

Chapter 7

Salinity Stress and Arbuscular Mycorrhizal Symbiosis in Plants

Asiya Hameed, Egamberdieva Dilfuza, Elsayed Fathi Abd-Allah, Abeer Hashem, Ashwani Kumar and Parvaiz Ahmad

Introduction

Plants being sessile experience various abiotic stresses including salt stress, which limits plant growth and yield and in severe cases leads to cell death. This mainly confers its ionic imbalances, nutritional deficiencies, and also due to changes in the osmotic effects (Zhang et al. 2010; Wu et al. 2010; Zou et al. 2013; Koyro et al. 2012). Various species of plants respond differently to salt stress, such as citrus and many others are salt-sensitive plants. Increasing rate of saline water in agricultural fields leads to a major threat to plant production and hence retards the growth and development of plants (Rabie and Almadini 2005; Pascal et al. 2005; Shokri and Maadi 2009) by affecting various metabolic processes.

A. Hameed
Department of Botany, Hamdard University, New Delhi, India

E. Dilfuza
Faculty of Biology and Soil Sciences, National University of Uzbekistan, Vuzgorodok, Tashkent, Uzbekistan100174,

A. Hashem
Botany and Microbiology Department, College of Science, King Saud University, P.O. Box. 2460 Riyadh 11451, Saudi Arabia

E. F. Abd-Allah
Plant Production Department, College of Food and Agricultural Sciences, King Saud University, PO Box 2460 Riyadh 11451, Saudi Arabia

A. Kumar
Department of Botany, Dr. H.S. Gour Central University, Sagar, Madhya Pradesh 470003, India

P. Ahmad (✉)
Department of Botany, S. P. College, Srinagar, Jammu and Kashmir 190001, India
e-mail: parvaizbot@yahoo.com

Toxicity of ions results in the disruption of enzyme activity, photosynthesis, respiration, as well as protein synthesis, and damaging of plasma membrane including cell organelles (Feng et al. 2002). Scientists have put an effort to minimize the crop loss due to salt stress by providing salt-tolerant crop plants (Gallagher 1985; Evelin et al. 2009) and also established salt-tolerant crops through breeding (Cuartero and Fernandez-Munoz 1999; Evelin et al. 2009). In addition, different genes have also been employed to enhance the salt tolerance in different plants (Wei-Feng et al. 2008; Tang et al. 2005; Evelin et al. 2009). Leaching of excess accumulated salts in groundwater also provides an alternative means to alleviate the salt stress. But these techniques are very costly and unaffordable to underdeveloped countries.

Among the environmental stress, soil salinity globally results in the greater loss in agricultural productivity and therefore affecting the lives of humans and animals (Aggarwal et al. 2012). Evelin et al. (2009) reported that 50 % loss of cultivated land affected by salinity and also the photosynthesis, protein synthesis, lipid and energy metabolism.

Salinity not only reduces yield of crops but also disrupts the ecological balance of the area (Aggarwal et al. 2012). Several literatures have reported that arbuscular mycorrhizal (AM) fungi act as growth regulator and mitigate the harmful effects of plants exposed to salt stress. Plants grown in fields are surrounded by various microorganisms such as bacteria and fungi that help and improve the plant growth and yield under various stress conditions (Creus et al. 1998). To cope with this stress, AM fungi play a key role in alleviating the toxicity induced by salt stress, thus normalizing the uptake mechanism in plants by supplying the essential nutrients. In this way, the plant recovers the water balance machinery, enhancing their tolerance capacity and thereby enduring the salt stress (Carretero et al. 2008; Porcel et al. 2012).

AM fungi form symbiotic associations with most of the plants and enhance the tolerance capacity to withstand the abiotic stresses including salinity besides increasing the uptake of inorganic nutrients (Hajbagheri and Enteshari 2011; Rabie and Almadani 2005). AM fungi supply mineral nutrients to plants, especially phosphorus, which is precipitated by the ions such as Ca, Mg, Zn (Al-Karaki et al. 2001).

Different mechanisms are required for the efficient growth and yield of plants. Reactive oxygen species (ROS) produced during salinity stress are detoxified by AM fungi as it has the tendency to enhance the production of antioxidant enzymes. Mycorrhizal plants regulate the various gene expressions affecting water balance in their tissues. AM fungi favor plant growth against the salt stress by improving the host plant nutrition, increasing K/Na ratios and efficiently influencing osmoregulation (i.e., osmotic adjustment) by accumulation of compatible solutes such as proline, glycine betaine, and soluble sugars (Porcel et al. 2012).

Mycorrhizal Plants Under Salt Stress

Mycorrhizae are ubiquitous in most temperate and tropical ecosystems including agricultural systems and form symbiotic relationship with the roots of higher plants (mycorrhizosphere). They act as channel for the exchange of energy and matter between plants and soil (Cardon and Whitbeck 2007). The most important property of AM fungi is to enlarge the surface area of the host plant roots due to an extensive hyphal network that helps to combat against stressed conditions. Mutual benefits between mycorrhizal fungi and the host plants include the exchange of carbon coming from photosynthesis and mineral nutrients, respectively (Mohammadi et al. 2011).

Formation of arbuscules in AM fungi is characterized by an extensive branched haustorium-like structure in the root cortical cells affecting nutrient exchange; however, these arbuscules are considered as the non-living part during the growth of AM fungi (Bonfante and Perotto 1995; Hause and Fester 2005) and are finally decomposed. Once grown inside, i.e., the cortical layer, the tree-like fungal structures called arbuscules are formed within the cortex of root by subsequent division of the fungal hyphae (Smith and Read 1997; Hause and Fester 2005). After the fungal entrance, these differentiated cortical cells simultaneously undergo reorganization by means of skeletal structures (i.e., microtubules and microfilaments).

Besides the exchange of mineral nutrients and phosphates, AM fungi show a positive effect toward stress conditions including osmotic potential (Augé 2001). Colonizing mycorrhizal fungi also play a key role as bioprotector under different pathogen attack (Slezack et al. 2000; Elsen et al. 2001; Strack et al. 2003). Alleviation of salt stress in plants by AM fungi is also mediated by growth hormones (Barker and Tagu 2000). Among these growth hormones, the level of cytokinin is found higher in shoots and roots of mycorrhizal plants as compared to non-mycorrhizal plants (Allen et al. 1980), whereas the amount of Abscisic acid (ABA) has also been found higher in AM roots (Bothe et al. 1994).

Anastomosing or networking hyphae of AM with the roots of plant attributes to an efficient soil texture as well as water relation (Bethlenfalvai and Schuepp 1994). Therefore, these AM fungi provide significant applications in sustainable agriculture (Schreiner and Bethlenfalvai 1995). Colonization of red tangerine (*Citrus reticulata*) by *Glomus mosseae* and *Paraglomus occultum* has shown better growth and increased photosynthetic performance and ionic balance implying the higher tolerance level under salt stress. These positive effects of AM fungi provide a good indicator of bio-amelioration of plants on exposure to salt stress (Zou et al. 2013).

The existence of AM colonization in the roots of halophytic plants has also been reported (Carvalho et al. 2001; Hilderbrandt et al. 2001). Besides this, AM fungi spores have also been obtained abundantly in extremely alkaline soils (Landwehr et al. 2002). It is likely that under increased levels of NaCl stress, mycorrhizal fungi do not affect the growth of the host plants, which is due to the

adverse effects of salinity on the growth and activity of the fungi (Sheng et al. 2008; Juniper and Abbott 2006). Mycorrhizal fungal symbioses have also been reported to enhance tolerance under salt stress in various host plants such as maize, clover, tomato, and lettuce (Feng et al. 2002; Al-Karaki et al. 2001). Mycorrhizal colonization improves not only the yield of plants but also the quality of fruit, for example in water melon (Kaya et al. 2009).

Plant Growth and Salinity

Salinity stress adversely affects plant morphology and physiology. Various studies reveal that AM fungi improve plant growth and yield under salt stress conditions (Al-Karaki et al. 2001; Tsang and Maun 1999). This could be possible by means of adequate supply of mineral nutrients, particularly phosphorus with the help of AM fungi by the host plant (Marschner 1986; Al-Karaki 2000). Published data showed the higher growth of mycorrhizal plants under salt stress (Giri et al. 2003; Sannazzaro et al. 2007; Zuccarini and Okurowska 2008).

Hajbagheri and Enteshari (2011) reported maximum plant growth and biomass under salt stress. Similarly, roots colonization by AM fungi resulted in the enhanced growth of tomato (Al-Karaki 2006), soybean (Sharifi et al. 2007), and citrus (Ying-Ning et al. 2013) on exposure to salt stress. Phosphorus limits plant growth due to its poor mobility in the soil. However, its increased availability due to AM fungi symbiosis with the host plant has been reported to enhance plant growth and biomass.

Application of mycorrhizal plants has proved to significantly increase plant growth as the uptake of phosphorus in chickpea (Azcón-Aguilar et al. 2003). Combination of mycorrhizal fungi with natural rock phosphate based on nutritional content is found to be more effective on *Sesbania* (Mohammadi et al. 2011). AM fungi colonization has found to be effective in several crop plants such as sunflower, maize, soybean, potato, and wheat (Dahlgren et al. 2004; Mohammadi et al. 2011).

Lin et al. (1991) reported phosphorus in double concentrations in the shoots and roots of mycorrhizal *Trifolium repens*, indicating that AM colonization provides higher percentage of phosphorus concentration than non-mycorrhizal plants (Ortas et al. 2011; Mohammadi et al. 2011). In another study, luxuriant growth has been observed in mycorrhizal garlic plants with increased fresh weight under salt stress (Cho et al. 2006; Al-Karaki 2006). Mehdi et al. (2006) also found the increased dry biomass of lentil shoots by mycorrhizal colonization.

In response to salt stress, reduction in root growth of tomato (Latef and Chaoxing 2011) and *Jatropha curcas* (Kumar et al. 2010) has been reported even when the plants were inoculated with the fungi. Similar results are also reported by Hajbagheri and Enteshari (2011). In this study, root dry weight increased due to enhanced salinity and root fresh weight decreased due to reduced osmotic potential of soil and also due to its low water absorption capacity (Hajbagheri and

Enteshari 2011). Similar results were obtained by Ghoulam et al. (2002) in beet root. When inoculated AM fungi were introduced, the fresh and dry weight of root increased because of its increased nutrient and water absorption by the fungal hyphae network. Mycorrhizal fungal fibers entering the plants increase cytokinin content resulting in higher water absorption and formation of extensive root system in plants. Other group of fibers presented outside the root system produces organic acids solubilizing phosphorus like malic acid, thereby enhancing phosphorus absorption and hence plant dry matter. Phosphorus plays a crucial role in cellular division by regulating the activity of growth hormones. Growth and biomass inhibition under salt stress is reported by Siddiqui et al. (2009) and Afroz et al. (2005) due to high accumulation of NaCl salt.

Chlorophyll Content

Chlorophyll content reduces under salt stress due to its enzyme inhibition required for biosynthesis of chlorophyll (Sheng et al. 2008; Murkute et al. 2006) and also by limited uptake of nutrients. Mycorrhizal plants in response to salt stress have been observed to increase the chlorophyll content (Sannazzaro et al. 2006; Colla et al. 2008; Zuccarini 2007), suggesting the less interference of salt with chlorophyll biosynthesis (Giri and Mukerji 2004). Also, the negative effect of Mg on chlorophyll molecules is counterbalanced in the presence of AM fungi under salt-stressed conditions (Giri et al. 2003; Zuccarini 2007). Salt stress causes alterations in the activities of enzyme, affecting the synthesis of chlorophyll, and results in the loss of pigments (Parida and Das 2005). El-Tayeb (2005) found the same in maize and barley plants. Reduction in chlorophyll activity is attributed to diffusional limitations, i.e., stomatal and mesophyll conductance (Paranychianakis and Chartzoulakis 2005).

With increasing the salinity level, photosynthesis is reduced in plants; however, in mycorrhizal plants, the chlorophyll activity is restored due to presence of specific enzymes required for its biosynthesis (Sheng et al. 2008; Hajbagheri and Enteshari 2011). Since mycorrhization increases the absorption of Mg in plants, the synthesis of chlorophyll increases in mycorrhizal plants. Increasing chlorophyll activity in AM-inoculated plants decreases Na level under salt stress. Zhu et al. (2010) found similar results in maize plants inoculated with *Glomus etunicatum*. These results are corroborated with the findings of Kumar et al. (2010). AM symbiosis enhanced the photosynthesis rate under salt stress in garlic plants (Borde et al. 2010). This is in accordance with the result of other studies (Sannazzaro et al. 2006; Sheng et al. 2008; Colla et al. 2008).

Yang et al. (2010) also reported the blockage of water absorbance by cucumber roots, thereby influencing stomatal opening and hence decreased biochemical reactions. According to Evelin et al. (2009), a tremendous loss in chlorophyll content and nutrient imbalances is among the adverse effects of salinity on the growth of plants.

Unavailability of carbon dioxide leads to increased stomatal closure due to its reduced consumption of NADPH produced by Calvin cycle (Ruiz-Lozano et al. 2012). Microorganisms such as bacteria and fungi increase plant growth and yield under adverse environmental conditions as they have the tendency to resist the damage and hence develop resistance against harmful effects of salinity stress.

The increased photosynthetic pigments by mycorrhizal colonization in plants is due to the inhibition of Na transport, which leads to better functioning of photosynthetic machinery (Borde et al. 2010; García-Garrido and Ocampo 2002). Production of proline by the application of mycorrhizal fungi demonstrates the high tolerance capacity in wheat plants by stabilizing the osmotic balance and scavenging the toxic radicals (García-Garrido and Ocampo 2002).

Under salt stress, AM fungi increase the rate of chlorophyll contents that is attributed to higher translocation of photosynthase by the fungi (Lösel and Cooper 1979). Levy and Krikun (1980) reported the same in mycorrhizal citrus plants related to water uptake as affected by stomatal regulation. Similar results were observed in grass by Allen and Allen (1981). This improvement with AM fungi is also due to enhancement in the cytokinin concentrations (Allen et al. 1980). Salinity stress adversely affects all different parameters, i.e., chlorophyll, growth, biomass, water status, nutrient uptake; however, inoculation with mycorrhizal fungal may simultaneously improve these parameters (Yohannes 2006).

Water Status

Kumar et al. (2010) have demonstrated normal levels of water in leaves of mycorrhizal *J. curcas* under salt stress. This symbiosis results in efficient water conductance in roots and simultaneously increases stomatal conductance and hence transpiration (Colla et al. 2008; Jahromi et al. 2008). AM inoculation helps the host plant to acquire nutrients and thereby improves the photosynthetic rate as well as water osmotic homeostasis (Porrás-Soriano et al. 2009; Sheng et al. 2008; Zuccarini 2007).

Water status is disrupted by salt stress; however, mycorrhizal colonization prevents the host plant from dehydration and thereby increases the root hydraulic conductivity at low water potential (Aroca et al. 2007). These inoculated plants allow fixing carbon dioxide freely relative to the non-colonized plants (Querejeta et al. 2007). Increased transpiration rate by AM symbiosis is related to the changes of ABA:cytokinin ratio (Gorcochea et al. 1997; Porcel et al. 2012). Mycorrhizal fungal colonization enables the host plants to absorb higher water through their hyphal network, and hence, water status (Khalvati et al. 2005; Bolandnazar et al. 2007; Porcel et al. 2012) and the intercellular carbon dioxide concentration are maintained in plant. Lower water saturation deficit and higher turgor potential in mycorrhizal plants efficiently regulate plant water status (Sheng et al. 2008).

Relative Cellular Permeability

Mycorrhizal plants improve the stability as well as the integrity of membrane proteins by maintaining higher relative permeability of the cell (Kaya et al. 2009; Garg and Manchanda 2008). This results in increased phosphorus uptake as well as antioxidant enzymes production (Feng et al. 2002). *Cajanus cajan* shows higher relative permeability when treated with AM fungi (Kaya et al. 2009). Also electrical conductivity of mycorrhizal plants was found higher in certain plant roots (Garg and Manchanda 2008). Mycorrhizal pigeon pea showed similar results as exposed to different levels of salt stress; this has been attributed to the higher electrolyte permeability of root plasma membrane (Feng et al. 2002), which is a result of higher phosphorus uptake and enhanced production of antioxidant enzymes. Proper combinations of mycorrhizal fungal species and the host plant result in the alleviation of the salt stress and make the cultivation of plants even more likely under stress.

Betaines

Betaines belong to *N*-methylated derivatives of amino acids and provide an effective indicator of salt stress like proline (Duke et al. 1986; Evelin et al. 2009). In addition, it has an osmotic regulating mechanism, protecting and stabilizing the integrity of cell membrane structure against the negative effects of excess salt accumulation. Mycorrhizal plants have found to be more effective during accumulation of betaines under salt stress (Al-Garni 2006; Evelin et al. 2009). In higher plants, proline is catalyzed by pyrroline-5-carboxylate synthetase (P5CS) and pyrroline-5-carboxylate reductase (P5CR). P5CS over-expressed gene in transgenic tobacco leads to enhanced production of proline under salinity (Kishor et al. 1995; Porcel et al. 2012). Glycine betaine protects the plants against adverse effects of salinity stress. Plants treated with mycorrhizal fungi accumulate betaine under stress and thus prevents plants from any stress damage. Various reports have shown that AM-treated plants enhanced the production of betaines that contribute to the osmotic adjustment of plants and hence results in a more efficient photosynthesis process (Sheng et al. 2011).

Proline

Proline accumulation is one of the natural means to adapt to environmental stress conditions. Proline is a non-toxic and good osmolyte and maintains the osmoregulation under salt stress (Ahmad and Jhon 2005; Ahmad and Sharma 2008; Ahmad 2010; Ahmad et al. 2010b, 2011, 2012a; Katare et al. 2012; Rasool et al. 2013a, b).

Plants when colonized by AM fungi show high degree of protection by accumulating more and more solute as it has been indicated in mung bean (Jindal et al. 1993; Evelin et al. 2009). Such solutes have been found more in roots than shoots as roots are the primary sites of water absorption. Proline accumulation is not only due to salinity stress but also by mycorrhizal colonization. In some plants, proline accumulation is observed due to salt stress and not by mycorrhizal colonization, and hence, it is required to clarify such finding to assess the mechanisms of salt tolerance in various plants. Proline also acts as energy storage (i.e., C and N) during salt stress (Goas et al. 1982; Aggarwal et al. 2012). Enhanced proline accumulation can be linked with increased N-fixing ability of plants as demonstrated by Evelin et al. (2009) in pigeon pea.

Symbiotic plants, under salt stress, are thought to prevent nodule destruction by avoiding the protein denaturation (Irigoyen et al. 1992). Maximum proline synthesis has been found in salt-stressed plants in the presence of bacteria *Burkholderia* (Barka et al. 2006), *Arthrobacter*, and *Bacillus* (Sziderics et al. 2007). The introduction of proBA gene extracted from *Bacillus subtilis* into *Arabidopsis thaliana* enhances proline accumulation and increased salt tolerance in transgenic plants (Chen et al. 2007). Proline accumulation was found to increase tremendously when the host plant gets stimulated by colonization under salt stress.

Carbohydrates

Carbohydrates lower the water potential of plants and provide defensive mechanism against salt stress (Thanna and Nawar 1994; Ahmad and Jhon 2005; Koyro et al. 2012). Increased carbohydrate content due to salinity stress has been observed in *Phragmites australis* and corresponds to mycorrhizal plants (*Glomus fasciculatum*) (Al-Garni 2006; Thomson et al. 1990). Similar results have been observed in soybean roots colonized by *Glomus intraradices* (Porcel and Ruiz-Lozano 2004). Enhanced level of soluble sugar in the host plants is resulted by mycorrhizal symbiosis (Evelin et al. 2009).

Trehalose among the non-reducing sugar is the main storage part of carbohydrate in extra-radical mycelium as well as in spores of AM fungi and plays a key role in maintaining the integrity of biological membranes against salt stress. Trehalose accumulation has been exploited as a stress protector and has the potential to adapt to hyperosmotic conditions of symbiotic bacteria and in turn provides a powerful tool in the response of AM fungi under salt stress (Lopez et al. 2008).

This forms the close association to withstand the capacity to endure salt stress (Borde et al. 2010). Conversely, some scientists have shown negative effects regarding the mycorrhizal association and sugar accumulation in host plants during salt stress.

Furthermore, carbohydrate accumulation is associated with the transport and supply of food to different parts of plants necessary for plant adaptation, growth,

photosynthesis, and biomass allocation (Balibrea et al. 2000). Eventually, the accumulation of carbohydrate in the sink associated with salt stress represents the first limiting step for salt tolerance and can be restored and enhanced in mycorrhizal plants (Perez-Alfocea et al. 2010; Dodd and Perez-Alfocea 2012). High sugar content in maize plants due to AM symbiosis was observed under salt stress by Feng et al. (2002). This result can lead to improved plant water level, efficient chlorophyll synthesis, and increased tolerance level (Sheng et al. 2008).

Polyamines

Polyamines play a significant role in response to various abiotic stresses including salinity (Krishnamurthy and Bhagwat 1989; Ahmad et al. 2012b) and high osmotic potential (Besford et al. 1993) as they act as a defense strategy (Kurepa et al. 1998). They also play an important role in the architecture of roots under salt stress (Couée et al. 2004). Salinity decreases the level of polyamines; however, in mycorrhizal plants, the activity of polyamines is improved (Sannazzaro et al. 2007).

Various species of salt-tolerant mycorrhizae have been observed to enhance the adaptability to salinity stress of *Lotus glaber* (Sannazzaro et al. 2007). Spermine and spermidine are formed from methionine and ornithine, whereas putrescine is produced from arginine. The initial step undergoes the loss of carbon dioxide catalyzed by ornithine decarboxylase (Ahmad et al. 2012b; Evelin et al. 2009). Nevertheless, associated enzymes linked with polyamines are increased under salinity (Lefevre and Lutts 2000). This might lead to an extensive enhancement of polyamines in plants when inoculated by mycorrhizal fungi. Polyamine also stimulates various protein biosyntheses via nucleic acid interaction and thereby stabilizes the biomembranes (Evelin et al. 2009).

Antioxidants

ROS generated under salt stress become a major devastating effect in plants. The radicals are leaked during the aerobic respiration in chloroplast and mitochondria (Møller 2001; Asada 1999). These in turn damage the photosynthetic machinery of the cell. ROS negatively affects biomolecules such as proteins, carbohydrates, nucleic acids, and membrane lipids. To combat the stressful environment, plants possess several antioxidant enzymes to protect them from such harmful effects of ROS. Therefore, antioxidative enzymes play a key role as a defense mechanism in various plant species and hence salt tolerance level (Yamane et al. 2004; Jiang and Zhang 2002; Evelin et al. 2009; John et al. 2007; Ahmad 2010; Ahmad et al. 2008a, b, 2009, 2010a, b, 2011, 2012a, c, 2013; Ahmad and Umar 2011; Koyro et al. 2012; Ahmad and Prasad 2012a, b; Rasool et al. 2013a, b).

Besides antioxidant enzymes, several non-enzymatic compounds such as carotenoids, glutathione, tocopherols, and ascorbic acid are also responsible to scavenge the oxygen radicals (Alguacil et al. 2003; Wu et al. 2006; John et al. 2007; Ahmad 2010; Ahmad et al. 2008a, b, 2009, 2010a, b, 2011, 2012a, c, 2013; Ahmad and Umar 2011; Koyro et al. 2012; Ahmad and Prasad 2012a, b; Rasool et al. 2013a, b). Incorporation of AM symbiosis helps to endure the salt stress and increases the antioxidant enzymes (Ocon et al. 2007; Harinasut et al. 2003).

Enhanced antioxidant enzymes associated with AM plants have been demonstrated by many scientists. Catalase (CAT), ascorbate peroxidase (APOX), and superoxide dismutase (SOD) have shown increased activity in *Olea europaea* and *Retana splaerocarpa* (Alguacil et al. 2003). Smirnov (1993) reported detoxification of superoxide to hydrogen peroxide by enhanced SOD. This produced hydrogen peroxide is in turn scavenged by CAT and peroxidase and APOX (Lopez et al. 1996; Benavides et al. 2000). Mycorrhizal plants enhance the production of antioxidant enzymes as affected by the micronutrients available to the enzymes such as CAT, POX, and SOD (Alguacil et al. 2003). Deficiencies and excess of micronutrients alter the expressions of metalloenzymes, e.g., Fe increases the CAT and APX activities in *Nicotiana plumbaginifolia* (Kamfenkel et al. 1995). Accumulation of ROS depends upon the balance between ROS production and ROS scavenging (Miller et al. 2010). There are many reports that showed mycorrhizal plants provide higher accumulation of antioxidative enzymes and thereby improve the whole plant growth under stress (Miller et al. 2010; Scheibe and Beck 2011).

Ascorbate plays a crucial role to protect the chlorophyll activity during salt stress (Shao et al. 2008; Noctor and Foyer 1998). Türkan and Demiral (2009) have reported the tremendous link between antioxidant capacity and salinity tolerance. Studies reveal that mycorrhizal symbiosis enables the host plant to survive under salt or water deficit stresses by enhancing the production of various antioxidant enzymes (Zhong Qun et al. 2007; Ruíz-Sánchez et al. 2010; Talaat and Shawky 2011).

Manchanda and Garg (2011) also reported that POX and CAT activity enhances salt tolerance in *C. cajan* (Mehdy 1994). Soybean plants colonized with AM fungi indicate the increased antioxidant capacity with the potential to adapt to the various salt stress conditions (Ghorbanli et al. 2004). Increased level of antioxidant enzymes might also result in the efficient colonization of mycorrhizal fungi under salt stress (Alguacil et al. 2003). Similar results were obtained with *Gmelina arborea* inoculated with *Glomus fasciculatum* (Dudhane et al. 2010; Aggarwal et al. 2012).

Root colonization by mycorrhizal fungi induces accumulation of proline and thereby facilitates osmotic adjustment (Sheng et al. 2011; Ruiz-Lozano and Azcon 1995). Proline is an indicator of salt and other stresses that scavenge the free radicals and stabilize the water balance mechanisms in plants (Yang et al. 2009; Dodd and Perez-Alfocea 2012). Under salt stress, levels of antioxidants enzymes vary depending on the species, metabolic state of plant, and also the intensity of stress (Reddy et al. 2004). Enhancement of antioxidant enzymes is

also associated with increased potential to withstand the stress indicating the tolerance of mycorrhizal garlic plants to salt stress (Borde et al. 2010). Evidences show the greater and increased growth of AM-treated plants on exposure to different levels of salt concentrations.

Abscisic Acid

AM fungi have the capacity to alter the levels of ABA and thereby adapt to different environmental stresses including salinity (Estrada-Luna and Davies 2003). ABA levels are found higher in *L. glaber* colonized by AM fungi (Sannazzaro et al. 2007). Spermine content in mycorrhizal plant tends to regulate the ABA activity in the shoot. Nevertheless, some authors have reported less accumulation of ABA in association with mycorrhizal fungi under salt stress (Evelin et al. 2009). ABA is one of the growth hormones responsible to protect the plant against salt stress (Miransari et al. 2013).

Nodulation and Nitrogen Fixation

During the symbiosis process, nitrogen-fixing bacteria form nodules on the roots, especially in leguminous plants. The number of nodules decreases under salt stress as the process of nitrogen fixation is adversely affected by the stress due to the inhibition of leg-hemoglobin production, thereby reducing the nitrogenase activity (Garg and Manchanda 2008; Rabie and Almadini 2005; Harinasut et al. 2003). Reduction in nodulation and nodule activity has also been observed by Serraj et al. (2001), Tejera et al. (2005), Bolanos et al. (2006), and Garg and Manchanda (2008) in different plants.

Under salt stress, mycorrhizal plants improve their productivity due to their adequate leg-hemoglobin content and nitrogenase activity. Therefore, nodulation seems to enhance at low salt concentration (Johansson et al. 2004; Rabie and Almadini 2005; Garg and Manchanda 2008). AM fungi possess the ability to alleviate the harmful effects of salinity during the process of nitrogen fixation and nodulation in legumes as AM fungi increase the number of nodules (Garg and Manchanda 2008; Giri and Mukerji 2004; Ruiz-Lozano et al. 2001; Porcel et al. 2003). Exogenous application of AM fungi improved the pink color of leg-hemoglobin, indicating the higher pigment content and hence higher nitrogenase activity and nitrogen fixation in mycorrhizal plants. This is also attributed to the free availability of phosphorus required for nitrogenase enzyme of bacterial symbionts and also uptake of essential micronutrients, leading to the enhanced growth and yield of plants (Founoune et al. 2002; Evelin et al. 2009). Therefore, to prevent from such harmful effects of abiotic stress, association of AM fungi under salinity stress can alter various changes and make the plants to adapt to different

types of stress including salt stress. Mycorrhiza-treated plants enhanced nodule formation, photosynthesis, and water status in *S. helvola* under salt stress (Tsang and Maun 1999).

Under extreme conditions of salinity stress, the AM fungi have been found to alleviate these stresses and create a strong association with their host plants (Dodel and Ruíz-Lozano 2012; Wilde et al. 2009; García-Garrido and Ocampo 2002). Several studies have reported a tremendous yield loss under salt stress (Al-Karaki et al. 2001; Cantrell and Linderman 2001; Hajiboland et al. 2010).

Nutrient Uptake

Nutrients are essential for the proper functioning of plants and any deficiency hamper plant growth and yield production. All essential nutrients seem to be adversely affected by salt stress. Accordingly, to combat the poor supply of nutrients from the soil, mycorrhizal fungi help their host plant to restore the uptake of mineral nutrients and hence plant growth (Giri and Mukerji 2004; Sharifi et al. 2007).

Phosphorus is essential for plant growth and is not readily available as the phosphate precipitates with some of the cations such as Ca, Mg, and Zn. However, AM fungal symbiosis plays a key role in supplying the poor mobility nutrients like phosphorus to the host plant by the roots and hence suppress the negative effects of salt (Feng et al. 2002; Al-Karaki and Clark 1998). This is attributed to the extensive network of AM fungal hyphae that explore higher volume of soil (Ruiz-Lozano and Azcón 2000). In fact, depleted areas around the plant roots can also become fertile due to the presence of mycorrhizal hyphae, which acquire nutrients from the soil under the salinity stress.

During salt stress, plants absorb Na more than K (Rus et al. 2001), thereby providing the competition for K within the same binding site. Potassium has its peculiar functions such as participating in the activities of various enzymes, regulating the stomatal movement, and also involving in the synthesis of proteins (Blaha et al. 2000). Salinity cause imbalance in K^+/Na^+ ratio adversely affecting the plant growth. Since mycorrhizal plants possess higher Na^+/K^+ (higher K^+ uptake in shoots), they are able to mitigate the salt stress by the dilution effect (Juniper and Abbott 1993). Similar results in the concentration of K have been demonstrated by Ojala et al. (1983) and Mohammad et al. (2003) who showed higher K^+ accumulation and hence higher K/Na ratio by mycorrhizal plants, favorably affecting the enzymatic processes as well as protein synthesis under salt stress (Audet and Charest 2006). Calcium act as a second messenger to transducer signals. Calcium ions have tendency to raise K uptake, thereby adapting various changes under salt stress. Therefore, Ca accumulation under salt stress has been found to enhance the colonization as well as sporulation of mycorrhizal fungi (Jarstfer et al. 1998).

Conclusion and Future Prospects

Salt stress has been shown to adversely affect plant growth and physiology; however, association with AM fungi seems to effectively enhance plant growth under stress through the accumulation of different solutes and higher uptake of water and nutrients. Investigations have been carried out to find the depth of mycorrhizal symbiosis and activity under stress. Enhanced production of antioxidative enzymes in mycorrhizal plants needs to be further evaluated to reveal the ultrastructure aspects of AM fungi. These in turn would open new avenues for the alternative way of increasing tolerance by AM symbiosis in order to overcome the adverse effects of salt stress. AM symbiosis plays a crucial role in plant growth promotion and prevents the plants from the adverse effects of various stresses including salinity. Genetic techniques and molecular approaches may indicate new insight in the alleviating role of mycorrhizal symbiosis under stress.

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