Scope for Microbial Amelioration of Salinity Stress in Plants

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Abstract

Presence of higher amount of soluble salts in soil and irrigation water is a major limiting factor for crop productivity in tropical and semi-arid regions of the world. Though physiological insights about the mechanisms of salt tolerance in plants have been gained, translation of such information to aid in crop improvement has been limited. The identification and exploitation of soil rhizosphere bacteria and mycorrhizal fungi for alleviating salinity stress opens new alternatives for salinity management. The organisms offer several beneficial effects to plants such as improved nutrient and water uptake, growth promotion, and alteration of plant metabolism under salinity stress. This review aims to evaluate the beneficial effects of soil rhizosphere bacteria and mycorrhizal fungi on the plant response to saline stress, with the possible application to improve the crop production under varying salinity conditions.

Key words: *salinity stress, ion homeostasis, mycorrhizae, rhizobacteria, phytohormones*

Introduction

Salinity is a key factor hampering crop productivity and a major cause of the abandonment of lands, particularly in the coastal areas for agricultural purposes. Over the years developing salt-tolerant crops has been given prominence and few major-determinant genetic traits of salt tolerance have been identified (Flowers, 2004; Munns and Tester, 2008). But these efforts could not produce desired results at field leaving lots of issues to address for adequately managing salinity stress on plants. Several recent studies have demonstrated that local adaptation of plants to their environment is driven by genetic differentiation in closely associated microbes (Rodriguez and Redman, 2008). Thus, an alternative strategy to improve crop salt tolerance lies at harnessing the salt-tolerant microbes that enhance crop growth. Enhancement of crop growth in a wide range of salinities by utilizing salinity tolerant soil microbes are discussed below, particularly this approach may succeed where it has proved difficult to develop salt-tolerant germplasm.

Though there are wide range of microbes having beneficial effect on crop plant under saline environment, much focus in this review is given on symbiotic relationships such as arbuscular mycorrhizal fungi (AMF), whose hyphal networks ramify throughout the soil and within the plant cells, and root-associated plant growth-promoting rhizobacteria (PGPR). These soil dwelling microbes in the rhizosphere region have evolved several mechanisms to protect themselves to survive in these adverse conditions and also trigger consequential changes in plants leading to crop adaptation to abiotic stresses. Further, in an effort to survive and prevail at the rhizosphere, some microbes possessing the cellulase enzyme capable of dissolving the cellulose cell wall of plant roots gain entrance into the apoplast of plants, the cell wall interior as well as the vascular bundle where they live and undergo normal metabolic activities (Khan *et al.* 2016). They also provide the plant with useful metabolites that are very essential for the plant to overcome abiotic stress.

Although changes in ion uptake by plant root occur within minutes of exposure to salinity (Davenport, 2007), ion (e.g. Na^+, Cl^-) accumulation to toxic levels in photosynthetically active mature leaves takes time providing scope for its amelioration. Thus understanding soil microbial role in alteration of ion homeostasis and improve plant nutrition in salinized crops is very important. As plant meristems are actively growing tissues where cell division and further expansion governs sink strength and affects plant carbohydrate status, microbial impacts on plant energetics are also briefly discussed. These mechanisms do not work in isolation but rather in an integrated manner to finally affect the major physiological

processes limiting growth under salinity. In general, studies proved that these microbes induce salinity tolerance in crops by production of phytohormones, volatile compounds, exo-polysaccharides, ACC deaminase and osmolyte, and triggering antioxidant activities (Wang *et al.*, 2003; Glick 2012). Thus this review seeks to evaluate microbial effects within the context of physiological and agronomic responses of plants to salinity (Munns, 1993) according to temporal changes in both osmotic and ionic stresses.

2. Soil-plant-microbial interactions and salinity stress

Several studies have shown that plant-microbe interactions not only depend on the plant and microbe alone but the surrounding environment as well. Soil and the soil microclimate are the two most important factors affecting the interactions among other factors (Fig. 1). Review of relevant literatures showed that soil properties influencing the microbial distribution and the plant-microbes interactions are soil type, moisture condition, organic matter content, fertility level, presence of toxic compounds, soil temperature etc. These properties are the key factors in deciding the microbial diversity and distribution, the interaction comes next only to this (Wagg *et al.* 2014). In managed ecosystem land use is important drivers of microbial distribution. It is important consideration in plant-microbe interaction because microbial diversity and composition are widely recognized as key factors in driving ecological functions (Vivant 2013).

Globally, in terms of environmental stresses, saline stress is considered the most severe stress that effect not only the soil and plant growth but also the living organisms. Salinity reduces plant growth chiefly in three ways, (i) osmotically induced water stress, (ii) specific ion toxicity due to high concentration of sodium and chloride ion and (iii) nutrient imbalances which hampers the uptake of water by plants (Greenway and Munns 1980). Ultimately photosynthetic rate decreases not only because of reduced leaf area and lesser gas exchange but also due to feedback inhibition of unused photosynthates, after exposure to salinity (Gayathri and Smith 2017).

Thus, it is essential to better understand the causes and controls of soil microbial distribution, effect of salinity on plants and the changes in plant system brought as a result of microbial-plant interaction under saline environment so as to harness its potential for amelioration of salinity stress in plants.
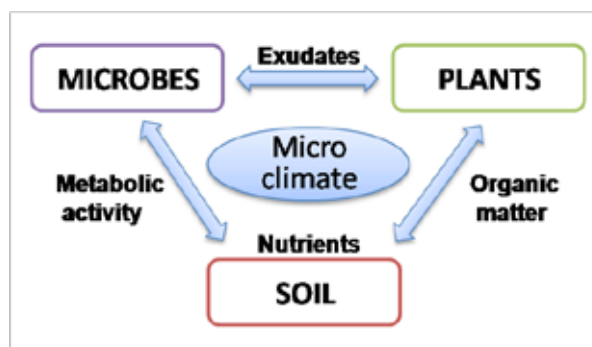

Fig.1 Soil-plant-microbe interactions

Soil microbes in alleviating salinity stress

Review of literatures indicated that many PGPR and MR have been investigated for their role in improving plant-water relations, ion homeostasis and photosynthetic efficiency in plants under salt stress. However, their amelioration mechanisms are intricate and often not completely understood in different crops under varying conditions. These mechanisms are regulated by a complex network of signaling events occurring during the plant–microbe interaction and consequently ensuing stress alleviation (Smith *et al.*, 2017). The classes of microbes belonging to these group/genera are Micrococcaceae, Bradyrhizobium, Bacillus, *Microbacterium, Pseudomonas, Curtobacterium, Variovorax, Paenibacillus, Pantoea,* and many others (Kasim *et al.* 2016). Here we discuss the beneficial effect of some of the PGPR and MRF on plant against salt induced stress.

Water homeostasis and osmolyte accumulation

Maintaining water homeostasis and the functioning of photosynthetic structures are essential for alleviating the impact of salinity on plant growth and crop yield, even if salinity-induced losses in turgor may be transient, owing to plant uptake of ions from the soil allowing foliar osmotic adjustment (Munns and Tester, 2008). Studies showed that

under stress, plants inoculated with mycorrhiza (Auge´, 2001) or PGPR (Creus *et al.*, 2004) often show enhanced osmotic adjustment. A schematic representation of salt stress alleviation by mycorrhizal fungi and plant growth-promoting rhizobacteria is represented in Fig. 2.

Root colonization by AMFs can induce major changes in the relative abundance of the major groups of organic solutes (Sheng *et al.*, 2011), such as modifying the composition of carbohydrates and inducing accumulation of specific osmolytes such as proline, thus facilitating osmotic adjustment. Nevertheless, the concentration of proline under saline conditions may not always indicate significant osmotic adjustment, unless subcellular compartmentation is considered (Pe´rez-Alfocea *et al.*, 1993). However, better growth of AM-inoculated *Jatropha curcas* compared with non-inoculated plants when exposed to salinity (1.7–8.5 dS m_1 NaCl for 60 d) resulted from increased soluble sugars and proline in the leaves of inoculated plants, allowing maintenance of leaf water status (Kumar *et al.*, 2010). Similarly the introduction of a proBA gene derived from *Bacillus subtilis* into *Arabidopsis thaliana* increased production of free proline, which was associated with increased salt tolerance in the transgenic plants (Chen *et al.*, 2007).

Further, improved exploitation of soil water due to the mycorrhizal hyphal contribution to water uptake and induced changes in root morphology also reported. Indeed, the mycorrhizal maintenance of root turgor during drought was apparently not related to osmotic adjustment, despite fungal alteration of concentrations of several key solutes, but to change apoplastic/symplastic water partitioning (Auge´ and Stodola, 1990). While these local changes contribute to root growth maintenance, soil microbes also affect the ability of the roots to take up water under both drought and saline stresses.

Source–sink relations and energetic metabolism

In addition to osmoregulation, stimulation of carbohydrate transport and metabolism between source and sink tissues has also been proposed as a mechanism to alleviate metabolic feedback inhibitions of photosynthesis, thus avoiding photo-inhibition during the osmotic phase of salinity when carbohydrates usually accumulate (Munns,

1993). Symbiotic microorganisms are known to directly modulate these source–sink relations by enhancing sink activity through increased exchange of carbohydrates and mineral nutrients. When colonized by AMF plant roots become a strong sink for carbohydrates, as these fungi can consume up to 20% of the host photosynthate (Heinemeyer *et al.*, 2006). It is also proposed that sugar accumulation may be due to the hydrolysis of starch in inoculated seedlings, as mycelium growth requirements mobilize carbon reserves, which could help decrease salinity-induced starch accumulation as a consequence of the inhibition of sink activity in growing tissues (Balibrea *et al.*, 2000). Thus maintenance of an active carbohydrate sink in symbiotic roots, when assimilate transport and use in other sink tissues is impaired, could help maintain the source activity of mature leaves for longer, thereby improving salt tolerance (Pe´rez-Alfocea *et al.*, 2010).

Ion homeostasis

Salt tolerance in glycophyte species is mostly related to the exclusion of toxic ions present in saline soil from the leaves thereby avoiding or delaying toxic effects (Munns and Tester, 2008). Microbes can alter root uptake of toxic ions and nutrients by altering host physiology and modifying physical barriers around the roots, or by directly reducing foliar accumulation of toxic ions (Na^+, Cl^-) while improving the nutritional status of both macro- (N, P, K) and micronutrients (Zn, Fe, Cu, Mn) mostly through selective uptake along with enhanced water flow into the root. Further, nutrients may also become more accessible to the plant due to microbial-induced changes in rhizosphere pH (organic acid excretion) and/or chelation with organic molecules (siderophores) exuded by microbes. Particular importance has been attached to microbial enhancement of K^+/Na^+ ratios in plants (Giri *et al.*, 2007). Hence, any contribution of the soil biota towards maintaining the homeostasis of toxic ions must benefit plant growth under salinity (Fig. 2).

It has been demonstrated that the AMF *Glomus intraradices* can selectively take up elements such as K^+, Mg^{2+}, and Ca^{2+} while avoiding Na^+ uptake to keep internal K^+/Na^+ and Ca^{2+}/Na^+ ratios within narrow limits, despite changes in concentration of the ions in the soil

environment. Concentrations and distributions of Na^+ and Cl^- within the fungal tissue suggest that this AMF acts to exclude Na^+ but include Cl^-. These selective mechanisms for ion uptake could partially alleviate salinity stress in host plants by improving their nutrition (Hammer *et al.*, 2011). If a significant proportion of the elemental uptake in plants occurs via the mycorrhizal fungi, this could explain the often higher K^+/Na^+ ratios in mycorrhizal plants (Giri *et al.*, 2007).
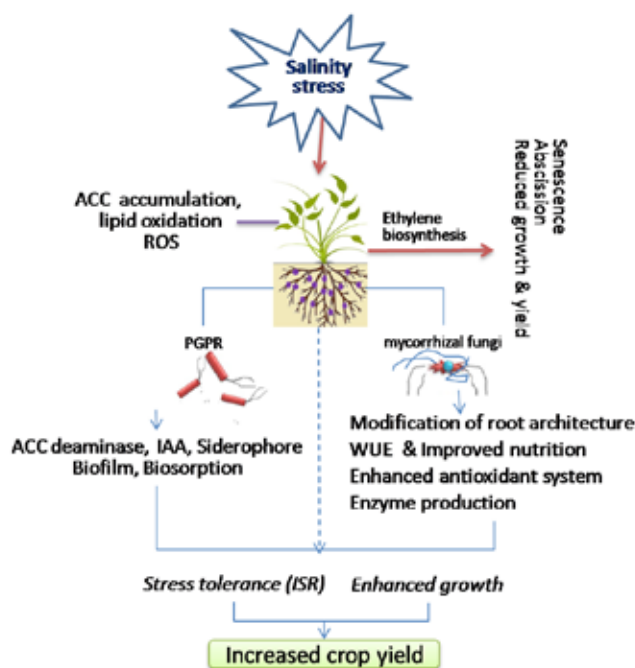

Fig. 2. A schematic representation of salt stress alleviation by mycorrhizal fungi (MF) and plant growth-promoting rhizobacteria (PGPR)

Stress tolerance through PGPR

Salinity impairs plant growth by causing osmotic imbalance and ion toxicity. Several studies have revealed that PGPRs and MRF are capable of maintaining optimum biological functions in cereals, legumes and vegetables grown under stress conditions. Some selected examples of growth promotion with inoculation of these rhizobacteria under stressful environments are included in Table 1.

One of the common hypotheses employed in most of the studies conducted under salinity stress was the lowering of ethylene level by the ACC-deaminase activities of PGPR. These studies conducted under both controlled and natural environments in greenhouse showed that inoculation with PGPR containing ACC-deaminase significantly increased plant growth and yield compared to that of un-inoculated control. In addition to regulating plant nutrition by enhancing K^+ uptake over Na^+ in plants under salt stress conditions (Nadeem *et al.*, 2009) inoculation with PGPR also enhances the uptake of other major nutrients as well as improves the water content of stressed plants. The inoculation with Pseudomonas spp. improved the eggplant growth by depressing the uptake of Na^+ and increasing the activities of antioxidant enzymes under salinity stress conditions. According to them, regulation of mineral uptake and increase in the antioxidant enzyme activities may be the two key mechanisms involved in alleviation of salt stress.

PGPR strains have been reported to be equally effective when applied with other microbial populations. For example, Figueiredo *et al.* (2008) evaluated the effect of co-inoculation with *Paenibacillus polymyxa* and *Rhizobium tropici* on growth, nitrogen content and nodulation of common bean (*Phaseolus vulgaris* L.) under abiotic stress environment in a greenhouse. The results showed that co-inoculation enhanced the plant growth, nitrogen content and nodulation of bean under drought stress compared to uninoculated control.

The PGPR strains are effective not only for improving plant growth under salinity stress but are also helpful for enhancing plant growth and development under heavy metals, flooding and drought stress (Glick *et al.*, 2007). Plant growth promoting rhizobacteria have been shown as effective biocontrol agents against a number of plant pathogens. The above discussion clearly indicates that PGPR strains are very helpful to enhance plant growth not only under salinity stress but also other stresses such as drought, flooding, heavy metals, pathogen attack, etc.

Table 1: A summary of beneficial effect of soil microbes on plants under salinity stress

Crop	Bacterial strain	Effect on plants	Reference
Tomato (*Solanum lycopersicum*)	*Achromobacter piechaudii*	ARV8 Inoculation increased fresh and dry weight as well as water use efficiency of tomato by decreasing the ethylene production under stress.	Mayak *et al.* (2004a)
	Pseudomonas fluorescens, P. aeruginosa, P. stutzeri	All PGPR strains enhanced the root and shoot growth of tomato. Sodium contents (Na) were low in plants inoculated with P. Stutzeri and showed relatively better grwoth compared to other two strains.	Tank and Saraf (2010)
Cotton (*Gossypium hirsutum*)	*Klebsiella oxytoca*	In addition to significant increase in height and dry weight of cotton plants, inoculation with PGPR uptake ofmajor nutrients like N, P, K, and Ca increased while Na deceased.	Yue *et al.* (2007)
Groundnut (*Arachis hypogae*a)	*P. fluorescens TDK1, P. fluorescens PF2 and P. fluorescens RMD1*	Bacterial strains proved useful for increasing salt tolerance of groundnut. The impact of strainswas variable and P. fluorescens TDK1 provedmost effective than other ones.	Saravanakumar and Samiyappan (2007)
Maize (*Zea mays*)	*Pseudomonas spp., Enterobacter aerogenes, Flavobactrium ferrugineum*	PGPR enhanced the growth of maize under salinity but with variable efficacy. Overall, high chlorophyll content, relative water content and K+/Na+ ratio was observed in inoculated plant than uninoculated control.	Nadeem *et al.* (2009)
Canola (*Brassica napus* L.)	*Pseudomonas spp.*	Rate of seed germination and seedling growth was significantly higher. ACCdeaminase producing Pseudomonas spp. enhanced canola tolerance against salinity stress.	Jalili *et al.* (2009)
Black gram	*Ochrobactrum pseudogrignonense*	Osmoregulation, ACCd, ROS	Saikia *et al.*, 2018
Mung bean (*Vigna radiata)*	*Pseudomonas syringae, Pseudomonas fluorescens,*	IAA production, siderophore activity nitrogenase activity, P- solubilization	Ahmad *et al.* (2011)
V. faba	*R. leguminosarum*	Osmoregulation and ACCd	Cordovilla *et al.*, 1999

Commercial prospects

The role of PGPR and MRF based bio-formulations has shown great potential toward sustainable agriculture and seen as an alternative to chemicals. Successful commercial application of microbial inoculants to improve crop growth and yield in saline soil implies that the inoculants are also salt tolerant, which highlights the potential of using microorganisms from saline habitats. Certain PGPR, whose ability to colonize the root system is undiminished by salinity (Paul and Nair, 2008), offer considerable potential as inoculants. Although some mycorrhizal species (e.g. *Scutellospora calospora*) reach maximum spore germination under high-salt conditions, spore germination of some AMF was delayed and the specific rate of hyphal extension was reduced in the presence of NaCl (Juniper and Abbott, 2006). The extent to which spore germination was inhibited was not the same for all species investigated but was similar for isolates of the same species, and was independent of the salinity of the environment of origin. However, the evidence that propagules from root pieces have a higher capacity to germinate under high salinity than the spores of the same species suggests that specific technologies can be developed to optimize fungal viability under saline conditions in order to optimize colonization of the host plant. One interesting proposition is to pre-treat mycorrhizal hyphae with salt prior to inoculation into saline environments (Sharifi *et al.*, 2007), which almost doubled root colonization and stimulated root and shoot growth of soybean plants. Thus, parallel programmes of independently increasing both microbial and plant salt tolerance may assist the productivity of crops grown in saline environments.

Conclusions

Significant improvement in plant tolerance to abiotic stress will improve yield and production of crops to feed humans and livestock. This can be achieved by two approaches. One approach is via development of salinity tolerant plant species. The other method is the use of PGPR and MRF which will go a long way in supporting the plant to develop both intrinsic and extrinsic ability to tolerate stressful conditions and sustain yield. However, a major

problem in rainfed agroecosystems is predominance of abiotic stresses like high temperature, salinity, and drought where the survival of bioinoculants is a problematic issue. The variations in results from laboratory to field are more compounded due to various abiotic stresses that prevail under field conditions for microbial inoculants to establish and to show the desired effect. Such problems can be overcome by sound screening programme for efficient stress tolerant PGPRs for effective deployment of these strains to draw one or more beneficial effects. Use of soil microbes for salinity alleviation will form the core of the future adaptation strategy to climate change as the salinity is projected to increase due to uncertainty in rainfall and sea water intrusion in the coastal areas.

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