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Salinity tolerance by mycorrhiza and plant growth – A review

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Abstract
Modern agriculture is facing twin challenge of ensuring global food security and executing it in a sustainable manner. However, the rapidly expanding salinity stress in cultivable areas poses a major peril to crop yield. Salinization occurs naturally in arid and semiarid regions where evaporation is higher than rainfall. In India nearly 6.74 million ha area is occupied by salt-affected soils out of which 2.96 million ha are saline soils (including coastal) and 3.79 million ha are alkali soils (CSSRI, 2020). The higher salinity level poses adverse effects on soil properties and plant physiology (Rajput *et al*., 2015). In the natural environment, plants can be colonized both by external and internal microorganisms. The activity of soil microbial communities is considered the lifeline of global ecosystem productivity and sustainability. Arbuscular mycorrhizae (AM) are considered as bio-ameliorators of saline soils and could develop salinity tolerance in crop plants. AM fungi colonize plant root systems and modulate plant growth in various ways under abiotic stress. Indeed AMF improve physiological processes and general metabolic activities of the plant and helps in the mitigation of salinity. It enhance the production of Strigolactones in root system, Abscisic acid, Jasmonic acid, Glomalin and helps the roots in uptake of water and other nutrient under saline condition. Hence, the Mycorrhizal fungi offers a potential solution to combat salinity problem, helps to mitigate from the stress and increase crop growth under adverse condition.

Keywords: Salinity tolerance, agriculture, plant growth

Introduction

Salinization is one of the most important problems affecting agricultural land worldwide. Salinization occurs naturally in arid and semiarid regions where evaporation is higher than rainfall. The remediation of salt-affected lands and their management will go a long way in meeting the desired 57% increase in global food production by the year 2050. (Arora *et al.*, 2017). Salt- affected soils are an important ecological entity in the landscape of any arid and semi-arid region. In India nearly 6.74 million ha area is occupied by salt-affected soils out of which 2.96 million ha are saline soils (including coastal) and 3.79 million ha are alkali soils (CSSRI, 2020). Indiscriminate use of poor quality waters in the absence of proper soil water-crop management practices poses grave risks to soil health and environment. The extend and distribution of salt affected soils in India is tabulated below.

Table 1: Extent and distribution of salt affected soils in India

Sl. No.	State	Saline soils (Mha)	Alkali soils (Mha)	Coastal saline soil (Mha)	Total (Mha)
1	Andhra Pradesh	0	196609	77598	274207
2	A & N islands	0	0	77000	77000
3	Bihar	47301	105852	0	153153
4	Gujarat	1218255	541430	462315	2222000
5	Haryana	49157	183399	0	232556
6	J & K*	0	17500	0	17500
7	Karnataka	1307	148136	586	150029
8	Kerala	0	0	20000	20000
9	Maharashtra	177093	422670	6996	606759
10	Madhya Pradesh	0	139720	0	139720
11	Orissa	0	0	147138	147138
12	Punjab	0	151717	0	151717
13	Rajasthan	195571	179371	0	374942
14	Tamil Nadu	0	354784	13231	368015
15	Uttar Pradesh	21989	1346971	0	1368960
16	West Bengal	0	0	441272	441272
	Total	1710673	3788159	1246136	6744968

(CSSRI, 2020)

Salinity Status in India and the world

India has a mainland coastline of 6100 km, which is prone to salinity problems. Apart from that, regions away from the coast also experience salinity issues. In India, about 6.74 million ha of land are affected by salinity (CSSRI, 2020). The affected soils are divided into three major categories:

saline soils, alkali soils, and coastal soils. Gujarat has the highest amount (almost 71% of the total saline soils in India) of salt-affected soils (1.2 million ha). The states affected with saline soils are in the following order, Gujarat > Rajasthan > Maharashtra > Haryana > Bihar > Uttar Pradesh > Karnataka. The problem of alkali soils is mainly faced by Uttar Pradesh, which accounts for almost 36% of the total alkali soils in India.

Soil Salinity in Indian Scenario

In India, around 6.74 Mha (million hectares) of the land area is covered with salt-affected soils, which is expected to reach up to 20 Mha by 2050 (Sharma and Singh, 2015; Bhattacharyya *et al*.,2015) [36]. According to Mandal *et al*. (2009), the salt-affected soil map of India shows the following regions affected - the Indo-Gangetic plain region (Uttar Pradesh, Bihar, Haryana, Punjab, and West Bengal); the peninsular region (Western Maharashtra, Vidarbha, and Marathwara); the Krishna, Godavari and Penneru deltas (Andhra Pradesh); the arid and semi-arid regions (Gujarat and Rajasthan); the Mahanadi delta (Orissa) and the Cauvery delta (Tamil Nadu).

Salinity effect on plants

Plants exposed to soil salinity are negatively affected with reduction in establishment, growth, and yield. Salinity present in the soil accumulates in the root zone of plants which eventually damages the crop and reduction in plant yield. Salinity affects plant in three different aspects. The effect of different levels of salinity on plant physiology and yield is listed below in (Table. 2)

Table 2: Effects of different level of salinity on plant physiology and yield

Soil salinity class	ECe (dS m^{-1})[a]	Effect on crop plants
Non-saline	0-2	Salinity effects negligible
Slightly saline	2-4	Yields of sensitive crops may be restricted
Moderately saline	4-8	Yields of many crops are restricted
Strongly saline	8-16	Only tolerant crops yield satisfactorily
Very strongly saline	>16	Only a few very tolerant crops yield satisfactorily

(Selvakumar *et al*., 2013)

Role of micro-organism alleviating Soil Salinity and improves plant growth

Salinity affects plants physiologically and biochemically and it triggers production of various enzymes and hormones. In the natural environment, plants can be colonized both by external and internal microorganisms. To overcome this, the biotic approach ("Plant-microbe interaction") for overcoming salinity/sodicity problems has recently received considerable attention throughout the world. Recently, the use of arbuscular mycorrhizal (AM) fungi as a practical way to alleviate soil stresses on plant growth has received increased attention (Al-Karaki 2006; Sannazzaro and others 2006; Miransari and others 2007, 2008) [18]. AM fungi are important soil organisms, fundamental for plant nutrition and soil fertility (Smith and Read, 1997) and represent a living bridge for the translocation of nutrients from the soil to plant roots and of carbon from plant roots to the soil (Zhu and Miller, 2003).

Mycorrhiza

Mycorrhiza is a type of fungi that are mutualistic symbiotic associations between soil fungi and the roots of most plant species.

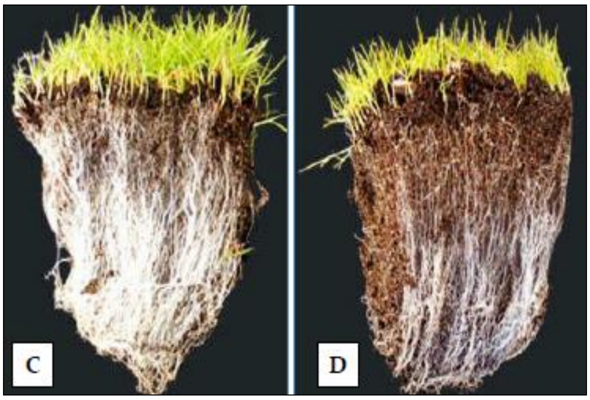


Fig 1: Plant showing with and without mycorrhizae

Occurrence of Mycorrhizosphere

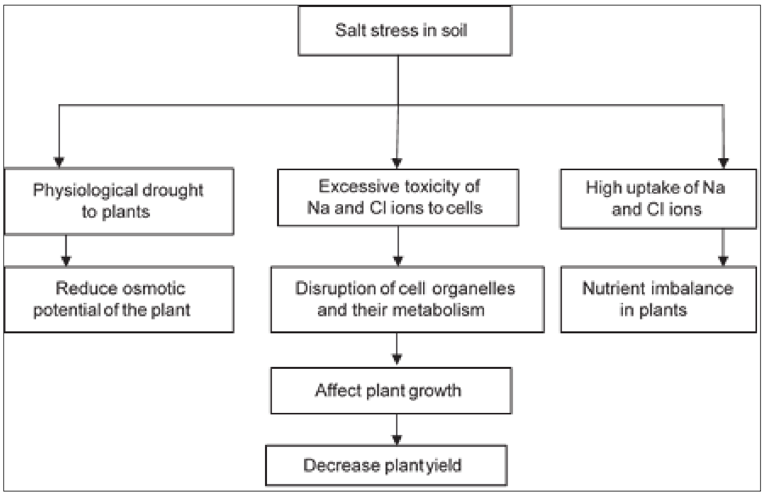
The natural role of mycorrhizosphere organisms may have been marginalized in intensive agriculture, since microbial communities in conventional farming systems have been modified due to tillage and high inputs of inorganic fertilizers, herbicides and pesticides. The roots of around 90% of higher plants form a symbiotic association with mycorrhizal fungi (Fig. 1). These fungi colonise roots, with the colonised root being termed a "mycorrhiza". The fungi benefit from the provision of plant carbon. The host plant may benefit in many ways, but the primary benefit is most often the ability to access inorganic nutrients from soil beyond the rhizosphere due to their transport into the root by hyphae of the fungi.

Arbuscular mycorrhizal fungi

Arbuscular mycorrhizal fungi (AMF) are ubiquitous among a wide array of soil microorganisms inhabiting the rhizosphere. It is being one of the most abundant obligate biotrophic organisms on earth that form a symbiotic association with plant roots (Paszkowski and Gutjahr, 2013). The association of AMF with plant root shows the ability to enhance plant growth by influencing plant hormones, nutrient accumulation, increasing the supply of phosphorus, water status, and affecting biochemical and physiological properties of plants growing in saline soils (Kumar *et al*., 2015; Selvakumar *et al*., 2018).

AMF forms intercellular hyphae, which develops vesicles that act as nutrient storage sites. In a study by Aliasgharzadeh *et al*. (2001), it was observed that some of the AMF species like *Glomus versiforme* and *Glomus etunicatum* were predominant in severe saline soil (162 dS m^{-1}). Kohler *et al*. (2009) found in their study that both species of AMF, *G. intraradices*, and *G. mosseae*, under moderately saline conditions, significantly stimulated the growth of lettuce plants (*Lactuca sativa*). Similarly, some other studies have been reported, which indicates that AMF when co-inoculated with certain bacterial species have an enhanced effect on growth and salt tolerance of some plant species (Lee *et al*., 2015; Hashem *et al*., 2016; Selvakumar *et al*., 2018).

Mechanism of Arbuscular mycorrhizal fungi alleviating soil salinity stress



Evelin *et al*. (2009) [13]

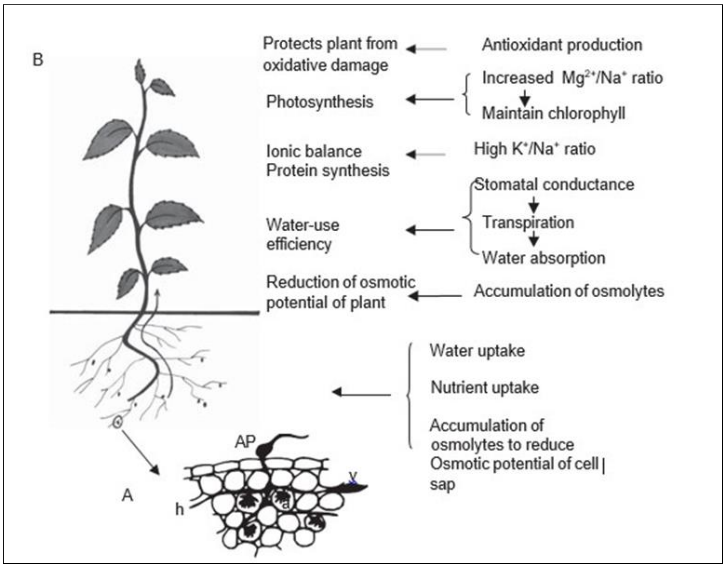
Fig 2: Primary effect of Salt Stress on plant system

There are several physiological, biochemical, and molecular approaches by which AM plants could alleviate salt stress these are:

1. increased accumulation of osmolytes;
2. control over ion uptake by roots, compartmentation of ions, and their transport into plant tissues to maintain ion homeostasis;
3. increased uptake of water and its distribution to plant tissues with the help of aquaporins;
4. enhanced production of antioxidants, which control oxidative damage;
5. selective build up or exclusion of salts;
6. managing adequate rate of photosynthesis for better plant growth,
7. maintaining membrane structure and integrity;
8. regulating phytohormone synthesis (Turkan and Demiral 2009);
9. Controlling ultrastructure damage (Evelin *et al*., 2013). These strategies seem to develop integrated responses in a concerted manner to improve plant salinity tolerance.

Arbuscular Mycorrhiza and Salt - Stress Amelioration

Several studies investigating the role of AMF in protection against salt stress have demonstrated that the symbiosis often results in increased nutrient uptake, accumulation of an osmo regulator, an increase in photosynthetic rate and water-use efficiency, suggesting that salt-stress alleviation by AMF results from a combination of nutritional, biochemical and physiological effects (Fig. 3).



Evelin *et al*. (2009) [13]

Fig 3: The intricate functioning of arbuscular mycorrhizal (AM) fungi in ameliorating salt stress in plants.

1. Plant growth and biomass

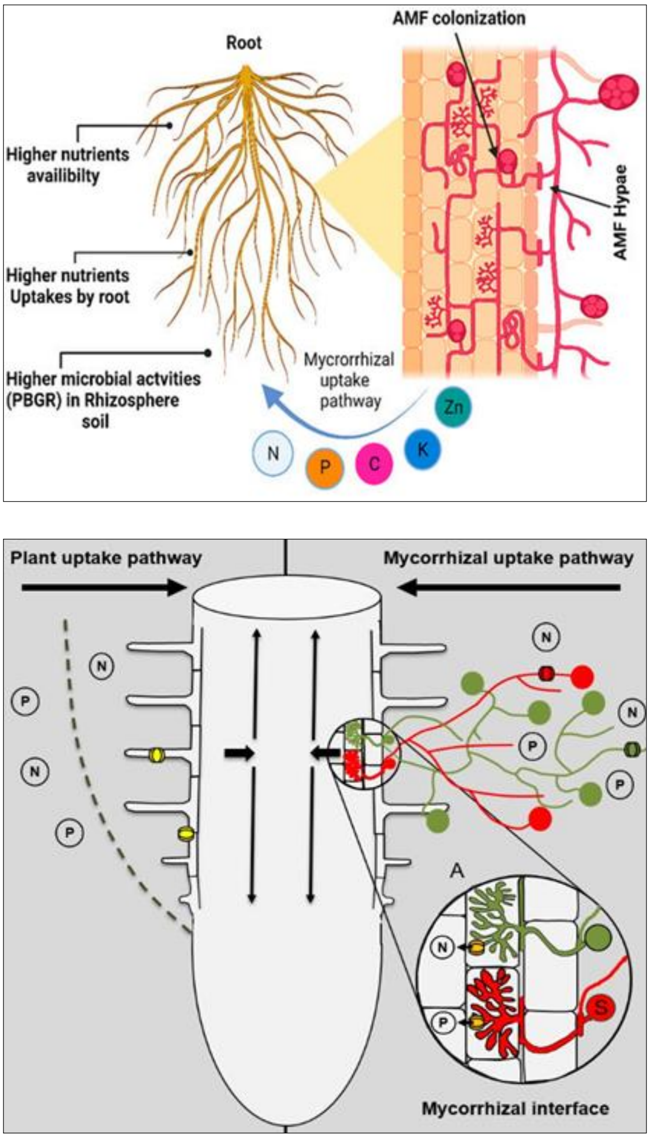
Under salt stress, plant growth and biomass suffered a setback. The reasons may be the non-availability of nutrients and the expenditure of energy to counteract the toxic effects of NaCl. However, mycorrhization was found to increase the fitness of the host plant by enhancing its growth and biomass. Al-Karaki (2000) [4] observed a higher shoot and root dry weight, fresh fruit yield, fruit weight and fruit number in a mycorrhizal tomato plant than in a non-mycorrhizal tomato plant.

2. Pathways for Nutrient uptake by Mycorrhizal roots

The arbuscular mycorrhizal (AM) symbiosis plays a key role for the nutrient uptake of more than 60% of land plants, including many important crop species such as wheat, corn, and soybean. AM fungi are ubiquitous and can account for up to 50% of the microbial biomass in soils. The extraradical mycelium (ERM) of the fungus acts as an extension of the root system and increases the uptake of phosphate (P), nitrogen (N), sulphur, and magnesium but also of trace elements, such as copper and zinc. In addition, AM fungi also provide non-nutritional benefits to their host plant, as they improve the resistance of plants against several abiotic (drought, salinity, heavy metals) and biotic (pathogens, herbivores) stresses

AMF have been shown to have a positive influence on the composition of mineral nutrients (especially poor mobility nutrients such as phosphorus) of plants grown in salt-stress conditions (Al-Karaki and Clark, 1998) by enhancing and/or selective uptake of nutrients.

Mycorrhizal roots have two uptake pathways for nutrients: the plant uptake pathway (PP) and the mycorrhizal uptake pathway (MP; Figure 4).



Bücking and Kafle, (2014)

Fig 4: Plant uptake and mycorrhizal uptake pathway under salinity

3. K^+: Na^+ ratio

Sodium and potassium ions, due to their similar physic - chemical nature, compete at the transport sites for entry into the symplast. Therefore, in saline soils where concentration of Na^+ in rhizosphere is very high, K^+ uptake faces a stiff competition from Na^+, eventually decreasing K^+: Na^+ ratio in the cytosol. Low K^+: Na^+ ratio in the cell subsequently disrupts protein synthesis, enzyme activity, photosynthesis, turgor maintenance, and stomatal movement (Maathuis and Amtmann, 1999). The integrity and selectivity of root membrane are also altered by Na^+ (Grattan and Grieve, 1999).

4. Chloride ions

Root cells take up Cl^- from soil solution through H^+ / Cl^- symporters at low cl^- and also through anion channels under saline conditions. To reach the xylem and then the shoot, Cl^- traverses the root by a symplastic pathway and is released from cells within the stele through specific anion channels. At high salinity, Cl^- accumulation increases greatly, though it remains constant in the roots (White and Broadley, 2002). The high tissue Cl^- concentrations can be toxic to crop plants and may restrict agriculture in saline regions (Xu *et al.*, 2000). This problem can be tackled to some extent by the application of arbuscular mycorrhiza, which can reduce the uptake of Cl^- ions (Zuccarini and Okurowska, 2008). The Cl^- ions can be compartmentalized in vacuolar membranes, thereby preventing them from interfering with the metabolic pathways in the plant (Cantrell and Lindermann, 2001). However, there are reports of increased Cl^- accumulation due to mycorrhizal colonization, the reason of which may be due to the carbon drain imposed by mycorrhizal hyphae on plants, which enhances the translocation of highly mobile anions like Cl^- from the soil (Bulwada *et al.*, 1983; Graham and Syversten, 1984).

5. Ca^{2+}: Na^+ and Ca^{2+}: Mg^{2+} ratio

Under salt stress, an elevated Na^+ concentration in the rhizosphere hampers the absorption of Ca^{2+} by replacing them in cell wall and plasma membrane. This results in translocation of less Ca^{2+}, thereby reducing Ca^{2+}: Na^+ ratio in salt stressed plants (Grattan and Grieve, 1999). Low Ca^{2+}: Na^+ ratio decreases hydraulic conductivity and cell turgor, and disturbs Ca^{2+} signaling (Läuchli and Lüttge, 2002). Ca^{2+} uptake is also challenged by the presence of Mg^{2+}. Magnesium is a macronutrient and is the central ion of the chlorophyll molecule. It is responsible for harvesting light for photosynthesis. It is also required for proper functioning of many enzymes, such as RNA polymerases, phosphatases, carboxylases, ATPases, protein kinases, and glutathione synthase (Shaul, 2002). Several studies have reported that Mg^{2+} concentration in plants decreases under salt stress conditions. However, Mycorrhizal plants possess higher concentration of Mg^{2+} than Non Mycorrhizal plants. It is interesting to note that Mycorrhizal plants, despite accumulating more Mg^{2+} than Non Mycorrhizal plants, are also shown to have desirable Ca^{2+}: Na^+ ratio by improving Ca^{2+} uptake under salt stress conditions (Evelin *et al.*, 2012).

6. Biochemical changes

As soil dries out and soil water potential becomes more negative, plants must decrease their water potential to maintain a favourable gradient for water flow from soil into roots. To achieve such an effect, plants develop a plethora of mechanisms, the most important being osmotic adjustment or osmoregulation. The most common of these include amino acids, amide and proteins; also quaternary ammonium compounds (betaines) and polyamines (Rabie and Almadini, 2005). These compounds are generally present in low concentrations when the plant is not under salt stress (Feng *et al.*, 2002) [17]. Accumulation of soluble sugars to adjust the osmotic potential of plants during salt stress constitutes an important plant protection mechanism (Evelin *et al*., 2009) [13].

Function of Proline under stress: (i) increase in the expression of gene encoding P5CS involved in proline biosynthesis; (ii) higher activity of the enzyme P5CS; (iii) higher activity of the enzyme, glutamate dehydrogenase, that is responsible for synthesizing glutamate, the precursor of proline; and (iv) inactivation of proline dehydrogenase, an enzyme that catalyze the degradation of proline.

7. Antioxidants mechanism

Salinity stress induces oxidative stress in plants and resulted in generation of ROS such as superoxide radical (O2), hydrogen peroxide (H_2O_2), hydroxyl radical (•OH) and singlet oxygen ($^1O_2$). The activated oxygen species thus generated can cause damage to plant cell structure and function if not controlled by protective mechanisms. Plant cells use several mechanisms to minimize the oxidative damage caused by ROS (Ahmad *et al*., 2010; Ashraf, 2009; Jamil *et al*., 2011). The induction of ROS-scavenging enzymes, such as superoxide dismutase (SOD), catalase (CAT), peroxidase (POD) and ascorbate peroxidase (APX) is the most common mechanism for detoxifying the ROS generated during stress conditions. AMF facilitate plant to modulate salinity stress by increasing the activities of antioxidant enzymes such as SOD, CAT, GR, and POX or by increasing the concentration of non-enzymatic antioxidant molecules such as ascorbate and glutathione (Alguacil *et al*., 2003; Porcel *et al*., 2003; Porcel and Ruiz-Lozano 2004; Garg and Manchanda 2009; Ruiz-Sanchez *et al*., 2010; Wu *et al*., 2010a, b; Talaat and Shawky 2011).

8. Physiological changes

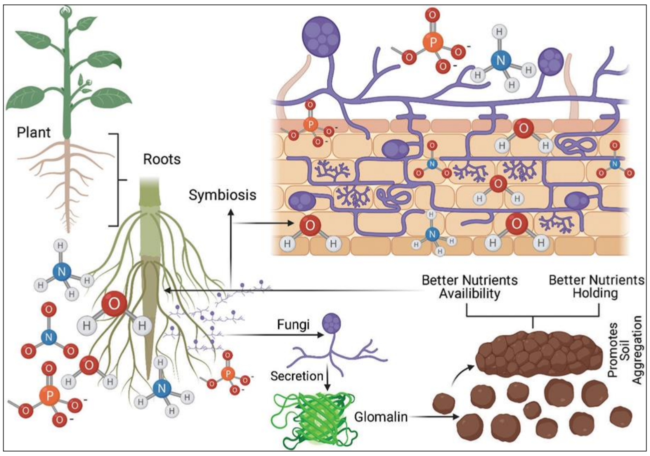
Salt stress can affect the plant by disrupting its physiological mechanisms such as decreasing photosynthetic efficiency, gas exchange, membrane disruption, water status, etc. There is evidence demonstrating that AM symbiosis can alleviate such effects by employing various mechanisms like increasing the chlorophyll content by altering the way for mg molecule. And notably changes in photosynthetic pigments and gas exchange parameters in which inoculation is performed.

9. Phytohormones signalling - ABA content

Phytohormones including cytokinins, ethylene, abscisic acid (ABA), auxin, jasmonic acid and salicylic acid can also act as signal molecules during the process of AMF symbiosis (Gutjahr and Paszkowski, 2009; Miransari *et al*., 2012). Research has also indicated that AMF roots contain high amounts of jasmonic acid in comparison with non-AMF roots (Hause *et al*., 2007; Meixner *et al*., 2005). This suggests that auxin may indirectly affect the symbiotic level as it is influenced by strigolactones. Hence, the role of Indole Acetic Acid (IAA) in mycorrhizal symbiosis has been suggested (Ludwig-Mu¨ller, 2010, 2011). The role of Jasmonic acid and salicylic acid to improve plant systematic acquired resistance is also well documented.

10. Maintenance of water homeostasis and aquaporins

Under stress condition, inoculation with mycorrhiza often improves plant water status due to the contribution of extraradical hyphae for absorbing more water, and change in root morphology and soil structure. Mycorrhizal fungi largely alters root hydraulic conductivity under salinity stress (Aroca *et al*., 2007). Arbuscular mycorrhiza fungi play a key role in soil aggregation. AMF affects the shoot to root ratio, plant physiology, nutrients uptake by plants and highly affect soil aggregates formation during symbiosis. When AMF affect the plant root system, the AMF increases the potential of plants roots and root hairs to bind soil particles. Hallett *et al*. (1998) reported that plants roots apply stress on soil particles and bind these soil particles to facilitate the formation of soil aggregates. The regulation of water across membranes, and hence the regulation of root hydraulic conductivity, has been mainly attributed to the transmembrane aquaporins. Aquaporins are membrane intrinsic proteins present in all living organisms, including fungi (Agre *et al.*, 1993), that facilitates the transport of water and another small uncharged molecules across cell membranes following a gradient (Maurel *et al*., 2008). Fungal mycelia contain their own aquaporins, is known about their contribution to the water transport of mycorrhizal plants (Aroca *et al.*, 2009). Aquaporins have a role in passive movement of water molecules following a water potential gradient and maintaining cellular osmoregularity (Maurel *et al.*, 2002; Kjelbom *et al*., 1999).



Wahid *et al*. (2021)

Fig 5: Regulation of nutrients and water by arbuscular mycorrhizal fungi (AMF)

11. Glomalin production

Just like plants, the AMF hyphae bind the microparticles of soil into macroparticles. AMF produces some glomalin - related protein and mucilage's that help soil aggregate formation in the soil and plant rhizosphere. These proteins increase the coating of these particles and enhance their stability and preventing them from dispersing and disintegrating.

Ecological significance of arbuscular mycorrhizal symbiosis

Ecological consequences of the interactions between plants and the AMF for plant nutrition, growth, competition, stress tolerance and fitness, as well as for soil structuring have been often addressed.

Key effects of AM symbiosis

The key effects of AM symbiosis can be summarized as follows:

1. Enhancing uptake of low mobile ions,
2. Improving quality of soil structure,
3. Enhancing plant community diversity,
4. Improving rooting and plant establishment,
5. Improving soil nutrient cycling, and
6. Enhancing plant tolerance to (biotic and abiotic) stress.

The contribution of AMF to plant nutrient uptake is mainly through the acquisition of nutrients (especially phosphorous, which is extremely immobile element in soils) from the soil by the extraradical fungal hyphae, especially from root-distant soil not depleted of nutrients by the root. Fungal hyphae are functionally analogous to fine root hairs, as both are nutrient uptake organs. Mycelium extends the plant's effective absorption surfaces beyond the nutrient depleted zone that develops around the root caused by direct root uptake processes.

Latest development in AM fungal research

The advancement of metagenomics and next generation sequencing technologies has characterized all-known AMF into a single clade, the phylum Glomeromycota, a sister group of Ascomycota and Basidiomycota on the basis of ribosomal RNA phylogeny. Lee and Young (2009) [24] demonstrated the feasibility of obtaining a high-quality sequence from both the nucleus and mitochondria after whole genome amplification of DNA from AM spores.

Tisserant *et al*. (2012) produced first genome-wide analysis of the transcriptome of *G. intraradices* DAOM 197198 and transcript profiling on symbiotic and a symbiotic fungal structures based on oligo array and pyro - sequencing data, which provided novel insights into the molecular basis of symbiosis-associated traits. The latest advances in the gene-based study contribute to our understanding of mechanisms involved in the establishment of AMF at every level. The complete sequencing of an AM fungal genome will advance our knowledge, and aid in the application of AMF to improve plant productivity under salinity stress and nutrient-limited soil conditions.

Conclusion & future perspective

Salt stress adversely affects the morphology as well as physiology of plants grown under saline soil by increasing the osmotic stress, ion toxicity and nutrient deficiency. However, colonization of plant with AM fungi significantly increased growth response. The real essence of mycorrhizal association is that it benefits the primary producers by combating diseases, supplying essential nutrients required for growth. In the light of the current scenario what seems to be essential is the identification of the mechanism and nature of interaction and the key genes from fungi as well as the plants that regulate the interaction. Despite all these benefits present day practices of agriculture may lead to the destruction of these beneficial associations. Anthropogenic activities like slash and burn cultivation, mining, waste disposal, and clear-cutting of forests are also detrimental to mycorrhizae. Ruthless use of pesticides & fertilizers have not only degraded the environment but also risked the lives of millions of living organisms, so stress on ecofriendly substitutes like mycorrhiza should be more. Stress should be laid on the identification of more useful strains of mycorrhiza which can thrive in any environmental condition. A well-documented knowledge about mycorrhizal tradeoffs as well as a complete understanding of the mechanism of interaction will be essential to advance mycorrhizal technology for a better tomorrow.

Although the performance of AMF under salt stress is well studied under controlled environment and field level, researches on the molecular mechanisms governing the process of salt amelioration in plants are limited. To improve the resistance of plants to salinity, the mechanisms of symbiosis between plants and microorganisms need to be addressed which can lead to improved selection of efficient microorganisms for specific plant species. In addition to this, studying microbe–microbe interaction in soil may reveal the mechanisms behind their interaction among each other and their co-inoculation effects which may eventually lead to improved selection of effective microorganisms. The utilization of effective AMF strains for the amelioration of plant growth under salt stress is a potential approach which can be used in synergy with other known technologies to increase crop productivity in salt-affected areas.

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