson GWT, Hartnett DC (1998) Interspecific variation in plant responses to mycorrhizal colonization in tallgrass prairie. Am J Bot 85:1732–1738

Wright DP, Read DJ, Scholes JD (1998) Mycorrhizal sink strength influences whole-plant carbon balance of *Trifolium repens* L. Plant Cell Environ 21:881–891

Wu QS, Xia RX, Zou YN, Wang GY (2007) Osmotic solute responses of mycorrhizal citrus (*Poncirus trifoliata*) seedlings to drought stress. Acta Physiol Plant 29:543–549

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

Xia T, Apse MP, Aharon GS, Blumwald E (2002) Identification and characterization of a NaCl-inducible vacuolar Na^+/H^+antiporter in *Beta vulgaris*. Physiol Plant 116:206–212

Yamada S, Katsuhara M, Kelly WB, Michalowski CB, Bohnert HJ (1995) A family of transcripts enpoding water channel proteins: tissue-specific expression in the common ice plant. Plant Cell 7:1129–1142

Yamada S, Komori T, Myers PN, Kuwata S, Kubo T, Imaseki H (1997) Expression of plasma membrane water channel genes under water stress in *Nicotiana excelsior*. Plant Cell Physiol 38:1226–1231

Yang CW, Chong JN, Kim CM, Li CY, Shi DC, Wang DL (2007) Osmotic adjustment and ion balance traits of an alkali resistant halophyte *Kochia sieversiana* during adaptation to salt and alkali conditions. Plant Soil 294:263–276

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

Zai XM, Qin P, Wan SW, Zhao FG, Wang G, Yan DL, Zhou J (2007) Effects of arbuscular mycorrhizal fungi on the rooting and growth of beach plum (*Prunus maritima*) cuttings. J Hortic Sci Biotechnol 82:863–866

Zeuthen T (2001) How water molecules pass through aquaporins. Trends Biochem Sci 26:77–81

Zhang X-H, Hodson I, Williams JP, Blumwald E (2001) Engineering salt-tolerant *Brassica* plants: characterization of yield and seed oil quality in transgenic plants with increased vacuolar sodium accumulation. Proc Natl Acad Sci USA 98:12832–12836

Zhang YF, Feng G, Li XL (2003) The effect of arbuscular mycorrhizal fungi on the components and concentrations of organic acids in the exudates of mycorrhizal red clover. Acta Ecol Sin 23:30–37

Zhang H, Wu X, Li G, Qin P (2011) Interactions between arbuscular mycorrhizal fungi and phosphate-solubilizing fungus (*Mortierella sp.*) and their effects on *Kostelelzkya virginica* growth and enzyme activities of rhizosphere and bulk soils at different salinities. Biol Fertil Soil 47:543–554

Zhi H, He CX, He ZQ, Zou ZR, Zhang ZB (2010) The effects of arbuscular mycorrhizal fungi on reactive oxyradical scavenging system of tomato under salt tolerance. Agric Sci China 9:1150–1159

Zhu JK (2003) Regulation of ion homeostasis under salt stress. Curr Opin Plant Biol 6:441–445

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