General Research Paper

Arbuscular Mycorrhiza: A Versatile Component for Alleviation of Salt Stress

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ABSTRACT

Salt-affected soil is one of the most serious abiotic stress that causes reduced plant growth, development and productivity worldwide. Plants, in their natural environment, are colonized both by external and internal microorganisms. These microorganisms, particularly beneficial bacteria and fungi, can improve plant performance under stress environments and, consequently, enhance yield. Arbuscular mycorrhizal (AM) fungi are associated with the roots of over 80% terrestrial plant species including halophytes, hydrophytes and xerophytes. In this respect, bioreclamation using mycorrhiza for alleviating salt stress would be a better option. AM fungi promote plant growth and salinity tolerance by different ways, such as enhancing nutrient acquisition, producing plant growth hormones, improving rhizospheric and soil conditions, altering the physiological and biochemical properties of the host and defending roots against soil-borne pathogens.

INTRODUCTION

Food and nutritional security of the ever increasing population calls for sustained productivity from the limited land and water resources, which is further thwarted by the multiplicity of resource degradation problems. Estimates on global salinization in land and water resources have shown that, about 7% of the world's total land area are affected by salt (Ghassemi et al. 1995, Ruiz-Lozano et al. 2001, Munns et al. 2002). About 23% of the world's cultivated lands are saline and 37% sodic (Khan & Duke 2001), and increased salinization of arable land will result into 50% land loss by the middle of the 21st century (Wang et al. 2003). The significance of soil salinity for agricultural yield is enormous (Tester & Davenport 2003) as it affects the establishment, growth and development of plants leading to huge losses in productivity (Giri et al. 2003, Mathur et al. 2007). The direct effects of salt on plant growth may involve: (a) Reduction in the osmotic potential of the soil solution that reduces the amount of water available to the plant causing physiological drought: To counteract this problem plants must maintain lower internal osmotic potentials in order to prevent water movement from roots to the soil (Feng et al. 2002, Jahromi et al. 2008), (b) Toxicity of excessive Na^+ and Cl^- ions towards the cell: The toxic effects include disruption to the structure of enzymes and other macromolecules, damage to cell organelles and plasma membrane, disruption of photosynthesis, respiration and protein synthesis (Juniper & Abbott 1993, Feng et al. 2002), and (c) Nutrient imbalance in the plant caused by nutrient uptake and transport to the shoot leading to ion deficiencies: To deal with this

problem and minimize crop loss, scientists have searched for new salt-tolerant crop plants and developed salt-tolerant crops through breeding. To tackle the detrimental effects of salinity, scientists are also in the process of engineering plants genetically using different genes. Leaching of excessive salts or desalinizing seawater for use in irrigation (Muralev et al. 1997) are other methods employed to combat salt stress. Though successful, these approaches are costly and beyond the economic means of developing nations (Cantrell & Linderman 2001). In recent years, the use of the biological application (mycorrhizal symbiosis) as a practical method to alleviate soil stresses like salinity on plant growth has received a greater attention (Abdel-Fattah et al. 1996, Daei et al. 2009, Wu et al. 2010).

Microorganisms differ in their ability to cope with the adverse effects of excessive salt. Specific associative bacteria or symbiotic eukaryotes could have the potential to alleviate salt stress of plants. Among all these, AM fungi could be of paramount importance in this field, since they were shown to have manifold positive effects on plant growth and health (Van der Heijden et al. 1998, Smith & Read 2008). It is often stated that 80% of all land plants are colonized by AM fungi. Major plant families such as Brassicaceae (DeMars & Boerner 1996), Caryophyllaceae, Chenopodiaceae and among the monocots, all families other than Poaceae (grasses) are generally non-AM fungi. Under salt stress conditions, plant tolerance and production are complicated mechanisms. AM fungi employ different mechanisms to enhance salt tolerance of host plants such as enhancing nutrient acquisition (P, N, Mg and Ca) (Azcon &

Atrash 1997, Giri & Mukerji 2004, Sheng et al. 2009), inhibiting high uptake of Na and Cl and their transport to plant shoots (Daei et al. 2009), improving water uptake (Ruiz-Lozano & Azcon 2000), accumulating of proline and polyamines (Evelin et al. 2009, Ibrahim et al. 2011) and increasing some of the enzymatic antioxidant defence system (SOD and CAT) (Wu et al. 2010). Other arbuscular mycorrhizal mechanisms may include an osmotic adjustment, which assist in maintaining the leaf turgor pressure, and the effects on the photosynthesis, transpiration, stomatal conductance and water use efficiency (Juniper & Abbott 1993).

DISTRIBUTION OF SALT AFFECTED SOILS

Salt affected soils alone have assumed significant global dimension, as about 1000 million ha area in more than hundred countries is affected by this menace. It is estimated that there are 76 million hectares of human-induced salt affected land (Table 1), representing 5% of the world's cultivated land (Ghassemi et al. 1995).

Saline soils contain excessive concentrations of soluble carbonate, chloride and sulphate salts that cause EC levels to exceed 4 dSm^{-1} and formation of a white crust on the soil surface (Table 2). Excess salts in the root zone reduce the amount of water available to plants and cause the plant to expend more energy to exclude salts and take up pure water. In contrast to saline soils, sodic soils have a relatively low EC, but a high amount of Na$^+$ occupying exchange sites, often resulting in the soil having a pH at or above 8.5, less plant available water, poor tilth and sometimes a black crust on the surface formed from dispersed organic matter. Saline-sodic soils are soils that have chemical characteristics of both saline soils (EC greater than 4 dSm^{-1} and pH less than 8.5) and sodic soils (ESP greater than 15).

MANIFESTATION OF SALINITY ON SOIL-PLANT SYSTEM

A saline soil contains Ca^{2+} salt, which increase flocculation and is beneficial in terms of soil aeration, root penetration, and root growth. Although increasing soil solution salinity has a positive effect on soil aggregation and stabilization, at high levels of salinity can have negative and potentially lethal effects on plants (Bauder & Brock 1992). Sodium has the opposite effect of salinity on soils. The primary physical processes associated with high sodium concentrations are soil dispersion and clay platelet and aggregate swelling. The forces that bind clay particles together are disrupted when too many large sodium ions come in between them. The three main problems caused by sodium-induced dispersion are reduced infiltration, reduced hydraulic conductivity, and surface crusting, which in turn prevents seedling emergence and inhibit plant growth (Sharma & Minhas

Table 1: Global distribution of saline and sodic soils (Szabolcs 1989).

S.NO	Continent	Area (million hectares)		
		Saline	Sodic	Total
1.	North America	6.2	9.6	15.8
2.	Central America	2.0	-	2.0
3.	South America	69.4	59.6	129.0
4.	Africa	53.5	27.0	80.5
5.	South Asia	83.3	1.8	85.1
6.	North and Central Asia	91.6	120.1	211.7
7.	Southeast Asia	20.0	-	20.7
8.	Europe	17.4	340.0	357.4
9.	Australasia	7.8	22.9	30.7
	Total	351.5	581.0	932.2

Table 2: Classification of salt affected soil (U.S. Soil Salinity Laboratory Staff 1954).

Parameter	Saline soil	Alkali soil	Saline alkali
pH	<8.5	>8.5	<8.5
EC	>4	<4	>4
ESP	<15	>15	>15
SAR	<13	>13	>13
TDS	>2500	-	-
OP (bar)	>1.44	-	-
Ca^{2+}	28.4 to 37	1.10 to 1.40	0.60 to 32.4
Mg^{2+}	22.8 to 37.2	0.30 to 1.42	0.90 to 38.3
K$^+$	0.21 to 1.10	0.28 to 4.10	0.48 to 1.60
Na$^+$	53 to 102	15.6 to 29.2	58.5 to 145
CO$_3$	0	8.0 to 8.4	0 to 5
HCO$_3^-$	4.50 to 7.20	3.29 to 18.6	2.35 to 19.5
SO$_4^{2-}$	62.2 to 90	3.80 to 8.48	20.1 to 105
Cl$^-$	29 to 78	2.86 to 16.7	16.3 to 105

*Cation and anion concentrations in mEq/L, TDS in mg/L and EC in dS/m

2005). Alkali soils have a high ESP, SAR and pH values. The chief characteristic of sodic soils from the agricultural stand point is that they contain sufficient exchangeable sodium to adversely affect the growth of most crop plants. Excess exchangeable sodium has an adverse effect on the physical and nutritional properties of the soil, with consequent reduction in crop growth, significantly or entirely. The soils lack appreciable quantities of neutral soluble salts, but contain measurable to appreciable quantities of salts capable of alkaline hydrolysis, e.g. sodium carbonate. The electrical conductivity of saturation soil extracts is, therefore, likely to be variable but is often less than 4 dSm^{-1} at 25°C. The pH of saturated soil pastes is 8.2 or more and in extreme cases may be above 10.5. Dispersed and dissolved organic matter present in the soil solution of highly sodic soils may be deposited on the soil surface by evaporation causing a dark surface which is why these soils have also been termed as black sodic soils. The hydrolysis of CaCO$_3$ and of MgCO$_3$, is limited due to their low solubility and therefore they tend to produce a pH in soils not higher than 8.0 to 8.2. Soils containing measurable quantities of Na$_2$CO$_3$, have a pH of

more than 8.2; the pH increases with increasing amounts of Na_2CO_3, and may be as high as 10.0 to 10.5. This is due to the higher solubility of Na_2CO_3 and therefore the greater potential for hydrolysis.

High salts content not only affect physical and chemical properties of the soil, but also affect microbiological properties of soil. Increase in salinity has been shown to decrease soil respiration rates and the soil microbial biomass (Laura 1976, Pathak & Rao 1998). The reason for the reduced size and activity of the microbial community with increasing salinity is likely to be osmotic stress which is caused by large concentrations of salts in soil solutions (Galinski 1995, Oren 1999). Osmotic stress usually limits microbial growth and activity in saline soil, while under sodic condition, ion toxicities and adverse pH conditions may also inhibit microbial growth (Rietz & Haynes 2003). The most commonly used microbial indicators for soil health monitoring are microbial biomass, microbial quotient and soil respiration (Nielsen & Winding 2002). Soil microbial biomass was highly sensitive to salinity and can be used as indicator for management of salt affected soils (Shah & Shah 2011). Similarly, increasing sodicity levels have had slight negative correlations with C mineralization (Nelson et al. 1997), and caused a decrease in the amount of soil microbial biomass (Chander et al. 1994). According to Tripathi et al. (2006), a decrease in microbial biomass C and microbial activities with a rise in salinity is probably one of the reasons for poor crop growth in coastal saline soils.

Soil salinity affects the establishment, growth, and development of plants, leading to huge losses in productivity (Evelin et al. 2009). Plants growing in saline soil are subjected to three distinct physiological stresses. First, the toxic effects of specific ions such as sodium and chloride, prevalent in saline soils, disrupt the structure of enzymes and other macromolecules, damage cell organelles, disrupt photosynthesis and respiration, inhibit protein synthesis, and induce ion deficiencies (Juniper & Abbott 1993). Second, plants exposed to the low osmotic potentials of saline soil are at risk of physiological drought because they must maintain lower internal osmotic potentials to prevent water moving from the roots into the soil. Finally, salinity also produces a nutrient imbalance in the plant caused by decreased nutrient uptake and/or transport to the shoot (Marschner 1995, Adiku et al. 2001). As a consequence, salt stress affects all the major processes, such as growth, photosynthesis, protein synthesis, and energy and lipid metabolisms (Ramoliya et al. 2004). Under salt condition plant produce some stress signal which is first perceived at the membrane level by the receptor, which results in the generation of secondary signal molecules, such as Ca^{2+}, inositol phosphates, reactive oxygen species (ROS) and abscisic acid (ABA). The stress signal, then transduces inside the nucleus to induce multiple stress responsive genes, the products of which ultimately lead to plant adaptation to stress tolerance.

RECLAMATION OF SALT AFFECTED SOIL

The first step in managing salt-affected soils is to determine the problem and identify its cause or source. If salt problems are suspected or likely, soil and water samples should be collected on an annual basis and analysed for EC, ESP, SAR, and pH. Other parameters, such as percent organic matter, clay content, CEC, and presence of lime, may also be useful (Schafer 1982). Second step is to determine a management plan. Choosing how to manage a salt problem and which techniques to employ will depend on a number of factors including, cropping systems, availability of water and cost. There are many different methods of reclamation of saline soils such as physical amelioration (deep ploughing, sub-soiling, sanding, profile inversion), chemical amelioration (amending of soil with various reagents e.g., gypsum, calcium chloride, limestone, sulphuric acid, sulphur, iron sulphate), water leaching, phytoremediation (Ahmad & Chang 2002, Sharma & Minhas 2005, Qadir et al. 2007, Feizi et al. 2010) and electro-reclamation (treatment with electric current) (Mahdy 2011). Although sanding, hauling, flushing, leaching and profile inversion (physical approach) are attractive, but there are several problems in their large-scale execution. For example, flushing and leaching require a huge amount of water, but in arid areas, where salt affected problem are most prevalent, water scarcity is a major issue. Chemical amendment costs have increased prohibitively over the past two decades due to competing demands from industry and reductions in government subsidies for their agricultural use in several developing countries. So under this situation, bioremediation like growing salt tolerant plants or using different microorganism like fungi, bacteria etc. to cope salt stress condition, can prove to be a best alternative. Bioreclamation has two advantages over traditional method with reference to its less amount of water requirement and its feasibility in areas with very shallow water table. In this review, we have elaborated the role of AM fungi symbiosis in mediating salt tolerance.

AM mediated salt tolerance mechanism: In Indian pipe (*Monotropa hypopitys* L.), Franciszek Kamienski in 1881 discovered a mutualistic association of fungus and roots. Farnk in 1885 named the symbiotic process between the fungi and roots by Greek word ''Mykorrhizen'', meaning ''Myco-rhiza (fungus-root)''. Amongst the mycorrhizal associations, the AM association is the most common one (Sjoberg 2005, Tahat & Sijam 2012). AM fungi belong to

the fungal phylum Glomeromycota (Schubler et al. 2001) with four orders, eight families and ten genera. The genera, which include most of the described species are *Acaulospora, Gigaspora, Glomus* and *Scutellospora* (Schubler 2005). Usually the AM fungi form a symbiotic association with vascular plants as their hosts and hence obtain their required energy; the fungi, may also inoculate the roots of nonvascular plants (Russell & Bulman 2005, Sjoberg 2005). The AM fungi are named according to their formation of highly branched intracellular fungal structures or ''arbuscules,'' which are the site of phosphate exchange between the fungus and the host plant. Vesicles, containing lipids, are highly vacuolated with carbon storage structures, and are usually formed in most genera of Glomeromycota, depending on the environmental conditions (Smith & Read 2008).

There are numerous studies reporting that mycorrhizal associations lead to crop improvement like growth rate, biomass, and mineral uptake under saline or drought conditions (Augé 2004, Evelin et al. 2009, Subramanian & Charest 1999). Mycorrhizae were shown to have beneficial effects in delaying or coping with toxic effects caused by soil salinity by maintaining an overall physiological balance (Sharifi et al. 2007, Shokri & Maadi 2009). AM fungi occur naturally in saline environments despite the fact that they have a low affinity with halophyte plants (Khan 1974). However, halophytes can benefit to some extent from AM symbiosis as in the case of *Phragmites australis,* for which the water content increased in salt AM plants (Al-Garni 2006). Interestingly, the most commonly observed AM fungus was among *Glomus* spp. (Landwehr et al. 2002). However, when comparing several *Glomus* spp., Porras-Soriano et al. (2009) observed that each AM fungal species has a different efficiency in alleviating plant salt stress. Recently, Khare & Rai (2012) have investigated taxonomic diversity of AM fungi in the alkaline soils of upper Gangetic plains of district Allahabad and adjoining areas and it was found that such soils have a detrimental effect on AM spore population, distribution and diversity. Some examples of AM improvement mechanisms and nutrient uptake under salinity stress are given in Table 3.

Effect of salt on AM fungi: Salinity can adversely affect the colonization capacity of the fungi, the germination of the spores, and the growth of fungal hyphae. The colonization capacity of plant roots by some AM fungi decreases with increasing NaCl level, indicating that salinity has negative effects on the growth of AM fungi. Before colonization occurs, spores need to be hydrated in order to germinate which is difficult in saline soil. It has been reported that the addition of various salts to soil inhibits hyphal growth with a subsequent decrease in the spread of mycorrhizal hyphal network (Abdel Latef & Chaoxing 2011a, 2014). In the presence of NaCl, germination of spores is delayed rather than being prevented (Juniper & Abbott 2006, Hajiboland 2013). The rate of germination and maximum germination of AM fungi spores may also depend on the salt type. According to Juniper & Abbott (1993), the different salts $NaNO_3$ and Na_2SO_4 with similar osmotic potentials impart differential effects on the rate and maximum germination of spores. They attributed the difference to a higher concentration of Na^+ in the latter. However, other studies showed that there is infact no reduction in AM colonization in the presence of NaCl (Aliasgharzadeh et al. 2001, Yamato et al. 2008) and even increase in sporulation and colonization occur (Peng et al. 2010). The discrepancies amongst studies suggest that various AM fungal spp. have varying tolerance to salinity, then questioning the host plant and AM fungus compatibility and tolerance (Porras-Soriano et al. 2009). These studies also suggest that AM fungal species have different capacities in protecting plants and that host compatibility might be an issue worth looking into when developing AM strategies in plant growth and tolerance under salt stress conditions. The relative tolerance of different types of the same fungal genus can vary as is reported in the case of *Glomus* sp. Propagules of *Glomus* sp. within the colonized root pieces grow in 300 mM NaCl, but the spores of the same fungi extracted from the soil did not. This may indicate a difference in the energy status between them, or differences in the amount of water and energy required to initiate germination (Juniper & Abbott 2006).

Effect of AM fungi on plant growth and biomass: Plant growth decreases under salt stress due to (a) the expenditure of energy to avoid the toxic enhance the efficiency of the host plants by increasing their growth. For example, Abdel Latef & Chaoxing (2011, 2014) have recently reported that, although salt stress reduced dry matter production of tomato and pepper plants, respectively, in all treatments mycorrhizal plants grew better than nonmycorrhizal plants. Shekoofeh & Sepideh (2011) observed that mycorrhizal inoculated plants grown under saline conditions experienced increase in root length, dry and fresh weights of shoot and content of photosynthesis. Studies have also indicated that some plants such as tomato (Al-Karaki 2006) and soybean (Sharifi et al. 2007) showed increased growth under saline conditions when their roots are colonized by AM fungi. Qiang-Sheng & Ying-Ning (2011) reported markedly increase in both, plant performance (leaf number, leaf area, shoot and root dry weights) and leaf relative water content of citrus seedlings in AM association when exposed to salt stress. The improved growth of mycorrhizal plants in saline conditions is primarily related to mycorrhiza-mediated enhancement of host plant P nutrition (Al-Karaki 2000).

Effect of AM fungi on mineral nutrition: *Nitrogen (N):* Nitrogen is the one of the most important nutrient for plant growth. It serves as an important part of many plant cell components, including amino acids and nucleic acids. N deficiency in a plant tissue rapidly inhibits plant growth, and induces chlorosis in leaves. Salinity adversely influences N acquisition and utilization by affecting different stages of N metabolism, such as NO_3^- uptake and reduction and protein synthesis (Frechill et al. 2001, Evelin et al. 2009). Application of AM fungi can result in a more efficient assimilation of N in the host plants, due to the following: (a) The extraradical mycelia take up inorganic nitrogen from the soil in the form of nitrate and assimilated it via nitrate reductase, located in the arbuscule-containing cells (Kaldorf et al. 1998) and the GS-GOGAT cycle leading to the formation of arginine. Arginine, so formed, is transported from the extra-radical to the intra-radical mycelia where it is catabolized and equilibrates with ammonium according to the pH; (b) increased production of enzymes controlling the primary nitrogen fixation in the extra-radical mycelia, whereas enzymes controlling arginine catabolism are up regulated in the intra-radical mycelia; (c) decreasing the toxic effects of Na^+ ions by deducing its uptake and this may indirectly help in maintaining the chlorophyll content of the plant (Evelin et al. 2009, 2012, Kapoor et al. 2013).

Phosphorus: Phosphorus is an essential macronutrient which is involved in energy transfer, photosynthesis, transformation of sugar and starch, nutrient movement within the plant and transfer of genetic characteristics from one generation to another generation. Under salinity stress, the uptake and concentration of P in plant tissues decreases, resulting in reduced and stunted growth, dark green coloration of the leaves, production of slender stems, and senescence of older leaves (Evelin et al. 2012). AM symbiosis plays a vital role in improving the P nutrition of the host plants under salt stress conditions. It has been seen that external hyphae of AM fungi deliver upto 80% of a plants P requirements (Marschner & Dell 1994). This is probably due to the extended network of AM fungal hyphae that allow them to explore more soil volume than non-mycorrhizal plants (Ruiz-lozano & Azcon 2000). Indeed, mycorrhizal hyphae extend beyond the depletion zones around roots and acquire nutrients that are several centimetres away from the root surface and thus suppress the adverse effect of salinity stress.

$K^+:Na^+$ ratio: Potassium plays a key role in plant metabolism. It activates a range of enzymes, and plays an important role in stomatal movements and protein synthesis. High concentrations of K^+ are required in protein synthesis as K^+ is used in the binding of tRNA to the ribosomes (Blaha et al. 2000). These functions cannot be replaced by Na^+ ions (Giri et al. 2007); a higher K^+ Na^+ ratio generated due to salinity

disrupts the ionic balance in the cytoplasm, consequently disrupting various metabolic pathways (Giri et al. 2007). Mycorrhizal colonization of a plant with AM fungi can reverse the effect of salinity on K^+ and Na^+ nutrition. Mycorrhizal colonization can enhance K^+ absorption under saline conditions (Alguacil et al. 2003, Giri et al. 2007, Sharifi et al. 2007, Zuccarini & Okurowska 2008) while preventing Na^+ translocation to shoot tissues. This increases the $K^+:Na^+$ ratio in roots and shoots of AM plants (Giri et al. 2007). It is accomplished by regulating the expression and activity of K^+ and Na^+ transporters and of H^+ pumps that generate the driving force to transport ions (Parida & Das 2005). The Na^+/H^+ antiporter catalyses the transfer of Na^+ out of the cytoplasm into either vacuoles or apoplasm (Ouziad et al. 2006).

Calcium (Ca): Calcium has some important roles in maintaining plant membrane integrity, cell wall structures, as well as ion transport regulation and selectivity (Maathuis 2009, Evelin et al. 2012). A higher Ca^{2+} concentration in mycorrhizal than nonmycorrhizal plants can favourably alleviate the toxic effects of NaCl by inducing a higher K^+/Na^+ ratio leading to salt adaptation (Rabie & Almadini 2005, Evelin et al. 2009). Moreover, a high Ca^{2+} concentration can also enhance colonization and sporulation of AM fungi (Jarstfer et al. 1998, Evelin et al. 2012). On the other hand, Giri et al. (2004) observed no visible change in Ca^{2+} uptake of mycorrhizal and nonmycorrhizal *Acacia uriculiformis* plants under salinity stress. It has been suggested that mycorrhiza may not be effective on the uptake of nutrients, such as Ca^{2+}, through absorbing to the plant roots by mass flow as compared with nutrients absorbed by diffusion. It is currently not clear how AM fungi may affect the transport and uptake of Ca^{2+} ions (Evelin et al. 2012).

Magnesium (Mg): Magnesium is a macronutrient and forms the integral part of the chlorophyll molecule (Evelin et al. 2012). AM fungi can increase chlorophyll concentration, by increasing the uptake of Mg^{2+} by the host plant (Giri et al. 2003). This suggests that salt interferes less with chlorophyll synthesis in mycorrhizal than nonmycorrhizal plants (Giri & Mukerji 2004). The enhanced Mg^{2+} uptake can increase the chlorophyll concentration and hence improve photosynthetic efficiency and plant growth (Evelin et al. 2009). Recently, Evelin et al. (2012) found that NaCl and mycorrhizal colonization had little or no effect on Mg^{2+} concentration in fenugreek plants. This may be attributed to elimination of the competition between Ca^{2+} and Mg^{2+} (Evelin et al. 2012).

Chloride (Cl): In saline regions, higher concentration of Cl⁻ may limit plant growth and can be toxic to crop plants (Xu et al. 2000, Evelin et al. 2009). Such a stress can be alleviated to some extent by using AM fungi, which can reduce the uptake of Cl ions (Zuccarini & Okurowska 2008). In

mycorrhizal plants, the ability of the host plant increases and hence compartmentalizes higher rate of Cl in the vacuoles, thereby preventing the ions from interfering with the metabolic pathways in the plant (Cantrell & Lindermann 2001, Evelin et al. 2009). However, there are reports of enhanced Cl accumulation due to the colonization of mycorrhizal fungi. Such a process has been attributed to the higher transfer of carbon from the host plant to the mycorrhizal hyphae, which enhances the translocation of highly mobile anions like Cl from the soil (Graham & Syversten 1984, Evelin et al. 2009).

BIOCHEMICAL CHANGES

The best characterized biochemical response of plant cells to osmotic stress is an accumulation of some inorganic ions such as Na^+ and compatible organic solutes like proline, glycine betaine, and soluble sugars (Flower & Colmer 2008). These compatible solutes can accumulate to high levels without disturbing intracellular biochemistry (Bohnert & Jensen 1996), protecting sub-cellular structures, mitigating oxidative damage caused by free radicals, and maintaining the enzyme activities under salt stress (Yokoi et al. 2002).

Proline and other osmolytes: Proline is one of the compatible organic solutes that is used by plant as osmoprotectant. In most plant species, the accumulation of proline has been observed under salinity stress (Abdel Latef 2010, 2011b; Hameed et al. 2014). Proline has a key role in the stabilization of cellular protein and membranes under high salinity concentrations. Abdel Latef et al. (2009) suggested that, proline can act as a sensor of salt-stress injury and not as an osmoprotectant. Proline and glycine betaine (N, N, N-trimethylglycine betaine) are two major osmoprotectant osmolytes, which are synthesized by many plants (but not all) in response to stress, including salinity stress, and thereby help in maintaining the osmotic status of the cell to ameliorate the abiotic stress effect. Proline also plays roles in scavenging free radicals, stabilizing sub-cellular structures, and buffering cellular redox potential under stresses. The salinity stress responsive genes, whose promoters contain proline responsive elements (ACTCAT), are also known to be induced by proline (Chinnusamy et al. 2005). In higher plants, proline is synthesized from glutamic acid by the actions of two enzymes, pyrroline-5-carboxylate synthetase (P5CS) and pyrroline-5-carboxylate reductase (P5CR). Overexpression of the P5CS gene in transgenic tobacco resulted in increased production of proline and salinity/ drought tolerance (Kishor et al. 1995). Proline accumulation, in terms of amount, has been found to increase when the plant is colonized by AM fungi. Several authors have reported a higher proline concentration in AM plants than in non-AM plants at different salinity

levels (Jindal et al. 1993, Sharifi et al. 2007). However, in contrast to the reports above, other authors reported that non-AM plants accumulated more proline that AM plants at various salinity levels (Wang et al. 2004, Rabie & Almadini 2005, Jahromi et al. 2008), suggesting that proline accumulation in plants may be a symptoms of stress in less salt-tolerant species or that this accumulation may be also due to salinity and not necessarily to mycorrhizal colonization. On the other hand, betaines can also stabilize the structures and activities of enzymes and protein complexes and maintain the integrity of membranes against the damaging effects of excessive salt (Gorham 1995).

Accumulation of betaines under salt stress was found to increase when the plant is colonized by AM fungi (Al-Garni 2006). Under saline conditions, sugar may contribute up to 50 % of the resulted osmotic potential in glycophytes (Paraviz & Satyawati 2008, Abdel Latef & Chaoxing 2014). They can act as osmoprotectants, adjust osmotic potential, store carbon, and scavenge radical products. In mycorrhizal plants, the sugar content increases (Abdel Latef & Chaoxing 2014, Talaat & Shawky 2014).

AM fungi increase the sugar content of the host plant because of (a) the sink effects that make the fungi demand sugars from the shoot tissues, (b) hydrolysis of starch to sugars in the seedlings inoculated with mycorrhizal fungi, (c) preventing structural changes in soluble protein, (d) maintaining the osmotic equilibrium in plant cell, and (e) keeping membrane integrity (Kapoor et al. 2013, Abdel Latef & Chaoxing 2014). On the other hand, some authors reported negative correlations between AM fungal colonization and sugar accumulation in host plants (Pearson & Schweiger 1993, Sharifi et al. 2007, Beltrano et al. 2013).

Antioxidant Enzymes: Plants subjected to environmental stresses, including salinity produce reactive oxygen species. Reactive oxygen species include free radicals such as superoxide anion (O_2^-), hydroxyl radical (OH), and nonradical molecules such as hydrogen peroxide (H_2O_2) and single oxygen (O_2). In plants, reactive oxygen species are always formed by the inevitable leakage of electrons onto O_2. This would result in the electron transport of mitochondria, chloroplasts, and plasma membranes or is as a byproduct of different metabolic pathways in various cellular compartments (Sharma et al. 2012). All reactive oxygen species are extremely harmful to organisms at high concentrations. When the level of reactive oxygen species is higher than the tolerance level, a cell is subjected to ''oxidative stress.'' The enhanced production of reactive oxygen species during environmental stresses can adversely affect the cellular activities by causing the oxidation of proteins, peroxidation of

lipids, and preventing the activity of enzymes, which eventually results in cellular deactivation (Sharma et al. 2012). Plants have both enzymatic and nonenzymatic mechanisms for scavenging reactive oxygen species. The enzymatic antioxidants include superoxide dismutase (SOD), catalase (CAT), guaiacol peroxidase (GPX), and the enzymes of ascorbateglutathione (AsA-GSH) cycle such as, ascorbate peroxidase (APX), dehydro ascorbate reductase (DHAR), mono dehydro ascorbate reductase (MDHAR), and glutathione reductase (GR). Ascorbate (AsA), glutathione (GSH), phenolics, carotenoids, and tocopherols, which act as potent nonenzymic antioxidant inside the cell (Sharma et al. 2012). Like other abiotic stresses, salinity also induces oxidative stress in plants (Abdel Latef 2011b, 2014). Several studies suggested that mycorrhizal symbiosis helps plants to alleviate salt stress by enhancing the activities of antioxidant enzymes (Hajiboland et al. 2010, Abdel Latef & Chaoxing 2011, 2014, Evelin & Kapoor 2013).

PHYSIOLOGICAL CHANGES

Salinity stress can adversely affect plant growth by disrupting different physiological mechanisms such as decreasing water potential, disruption of membrane, photosynthetic efficiency, gas exchange, etc. Research work has indicated that AM symbiosis can alleviate such effects by using various mechanisms, which are discussed below.

Chlorophyll content: Increasing salinity causes a reduction in chlorophyll content (Sheng et al. 2008) due to suppression of specific enzymes that are responsible for the synthesis of photosynthetic pigments (Murkute et al. 2006). A reduction in the uptake of minerals (e.g. Mg) needed for chlorophyll biosynthesis also reduces the chlorophyll concentration in the leaf (El-Desouky & Atawia 1998). A higher chlorophyll content in leaves of mycorrhizal plants under saline conditions has been observed by various authors (Giri & Mukerji 2004, Sannazzaro et al. 2006, Zuccarini 2007, Colla et al. 2008, Sheng et al. 2008). This suggests that salt interferes less with chlorophyll synthesis in mycorrhizal than in non-mycorrhizal plants (Giri & Mukerji 2004). In the presence of mycorrhiza, the antagonistic effect of Na on Mg uptake is counterbalanced and suppressed (Giri et al. 2003). Inoculated plants under salt stress reach levels of photosynthetic capacity (estimated by chlorophyll content) even superior to those of non-stressed plants, showing that in this respect, mycorrhization is capable of fully counterbalancing stress (Zuccarini 2007).

Relative permeability: AM fungal inoculation concentration than the non-mycorrhizal plants by maintaining the improved integrity and stability of the membrane (Feng et al. 2002, Garg & Manchanda 2008, Kaya et al. 2009). Consequently, electrical conductivity of mycorrhizal roots was found to be higher than the non-mycorrhizal roots (Garg & Manchanda 2008). The mycorrhizal *Cajanus cajan* roots showed a higher relative permeability than the nonmycorrhizal plants at different levels of soil salinity (4, 6 and 8 dS m21 ECe; Garg & Manchanda 2008). Kaya et al. (2009) reported that the electrolyte leakage in leaves of *Capsicum annum* treated with 50 mM and 100 mM concentrations of NaCl were 31.66 and 42.45 respectively, while the AM fungi-inoculated plants had a relatively lower electrolyte leakage of 26.87 and 30.98 respectively, This suggests that mycorrhizal plants had a much lower root plasma membrane electrolyte permeability than the non-mycorrhizal plants. The increased membrane stability has been attributed to mycorrhiza mediated enhanced P uptake and increased antioxidant production (Feng et al. 2002).

Water Status: Plants under salinity stress are subjected to physiological drought as Na^+ and Cl ions bind water that is required to be utilized by plants (Fuzy et al. 2008). Mycorrhizal plants have a higher water content compared with non inoculated plants because: (a) mycorrhizal roots have a higher hydraulic conductivity at low water potential (Kapoor et al. 2008); (b) altered morphology of root system induced by mycorrhizal fungi (Kothari et al. 1990); (c) higher stomatal conductance, which increases the demand for transpiration (Sheng et al. 2008); (d) the fungi accumulate solutes, and hence improve plant osmotic adjustment (Abdel Latef & Chaoxing 2014). All these improved processes resulted by mycorrhizal colonization make the host plants to use water more efficiently. Accordingly, a lower intercellular concentration of carbon dioxide is resulted in the host plant. As a consequence, the gas exchange capacity increases in mycorrhizal plants (Evelin et al. 2009, Porcel et al. 2012, Hameed et al. 2014).

Abscisic Acid: The plant hormone, abscisic acid (ABA), is able to make the plant to respond to different stresses including drought and salt stress. ABA can also act as the major internal signal and hence enables plants to survive under adverse environmental conditions such as salt stress (Keskin et al. 2010, Javsari et al. 2014). When plants are under salinity stress, the concentration of ABA in plants increases. This is in most cases related with leaf or soil water potential, indicating that the production of endogenous ABA is resulted by water deficit and not by the specific effects of salt (Zhang et al. 2006, Javid et al. 2011). It has been reported that mycorrhization can alter the ABA levels in the host plant (Estrada-Luna & Davies 2003). AM plants are less affected by salinity stress than non-AM plants, and hence, less amounts of ABA are accumulated in mycorrhizal plants. However, depending on the properties of the host plant, the

Table 3: Some examples of AM improvement mechanisms and nutrient uptake under salinity stress.

Crop	Condition	Mycorrhiza	Mechanism	Result	Reference
Zea mays L.	(0–100 mM)	Glomus mosseae	Higher soluble sugars and electrolyte concentrations in plant root suggested a higher osmo regulating capacity	higher root and shoot dry weight, Concentrations of chlorophyll, P and soluble sugars were higher than non AM plants	Feng et al. (2002)
Sesbania aegyptiaca and S. grandiflora	15·8 dSm⁻¹ (1·58 S/m)	Glomus macrocarpum	The reduction in Na uptake together with a concomitant increase in P, N and Mg absorption and high chlorophyll content may be important salt-alleviating mechanisms	AM inoculated plant have higher root and shot biomass and increase P, N and Mg concentration in seedling tissue	Giri & Mukerji (2004)
Cajanus cajan	4,6 & 8 dSm⁻¹	Glomus mosseae	Enhanced levels of antioxidant enzyme activities, reduced membrane permeability, reduced lipid peroxidation,	greater nodulation and nitrogen fixation,	Garg & Manchanda (2008)
Lactuca sativa	(0, 50, 100 mM NaCl)	Glomus intraradices	lower proline content, and expression of Lsp5cs, lower expression of the stress marker gene Lslea gene, abscisic acid and enhanced the expression of LsPIP1	Enhanced root water permeability	Jahromi et al (2008)
Glycine max L.	6-12 dSm⁻¹	Glomus mosseae	High proline concentration was suggested to protect nodule metabolism. high antioxidant capacity under stress conditions can prevent damages due to ROS formation & high SOD activity	Increase nitrogen fixation & higher plant growth	Younesi et al. (2013)
Gmelina arborea Roxb.	100-200 mM NaCl	Glomus fasciculatum	Significant induction of antioxidative enzyme activities such as SOD, POX and CAT that could help the plants protect themselves from the oxidative effects of the ROS.	increase in fresh and dry weight, greater percentage of mycorrhizal colonization, higher accumulation of proline and chlorophyll content	Dudhane et al. (2011)
Vicia faba	(0.0 – 6.0 dSm⁻¹)	Glomus clarum+ NFB	Selective accumulation or exclusion of ions, control of ion uptake by roots and transport into leaves and compartmentalization of ions at the cellular and whole plant levels	Better ionic balance increase N,P, proline content, Phosphates' & nitrogenase enzymes	Rabie & Almadini (2005)
Capsicum annuum	25- 50 mM NaCl	Glomus intraradices	producing plant growth hormones, increase in electrolyte leakage, accumulate proline as a non-toxic protective osmolyte to maintain osmotic balance	Increase Growth and Yield of Chilli	Selvakumar & Thamizhiniyan (2011)
Trifolium subterraneum L.	2.2-12 dSm⁻¹	Glomus intraradices	increased P concentrations and Root K/Na ratio possibly contributing to salinity tolerance	promoting seedling growth and establishment of Trifolium subterraneum in saline conditions	Asghari (2008)
Cluster bean	4,8,12 dSm⁻¹	Glomus mosseae and Acaulospora laevis + bradyrhizobium	alleviate the detrimental effect of salinity through improved water and nutrient uptake & maintain ionic balance	increased growth parameters as well as nutrient uptake	Kadian et al. (2013)
Lycopersicon esculentum	0, 50 and 100mM NaCl	Glomus mosseae	protect plants against salinity by alleviating the salt induced oxidative stress	am induced root colonization, growth, leaf area, chlorophyll content, fruit fresh weight and fruit yield	Latef & Chaoxing (2011)

...cont. Table

Plant	NaCl	Glomus species	Effects	Reference
Citrus tangerine	100mM NaCl	*Glomus mosseae and Paraglomus occultum*	increase both plant performance (leaf number, leaf area, shoot, and root dry weights) and leaf relative water content of citrus seedlings, increase The K^+/Na^+, Ca^{2+}/Na^+, and Mg^{2+}/Na^+ ratios	Wu & Zou (2009)
Olive tree	6g NaCl kg-1	*Glomus mosseae, Glomus intraradices or Glomus claroideum*	increased plant growth and the ability to acquire nitrogen, phosphorus, and potassium from non-saline as well as saline media.G. mosseae was the most efficient fungus in reducing the detrimental effects of salinity. K content was enhanced under salt conditions by 6.4-foldwith G. mosseae, 3.4-fold with G. intraradices, and 3.7-foldwithG. claroideum. K, as the most prominent inorganic solute, plays a key role in the osmoregulation processes and the salinity tolerance	Soriano et al (2009)
wheat	1.20,6.09, 10.63 dSm-1	*Glomus mosseae + spermine*	positive effect on growth, salt tolerance and mycorrhizal root colonization in wheat plants. salt alleviation by enhancing photosynthetic pigments, proline, protein, spermine and spermidine, and lowered putrescine contents	fattah et al. (2013)
peanut	0, 0.1, 0.2, 0.3 and 0.5MNaCl	*Glomus mosseae*	improve growth. enhanced nutrient absorption and Chlorophyll content	Khaliel (2010
Triticum aestivum L.	0.75, 1.50, 3.0 g NaCl kg-1 soil	*Glomus clarum*	mycorrhiza enhanced the growth and accumulation of nutrients and soluble solutes that might be responsible for osmotic adjustment of plant to counteract oxidative damage generated by salinity. improving the accumulation of nutrients and soluble sugars, total soluble carbohydrates, Chlorophyll, carotene, proline and protein	Amri et al. (2013)

effects of AM fungal species on ABA content in the host plant differs (Evelin et al. 2009, Porcel et al. 2012).

CONCLUSIONS

From the above review it is evident that under stress condition mycorrhiza can be proven as a good strategy to alleviate salt tolerance by making root symbiosis with the host plant. However, in the presence of the fungi, the plant's ability to resist the stress increases as a result of morphological and physiological changes. Production of different solutes, plant hormones, antioxidant products, the adjusted rate of K^+/Na^+, extensive network of the mycorrhizal plant roots, and enhanced nutrient uptake are all among the processes that make the plant to survive under stress.

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