

SALINITY STRESS IN PLANTS: CAN ARBUSCULAR MYCORRHIZAL FUNGI BE A PROMISING SOLUTION?

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Abstract. Abiotic stress is increasing, which needs dire attention to tackle this issue. Recently, microbial application emerged as a promising solution to mitigate adversities of abiotic stresses. Arbuscular mycorrhizal fungi (AMF) form a symbiotic association with plants, and it can counter the toxic impacts of salinity. Salinity stress induces oxidative, ionic, and osmotic stresses, which impair plant physiological, metabolic, and biochemical functioning, membrane stability, nutrients and water uptake, resulting in substantial growth and yield losses. AMF improves membrane stability, water uptake, and nutrients and decreases the production of reactive oxygen species. Moreover, AMF also improves photosynthetic efficiency, protects photosynthetic apparatus and gene expression, and maintains a better osmolyte and hormonal balance, leading to better plant performance in saline conditions. In addition, AMF also participates in gene expression involved in the extrusion of sodium (Na) to soil solution and potassium (K) acquisition. It also affects the expression of tonoplast aquaporins, which improve the water uptake and plant water status under saline conditions. Thus, we discussed the mechanisms induced by AMF to enhance salinity tolerance plants. Different research gaps that must be fulfilled in future studies are also discussed in the present review. The present review provides insights to improve crop production by using AMF under increasing intensity of salinity and climate change.

Keywords: *antioxidants, aquaporins, gene expression, nutrient uptake, photosynthesis*

Introduction

Soil salinity (SS) is a serious global threat that affects 1100 Mha globally (FAO, 2023). Soil salinity negatively affects plant growth by inducing osmotic, oxidative and ionic toxicity (Munns, 2005). The extent of soil salinity is soaring owing to poor drainage, climate change and global warming (Hassani et al., 2021). The global population is continuously increasing, which requires a substantial increase in food production in saline soils (Chang et al., 2019). Salinity significantly limits crop production across the globe, particularly in semi-arid and arid regions (Munns and Gilliam, 2015). Generally, SS reduces water availability by decreasing soil water potential, which decreases water availability, leading to serious growth reduction (Dastogeer et al., 2020). Saline conditions also decrease nutrient and water uptake and cause ionic and nutrient imbalance, resulting in significant yield losses (Dastogeer et al., 2020). Moreover, SS also decreases water absorption and increases ethylene production, which negatively affects cell growth and metabolism and decreases plant growth (Dastogeer et al., 2020). In addition, high salt concentration increases reactive oxygen species (ROS) production, which causes oxidation of proteins, membranes and major molecules (*Fig. 1*) (Hanin et al., 2016).

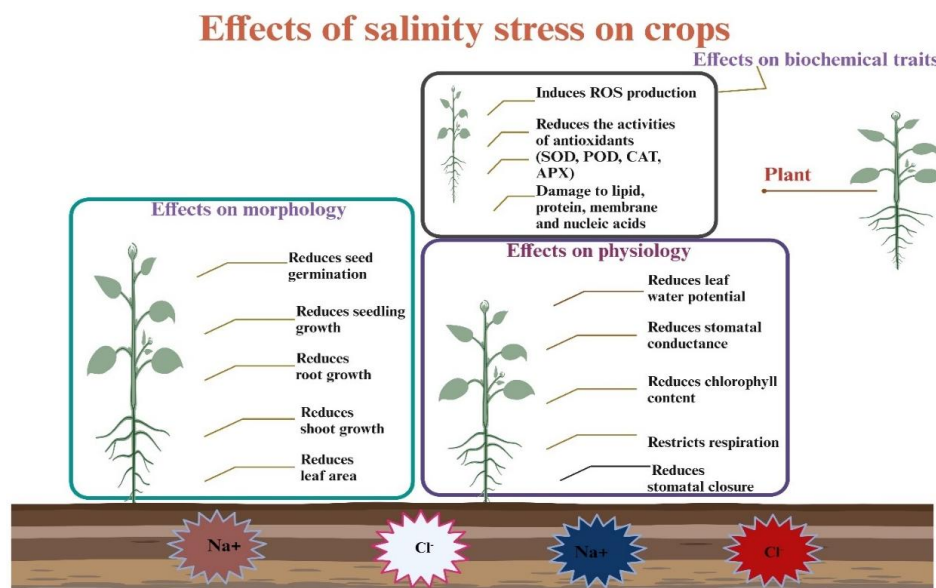


Figure 1. Salt stress reduces growth, and shoot growth. Salinity stress decreases rate of photosynthesis and antioxidant activities. This figure was made with Biorender.com

The rapid industrialization and urbanization are shrinking the global cultivated area and decreasing the crop productivity. The changing climate conditions are leading to more global warming and more drought that is negatively affecting crop productivity and international security (Kastner et al., 2021). Thus, it is mandatory to develop the appropriate measures to improve crop production under saline soils to ensure global food security (Finucane et al., 2020). Globally, different methods are being employed for mitigating the toxic impacts of SS. Among these methods, the use of AMF has shown promising results in reducing the toxicity of salinity (Spatafora et al., 2016). The survival of AMF depends on its symbiotic association with the roots of the plants as they acquire nutrients and carbohydrates from plants. In return, they substantially increase the water and nutrient absorption by plant roots by increasing root surface area (Goddard et al., 2021). The AMF association with plant roots improves soil quality and resistance to abiotic stresses (Giovannini et al., 2020; Klinsukon et al., 2021). AMF increases nutrient and water uptake, osmolyte accumulation, photosynthetic efficiency and antioxidant activities, thereby ameliorating toxicity of salinity (Hashem et al., 2018; Porcel et al., 2015).

It is also documented that AMF secrete enzymes and increases nutrient uptake, which boosts plant growth (Riaz et al., 2021; Taghvaei et al., 2023). Besides this, AMF also releases different hormones, which help to develop the extensive root system and result in better nutrient and water uptake. In addition, plants also provide sugar to AMF for their energy requirements and survival (Chanclud and Morel, 2016). AMF inoculation also improves chlorophyll synthesis and leaf water status and reduces ROS production through an increase in antioxidant efficacy and synthesis of osmolytes (Fernández et al., 2022; Ngosong et al., 2022). Therefore, in the current review, we elaborated on the diverse mechanisms mediated by AFM to counter salinity stress. We also shed light on different research gaps and indicated future research gaps to improve crop production by using AMF.

Plant responses to salinity stress

Soil salinity causes a significant reduction in plant growth (*Fig. 1, Table 1*). However, the reduction in growth rate largely depends on plant species, stage of plant life and salt concentration (Yadav et al., 2019). Salinity stress also reduces the expression of different genes involved in cell cycle progression, which decreases the number of cells in the meristem and leads to growth inhibition. Salinity stress also causes cell shrinkage, and it also reduces cell division and root and shoots growth. This response in growth reduction is due to changes in plant water relations owing to oxidative stress (*Table 1*). The onset of osmotic stress reduces water absorption, leading to a decrease in plant growth and yield (Denaxa et al., 2022; Petretto et al., 2019).

SS impairs photosynthesis by reducing chlorophyll synthesis, stomata closure, altering enzyme activity, reducing CO₂ intake and damaging the photosynthetic apparatus (Qin et al., 2020; Zahra et al., 2022) (*Table 1*). Salinity-induced ROS production increases oxidation and degradation of chlorophyll, which decreases chlorophyll contents under saline conditions (Taïbi et al., 2016). Besides this, excessive ROS production also inhibits the electron transport chain, which leads to Pseudo-cyclic electron transport (Zahra et al., 2021). In addition, saline conditions also disturb the ultra-structure of chloroplast by inducing the accumulation of starch and swelling of thylakoid (Goussi et al., 2018). Soil salinity also decreases nutrient uptake owing to competition between nutrients Na⁺ and Cl⁻ ions (Berry and Wallace, 1981).

These interactions often cause a deficiency of Ca²⁺, K⁺, and Mg²⁺ (Balasubramaniam et al., 2023). Salinity stress increases Cl uptake and accumulation, which decreases N uptake by plants owing to the antagonism of Cl⁻/NO₃³⁻ (Balasubramaniam et al., 2023). Potassium (K) is also a vital nutrient needed for water relations and protein synthesis, and SS significantly decreases K uptake.

Salinity-induced increase in Na⁺ concentration decreases the concentration of K and Ca²⁺ owing to the fact that Na⁺ competes with K⁺ at the uptake sites of the root (Grattan and Grieve, 1999). The increase in Na accumulation also negatively affects the plant water relations owing to the fact that the SS, the osmotic potential of cells becomes more negative, which drives water out of the cells and causes a reduction in cell turgor pressure (Betzen et al., 2019). Further, salinity also caused a decrease in RWC, water uptake, and transpiration rates (Chaudhuri and Choudhuri, 1997). It also decreases protein synthesis and impairs cell signaling and energy metabolism (Munns and Gilliam, 2015).

Plants accumulate different osmolytes that play a significant role in mitigating adversities of salinity stress (*Fig. 2*). These osmolytes maintain the osmotic adjustment and detoxify ROS, which protects the cellular membranes and the cellular metabolism (Sharma et al., 2019). Plants synthesize glycine-betaine (GB) in chloroplast, and it protects the thylakoid membranes from oxidative damage, thus maintaining the plant's photosynthetic efficiency (Alasvandyari and Mahdavi, 2018; Zhu et al., 2022). Proline is an important osmolyte, and its concentration significantly increases under salinity conditions. It helps the plants maintain the cell turgor. The increased proline concentration substantially improves salt tolerance (Abdelhamid et al., 2013; Nguyen et al., 2013). Likewise, exogenously applied proline also mitigates the adverse impacts of salinity (Jamil et al., 2018). Moreover, proline accumulation also increases antioxidant activities and up-regulates the production of stress-protective dehydrin proteins, which improves salinity tolerance (Balasubramaniam et al., 2023). Plants also accumulate different sugars to counter the toxic impacts of salinity. For instance, trehalose (Tre)

improves water absorption, protects the cellular membrane, and improves photosynthetic efficiency under SS (Nawaz et al., 2022).

Table 1. *Effect of salinity stress on plant growth, physiological and biochemical processes under salinity stress*

Plant species	Salinity stress	Study type	Major effects	References
Rice	0.3, 2, 4, 6, 8, 10 and 12 dS m ⁻¹)	Hydroponic culture	Salinity stress reduced root and shoot growth and biomass production	(Ikbal et al., 2024)
Wheat	0, 100, and 200 mol/L	Hydroponic culture	Salinity stress decreased chlorophyll content, increased Na ⁺ content in leaves and reduced shoot length and root length	(Saddiq et al., 2021)
Wheat	100 and 200 mM NaCl	Pot experiment	Salinity stress decreased N uptake, RWC, leaf area and increased Na uptake	(Lekshmy et al., 2013)
Maize	100 mM	Pot experiment	Salinity stress reduced germination, seedling growth and biomass production	(Zahra et al., 2020)
Barley	0, 100, 200 and 300 mM	Pot experiment	Salinity stress reduced dry weight, and photosynthetic rate	(Narimani et al., 2020)
Barley	100 mM	Hydroponic study	Salinity stress induced necrosis and chlorosis, and caused lipid peroxidation in barley genotype	(Zeeshan et al., 2020)
Sorghum	0, 50, 100, 200 mM	Pot experiment	Salinity stress decreased growth, germination and gas exchange of sorghum cultivars	(AL-Shoaibi, 2020)
Sorghum	3 and 12 dS m ⁻¹	Pot experiment	Salinity stress decreased antioxidant activities and proline synthesis	(Zamani et al., 2021)
Cotton	15 dS m ⁻¹	Pot experiment	Salinity stress reduces bolls production, fiber strength, fiber length, chlorophyll content, and relative water content in cotton	(Zafar et al., 2022)
Cotton	0, 120, 180, 240, 300, and 360 mM	Pot experiment	Salinity stress reduced biomass, root growth, and volume	(Yan et al., 2019)
Chickpea	0, 50 and 100 mM	Pot experiment	Salinity stress decreased germination percentage, stem diameter, plant height and fresh weight in chickpea	(Ceritoğlu et al., 2020)
Cabbage	75 and 150 mM	Greenhouse experiment	Salinity stress enhanced electrolyte leakage, hydrogen peroxide (H ₂ O ₂) content in cabbage. Salinity stress also decreased stomatal conductance, intercellular CO ₂ content (Ci) and transpiration rate (Tr)	(Sahin et al., 2018)
Sunflower	50, 150 and 250 mM	Pot experiment	Salinity stress reduced dry matter and water content. Salinity stress also reduced the activity of glutathione reductase (GR) and ascorbate peroxidase (APX)	(Taher et al., 2018)

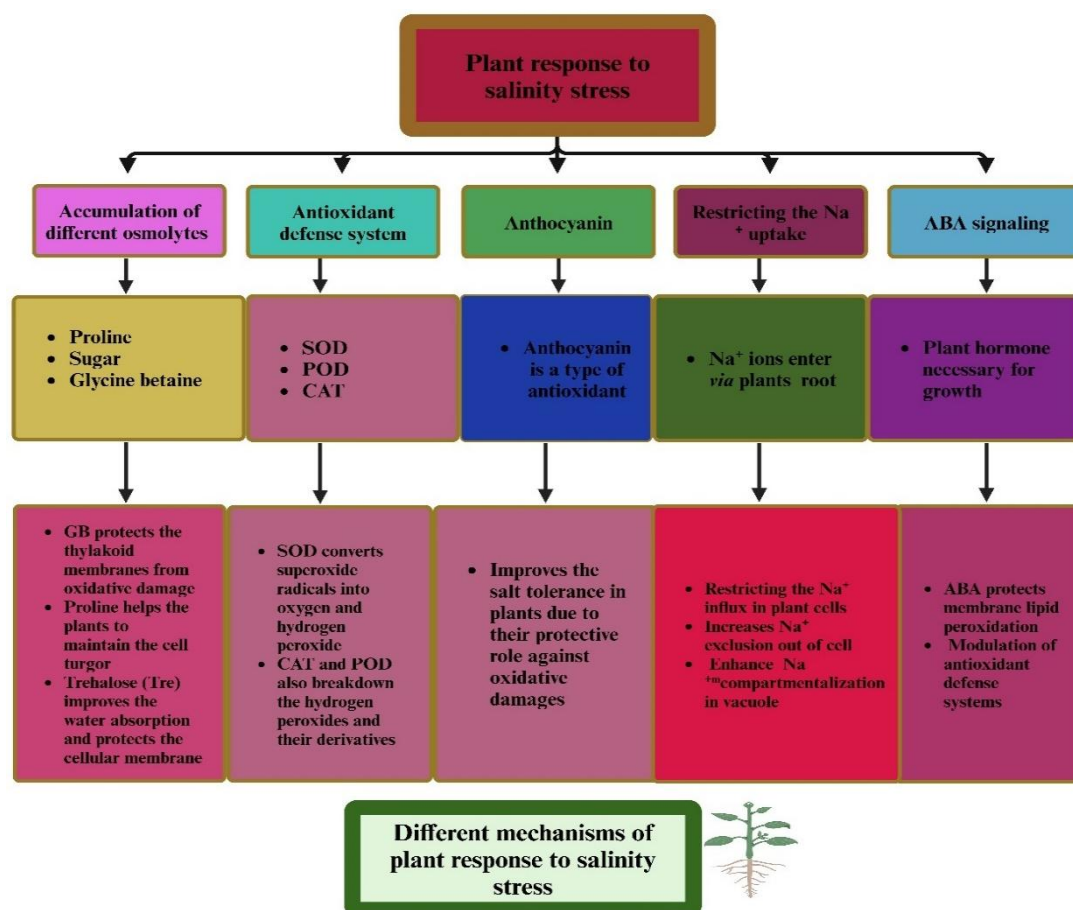


Figure 2. Responses of plants to salinity stress. This Figure was made with BioRender.com

Salinity stress induces excessive ROS production, which causes damage to cellular structure and causes irreversible metabolic dysfunction. The plant has excellent antioxidant defense systems that scavenge or quench these ROS (Azeem et al., 2023). SOD is an important antioxidant that works as the first defense line to eliminate superoxide radicals by converting superoxide radicals into oxygen and hydrogen peroxide. Further, CAT and POD also break down the hydrogen peroxides and their derivatives (Qamer et al., 2021; Sarker and Oba, 2020).

The concentration of malondialdehyde (MDA) also increases under SS. However, salt-tolerant genotypes showed less MDA production (Hussain et al., 2022). Anthocyanin is also an important antioxidant, and it appreciably improved the salt tolerance in plants due to its protective role against oxidative damage (Van Oosten et al., 2013).

Background of AMF

AMF has a promising ability to survive under extreme climatic conditions. Since fungi are parasites or symbiotes, there is a complex relationship between plant roots and fungi (Panstruga et al., 2023; Tang et al., 2023). The cell wall of fungi contains chitin, which is considered a flexible polysaccharide. In fungal hyphae, different auxiliary cell walls are present, which contain large pores that allow the ribosome, mitochondria and

nuclei to pass (Tajuddin et al., 2023). Besides this, mycelium also possesses a multi-cellular structure. It forms a hypha when it matures. The mycelium of sugar spreads over a large area, which allows the roots to obtain phosphorus and minerals. In contrast, plants provide sugar to fungi (Sun et al., 2017). AMF also helps plants with water and nutrient absorption, and they also provide protection for plants (Spatafora et al., 2016). Apart from this, fungal mycelium also breaks down the soil organic matter, which releases nutrients for plants, while plants get carbohydrates and energy, and this relationship gets mutual benefits (Redecker et al., 2013). The fungal-mediated increase in nutrient absorption increases plant performance in stress conditions (Spatafora et al., 2016). It is also documented that AMF also shields the plants from disease and ensures better plant growth (Astapati and Nath, 2023; de Andrade et al., 2023; Woo et al., 2023).

Can AMF ensure agricultural sustainability?

To harness the natural ability of soil, it is compulsory to decrease the use of chemical inputs that are harmful to the environment (Li et al., 2023b; Liu et al., 2023). The plants and microbes work together; therefore, AMF can ensure the sustainability of agriculture (Díaz-Urbano et al., 2023). AMF is invaluable in mobilizing nutrients into a usable form, which ensures better plant growth (Li et al., 2023a). The mycelium produced by AMF is invaluable because AMF proliferation improves soil quality and structure stability, which encourages plant growth. Utilizing the AMF association can ensure better productivity by reducing the use of insecticides and fertilizers (Janowski and Leski, 2022). Legume crops improve soil health and microbial growth and increase nutrient availability, leading to better plant growth (Bhupenchandra et al., 2022). Soil fungi have different functions, as they decompose organic matter and provide nutrients to plants. AMF plays a vital part in ecology owing to its role in nutrient cycling and the production of biomass by microbes (Mathur & Jajoo, 2020). Thus, the germ plant of plants must be tailored for specific environments (Etikala et al., 2021), and this will allow the plants to get essential nutrients for plant growth, resulting in a substantial increase in tolerance against stress conditions (Lin et al., 2020).

Role of AMF to mitigate salinity stress

Soil salinization poses a serious threat to crop production. AMF possesses a tremendous ability to mitigate adversities of salinity, and the mechanism of AMF to induce salt tolerance is described below.

AMF improves plant photosynthetic efficiency under saline conditions

Salinity stress negatively affects plant physiological processes and hinders photosynthesis, which reduces plant growth and development (Sheng et al., 2008). AMF can mitigate the toxic effects of SS photosynthesis by increasing leaf area, stomata conductance and CO₂ assimilation (Chen et al., 2017) (*Fig. 3*). The concentration of chlorophyll contents is significantly decreased under saline conditions due to an increase in chlorophyll degradation because of an increase in chlorophyllase activity (Murkute et al., 2006; Bargaz et al., 2016). The study findings of Aroca et al. (2013) indicated that AMF enhances chlorophyll synthesis and increases plant growth

(Zuccarini and Okurowska, 2008). AMF fungi trigger chlorophyll synthesis by an increase in Mg^{2+} uptake (Sheng et al., 2008). The recent discoveries also showed that AMF increases RuBisCO activity (Hashem et al., 2015). AMF counteracts the antagonistic impacts of Na^+ on Mg^{2+} , which ensures better plant performance. Salinity stress also negatively affects the reaction center of PS-II and the electron transport chain; however, these negative effects can be minimized by AMF symbiosis (Sheng et al., 2008).

AMF protects cellular membranes and maintains water relations to counter toxic effects of salinity

The cell membrane controls the transport of ions, and salinity stress significantly damages the cellular membranes. AMF reduces electrolyte leakage, which leads to a reduction in the loss of important solutes (Garg and Manchanda, 2008). Feng et al. (2002) noted that AMF decreased EL due to increased P uptake and activity activities. Likewise, Yang et al. (2014) witnessed that AMF inoculation in *Malus hupehensis* enhanced the turgidity of the leaf and lowered the osmotic potential. Further, AMF inoculation also maintains higher water contents by increasing water uptake (Jahromi et al., 2008; Jiang et al., 2017). AMF also maintains lower osmotic potential, possibly due to an increase in solute accumulation, resulting in improved osmotic adjustments and turgor potential (Al-Garni, 2006). Additionally, AMF allows the host plants to use the water more efficiently and maintain a lower intercellular CO_2 concentration, which in turn improves the gas exchange capacity and subsequent assimilate production and plant growth (Graham and Syvertsen, 1984).

AMF improves nitrogen fixation to ensure better plant growth under saline conditions

It has been documented that AMF increases root nodulation and N fixation in legumes, and different authors have reported that AMF increases N fixation under saline conditions, which ensures better plant growth and seedling vigor (Evelin et al., 2009). For instance, Garg and Manchanda (2008) pigeon pea plants treated with *Glomus mosseae* showed a substantial improvement in dry mass production and N fixation. Further, nodules of legume plants are vulnerable to salinity, and their density significantly decreases under saline conditions (Garg and Manchanda, 2008). Salinity stress triggers premature nodule senescence, which induces the formation of green pigments in hemoglobin, leading to a decrease in N fixation (Matamoros et al., 2010). AMF decreases premature nodule senescence (Rabie and Almadini, 2005) and increases N fixation and nitrogenase activities (Founoune et al., 2002).

AMF improves osmolyte accumulation and maintain hormonal balance to counter deleterious impacts of salinity

Osmolyte accumulation is an important strategy used by plants to mitigate SS (Kaur and Asthir, 2015). For instance, some authors found that AMF inoculation increased proline synthesis under saline soils. The inoculation with AMF increases gene expression encoding P5CS involved in proline biosynthesis. It increases the activity of P5CS enzymes, which increases the proline synthesis (Fig. 3). Besides this, AMF also increases the activity of glutamate dehydrogenase, which is precursor of proline and they also cause the inactivation of proline dehydrogenase, which catalyzes the proline

degradation therefore, all these reasons increasing proline synthesis (Abo-Doma et al., 2011). Apart from this proline is also a stress marker and AMF inoculation plants accumulate more proline (Sannazzaro et al., 2007).

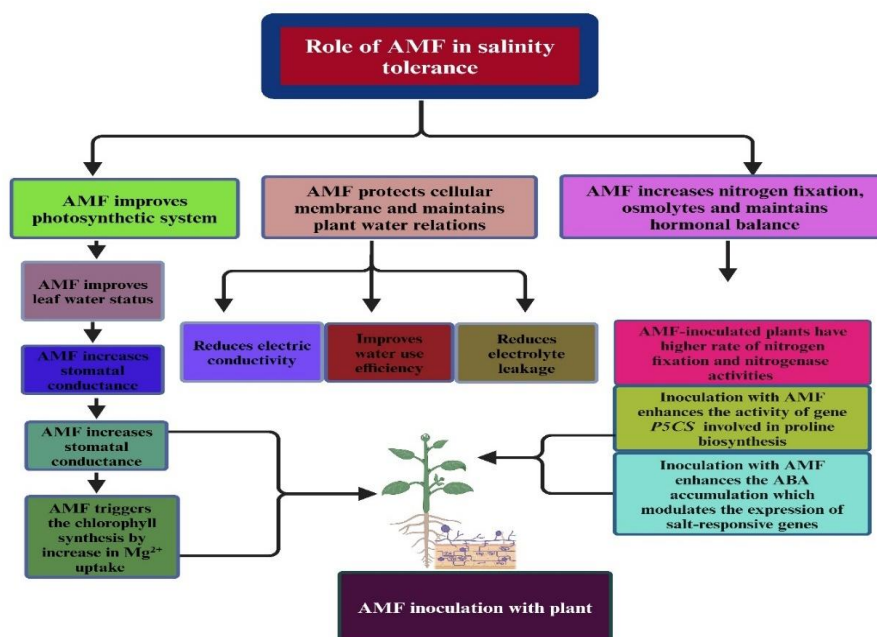


Figure 3. AMF improves salinity tolerance in plants via improving photosynthesis, increasing osmolytes, maintenance of plant water relation, and increasing nitrogen fixation. This Figure was made with BioRender.com

Salinity stress increases the accumulation of Tre which can be further increased by AMF inoculation (Garg and Pandey, 2016). The increase in synthesis of Tre substantially improves the salinity stress. The high concentration of Tre in AMF inoculated plants is linked with enhanced activity of TPS and TPP enzymes (Garg and Pandey, 2016). AMF also increases synthesis of acetic, citric, fumaric, malic, and oxalic acids, and decrease in concentration of formic acid and succinic acid decreased (Sheng et al., 2011). AMF protect enzymes involved in synthesis of organic acids which help to counteract SS (Talaat and Shawky, 2011) (Table 2).

AMF-inoculated plants had a high ratio of Spd + Spm:Put as compared to non-inoculated plants (Evelin et al., 2013). Moreover, the mechanism of AMF to induce polyamine synthesis has not been discovered. Thus, more investigations are needed on polyamine metabolism. Garg and Bharti (2018) witnessed that salt-tolerant chickpea cultivars accumulate more sugars than salt-sensitive cultivars, which indicates that an increase in the accumulation of sugars can enhance salt tolerance. The AMF-induced increase in α - and β -amylases activity induces rapid hydrolysis of starch in glucose, which results in better accumulation of sugars in AMF-inoculated plants (Garg and Bharti, 2018). The exogenous application of salicylic acid in combination with AMF improves salt tolerance by decreasing lipid peroxidation and increasing proline, soluble sugars and K accumulation while decreasing lipid peroxidation (Shekoofeh et al., 2012). Hashem et al. (2018) found that the concentration of jasmonic acid (JA) was increased under saline conditions, which was further boosted by the presence of *Rhizophagus*

irregularis in *Cucumis sativus* seedlings. This indicated that JS plays a critical role in imparting salinity tolerance. In another study, Aroca et al. (2013) found an increase in ABA synthesis in *Lotus glaber* plants inoculated with *Rhizophagus regularis* and *Lotus glaber* (Sannazzaro et al., 2007). The production of ABA is increased in plants under saline conditions, which is linked with soil or leaf water potential; this indicates the ABA production in plants resulting from water deficiency instead of direct impact of salts (Javid et al., 2011).

Table 2. Effects of AMF oxidative stress markers and antioxidant activities under salinity stress

Plant species	Salinity stress	Fungal species	Major effects	References
<i>Stevia rebaudiana</i> Bertoni	80 mM of NaCl	AMF consortium (MC) or <i>Rhizophagus irregularis</i> (Ri)	AMF enhanced growth and antioxidant activities and decreased oxidative damages	(Janah et al., 2021)
Pepper	0, 25 and 50 mM NaCl	<i>Arbuscular mycorrhizal fungi (Glomus irradicans 10% w/w)</i>	AMF inoculation increased antioxidant activities	(Hegazi et al., 2017)
<i>Gleditsia sinensis</i>	0, 50, 100, and 150-mM NaCl	AMF	AMF increased activities of CAT and POD	(Wang et al., 2022)
Cowpea	200 mM NaCl		AMF enhanced the activity of CAT, POD and SOD	(Hashem Abeer et al., 2015)
<i>Cucumis sativus</i> L.			AMF enhanced the salinity tolerance by increasing the activity of SOD, POD, and APX and reduced the electrolyte leakage	
Soybean	100, 200 and 300 mM NaCl	<i>Unneliformis mosseae</i> (syn. <i>Glomus mosseae</i>)	AMF inoculation reduced ROS production	(Hashem et al., 2019)
Tomato	0, 0.63, 5, and 10 dSm ⁻¹ NaCl	<i>Glomus intraradices</i>	AMF reduced ROS production, and lowered H ₂ O ₂ and lipid peroxidation	(Hajiboland et al., 2010)
Wheat	4.7 and 9.4 dS m ⁻¹ NaCl		AMF reduced H ₂ O ₂ , electrolytes leakage (EL) and MDA concentration in salt stressed plants and decreased oxidative damage by eliminating ROS and enhanced activities of SOD, POD and CAT	(Talaat and Shawky, 2014a)
Cotton	50 mM·L ⁻¹ NaCl	<i>Paraglomus occultum</i>	AMF inoculation increased salt tolerance by increasing SOD, POD and CAT	(Zhang et al., 2024)
Sorghum	150 and 300 mM	<i>Funneliformis mosseae</i> and <i>Rhizophagus intraradices</i>	AMF-treated plants showed enhanced activity of CAT, APX and SOD while MDA and H ₂ O ₂ concentration was reduced	
Sweet Basil	0 and 150 mM		AMF decreased the concentration of MDA and H ₂ O ₂ and enhanced APX, and CAT activities	(Yilmaz et al., 2023)

AMF improves antioxidant activities to counter deleterious impacts of salinity

Salinity stress induces oxidative stress by disturbing the equilibrium between the production of ROS and the scavenging of antioxidants (Gill and Tuteja, 2010). Excessive ROS production upsets cellular functioning by attacking the lipids, DNA and proteins (Zhang et al., 2018). AMF improves the expression of different antioxidant enzymes involved in the protection of plants from ROS (Rai et al., 2011). Different studies have documented that AMF symbiosis mitigates salinity toxicity in plants by increasing antioxidant activities (He et al., 2007). SOD is an important enzyme that plays a critical role in protecting the electron transport system by scavenging the free radicals of superoxide. The AMF-mediated increase in SOD has been reported in different crops like cotton, sorghum and cowpea growing in saline conditions (Wu et al., 2016). The increase in SOD activity by AMF could be attributed to an increase in Zn, Mg, copper and Fe uptake, which are co-factors of SOD iso-enzymes (Kohler et al., 2009). It is also documented that AMF mediated the breakdown of H₂O₂ by increasing APX and CAT activity, therefore protecting the plants from oxidative damage (Abd_Allah et al., 2018). The study findings of Alguacil et al. (2003) showed an increase in APX, CAT and SOD in *Olea europaea* and *Retama sphaerocarpa* plants treated with AMF. Moreover, AMF also improves the accumulation of polyphenols, which contribute to increasing plant growth under saline conditions (Engel et al., 2016). Nonetheless, the role of AMF in the synthesis of non-enzymatic antioxidants (carotenoids, tocopherols, and ascorbic acid) has not been studied; therefore, in-depth research is needed.

AMF maintains nutrient homeostasis to country salinity stress

Salinity stress disturbs nutrient homeostasis and decreases the uptake of essential nutrients, which causes a significant reduction in plant growth (Hajiboland et al., 2010; Zuccarini and Okurowska, 2008). The increase in plant growth under saline conditions following AMF inoculation is linked with the improved acquisition of nutrients, particularly P (Planchette and Duponnois, 2005). The extensive fungal hyphae network ensures the better uptake of nutrients, which ensures better nutrient availability of plants, and this phenomenon is well echoed in the literature (Shokri and Maadi, 2009). The high concentration of P in AMF-inoculated plants improves O nutrition, which ensures better growth and antioxidant activities (Garg and Manchanda, 2008). The research findings indicate AMF inoculation resulted in more accumulation of N in shoots of *Sesbania grandiflora* and *S. aegyptiaca* plants as compared to non-inoculated plants (Giri and Mukerji, 2004).

Calcium works as a second messenger, and its concentration is significantly increased under saline conditions with transduced signals. Different studies showed that AMF association increased uptake as well as concentration of Ca²⁺ in diverse plants like bananas and lettuce as compared to non-inoculated plants (Yano-Melo et al., 2003). Further, AMF also improves the selective absorption of Ca²⁺ over Na⁺ and helps to sustain the low Na/K ratio. In another study, Elhindi et al. (2017) noted that AMF inoculation substantially increases the Ca²⁺ concentration and maintains a higher Ca²⁺/Na⁺ ratio in *Ocimum basilicum*. The recent findings of Cui et al. (2019) showed that Ca worked as a modulator in AMF colonization, and AMF inoculation increases Ca²⁺ absorption by host plants. Further, AMF inoculation also helps to sustain a low Na/K ratio by increasing K uptake and decreasing Na uptake (Kadian et al., 2013). In another

study, Namdari et al. (2017) noted that AMF inoculation increases K uptake and decreases the Na^+/K^+ and $\text{Na}^+/\text{Ca}^{2+}$ ratios in AMF-inoculated *Medicago sativa*. The plants inoculated with AMF showed selective K and Ca absorption over Na, thus sustaining a lower Na/K ratio (Ahmad et al., 2014). The maintenance of a lower Na/K ratio is considered an excellent strategy used by plants to mitigate the adverse impacts of salinity (Wu et al., 2010).

AMF improves plant performance under saline conditions

Salinity stress induces oxidative, ionic and osmotic stresses, which cause significant reduction in plant growth and pose a serious threat to crop productivity. AMF improves plant performance under salinity stress conditions (Table 3).

Table 3. Effects of AMF on plant physiological and biochemical functioning under salinity stress

Plant species	Salinity stress	Fungal species	Major effects	References
Wheat	200 mM NaCl	<i>Glomus</i> spp.	AMF increased the uptake of micronutrients like zinc (Zn) and iron (Fe) and also regulated decrease in Na and increase in K. AMF increase the carotenoids content in wheat	(Huang et al., 2023)
Hemp	0 100, and 200 mM NaCl	<i>Funneliformis mosseae</i>	AMF enhanced photosynthetic activity and content of secondary metabolites like flavonoid and phenol	(Yuan et al., 2024)
Rice	150 mM NaCl	<i>Glomus etunicatum</i> (GE)	AMF inoculation-maintained yield trait (100-grain weight) and regulate anthocyanins enrichment in in grains	(Tisarum et al., 2020)
Wheat	0, 50, 100, and 150 mM NaCl	<i>Glomus mosseae</i>	AMF increased plant height, shoot fresh biomass, root fresh biomass and enzymatic activities under salinity stress	(Ndiate et al., 2022)
Maize	0–5 g NaCl kg ⁻¹ soil	<i>Rhizoglomus irregulare</i>	AMF inoculation improved biomass and nutritional status of maize	(Moreira et al., 2020)
Barley	Saline soil	AMF	AMF improved plant height, weight of 1000-grain, grain yield and uptake of nitrogen (N), phosphorous (N) and potassium (K) in barley	(Masrahi et al., 2023)
Sorghum	Saline soil	<i>Funneliformis mosseae</i>	AMF increased P content, P uptake, and K^+/Na^+ ratio	(Chandra et al., 2022)
Cotton	100 mM L ⁻¹ NaCl	<i>Funneliformis mosseae</i> (GM)	AMF inoculation increased biomass, plant height, chlorophyll content and photosynthetic levels	(Peng et al., 2024)
Maize	Saline soil (5.74 dS/m)	<i>Glomus</i> species	AMF improved chlorophyll content, stomatal conductance and gas exchange in maize	(Huang et al., 2024)
Flax	0, 50, 100, and 150 mM NaCl	<i>Claroideoglomus etunicatum</i>	AMF increased total chlorophyll content, seed and stem fiber yield	(Kakabouki et al., 2023)
Sunflower	0, 0.5, 1 and 1.5 g kg ⁻¹ NaCl		AMF increased total dry weight and water use efficiency	(Zhou et al., 2020)

The recent findings of Afrangan et al. (2023) showed a regulatory role of *Glomus versiforme* and *Micrococcus yunnanensis* in maintaining the ionic and redox homeostasis in *Brassica napus* L. crops. Besides improving crop productivity, AMF can be applied to mitigate the adverse impacts of salinity on plants (Ait-El-Mokhtar et al., 2019). Different studies revealed that AMF increases the plant growth and yield of plants subjected to salinity stress. AMF symbiosis is beneficial for saline conditions, and it can reduce the harmful impacts of salinity on photosynthesis (Ait-El-Mokhtar et al., 2019; Elhindi et al., 2017). AMF inoculation significantly increases the photosynthetic efficiency, chlorophyll synthesis and WUE, which ensures better plant performance under saline conditions (Borde et al., 2010). *Allium sativum* plants treated with AMF showed better leaf area, fresh and dry biomass production (Wang et al., 2018).

AMF inoculation also promotes the synthesis of growth hormones (CK), which ensures higher photosynthetic efficiency and subsequent plant growth (Talaat and Shawky, 2014b). Apart from this, a mediated increase in plants is also associated with an increase in polyamine synthesis. For instance, AMF inoculation increased the strigolactone levels, which mitigated the adverse impacts of salinity and improved plant growth (Abdel Latif and Chaoxing, 2014). Further, AMF inoculation also reduces oxidative damage and increases the synthesis of organic acids and osmolytes, which mitigates the toxic effects of salinity and ensures better plant growth (Elhindi et al., 2017). AMF also modifies the plant's physiological and morphological properties, which help to counter the toxic effects of salinity (Ait-El-Mokhtar et al., 2019). Moreover, AMF also promotes the survival of plants under saline conditions by increasing the uptake of nutrients and water and promoting root development (Diagne et al., 2020; Lutts and Lefèvre, 2015). Additionally, AMF also aids in increasing the uptake of N and PK and up-grade the synthesis of vitamins, which ensures better plant growth (Zheng et al., 2022).

Conclusion and future prospects

It is clear from the above discussion that salinity stress reduces plant growth by disturbing membrane stability, nutrient and water uptake, antioxidant activities, hormonal balance, and nutrient homeostasis. AMF regulates plant growth under saline conditions by improving nutrient homeostasis, hormonal balance, nutrient and water uptake, antioxidant activities, and membrane stability. Further, AMF also improves gene expression and protects the plants from salinity-induced oxidative and ionic damages, which ensure better plant growth. Despite the recent progress in using the AMF to mitigate adversities of salinity, there are many unanswered questions. For instance, the role of AMF on nutrient uptake channels, signaling, and transport systems must be explored. Likewise, the effect of AMF on germination mechanisms is not yet understood; therefore, it is essential to determine its impact on germination mechanisms. The main focus of research is to identify gene expression and how gene expression impacts the growth of AMF, nutrients, and water uptake under saline conditions. Further, more research is also needed to explore the interactions of AMF and nitrogen-fixing bacteria under saline conditions. The identification of targeted genes by using biotechnology could also be an area of fascinating research to induce salt tolerance in plants. The identification of diverse genes involved in osmolyte synthesis and antioxidant activities will provide a molecular basis of AMF to induce salt tolerance

in plants. In addition, there is also a need to explore the transporter systems involved in the localization of nutrients in plants and host plants. In the literature, there are limited studies available about the impact of AMF on hormone synthesis under saline conditions. Thus, future research should investigate the impact of AMF on hormone interaction to counter adversities of salinity.

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