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Arbuscular mycorrhizal symbiosis and alleviation of salinity stress

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Abstract: Several environmental factors adversely affect plant growth and development and final yield performance of a crop. Drought, salinity, nutrient imbalances (including mineral toxicities and deficiencies) and extremes of temperature are among the major environmental constraints to crop productivity worldwide**.** Development of crop plants with stress tolerance, however, requires, among others, knowledge of the physiological mechanisms and genetic controls of the contributing traits at different plant developmental stages**.** In the past two decades, biotechnology research has provided considerable insights into the mechanism of biotic stress tolerance in plants at the molecular level**.** Furthermore, different abiotic stress factors may provoke osmotic stress, oxidative stress and protein denaturation in plants, which lead to similar cellular adaptive responses such as accumulation of compatible solutes, induction of stress proteins, and acceleration of reactive oxygen species scavenging systems. Recently, various methods are adapted to improve plant tolerance to salinity injury through either chemical treatments (plant hormones, minerals, amino acids, quaternary ammonium compounds, polyamines and vitamins) or biofertilizers treatments (Asymbiotic nitrogen-fixing bacteria, symbiotic nitrogen-fixing bacteria) or enhanced a process used naturally by plants (mycorrhiza) to minimise the movement of Na+ to the shoot. Proper management of Arbuscular Mycorrhizal Fungi (AMF) has the potential to improve the profitability and sustainability of salt tolerance. In this review article, the discussion is restricted to the mycorrhizal symbiosis and alleviation of salinity stress.

Keywords: Arbuscular mycorrhizal fungi, Growth improvement, Nutrient uptake, Salinity stress

INTRODUCTION

Environmental factors can act as stressors that impact the evolution of living organisms on Earth (Schluter, 2001). Indeed, survival necessitates the ability to rapidly adapt to changes in the environment, especially those which represent long term or chronic changes. Whenever possible, one of the easiest ways to counteract such stresses is to relocate to a more suitable niche (Huey *et al*. 2002). However, such a strategy is obviously restricted in a short term period and is not achievable with stationary organisms such as plants. Consequently, plants have developed a variety of strategies to cope against biotic stresses such as herbivory or parasitism, and abiotic stresses such as salinity, drought, heat or toxic metal contamination (Hodges *et al*., 1995; Subramanian and Charest, 1998, 1999; Audet and Charest, 2006, 2008, 2009). Among abiotic stresses, soil salinization is probably one of the most important in the world (Hasegawa *et al*., 2000; Zhu, 2003). High soil salinity is a growing setback in agricultural development in many parts of the world, especially in arid and semiarid areas. Currently, high soil salinity occupies 7% of Earth's land surface and it is predicted that 50% of arable land will be affected by salinity by the half of the 21th century (Evelin *et al.*, 2009). This could mostly occur due to soluble minerals found in irrigation water and the high fertilizer input from agricultural practices (Schilfgaarde, 1994; Al-Karaki, 2006). In addition, high temperature and low precipitation leading to salt accumulation at the soil surface affect the establishment, growth and development of plants and even more as salinity increases. The delay in root growth can be caused by too low soil water potential and salt cell toxicity (Psarras *et al.*, 2008). The latter causes cell death and root necrosis in the very sensitive genotypes. In addition to these deleterious effects on roots, growth of shoots is also affected and as a result the root/shoot ratio is disturbed (Maggio *et al*., 2007). Overall, salinity leads to many deleterious effects on plants and that at different life stages. To counteract this problem, many strategies were proposed to overcome salt detrimental effects such as searching for new salt-tolerant crops, genetically engineering plants, removing excessive salt accumulation in groundwater and desalinizing water for irrigation (Ashraf and Harris, 2004; Flowers, 2004; Zhang and Blumwald, 2001). Although these strategies appear efficient, yet they are costly and out of reach for developing countries that are the most affected.

Even nowadays, with the advent of modern agricultural practices and new management measures, the loss of crops due to field salinization remains a major concern. The main reason why agricultural fields are affected by salt is generally due to continued irrigation and a lack of sufficient drainage resulting in waterlogged soils which leads to increased surface salt concentrations as a consequence of evaporation (Ritchie *et al*., 1972). Consequently, a reduction in crop yields, mainly because of osmotic stress, as well as nutritional and toxic effects occurred. It is estimated that at least one third of all irrigated agricultural lands are affected to some degree by salinity (Williams, 1999). Furthermore, the increasing demands in food production constantly push agricultural fields to areas where water and soils have naturally or not high salt levels (Araus *et al*., 2007).

The sustainability of irrigated agriculture in many arid and semiarid areas of the world is at risk because of a combination of several interrelated factors, including lack of fresh water, lack of drainage, the presence of high water tables, and salinization of soil and groundwater resources. Soil salinity often leads to the development of other problems in soils such as soil sodicity and alkalinity. Soil sodicity is the result of the binding of Na^+ to the negatively charged clay particles, which leads to clay swelling and dispersal. Hydrolysis of the Na–clay complex results in soil alkalinity. Thus, soil salinity is a major factor limiting sustainable agriculture. Natural soil salinity predates human civilization. When early man, looking for better sources of livelihood, moved to arid lands along the riverbanks, he restored to irrigated agriculture. With the practice of irrigation began salinity, the first man-made environmental problem. Salt-affected lands occur in practically all climatic regions, from the humid tropics to the polar regions. Saline soils can be found at different altitudes, from below sea level (e.g. around the Dead Sea) to mountains rising above 5,000 m, such as the Tibetan Plateau or the Rocky Mountains. Of nearly, 160 million ha. of cultivated land under irrigation worldwide, about one-third is already affected by salt, which makes salinity a major constraint to food production. It is the single largest soil toxicity problem in tropical Asia (Greenland, 1984).

TYPES AND CAUSES OF SALINITY

Salinity is the concentration of dissolved mineral salts present in the soils (soil solution) and waters. The dissolved mineral salts consist of the electrolytes of cations and anions. The major cations in saline soil solutions consist of Na^+, Ca^{2+}, Mg^{2+} and K^+ and the major anions are Cl^-, SO_4^{2-}, HCO_3^-, CO_3^{2-} and NO_3^-. Other constituents contributing to salinity in hypersaline soils and waters include B, Sr^{2+}, SiO^{2+}, Mo, Ba^{2+} and Al^{3+} (Hu and Schmidhalter, 2002). Water soluble salts accumulate in the soil solum (the upper part of the soil profile, including the A and B horizons) or regolith (the layer or mantle of fragmental and unconsolidated rock material, whether residual or transported) to a level that impacts on agricultural production, environmental health, and economic welfare (Rengasamy, 2006).The dominant sources of salt are rainfall and rock weathering. Rainfall contains low amounts of salt, but over time, salt deposited by rain can accumulate in the landscape. Wind-transported (aeolian) material from soil or lake surfaces is another source of salt. Poor quality irrigation water also contributes to salt accumulation in irrigated soils. Seawater intrusion onto land, as occurred in recent tsunami-affected regions, can deposit huge amounts of salts in soils of coastal lands. The particular processes contributing salt, combined with the influence of other climatic and landscape features and the effects of human activities, determine where salt is likely to accumulate in the landscape (Rengasamy, 2006). Naturally salt-affected areas occur widely in arid and semi-arid areas (Rengasamy *et al*., 2003). The most common causes are (1) land clearing and the replacement of perennial vegetation with annual crops, and (2) irrigation schemes using salt-rich irrigation water or having insufficient drainage.

IMPACTS OF SALINITY

Salinity not only decreases the agricultural production of most crops, but also, as a result of its effect on soil physicochemical properties, adversely affects the associated ecological balance of the area. The harmful impacts of salinity include-low agricultural production, low economic returns due to high cost of cultivation, reclamation management, soil erosion due to high dispersibility of soil, ecological imbalance due to halophytes and marine life forms from fresh water to brackish water, poor human health due to toxic effects of elements such as B, F, and Se (Hu and Schmidhalter, 2002). Crop species show a spectrum of responses to salt, although all have their growth, and eventually, their yield reduced by salt. Salt effects are the combined result of the complex interaction among different morphological, physiological, and biochemical processes (Singh and Chatrath, 2001). Salinity may directly or indirectly inhibit cell division and enlargement and finally the growth of the whole plant. In addition to these factors, some other factors like water deficit (drought stress), ion toxicity, ion imbalance and soil compaction may cause growth reduction, injury of foliage, nutrient deficiencies, destruction of soil structure which ultimately hampers the growth of the plant. Some above ground visible morphological symptoms of plants are marginal yellowing/browing of foliage, premature fall of leaves, twig and branch die back, loss of vigor and stunted growth.

There are some examples available classifying tree/shrub species according to their sensitivity to salt which are given below:

Salt sensitive tree/shrub species:

Platanus hispanica	*Acer spp.*
Fagus sylvatica	*Carpinus betulus*
Aesculus hippocastanum	*Tilia spp.*
Rosa spp.	*Larix decidua*
Picea abies	*Pseudotsuga menziesii*

Salt tolerant tree/shrub species:

Robinia pseudoacacia	*Quercus spp.*
Populus spp.	*Rosa rugosa*
Acacia spp.	*Eucalyptus spp.*
Pinus halepensis	*Pinus nigra*
Eleagnus angustifolia	

MYCORRHIZA AND ALLEVIATION OF PLANT SALT STRESS

In nature, plants interact with several microorganisms such as bacteria and fungi that improve their performance when facing various environmental pressures. Indeed, most of terrestrial plants are involved in mutualistic associations with other organisms beneficial to both parties (Brundrett, 2002). One of these associations is referred to as mycorrhiza. Mycorrhizae form close symbiosis between fungi and plant roots. There are two major categories of mycorrhizae namely, ectomycorrhizae and endomycorrhizae which are formed by mostly Basidiomycetous and Glomeromycetous fungi. The endomycorrhizae usually produce vesicles, arbuscules, inter and intra-cellular mycelium in the cortex of the host plants, and also produce extrametrical hyphae with spores and sporocarps. The endomycorrhizae are represented by *Acaulospora*, Gigaspora, Glomus, Entrophospora, Scutellospora and Sclerocystis. AM fungi are an ubiquitous group of soil fungi which are known to colonize roots of plants belonging to more than ninety per cent of plant families (Trappe, 1987). Several tree taxa (e.g. *Salix, Populus, Alnus, Eucalyptus*) can form both endo- and ectomycorrhiza (Aggarwal *et al*., 2011). Due to an extended network of fine hyphae, the AM fungi can considerably improve the uptake of mineral nutrients to their host plant, whereas the plant supports the fungus with assimilation products (Harley and Smith, 1983; Smith and Read, 1997; Aggarwal *et al*., 2011).

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 and Charest, 1998, 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 and 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 and Rai (2012) have investigated taxonomic diversity of AM fungi in 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. Here in this review article, we shall be discussing the effects of salinity on various morphological, physiological parameters of plant.

EFFECT OF SALINITY ON AM COLONIZATION AND SPORE NUMBER

Soil salinity can affect AM fungi by slowing down root colonization, spore germination, and hyphal growth (Juniper and Abbott, 1993). Before colonization occurs, spores need to be hydrated in order to germinate which is difficult in saline soil. To some extent, salinity hampers AM fungi at early stages of the symbiosis which is delayed rather than inhibited (Juniper and Abbott, 2006). However, other studies showed that there is in fact no reduction in AM colonization in the presence of NaCl (Aliasgharzadeh *et al*., 2001; Yamato *et al*., 2008) and even increases 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.

Mycorrhizal fungi have been reported on the roots of cultivated and non-cultivated plants growing in disturbed or undisturbed saline soil. These have been linked with increased plant biomass and development in saline soil (Ruiz-lozano and Azcon, 2000). Sporulation by AM fungi does not appear to be affected by salinity. Thus, in plants adapted to saline soil, salinity appears to have little effect on the formation of AM spores. However salinity may dramatically affect mycorrhizal formation in plant unadapted to salt stress. One general concept about pH and AM fungi is that some AM fungi do not radily adapt to soil with a Ph different from their soil of origin and that pH change restricts AM establishment (Sylvia and Williams, 1992). Neutral to alkaline pH favours germination of *Glomus mosseae* while spores of *Gigaspora* germinated best between pH 5-6. Hepper (1984) determined the germination of *Acaulospora laevis* in soils having different pH and concluded that optimum range for germination was 4-5. In addition, a number of studies have shown that changing the soil pH affects the activity of indigenous and certain introduced AM fungi (Wang *et al*., 1985)

Soil microorganisms face similar problems as plants in saline soils. However, the effects of salinity on soil microbionts and their symbiotic relationships with plants are much less investigated. Dixon *et al.* (1993) reported that *in vitro* growth and *in situ* symbiosis of ectomycorrhizal fungi generally declined with increasing substrate salinity. However, salt tolerance of the tested fungi varied significantly between species and between isolates within a species. The genera *Pisolithus, Laccaria* and *Suillus* appeared more tolerant of sodium salts than *Thelephora* or *Cenococcum*. Reddell *et al*. (1986) and Dixon (1988) observed that dual inoculation of *Frankia*- a actinomyceteous fungus and *Suillus* species compartmentalized salt and toxic metals in vacuoles and cell walls, thus partially excluding these agents from metabolic pathways. Most of the eighteen isolates of three Australian *Pisolithus* species were found to be resistant to NaCl concentrations of very saline soils (Chen *et al*., 2001). Also the development of arbuscular mycorrhizal fungi from spore germination till root colonization is generally reduced by increasing salt concentrations (Juniper and Abbott, 1993). However, AM fungal colonized halophytes like *Aster tripolium* occur in salt marshes world-wide and the content of AM fungal spores in saline soils can be high (Mason, 1928, Rozema *et al*., 1986, Carvalho *et al*., 2001, Hildebrand *et al*., 2001). Carvalho *et al*. (2001) reported low AM fungal diversity with *Glomus geosporum* dominant in salt marches of the Portuguese Tagus estuary. They concluded that the distribution of mycorrhizas in salt marsh is more dependent on host plant species than on environmental stresses. Most halophyte species are non-mycorrhizal. Molecular biological techniques revealed that 80%, on average, of the AM spores isolated from a range of European saline soils belonged to one single species, *Glomus geosporum*, which occurred much less in the surrounding non-saline habitats(Hildebrand *et al*., 2001; Landwehr *et al*., 2002). The authors speculate that specific AM ecotypes may be particularly adapted to saline conditions and that they could have a great potential in conferring salt tolerance to plants. On the other hand, Cantrell and Linderman (2001) reported that AM fungi from saline soil were not more effective than those from non saline soil in reducing growth inhibition of lettuce and onion plants by salt. In another study (Copeman *et al*., 1996) AM fungi originating from saline soil, in contrary to fungi from non saline soil, did not promote growth of tomato under saline conditions. However, reduction in leaf chloride concentrations mediated by these fungi may have beneficial implications for plant survival in saline soil. Increasing salinity decreased the hyphal development of *Glomus sp.* from saline soil to a higher extent than that of *Glomus deserticola* from non saline soil (Ruiz-Lozano and Azcon, 2000). Though both AMF protected host plants against salinity, they differed in their symbiotic efficiencies and mechanisms to mediate plant salt tolerance. Rosendahl and Rosendahl (1991) demonstrated large variations in salt tolerance of AM fungal species and isolates.

PLANT GROWTH AND BIOMASS

Plant growth and biomass suffered a lot under salt stress. There is considerable evidence that arbuscular mycorrhizal (AM) fungi can enhance plant growth and vigor under salt stress conditions (Pond *et al*., 1984; Pfeiffer and Bloss, 1988; Juniper and Abbott, 1993; Ruiz-Lozano *et al*., 1996; Tsang and Maun, 1999; Al-Karaki *et al*., 2001). This has been attributed due to a more efficient nutrient uptake, particularly phosphorus by AM fungi (Hirrel and Gerdemann, 1980; Ojala *et al*., 1983; Marschner, 1986; Pfeiffer and Bloss, 1988; Al-Karaki, 2000). Phosphorus (P) is the macronutrient with the lowest mobility in soil and thus often limiting plant growth, particularly when soil water potential and P diffusion rate is lowered in dry or saline soils. However, mycorrhization was found to increase the fitness of the host plant by enhancing its growth and biomass. Several researchers have reported that AMF-inoculated plants grow better than non-inoculated plants under salt stress (Al-Karaki, 2000; Cantrell and Linderman, 2001; Giri *et al*., 2003; Sannazzaro *et al*., 2007; Zuccarini and Okurowska, 2008). It has been reported that mycorrhizal treated *Poncirus trifoliata* seedlings exhibited significantly higher dry biomass in saline soil as compared to non- AMF seedlings. Shhekoofeh and 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 photosynthetic. 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 and Ying-Ning (2011) reported markedly increase 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. Jain *et al*. (1989) reported AM application improved productivity of multipurpose trees on substandard soils in India. In another study with trees, double inoculation of *Acacia cyanophylla* with rhizobia and AM fungi significantly increased salt tolerance (Hatimi, 1999). In contrast with AM fungi, we know much less about the impact of ectomycorrhizal fungi on trees in saline environments. Recently Muhsin and Zwiazek (2002) demonstrated that *Hebeloma crustiliniforme* alleviated salt stress from white spruce (*Picea glauca*) seedlings and further reported the reduction of shoot Na uptake while increasing N and P absorption and maintaining high transpiration rates and root water conductance as important salt tolerance mechanisms related to ectomycorrhizal symbiosis. This enhancement in growth and salt tolerance may be due to the better nutritional status of the plants. To some extent, these AM fungi have been considered as bio-ameliorates of saline soils (Tain *et al.*, 2004).

MINERAL NUTRITION

AMF have been shown to have a positive influence on the composition of mineral nutrients (especially poor mobility nutrient such as phosphorus) of plants grown in salt-stress conditions (Al-Karaki and Clark, 1998) by enhancing and/or selective uptake of nutrients. This is primarily regulated by the supply of nutrients to the root system (Giri and Mukerji, 2004) and increased transport of water by AMF (Al-Karaki, 2000; Sharifi *et al.*, 2007). Mycorrhizal dependency increases with increasing salt concentrations (Giri and Mukerji, 2004). The impact of mycorrhizal fungi on different mineral nutrients is discussed below:

Phosphorus: The phosphorus concentration in plant tissues rapidly lowered under salt stress because phosphate ion precipitates with Ca, Mg and Zn, then being unavailable to plants (Evelin *et al.*, 2009; Park *et al.*, 2009; Wang *et al.*, 2008). Consequently, P solubilization or added in fertilizer is required for plant growth. It was further observed that AM symbiosis seems to be positively influenced by the composition of mineral nutrients (especially poor mobility nutrients such as P) of plants under salt stress conditions (AL-Karaki and Clark 1998). Higher P uptake under saline conditions increases the plants ability of reducing of negative effects Na and Cl (Feng *et al.*, 2002). Nutrient balanced plants were shown to sequester these elements in vacuoles to maintain metabolic pathways and better growth (Cantrell and Linderman, 2001). 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 and 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 and Azcon, 2000). Indeed, mycorrhizal 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.

K/Na: In saline soils, plants tend to absorb more Na than K hence competes for the same cell binding site (Rus *et al.*, 2001). Even though this site cannot discriminate between ions, only K has a cellular function, as it is involved in the activity of a wide range of enzymes, operates stomatal movement and protein synthesis (Blaha *et al.*, 2000). Salinity disrupts K/Na balance thus hampering plant growth. Grattan and Grieve (1998) showed that AM inoculated plants have higher K/Na ratio due to an increase of K uptake in shoot. Since AM colonization may increase plant growth, it then also reduces salt stress by growth dilution effect (Juniper and Abbott, 1993). So, AM colonization was shown to increase the Na uptake in *Distichlis spicata* (Allen and Cunningham, 1983). With time, AM treated plants may accumulate Na through water uptake, then decrease it at high salt level. This implies that AM fungi may act as buffers from toxic conditions (Audet and Charest, 2006).

Calcium: Calcium is essential as a second messenger among other functions. Under salt stress conditions, its concentration increases presumably to transduce signals (Cantrell and Linderman, 2001). High Ca levels help plants to cope with salt stress as raising selectivity in K uptake and leading to better salt adaptation. Hence, Ca accumulation has been found to increase colonization and sporulation (Jarstfer *et al.*, 1998).

Magnesium: Chlorophyll synthesis impaired by salt stress may reduce photosynthetic rate that however can be improved with Mg by AMF uptake (Giri and Mukerji, 2004). A higher chlorophyll concentration has been shown in AM plants of lettuce under salt stress (Zuccarini, 2007).

WATER OSMOTIC HOMEOSTASIS

The water status in AM treated plants of *Jatropha curcas* was maintained at relatively normal levels under saline conditions (Kumar *et al.*, 2010). Mycorrhizal colonization was shown to improve water conductance in roots and increase stomatal conductance thereby enhancing transpiration (Colla *et al.*, 2008; Jahromi *et al.*, 2008). AM colonization was also shown to lower osmotic potential by increasing plant compatible solutes. Several studies showed that AM symbiosis results in increasing nutrient uptake, photosynthetic rate and water status (Porras-Soriano *et al.*, 2009; Sheng *et al.*, 2008; Zuccarini, 2007).

PHYSIOLOGICAL CHANGES

Salt stress can affect the plant by disrupting its physiological mechanisms such as decreasing photosynthetic efficiency, gas exchange, membrane disruption, water status, etc. There is evidence demonstrating that AM symbiosis can alleviate such effects by employing various mechanisms.

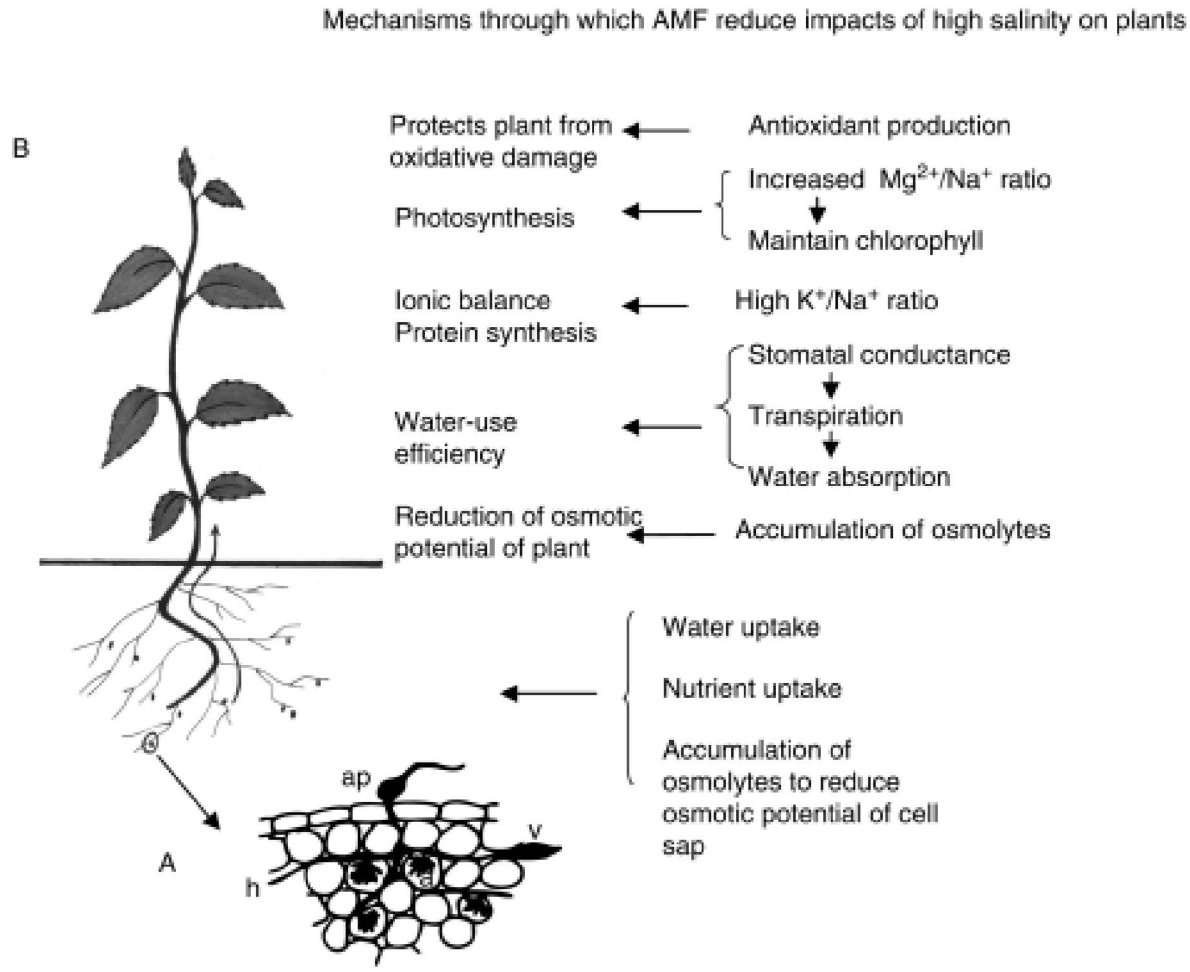

Fig. 1. *Intricate functioning of arbuscular mycorrhizal (AM) fungi in ameliorating salt stress in plants. In AM symbiosis, the fungus forms an appressorium (ap) on the root surface and enters the root cortex by extending its hyphae (h). The hyphae form arbuscules (a) and vesicles (v) in the cortex. Salinity deprives plants of the basic requirements of water and nutrients, causing physiological drought and a decrease in osmotic potential accompanied by nutrient deficiency, rendering plants weak and unproductive. Arbuscular mycorrhiza help plants in salt stress by improving water and nutrient uptake (Evelin et al., 2009).*

Chlorophyll content: The high level of salinization induced a significant decrease in the contents of pigment fractions (chlorophyll a and b) and consequently of the total cholophyll content due to suppression of specific enzymes that are responsible for the synthesis of photosynthetic pigments (Murkute *et al*., 2006). Salt stress opens porphyrin rings and harmful matters resulting from this dissolution are transferred to vacuole. Existance of these compositions demolishes green color of leaf (Parida and Das, 2005) and ultimately reduces the chlorophyll concentration in the leaf (El-Desouky and Atawia, 1998). A higher cholorophyll content in leaves of mycorrhizal plants under saline conditions has been observed by various authors (Giri and Mukerji, 2004; Sheng *et al*., 2008; Shekoofeh and Sepideh , 2011). Photosynthetic pigments were found to be increased under the influence of mycorrhizal inoculation. One reason of cholorophyll decrease in salt stress is antagonistic effects of sodium ion on Mg absorption. Since mycorrhiza helps in absorption of Mg in plants in some cases, it can increase chlorophyll synthesis in mycorrhizal treated plant. Also chlorophyll increase can be resulted from sodium decrease in shoot of mycorrhizal plants relative to non-mycorrhizal plants. Mycorrhizing decrease role of salt in chlorophyll synthesis (Giri and Mukerji, 2004). In *Glomus etunicatum* inoculated maize plant, increase in photosynthesis speed, transpiration and chlorophyll a, b density was reported under cold stress (Zhu *et al*., 2010). Also in *Jatropha curcas* mycorrhizal plants higher chlorophyll were reported than non-mycorrhizal plants under salt stress conditions (Ashwani *et al*., 2010).

Relative permeability: Inoculation of arbuscular mycorrhizal fungal with host plant enables plant to maintain a higher electrolyte concentration than the non-mycorrhizal plant by maintaining improved integrity and stability of the membrane (Garg and Manchanda, 2008; Kaya *et al*., 2009). Consequently, electrical conductivity of mycorrhizal roots was found to be higher than the non-mycorrhizal roots (Garg and Manchanda, 2008). The mycorrhizal pigeon pea roots showed a higher relative permeability than the non-mycorrhizal plants at different salinity levels of soil salinity. This suggests that mycorrhizal plants had much higher 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).

Nitrogen fixation and Nodulation: Nodules, formed through symbiosis with nitrogen-fixing bacteria are considered a soft target for salt stress and their occurrences decreases due to salt stress (Harisnaut *et al*., 2003; Rabie and Almadini, 2005; Garg and Manchanda, 2008). Nodulation suffered more than plant growth, as normalized nodule weight showed marked decline with salinity. The process of nitrogen fixation was affected negatively by salt stress, as revealed by declined leghemoglobin content and reduced nitrogenase activity. Similar decline in nodulation and nodule activity has also been reported earlier by Serraj *et al.* (2001); Tejera *et al.* (2005); Bolanos *et al.* (2006); Garg and Manchanda, (2008). Despite a decline in the functional efficiency of nodules, AM plants had considerably higher leghemoglobin content and nitrogenase activity than corresponding non-AM plants under salt stress. AM markedly increased nodulation at low saline concentration. Evidences from the previous studies (Johansson *et al*., 2004; Rabie and Almadini, 2005; Garg and Manchanda, 2008) indicate that the presence of AM fungi enhances nodulation and nitrogen fixation by legumes.

BIOCHEMICAL CHANGES

Soil water potential becomes more negative as soil dries out and plants must decrease their water potential to maintain a favorable gradient for water flow from soil into roots. To cope up from such an adverse effect, plants develops an osmotic adjustment, which may require a reduction in the plant osmotic potential which is mitigated by active accumulation of organic ions or solutes (Hoekstra *et al*., 2001). The compatible osmolytes generally found under saline stress plants are of low molecular weight sugars, organic acids, polyols, and nitrogen containing compounds such as amino acids, amides, imino acids, ectoine (1, 4, 5, 6-tetrahydro-2-methyl-4-carboxylpyrimidine), proteins and quaternary ammonium compounds. The following some biochemical changes are briefly discussed.

Proline: Accumulation of amino acid proline is one of the most frequently reported modifications induced by water and salt stress in plants. Under saline conditions, many plants accumulate proline as a non-toxic and protective osmolyte to maintain osmotic balance under low water potentials (Stewart and Lee, 1974; Jain *et al*., 2001; Parida *et al*., 2002; Ashraf and Foolad, 2007). It also acts as a reservoir of energy and nitrogen for utilization during salt stress conditions (Goas *et al*., 1982). Proline levels were found to be increased significantly with salinity stress in mycorrhizal plants when compared to non-mycorrhizal plants. Marked increase in proline occurs in mainly plants during moderate or serves salt stress and this accumulation, mainly as a result of increased proline biosynthesis, is usually the most outstanding change among free amino acids (Hurkman *et al*., 1989). This higher accumulation of proline contents in the nodules of mycorrhizal-stressed plants was correlated with the enhanced nitrogen fixing ability of these pigeon pea plants. Although proline normally crosses the peribacteroid membrane more slowly than succinate or malate (Udvardi and Day, 1997), under osmotic stress, there is an increase in the rate of proline uptake into symbiosomes (Pedersen *et al.*, 1996). High proline concentration was suggested to protect nodule metabolism by avoiding protein denaturalization and maintaining cell pH levels (Irigoyen *et al*., 1992).

Betaine: Betaines are quaternary ammonium compounds which are N-methylated derivatives of amino acids. Once formed, they are seldom metabolized (Grattan and Grieve, 1985; Duke *et al*., 1986). These are not merely non-toxic cellular osmolytes but they can also stabilize the structures and activities of protein complexes and maintain the integrity of membrane against the damaging effects of excessive salt (Gorham ,1995). It was found that at higher salinity levels the glycine betaine content of AM treated pigeon-pea plants was about 2-fold greater than that of non-AM plants (Manchanda and Garg, 2011).

Enzymes activity: There is accumulating evidence that production of reactive oxygen species (ROS) is a major damaging fac-tor in plants exposed to different environmental stresses, including salinit. Plants have evolved specific protective mechanisms, involving anti-oxidant molecules and enzymes in order to defend them-selves against oxidants (Jiang and Zhang 2002; Nunez *et al.*, 2003).

Antioxidant mechanisms may provide a strategy to enhance salt tolerance in plants. Peroxidase (POX) and catalase (CAT) are involved in the defense mechanisms of plants in response to pathogens either by their participa-tion in cell wall reinforcement, or by their antioxidant role in the oxidative stress generated during plant pathogen interaction (Mehdy, 1994). Manchanda and Garg (2011) reported that low and moderate salinity further increased the antioxidant enzymes activity in the nodules of mycorrhizal-stressed *Cajanus cajan* plants. Soybean plants inoculated with salt pretreated mycorrhizal fungi showed salt adaptation through increased SOD and POX activity in shoots, to those inoculated with the nonpretreated fungi (Ghorbanali *et al*., 2004). Alguacil *et al*., (2003) have reported that increased antioxidative enzyme activities could be involved in the beneficial effects of mycorrhizal colonization on the performance of plants grown under semi-arid conditions. Further, Garg and Manchanda (2011) have suggested that in addition to improving the ionic balance and osmolyte accumulation in the nodules, AM inoculation was an important factor in alleviation of oxidative stress as well. Dudhane *et al.* (2010) reported that there was an increased growth and also antioxidant activities in *Gmelina arborea* when inoculated with *Glomus fasciculatum.*

ULTRA-STRUCTURAL CHANGES

Salinity leads to structural and ultrastructural effects, particularly in salt-sensitive species. Some of them are indicative of the onset of injury, for example the aggregation of chloroplasts accompanied by a swelling in the granal and fret compartments or the complete distortion of chloroplastic grana and thylakoid structures. Others structural changes are associated with metabolic acclimation to salinity stress. For instance increased density of mitochondria enhanced ATPase particle frequencies in membranes may be related to enhanced energy demand at moderate salinity. Salinity-induced ultrastructural changes, such as the build up of transfer cells and many small vesicles, may be a sign of extensive exchange of substances across membranes.Up till now; there have been no published reports on the effect of AM in plants under this aspect of salt stress. Since, AMF inoculation can increase antioxidant activities in plants, it may be suggested that AMF can be applied to counteract the activities of reactive oxygen species and alleviate salt stress. Unfortunately, the role of AMF in this aspect has not yet been deciphered. Therefore, this aspect seeks more attention from the researchers to unveil the mechanism of salt-stress alleviation by AMF.

Conclusion

In conclusion, the results confirm that AMF alleviate the detrimental effect of salinity through improved water and nutrient uptake especially P through AM hyphae and colonized roots of plants. This suggests that phosphatases might be involved in P trans-fer and uptake mechanism which leads to higher P from saline soil. Exposure of mycorrhizal inoculated plants to salinity resulted in sig-nificant induction of antioxidative enzyme activities such as SOD, POX and CAT that could help the plants pro-tect themselves from the oxidative effects of the ROS. This cumulative effect increases the physiological performance and tolerance of the mycorrhizal plants under saline condi-tion.

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