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Halotolerant Plant Growth-Promoting Fungi and Bacteria as an Alternative Strategy for Improving Nutrient Availability to Salinity-Stressed Crop Plants

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Abstract

Nowadays, it is imperative to address the management of crop production in difficult environmental conditions in order to achieve the maximum potential of plant growth and yield for providing enough food. Increasing demand for plant products has been coupled with decreasing cultivated land due to the limitation of water and soil resources. Salinity is one of the most important abiotic stresses that both limit the production of agricultural products in arid and semiarid areas and decrease arable land across the world. Plant nutrition imbalances due to excessive absorption of sodium (Na^+), and chloride (Cl^-) ions also reduce the absorption of macronutrients such as potassium (K), calcium (Ca), magnesium (Mg), nitrogen (N), and phosphorus (P) and micronutrients such as iron (Fe), zinc (Zn), copper (Cu), manganese (Mn), and boron (B). To satisfy crop nutritional requirements under salinity stress, micro- and macronutrients are usually added to soil as chemical fertilizers; however synthesis of these fertilizers is highly energy-intensive processes and has long-term impacts on the environment in terms of eutrophication, soil fertility depletion, and carbon footprint. Such environmental concerns have led to the search for sustainable way of providing crops with nutrients. In this regard, plant growth-promoting salinity-tolerant microorganisms have been seen as best eco-friendly means for nutrition of salinity-stressed crop plants. These microorganisms increase the nutrient bioavailability through N_2 fixation and mobilization of key nutrients (P, K, and micronutrients) to the crop plants. Use of salinity-tolerant microorganisms is also known as an alternative, innovative, environmental friendly option to reduce the use of costly and

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non-environmental friendly chemical fertilizers and can represent a promising approach to increase nutrient bioavailability and facilitate the development of saline soil-based agriculture. In this chapter, current knowledge on the mechanisms used by plant growth-promoting rhizobacteria (PGPR) and arbuscular mycorrhizal (AM) fungi to influence soil nutrient bioavailability (N, P, K, and micronutrients) under salinity stress is discussed.

Keywords
Arbuscular mycorrhizal fungi · PGPR · Salinity stresses · Agriculture crops · Plant-microbe interactions · Saline soil-based agriculture

5.1 Introduction

Given the growing population of the world with an annual growth rate of 80 million per year and the food shortage crisis of the present century, it is necessary to look for a proper way to meet the food needs of the community in an adequate and desirable quality because one of the indicators of sustainable development is the issue of food security. In order to meet the food needs, given the declining trend in agricultural land that is mostly due to soil salinization, there is no solution other than the strategy of increasing production per unit area (maximum production) (Etesami and Beattie 2018). Due to the ever-increasing demand for food and the lack of salt non-affected soils, we should inevitably use the potential of salinity-stressed soils to produce important crop plants. Salinity of water and soil is among the most important factors limiting the growth of crop plants and production of agricultural products. The total area affected by salt in the world is constantly rising. According to the estimates, around 30–50% of the world's land is under salt stress, and in Iran, about 50% of the cultivated land is facing a salinity problem. In saline conditions, sodium ion (Na^+) concentration is usually higher than the concentration of micro- and macronutrients, and this leads to nutritional imbalances in plants under salt stress in a variety of ways. In general, the presence of excess salts in soil or irrigation water confronts the plant with salt stress. Salinity stress, irrespective of the mechanism of salinization, occurs due to excessive accumulation of cations and anions in the soil solution. These salts consist primarily of ions such as Na^+ and chlorine (Cl^-) and then bicarbonate (HCO_3^-), sulfate (SO_4^{2-}), calcium (Ca^{2+}), magnesium (Mg^{2+}), borate (BO_3^{-3}), and rarely nitrate (NO_3^-) (Sha Valli Khan et al. 2014). The presence of these cations and anions in the soil prevents the absorption of other essential nutrients such as nitrogen (N), phosphorus (P), potassium (K), iron (Fe), cupper (Cu), zinc (Zn), etc. (Giri et al. 2007; Munns and Tester 2008; Tester and Davenport 2003). To increase the availability of nutrients for salinity-stressed plants, large amounts of chemical fertilizers are required on a regular basis. In areas where there is a problem of water and soil salinity, salinity causes a 10–60% reduction in the yield of crops (FAO 2005). In these areas, farmers are trying to compensate for the damage caused by salinity by using more inputs such as fertilizer, seeds, and water, which sometimes accounts for up to 65% of the income of the farmers. But, in addition to increasing production costs, the excessive use of these fertilizers causes a lot of environmental problems including increasing pollution of water and soil resources (greenhouse gaseous emissions) as well as water eutrophication, imbalance of nutrients in the soil, decrease in the yield of agricultural products, and endangering the health of humans and other living organisms (Adesemoye and Kloepper 2009). Moreover, the use of chemical fertilizers in salt-affected soils is not a right choice and, if used, increases the salinity of the soil. Most crop plants are sensitive to salinity and cannot survive under high salinity concentrations (Siddiqui et al. 2009). In other words, such plants need microorganisms to grow in saline soils (Etesami and Beattie 2018). For this reason, in recent years, the use of plant growth-promoting microorganisms (PGPMs) as bio-fertilizers or biocontrol agents in agriculture has been considered by many researchers, and the increased growth of different crops by these microorganisms has been proven in greenhouse and field experiments. Use of PGPMs is known as an alternative, innovative, environmental friendly option to reduce the use of costly and non-environmental friendly chemical fertilizers (Rashid et al. 2016). PGPMs increase plant growth and yield through various mechanisms (Etesami and Maheshwari 2018).

Rhizosphere free living bacteria that directly and indirectly improve plant growth and health are named as plant growth-promoting rhizobacteria (PGPR). In indirect mechanisms, the PGPR indirectly modify the harmful effects of plant pathogens by using specific mechanisms, thereby increasing plant growth. But in direct mechanisms, these bacteria, by fixing nitrogen, producing the metabolites effective at plant growth, such as plant hormones indole-3-acetic acid (IAA), cytokinins (CK), and gibberellins (GAs), increasing the solubilization of insoluble compounds such as P and K through the production of organic and inorganic acids, producing siderophores (increase in the availability of micronutrients such as Fe, Zn, etc.), and reducing the effects of stress ethylene by the production of enzyme ACC (1-aminocyclopropane-1-carboxylate) deaminase, help plants to grow more efficiently (Etesami 2018; Etesami and Maheshwari 2018; Gamalero and Glick 2011; Glick 2014). Various genera of bacteria such as *Pseudomonas*, *Azospirillum*, *Azotobacter*, *Klebsiella*, *Enterobacter*, *Alcaligenes*, *Arthrobacter*, *Burkholderia*, *Bacillus*, *Serratia*, *Erwinia*, *Flavobacterium*, and *Rhizobium* have been reported as PGPR (Egamberdiyeva 2005; Glick 2014).

Another group of microorganisms that are closely associated with plants are fungi. Fungi, like bacteria, can colonize the rhizosphere, the rhizoplane, and in many cases within root tissues (endophyte). Arbuscular mycorrhizal (AM) fungi are among the most abundant fungi in agricultural soils. Mycorrhizal fungi are the fungi that form a symbiotic association with the roots of 83% of dicotyledonous plants and 79% of monocotyledons (Peterson et al. 2004). The role of mycorrhizal fungi in increasing the absorption of nutrients is important only in ecosystems that have nutrient deficiency (Cardoso and Kuyper 2006). These fungi can also confer plant beneficial effects through several mechanisms (Owen et al. 2015; Rawat and Tewari 2011; Waller et al. 2005).

In addition to negatively influencing plant growth, salinity also negatively affects microorganisms including bacteria (Greaves 1922) and AM fungi (e.g., negative effect on colonization capacity, spore germination, growth of fungal hyphae, and the formation and function of mycorrhizal symbiosis) (Giri et al. 2007; McMillen et al. 1998; Porcel et al. 2012; Sheng et al. 2008). Moreover, there are reports that activity of plant growth-promoting bacteria (PGPB), such as their ability to solubilize phosphate (Sharma et al. 2013) or produce enzyme ACC deaminase (Upadhyay et al. 2009), is affected by environmental conditions such as salinity stresses (Sánchez-Porro et al. 2009). Therefore, the microorganisms can increase levels of nutrients for plants under conditions of environmental stresses that are themselves resistant to these stresses (Etesami and Beattie 2018; Etesami and Maheshwari 2018). It has been known that microorganisms isolated from saline environments or halophytic plants have been able to well maintain their plant growth-promoting (PGP) traits under salinity stress (Etesami and Beattie 2018). These microorganisms usually have strategies to maintain their survival in saline environments (Vreeland 1987).

Halophiles are salt-loving organisms that grow well in relatively high salt concentrations in saline and hypersaline environments. Halophiles are present in all major groups of microorganisms (archaea, bacteria, and eukarya), and their salt differentiation is based on their salt tolerance level and salt needs (Ma et al. 2010). Halotolerant or halophilic bacteria form a diverse set of microorganisms that physiologically belong to different genera. Salt-resistant microorganisms usually have strategies to maintain their survival in saline environments (Vreeland 1987). Salinity-resistant bacteria through various mechanisms such as sodium excretion of cells; production of extracellular polysaccharides (EPS); intracellular accumulation of compatible soluble compounds, such as proline, trehalose, glycinebetaine (GB), sucrose, and glycerol; adaptation of proteins and enzymes to high concentrations of soluble ions; and the accumulation of K can withstand high levels of salt (Ruppel et al. 2013). Such halotolerant PGPR have been isolated both from halophytes (Etesami and Beattie 2018) and from salt-affected soils (Hingole and Pathak 2016; Orhan and Gulluce 2015). These bacteria could also increase the resistance of salinity-sensitive crop plants to salinity and improve the growth and yield of these plants under salinity stress (Etesami and Beattie 2018). For example, salinity-resistant bacteria with the ability to N_2 fixation or phosphate solubilization have potential for growth and yield of crop plants in saline soils as bio-fertilizers (Delgado-García et al. 2013). Also, these bacteria can play a special role in counteracting environmental stresses such as salinity and drought by producing bio-surfactants and EPS (Margesin and Schinner 2001).

AM fungi are also widely found in natural ecosystems and in salt-affected soils (Sengupta and Chaudhuri 2002) and are considered as suitable candidates for alleviating salinity stress in salinity-stressed plants (Garg and Chandel 2011). Mycorrhizal fungi such as *Glomus* sp. and *G. mosseae* also occur naturally in saline environments (Evelin et al. 2009). There are reports that salinity has not been able to prevent AMF sporulation and colonization of AM fungi (Aliasgharzadeh et al. 2001). Previous studies showed that AMF-inoculated plants grew better under salinity stress compared to non-inoculated plants (Feng et al. 2002; Giri et al. 2007; Hajiboland et al. 2010; Porcel et al. 2012; Sannazzaro et al. 2007; Zuccarini and Okurowska 2008). These fungi were able to improve plant growth, vigor, and performance and protect plant against the detrimental effects of salinity (Evelin et al. 2009; Garg and Chandel 2011; Giri et al. 2007; Kaya et al. 2009a; Kumar et al. 2010;

Porras-Soriano et al. 2009). In general, AM fungi can increase the resistance of AM plant to salinity by many mechanisms (including a combination of nutritional, biochemical, and physiological effects) (Evelin et al. 2009) such as:

1. Accumulating osmoregulators (e.g., proline, glycine betaine, etc.) (Garg and Manchanda 2009). These fungi can also synthesize trehalose in the extraradical mycelium, which serves as the main storage carbohydrate and also as an abiotic stress protectant (Garg and Chandel 2011; Ocón et al. 2007).
2. Improving host mineral micro- and macronutrient uptake (e.g., P, Zn, and Fe) (Asghari 2012; Miransari and Smith 2008) and ion balance (Giri et al. 2007; Wu et al. 2010).
3. Enhancing photosynthetic rate and water-use efficiency (WUE) (Colla et al. 2008; Wu et al. 2010).
4. Improving physiological processes such as water absorption capacity of salinity-stressed plants (e.g., by enhancing root hydraulic conductivity, WUE, higher K^+/Na^+ ratios, and compartmentalization of sodium within some plant tissues and favorably adjusting the osmotic balance and composition of carbohydrates) (Al-Karaki 2006; Giri et al. 2003; Ruiz-Lozano 2003).
5. Maintaining membrane integrity that facilitates compartmentalization within vacuoles and selective ion uptake (Rinaldelli and Mancuso 1996).
6. Lowering Na concentrations in salinity-stressed plants by dilution effects due to growth enhancement (Al-Karaki 2006).
7. Positively influencing the composition of mineral nutrients of plants grown under salt stress conditions (Al-Karaki and Clark 1998) by increasing and/or selective uptake of nutrients (Porcel et al. 2012). The extensive mycelial system of fungi can absorb nutrients such as N, P, K, Zn, Cu, and Fe. The nutrients absorbed by AM fungi are not only for these fungi, but only some of them are transmitted to host plant (Gosling et al. 2006).

Extensive research has been carried out on occurrence and functional diversity of agriculturally important microbes in stressed environments as reviewed by several authors (Grover et al. 2011; Paul 2013; Paul and Lade 2014; Venkateswarlu et al. 2008; Yang et al. 2009). Beneficial bacteria and fungi could improve plant performance under stress environments and, consequently, enhance yield both directly and indirectly (Banik et al. 2006; Barassi et al. 2006; Chakraborty et al. 2015; Choudhary 2012; Choudhary et al. 2015; Dahmardeh et al. 2009; Damodaran et al. 2014; Davies et al. 2011; del Amor Francisco and Cuadra-Crespo 2012; Dimkpa et al. 2009; Dolkar et al. 2018; Egamberdieva et al. 2008; Etesami and Alikhani 2016b; Fu et al. 2010; Gray and Smith 2005; Hamilton et al. 2016; Kaymak et al. 2009; Khan et al. 2012; Mayak et al. 2004b; Milošević et al. 2012; Nadeem et al. 2007; Paul 2012; Paul and Nair 2008; Ramadoss et al. 2013; Rojas-Tapias et al. 2012; Shrivastava and Kumar 2015; Soleimani et al. 2011; Tiwari et al. 2011; Upadhyay et al. 2009; Yang et al. 2009; Yao et al. 2010; Yildirim and Taylor 2005). The main objective of the present chapter is to highlight and discuss current knowledge on the mechanisms used by PGPR and AM fungi to influence soil nutrient (N, P, K, and Fe) bioavailability under salinity stress.

5.2 Salinity Stress

Among various environmental stresses, soil salinity, either resulting from natural or man-made processes, is one of the main concerns for agriculture because it converts arable land to nonarable land and affects crop production and agricultural sustainability especially in arid and semiarid regions of the world (Flowers 2004; Munns 2005). Soil salinization reduces 1–2% of the area that can be used for agriculture each year. Approximately 7% of the land on the planet and 20% of the total arable land are adversely affected by salinity. Soil salinity affects extensive areas of land in both developed and developing countries. The agricultural intensification, together with unfavorable natural conditions, has accelerated soil salinity in many parts of the world. A soil is considered to suffer from salinity if the electrical conductivity (EC) of its saturation is above 4 dS m^{-1} (America 2001), which is equivalent to approximately 40 mM NaCl (Munns and Tester 2008). Cultivated soils worldwide are becoming more saline from marginal irrigation water, excessive fertilization, and desertification processes (Munns and Tester 2008). The Food and Agriculture Organization (FAO) reported that more than 1 billion ha of land throughout the world were affected by salinity (Ahmad 2013; FAO 2008). Because of global climate change, the area of land affected by salinity is increasing day by day (Shrivastava and Kumar 2015). It has been estimated that more than 50% of the arable land would be salinized by the year 2050 (Jamil et al. 2011).

Salinity limits the productivity of agricultural crops in varying degrees with adverse effects on germination, plant vigor, and crop yield such as cereals (rice, wheat, and maize), forages (clover) or horticultural crops (potatoes and tomatoes) (Munns and Tester 2008). These crops are relatively susceptible to excessive concentration of salts, either dissolved in irrigation water or present in soil (rhizosphere) solution. At plant level, response to salinity stress is very complicated because it reflects the combination of the effects of drought stress and the special effect of ions. In order to understand the nature of salt stress, a definition must first be provided. Different definitions have been made for salinity so that, according to Shannon and Grieve (1998), salinity is the excessive concentration of soluble salts and mineral elements in soil solution that result in salt accumulation in the root area (rhizosphere), which makes water uptake by plant difficult. Soil salinization is a process in which the accumulation of soluble salts in the surface layer of the soil increases, and, as a result, the surface layer loses its potential as a growth medium for plants. In arid and semiarid soils, the problem is excess salts, which are mainly due to the lack of rainfall and high evaporation. Soil salinity is also due to other causes such as excessive use of chemical fertilizers, improper water quality for irrigation, deforestation, or compact cropping. Salinity also results in low osmotic potential of soil solution (osmotic effect) (Munns 2005; Munns and Tester 2008), and as a result, plants suffer from water shortages, resulting in excessive production of reactive oxygen species (ROS) such as peroxide anions, hydroxyl radical, hydrogen peroxide, and single oxygen, each of which can disrupt normal plant metabolism and lead to the destruction of plasma membranes and internal membrane systems (Parida and Das 2005). It has been widely reported that salinity limits plant growth and development, which leads to changes in physiology, morphology, and biochemical properties of plants. In general, salinity-induced stress reduces the yield of many crop plants because salt inhibits plant photosynthesis, protein synthesis, lipid metabolism, plant biomass, green pigments, stomatal conductance, and transpiration rate and lead to change in activity of enzymes such as superoxide dismutase (SOD), peroxidase (POD), ascorbate peroxidase (APX) and catalase (CAT), and osmolyte accumulation (such as proline, glycine betaine, total free amino acids, soluble sugars, and so on). In salinity stress conditions, seed germination stage, as one of the most important plant life stages, which plays an important role in plant establishment, is negatively affected by salinity. Salinity also leads to an imbalance of phytohormones (in particular IAA and ethylene) and thus decreases plant growth (Kaya et al. 2009b). High concentrations of soluble salts and some ions (Na^+ and Cl^-), due to causing specific ion effects (mainly Na^+ and Cl^-) (specific ion effect), which result in nutritional imbalances or ion cytotoxicity (Munns 2005; Munns and Tester 2008), undesirably also affect plant growth by limiting the absorption and transfer of essential nutrients to plant roots (Shrivastava and Kumar 2015), resulting in deficiency symptoms, and reduce the availability of nutrients (N, P, K, Ca, Mg, Fe, Cu, Zn, etc.) in soil (Barea et al. 2005; Moradi et al. 2011). Almost all micro- and macronutrient contents decrease in the roots and shoots of the plant with increasing NaCl concentration in the growth medium (Paul and Lade 2014).

In general, one of the most important consequences of salinity is the nutritional imbalances or ion cytotoxicity. The imbalance of nutrients, in turn, leads to a decline in the growth and development of plants. Plant nutrient management is the most practical and easiest way to overcome stress. The nutritional status of the plant mainly affects their ability to adapt to adverse environmental conditions and in particular non-biological stress factors. Several studies have shown that plants exposed to environmental stresses need the higher amount of nutrients to adapt to stress and reduce the negative effects of these stresses. In addition to having toxic effects on plant cells, soil nutrient imbalances can affect the plant's ability to survive or absorb water (Etesami 2018; Etesami and Maheshwari 2018). However, it has been found that salinity-resistant microorganisms can grow well in salt and high osmotic pressure conditions and partially meet the nutritional needs of the plant under salinity stress (Fig. 5.1 and Table 5.1) (Etesami and Beattie 2018).

5.3 PGPR and AM Fungi-Mediated Increase of N Availability Under Salinity Stress

Nitrogen (N) is the most vital nutrient for plant growth and productivity. Although there is about 78% N_2 in the atmosphere, soil N is mostly in organic forms and unavailable for plants. Deficiency of this nutrient in the soil results in a significant reduction in plant growth and yield. As mentioned above, one of the adverse effects of soil salinity on plants is to alter the uptake of nutrients by plants (decrease in uptake of nutrients with increase in soil salinity) (Cheng-Song et al. 2010; Rawal and Kuligod 2014). Studies indicate that salinity reduces N uptake/accumulation (Feigin

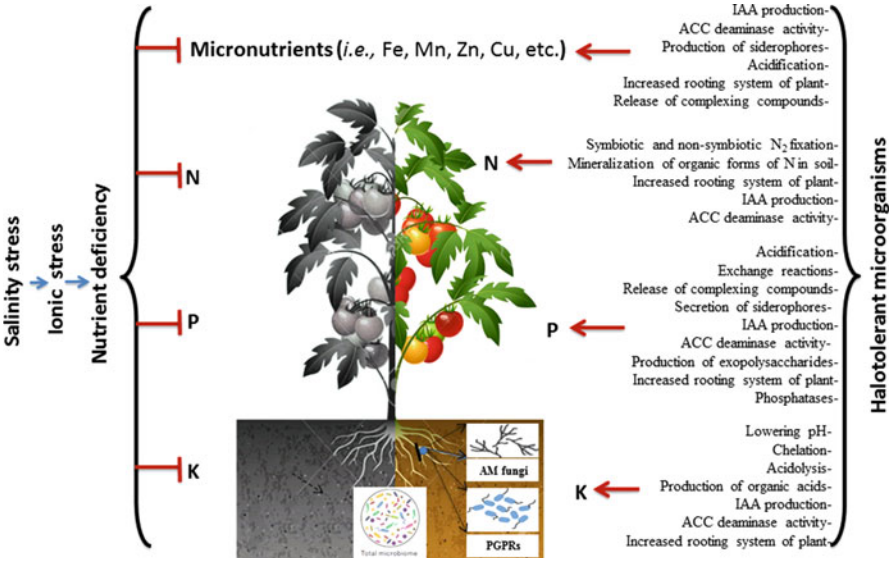

Fig. 5.1 An overview on the role of PGPR and mycorrhizal fungi to promote nutrient acquisition under salinity stress

1985). One of the ways to alleviate, to some extent, the detrimental effects of salinity and help to improve the yield of crops is to use chemical fertilizers. According to Rawal and Kuligod (2014), under salinity conditions, application of higher doses of N resulted in increased yield. In general, in most soils of saline and drought areas, the available N shortage for plants is present, and this shortage cannot be compensated for by using only chemical fertilizers at global level. On the other hand, the use of biological nitrogen fixation (BNF) process is more efficient and more favorable than chemical fertilizers (Shamseldin and Werner 2005). The atmospheric N_2 is converted into plant-utilizable forms by BNF which changes N_2 to ammonia (NH_4^+) by nitrogen-fixing PGPR using a complex enzyme system known as nitrogenase (Kim and Rees 1994). The importance of this process is saving on the use of chemical fertilizers, providing N in line with the plant's requirements and, consequently, increasing plant yield. Also, the excessive use of bio-fertilizers does not create environmental problems unlike chemical fertilizers. On the other hand, following the planting of leguminous plants, the soil is enriched in terms of N absorption, and the remaining effects of leguminous plants will be useful for subsequent planting (Shamseldin and Werner 2005). Today, in planning for sustainable agricultural systems, the use of this type of symbiosis is considered a basic necessity.

It is known that most legume plants are sensitive or relatively resistant to salinity (Dulormne et al. 2010; Garg and Chandel 2011; Jebara et al. 2010; Khadri et al. 2006; López and Lluch 2008). These plants are dependent on nitrogen fixation for their optimal growth (Chalk et al. 2010; Jebara et al. 2010). Salinity, in addition to its

Table 5.1 Potential application of PGPR and mycorrhizal fungi to improve nutrient availability to salinity-stressed plants

Nutrient	Experimental plant(s)	Microorganism(s)	Amelioration effect of microorganism on salinity-stressed plant	References
N	*Cajanus cajan* (L.)	*Glomus mosseae*	The symbiotic association with AM led to significant improvement in plant dry mass and nitrogen-fixing potential of nodules under salt stress. AM plants had lower trehalase activity under saline and non-saline conditions	Garg and Chandel (2011)
P, K, Zn, and Cu	*Acacia nilotica*	*Glomus fasciculatum*	Mycorrhizal plants maintained greater root and shoot biomass at all salinity levels compared to non-mycorrhizal plants. AM-inoculated plants had higher P, Zn, and Cu concentrations than un-inoculated plants	Giri et al. (2007)
			Mycorrhizal plants accumulated a higher concentration of K at all salinity levels. Mycorrhiza-inoculated plants had lower concentration of Na in shoot tissue. Mycorrhizal fungus alleviated deleterious effects of saline soils on plant growth that could be primarily related to improved P nutrition. The improved K^+/Na^+ ratios in root and shoot tissues of mycorrhizal plants may help in protecting disruption of K-mediated enzymatic processes under salt stress conditions	
P, K, and Zn	Soybean (*Glycine max* L.)	*Glomus etunicatum*	Soybean plants inoculated with the AM fungus had significantly higher fresh and dry	Sharifi et al. (2007)

(continued)

Table 5.1 (continued)

Nutrient	Experimental plant(s)	Microorganism(s)	Amelioration effect of microorganism on salinity-stressed plant	References
			weight, root proline, P, K and Zn compared to non-AM plants	
P, N, and Mg	*Sesbania aegyptiaca* and *S. grandiflora*	*Glomus macrocarpum*	Mycorrhizal seedlings had significantly higher root and shoot dry biomass production than non-mycorrhizal seedlings grown in saline soil. The content of chlorophyll was greater in the leaves of mycorrhiza-inoculated seedlings as compared to un-inoculated seedlings. The number of nodules was significantly higher in mycorrhizal plants than non-mycorrhizal plants. Mycorrhizal seedling tissue had significantly increased concentrations of P, N, and Mg but lower Na concentration than non-mycorrhizal seedlings	Giri and Mukerji (2004)
N	*Cajanus cajan* (L.) Mill sp.	*Glomus mosseae*	AM significantly improved nodulation, leghemoglobin content, and nitrogenase activity under salt stress. Activities of superoxide dismutase (SOD), catalase (CAT) and peroxidase (POX), and glutathione reductase (GR) increased markedly in mycorrhizal-stressed plants	Garg and Manchanda (2008)
P	*Phyllanthus amarus*	*Acinetobacter* sp. and *Bacillus* sp.	Both bacteria alone or in combination promoted a higher vigor index, germination (%), plant biomass, P	Joe et al. (2016)

(continued)

Table 5.1 (continued)

Nutrient	Experimental plant(s)	Microorganism(s)	Amelioration effect of microorganism on salinity-stressed plant	References
			content, plant phenolic content, radical scavenging, and antioxidative activity, compared to un-inoculated control	
N, K, and P	Wheat (*Triticum aestivum* L.)	*Bacillus pumilus*, *B. aquimaris*, *B. arsinicus*, *Arthrobacter* sp., *B. cereus*, *P. mendocina*, and *B. subtilis*	Wheat root dry weight and shoot biomass, proline and total soluble sugar accumulation, and percentage of N, K, and P in leaves of wheat increased significantly after inoculation with PGPR, as compared to un-inoculated plants. These PGPR showed maximum reduction of Na content in wheat leaves of about 23% at both 60 and 90 days after sowing and produced the best yield of around 17.8% more than the control	Upadhyay and Singh (2015)
N and P	*Salicornia bigelovii*	*Azospirillum halopraeferens*, *Azospirillum brasilense*, *Vibrio aestuarianus*, *Vibrio proteolyticus*, *Bacillus licheniformis*, and *Phyllobacterium* sp.	At the end of the growing season, the N and protein content of seeds significantly increased. The P content in foliage increased significantly in plants treated with bacterial strains	Bashan et al. (2000)
P	*Avicennia marina*	*Oceanobacillus picturae*	*O. picturae* significantly increased available P, decreased pH, positively enhanced nutrient uptake parameters in roots and shoots, increased stem circumference, number of xylem vessels, mean xylem diameter, and the hydraulically weighted xylem vessel diameter, compared with non-inoculated plants	El-Tarabily and Youssef (2010)

(continued)

Table 5.1 (continued)

Nutrient	Experimental plant(s)	Microorganism(s)	Amelioration effect of microorganism on salinity-stressed plant	References
N, P, K, and Ca	Groundnut (*Arachis hypogaea* L.)	*Brachybacterium saurashtrense* (JG-06), *Brevibacterium casei* (JG-08), and *Haererohalobacter* (JG-11)	Plant length, root length, shoot dry weight, root dry weight, and total biomass were significantly higher in inoculated plants compared to un-inoculated plants. The PGPR-inoculated plants were quite healthy and hydrated, whereas the un-inoculated plant leaves were desiccated in the presence of 100 mM NaCl. The inoculated plants also had a higher K^+/Na^+ ratio and higher Ca^{2+}, P, and N content	Shukla et al. (2012)
N, P, and K	Maize (*Zeya mays* L.)	*Pseudomonas* and *Enterobacter* spp.	Under stress conditions, more N, P, and K uptake and high K^+/Na^+ ratios were recorded in inoculated plants compared with the control	Nadeem et al. (2009)
N	Peanut	*Klebsiella*, *Pseudomonas*, *Agrobacterium*, and *Ochrobactrum*	A significant increase in total nitrogen (N) content (up to 76%) was observed over the non-inoculated control. Under salt stress, inoculated peanut seedlings maintained ion homeostasis, accumulated less reactive oxygen species (ROS), and showed enhanced growth compared to non-inoculated seedlings	Sharma et al. (2016)
K and Ca	Wheat	*Bacillus licheniformis* HSW-16	Inoculation of *B. licheniformis* HSW-16 protected wheat plants from growth inhibition	Singh and Jha (2016)

(continued)

Table 5.1 (continued)

Nutrient	Experimental plant(s)	Microorganism(s)	Amelioration effect of microorganism on salinity-stressed plant	References
			caused by NaCl and increased plant growth (6–38%) in terms of root length, shoot length, fresh weight, and dry weight. Ionic analysis of plant samples showed that the bacterial inoculation decreased the accumulation of Na^+ content (51%) and increased K^+ (68%) and Ca^{2+} content (32%) in plants at different concentration of NaCl	
N, K, P, Ca, Mg, S, Mn, Cu, and Fe	Strawberry	*Bacillus subtilis* EY2, *B. atrophaeus* EY6, *B. sphaericus* EY30, *Staphylococcus kloosii* EY37, and *Kocuria erythromyxa* EY43	PGPR inoculations significantly increased the growth, chlorophyll content, nutrient element content, and yield of strawberry plants. The highest N, K, P, Ca, Mg, S, Mn, Cu, and Fe concentrations were observed in the inoculated plants	Karlidag et al. (2013)
K, Ca, Mg, and P	Pea (*Pisum sativum* L. cv. Alderman)	*Variovorax paradoxus* 5C-2	*V. paradoxus* 5C-2 increased K, Ca, Mg, and P uptake and root to shoot K flow but decreased Na flow and increased Na deposition in roots. Thus, shoot K^+: Na^+ ratio increased following *V. paradoxus* 5C-2 inoculation	Wang et al. (2016)
N, P, and K	Wheat	*Pseudomonas putida*, *Enterobacter cloacae*, *Serratia ficaria*, and *Pseudomonas fluorescens*	Inoculation with the PGPR resulted a significant increase in the growth and yield parameters of wheat. The inoculated plants also improved the nutrient status of the wheat plants. The	Nadeem et al. (2013)

(continued)

Table 5.1 (continued)

Nutrient	Experimental plant(s)	Microorganism(s)	Amelioration effect of microorganism on salinity-stressed plant	References
			inoculated plants had low Na and high N, P, and K contents	
N, P, K, Ca, and Fe	Cotton	*Raoultella planticola*	*Raoultella planticola* reduced the quantities of ethylene and abscisic acid in cotton seedlings and increased indole-3-acetic acid content in cotton seedlings under salinity stress. The accumulation of N, P, K, Ca, and Fe in the cotton plants was increased significantly in *Raoultella planticola* treatment, whereas the uptake of Na in cotton seedlings decreased	Wu et al. (2012)
K, Ca, and Mg	Maize (*Zea mays* L.)	*Azotobacter sp. C5*	Chlorophyll, Mg, K, Ca, Mg, total polyphenol, and proline of the inoculated plant increased	Rojas-Tapias et al. (2012)

References: Bashan et al. (2000), El-Tarabily and Youssef (2010), Garg and Chandel (2011), Garg and Manchanda (2008), Giri et al. (2007), Giri and Mukerji (2004), Joe et al. (2016), Karlidag et al. (2013), Nadeem et al. (2009, 2013), Rojas-Tapias et al. (2012), Sharifi et al. (2007), Sharma et al. (2016), Shukla et al. (2012), Singh and Jha (2016), Upadhyay and Singh (2015), Wang et al. (2016), and Wu et al. (2012)

negative effect on plant growth, has a negative effect on the nitrogen fixation process, such as nodule growth (Abdelmoumen and El Idrissi 2009), symbiotic activity (Dulormne et al. 2010; Jebara et al. 2010), activity of the nitrogenase enzyme (Jebara et al. 2010), nodule respiration (Dulormne et al. 2010; López and Lluch 2008), nodule establishment (Aydi et al. 2008), leghemoglobin, acetylene-reduction activity, and nitrogen content of legume plants (Garg and Chandel 2011), for example, in soybean (*Glycine max*) (van Hoorn et al. 2001), mung bean (*Vigna mungo* L. Hepper) (Mensah and Ihenyen 2009), common bean (*Phaseolus vulgaris*), faba bean (*Vicia faba*) (Rabie and Almadini 2005), and goat's rue (*Galega officinalis*) (Egamberdieva et al. 2013; Paul and Lade 2014).

In addition to the effect of salinity on the nitrogen fixation process, salinity also affects the establishment and activity of the legume-*Rhizobium*, which is susceptible to salinity (Jebara et al. 2010). It is known that environmental stresses including salinity stress have a negative effect on the number of rhizobial isolates, BNF capacity (Duzan et al. 2004), and the ability to produce some bacterial metabolites

(Sánchez-Porro et al. 2009; Upadhyay et al. 2009; Yoon et al. 2001). There are different rhizobial strains in soil that their effect on their host is not the same in terms of BNF and dealing with environmental stresses (Rehman and Nautiyal 2002). In order to obtain the best bio-fertilizers, the exact identification of the isolates of each region and their biological ecology, the isolation of the specific rhizobial isolates of each plant, and the adaptation of these rhizobial isolates to different climatic conditions are necessary. Therefore, selection and breeding of genotypes and halotolerant rhizobial strains that can grow under stress conditions might be an effective tool at resolving the soil reclamation practices.

The combined use of AM fungi with rhizobial bacteria has also been suggested as an effective strategy to increase plant growth and nitrogen fixation under salinity stress (Chalk et al. 2006; Franzini et al. 2010; Garg and Chandel 2011). AM fungi could neutralize harmful effects of salinity on nodulation and nitrogen fixation and thereby alleviate the salinity-induced premature nodule senescence (Garg and Chandel 2011; Garg and Manchanda 2008, 2009; Goss and De Varennes 2002; Patreze and Cordeiro 2004) by different ways such as (i) increasing the fitness of host plants by enhancing shoot and root biomass (Garg and Chandel 2011); (ii) enhancing host plant P nutrition and other nutrients with low mobility, such as Fe, Cu, and Zn (Kaya et al. 2009a; Miransari and Smith 2008); (iii) decreasing uptake of Na by salinity-stressed plant (Al-Karaki 2006; Chakraborty et al. 2008; Giri et al. 2007); and (iv) stimulating the salinity-induced accumulation of trehalose, a carbohydrate in osmoprotection and osmotic adjustment against salinity stress, by inhibiting trehalase activity in AM plants and increasing total soluble sugars (Garg and Chandel 2011).

One of the responses of salinity-stressed plants (osmotic adjustment) against salt stress is various organic compounds, collectively known as compatible solutes or osmolytes (Contreras-Cornejo et al. 2009; Cortina and Culiáñez-Macià 2005). These compounds play an important role as an abiotic stress protectant in a wide variety of organisms (Contreras-Cornejo et al. 2009; Elbein et al. 2003; Fernandez et al. 2010; Garg and Chandel 2011). Trehalose (α-ᴅ-glucopyranosyl-1,1-α-ᴅ-glucopyranoside) is one of these osmolytes that has been detected in symbiotic nitrogen-fixing bacteria such as *Rhizobium* (the accumulation in bacteroids and in nodules of leguminous plants) (Müller et al. 2001). This compatible solute plays an important role in the maintenance of efficient nitrogen fixation, protection of bacterial nitrogenase activity, and whole plant tolerance under drought and salinity stresses (Farías-Rodríguez et al. 1998; Garg and Chandel 2011; López et al. 2008; Zacarías et al. 2004). The ability of AM fungus has been shown to increase plant nitrogen content under saline conditions. For an example, in a study, Giri and Mukerji (2004) showed that AM-inoculated plants had significantly greater concentration of N and the greater number of nodules than non-mycorrhizal plants under salinity stress. Increased N concentration under saline conditions may help to decrease Na uptake, which may be indirectly related to maintaining the chlorophyll content of the plant (Giri and Mukerji 2004). Improved nodulation and N fixation in mycorrhizal plants may be because of alleviation from P stress and possibly to absorption of some essential micronutrients, which leads both to enhanced growth of plants and has an indirect effect on the N-fixing system (Founoune et al. 2002).

Environmental conditions such as stresses affect the production of extracellular polysaccharides (EPS) of rhizobia strains, so that these strains produce more EPS to withstand adverse environmental conditions (Ashraf et al. 2004; Delavechia et al. 2003). It has been reported that salinity- and drought-tolerant rhizobial strains produce more EPS content and, by increasing the amount of EPS, tolerate unsatisfactory conditions and continue to grow (Ashraf et al. 2004; Delavechia et al. 2003). On the other hand, the survival of rhizobial strains in soil depends on the ability of these strains to bind to the host plant and to create a symbiotic relationship. Among these, EPS are of particular importance in the specialization of rhizobia in identifying these strains by the host plants (Werner 1992). The EPS of the rhizobial strains play an important role in the process of recognizing legume-rhizobium as well as protecting the bacterial cell against environmental stresses (Werner 1992). Therefore, EPS-producing salinity-resistant rhizobial strains can not only tolerate the conditions of salinity stress but can also act more successful in creating a symbiotic relationship with the host plant than salinity-sensitive rhizobial strains. In several experiments conducted in salinity and drought regions, it was observed that the salinity- and drought-resistant rhizobial isolates isolated from salt-affected soils were of significant efficiency (Shamseldin and Werner 2004, 2005).

Since essential plant nutrients are taken up from the soil by roots (Mills et al. 1996), good root growth is considered a prerequisite for enhanced plant development. The morphological modification of roots plays an important role in the mechanisms of stress response (Carmen and Roberto 2011). Microorganisms increase root system of plants by production of phytohormone IAA and ACC deaminase. In addition to the production of IAA, gibberellins and other growth regulators produced by PGPR can support the increase of root length, root surface area, and number of root tips, leading to enhanced uptake of nutrients, thereby improving plant health under stress conditions (Egamberdieva and Kucharova 2009; Etesami and Maheshwari 2018). Rhizobacteria-mediated root proliferation has been well proved, and it also works in stressed soils (Diby et al. 2005a). Inoculation of various plant species with PGPR has also reported to lead to enhanced formation of lateral roots and root hairs that can result in enhanced tolerance to abiotic stress (Etesami and Maheshwari 2018; Paul and Lade 2014). Promotion of root growth results in a larger root surface and can, therefore, have positive effects on water acquisition and nutrient (i.e., N) uptake (Diby et al. 2005b; Paul and Sarma 2006) that is expected to alleviate the stress effects in the plant (Chakraborty et al. 2006; Hamdia et al. 2004; Long et al. 2008; Paul and Sarma 2006). Microbial IAA is involved in many processes of nodule formation by rhizobia in legume plants, such as founder cell specification, nodule initiation and differentiation (IAA accumulation), nodule numbers, vascular bundle formation, and cell division and differentiation (Etesami et al. 2015b; Etesami and Beattie 2017). These three later events are more necessary for nodule formation (Glick 2012; Theunis 2005). In addition, due to having the function in increased root system, IAA-producing bacteria can provide more number of active sites and access to colonization for N_2-fixing bacteria or PGPR.

Previous studies indicate that salinity can either decrease (300 mM NaCl) (Dunlap and Binzel 1996) or increase (100 mM NaCl) (Albacete et al. 2008) root IAA accumulation in plant, which might affect cell elongation and root growth. It has been known that the bacteria isolated from saline environments have been able to produce IAA in the presence of salinity (Etesami and Beattie 2018). In a study, Sadeghi et al. (2012) demonstrated that a *Streptomyces* isolate increased plant growth in wheat and produced IAA in the presence of salt. The ability to modify plant stress levels by providing IAA, a molecule involved in the development of lateral roots, has also been reported for halotolerant bacteria isolated from saline habitats and halophytes (Bian et al. 2011; Marasco et al. 2012; Naz et al. 2009; Piccoli et al. 2011; Sgroy et al. 2009; Siddikee et al. 2010; Tiwari et al. 2011). *Arthrobacter* sp., *Nitrinicolalacis aponensis*, *Brachybacterium* sp., *B. saurashtrense*, *Brevibacterium casei*, *Br. halotolerans*, *Haererohalobacter* sp., *Klebsiella* sp., *Pseudomonas* sp., *P. stutzeri*, *P. pseudoalcaligenes*, *P. putida*, *P. mendocina*, *Agrobacterium tumefaciens*, *Ochrobactrum anthropi*, *Bacillus* sp., *B. cereus*, *B. pumilus*, *B. simplex*, *B. mycoides*, *B. aquimaris*, *B. licheniformis*, *B. mycoides*, *B. subtilis*, *Sporosarcina aquimarina*, *Serratia marcescens*, *S. plymuthica*, *S. plymuthica*, *Thalassospira permensis*, *Acinetobacter*, *Microbacterium* sp., *M. oxydans*, *Streptomyces* sp., *S. avidinii*, *S. europaeiscabiei*, *S. exfoliatus*, *S. umbrinus*, *S. griseoplanus*, *Rhodococcus* sp., *R. equi*, *R. erythropolis*, *Micrococcus luteus*, *Marinococcus halophilus*, *Nocardia* sp., *Halomonas* sp., *H. elongata*, *H. eurihalina*, *H. sinaiensis*, *H. halmophila*, *H. ilicicola*, *H. indalina*, *H. variabilis*, *H. xinjiangensis*, *H. taeheungii*, *Halobacillus trueperi*, *Nesterenkonia halobia*, *Oceanobacillus picturae*, *Kushneria*, *Virgibacillus olivae*, *Lysinibacillus fusiformis*, *Achromobacter xylosoxidans*, *Mesorhizobium* sp., *Zhihengliuella* sp., *Vibrio alginolyticus*, and *Cronobacter sakazakii* are some examples of IAA-producing salt-tolerant PGPR isolated from halophytes (Gontia et al. 2011; Mapelli et al. 2013; Sgroy et al. 2009; Sharma et al. 2016; Shukla et al. 2012; Tiwari et al. 2011). According to the above studies, it can be concluded that salinity-resistant rhizobacteria or rhizobial bacteria with the ability to produce IAA may help to increase the resistance of plants to salinity stress and increase the amount of N in the plants.

One of the responses of plants under stress conditions such as salinity stress is the increase in the level of intracellular ethylene inside the plant (stress ethylene). Stress ethylene reduces the vegetative stage of plant growth and eventually decreases the plant yield (Etesami and Maheshwari 2018; Glick 2005). Siddikee et al. (2011) also stated that the ethylene produced in response to salinity stress reduced root growth and thus reduced water and nutrient uptake and finally decreased plant growth. Previous researchers found that formation and function of nitrogen-fixing nodules on legume roots were severely inhibited by addition of exogenous ethylene (Peters and Crist-Estes 1989). Ethylene inhibits the elongation of infection threads and, consequently, the formation of nodules in most legumes (Etesami et al. 2015b; Sugawara et al. 2006). In addition, production of ethylene, a signal molecule for induced systemic resistance in plants, decreases endophytic colonization in plants (Iniguez et al. 2005). The overproduction of ethylene can also cause the inhibition of root elongation, lateral root growth, and root hair formation (Belimov et al. 2009; Mayak et al. 2004b; Saleem et al. 2007), which subsequently results in decreasing the nodule number of on root. Some soil bacteria produce ACC deaminase enzyme. This enzyme converts ACC (a substrate for ethylene production) to α-ketobutyrate and ammonium. By modifying the ACC production in plants, ACC deaminase-producing bacteria can prevent the excess ethylene production in the plant (Glick 2014). The ACC deaminase trait has been extensively studied in numerous soil microbial species, that is, bacteria, fungi, and endophytes; however, this trait is most common among PGPR (Etesami and Maheshwari 2018; Glick 2005) such as the genera *Achromobacter*, *Acidovorax*, *Alcaligenes*, *Enterobacter*, *Klebsiella*, *Methylobacterium*, *Pseudomonas*, *Rhizobium*, and *Variovorax* (Esquivel-Cote et al. 2010). Ahmed et al. (2004) found that ACC deaminase-producing bacteria increased grain yield, root weight, root length, and more nitrogen uptake in straw and wheat grain by decreasing stress ethylene level compared to control.

Salinity has been shown to cause PGPR to lose their ACC deaminase enzyme production (Upadhyay et al. 2009). However, it has been found that ACC deaminase-producing salt-tolerant PGPR can survive well in a saline environment and that their beneficial properties help plants to overcome stress effects by reducing ethylene levels (Mayak et al. 2004a). The production of enzyme ACC deaminase has also been well reported in halotolerant bacteria isolated from halophytic plants and from saline environments (Jha et al. 2012; Siddikee et al. 2010; Zhou et al. 2017). The roots of halophytes may be associated with promising ACC deaminase-producing bacterial candidates for promoting growth and salt tolerance in crops (Etesami and Beattie 2018). For example, novel diazotrophic halotolerant bacteria from roots of *Salicornia brachiata* featured ACC deaminase activity and these isolates included *Brachybacterium saurashtrense*, *Brevibacterium casei*, *Cronobacter sakazakii*, *Haererehalobacter*, *Halomonas*, *Mesorhizobium*, *Pseudomonas*, *Rhizobium radiobacter*, *Vibrio*, and *Zhihengliuella* (Jha et al. 2012). Examples of halotolerant ACC deaminase-producing PGPR include *Micrococcus yunnanensis*, *Planococcus rifietoensis*, *Variovorax paradoxus*, *Brachybacterium saurashtrense*, *Klebsiella* sp., *Pseudomonas* sp., *P. stutzeri*, *P. putida*, *Agrobacterium tumefaciens*, *Ochrobactrum anthropi*, *Serratia marcescens*, *S. plymuthica*, *Thalassospira permensis*, *Microbacterium* sp., *M. oxydans*, *Bacillus* sp., *B. cereus*, *B. licheniformis*, *B. pumilus*, *B. subtilis*, *B. mycoides*, *S. plymuthica*, *M. oxydans*, *Microbacterium* sp., *Streptomyces* sp., *Rhodococcus* sp., *Rh. erythropolis*, *Nocardia* sp. *Halomonas taeheungii*, *H. xinjiangensis*, *Brevibacterium halotolerans*, *Achromobacter xylosoxidans*, *Zhihengliuella* sp., *Mesorhizobium* sp., *Brachybacterium* sp., *Vibrio alginolyticus*, *Brevibacterium casei*, *Cronobacter sakazakii*, *P. pseudoalcaligenes*, *Haererehalobacter* sp., *Pantoea agglomerans*, *P. oryzihabitans*, and *Halomonas* sp. (Gontia et al. 2011; Jha et al. 2012; Mapelli et al. 2013; Sgroy et al. 2009; Sharma et al. 2016; Szymańska et al. 2016; Teng et al. 2010; Zhou et al. 2017), which were isolated from species of halophytes. Generally, it seems that the production of IAA and ACC deaminase by salinity-tolerant PGPR might be an important tool in salt tolerance of plants/legumes in salt-affected soils (Etesami and Beattie 2018; Etesami and Maheshwari 2018).

5.4 PGPR and AM Fungi-Mediated Increase of P Availability Under Salinity Stress

Phosphorus (P) is an important and essential macronutrient for plants and microorganisms that its shortage restricts plant growth and development and, unlike N, does not have a large atmospheric source (Katznelson et al. 1962). Stem development, root and shoot firmness, fixation of nitrogen in legumes, macromolecular biosynthesis, improvement in crop quality, production and transfer of energy, photosynthesis, and resistance to plant diseases are related to P nutrition (Roychoudhury and Kaushik 1989). The deficiency of P supply and availability also remains a severe limitation on nitrogen fixation and symbiotic interactions (Pereira and Bliss 1989). In contrast to N, phosphate compounds are relatively insoluble and therefore are not easily leached from the soil profile. Usually, low amounts of P in soils and its tendency to react with soil constituents and the production of relatively insoluble compounds and therefore nonabsorbable compounds for plants make P very important for soil fertility. It is worth mentioning that the total amount of P in soil is much more than available P, but the importance of the available P in plant growth is higher. Phosphorus is predominantly found in mineral soil parts, either as adsorbed on mineral surfaces of soil or as relatively soluble sediments, or in organic forms that are either as adsorbed on mineral surfaces of soil, or as a part of microbial biomass or with organic matters. Phosphorus is extracted from phosphate rock (over 80% of phosphate rock reserves are utilized for fertilizer production) (Owen et al. 2015), which is a nonrenewable resource. This is very important for a number of countries without phosphate rock (Van Vuuren et al. 2010). The extraction of P minerals and spread of P fertilizers in agricultural land are not sustainable due to the limited resources of P, and this will make production of this fertilizer in the future difficult. In addition, in practice, P use efficiency (recovery of fertilizer P) is between 10% and 25%. That is, about 75% of this fertilizer in soil is converted into insoluble forms by reacting with metal cations (formation of complexes with Fe^{3+}, Al^{3+} and Ca^{2+}) (Gyaneshwar et al. 2002; Stevenson and Cole 1999).

Plants absorb P mainly as primary and secondary ions of orthophosphates ($H_2PO_4^-$ and HPO_4^{2-}), which are present in the soil solution. The concentration of these ions in the soil solution at any time is negligible (Marschner 1995) and often is less than 0.1 mg L^{-1}. The P in the soil solution should be renewed continuously; otherwise the plant will not have sufficient P to complete its growth. The concentration of various P ions in soil solution is closely related to the pH of environment. Acidic environments are suitable for $H_2PO_4^-$ ions and pH-containing environments higher than 7 for HPO_4^{2-} ions. According to a general experimental law, the maximum usable P for most agricultural plants is when the soil pH is in the range of 5.5–7. The P in calcareous soils is converted into insoluble calcium and magnesium compounds and in acid soils into iron and aluminum phosphates, thereby reducing its access to plants. In general, different forms of P in soil are controlled by the soil's natural properties, including pH, the soluble and exchangeable cations (Ca^{2+}, Mg^{2+}, Fe^{2+}, etc.), the type of soil particles, and their surface (Penfold 2001).

Salinity also reduces phosphorus (P) uptake/accumulation in crops grown in soils primarily by reducing P availability (Etesami and Maheshwari 2018; Paul and Lade 2014) because phosphate ions precipitate with Ca^{+2} ions (Navarro et al. 2001; Parida and Das 2005; Rogers et al. 2003). In addition, the reduction in P availability in saline soils was suggested to be a result of ionic strength effects that reduce the activity of phosphate and the tight control of P concentrations by sorption processes and by low solubility of Ca-P minerals. In saline soils, due to the presence of cations (e.g., Ca^{2+} and Mg^{2+}) in high concentrations, it is possible to form insoluble cation-phosphorus compounds in salt-affected soils (Etesami and Maheshwari 2018). Previous studies also showed that salinity could reduce the P uptake by plant (Barea et al. 2005; Patel et al. 2010). For example, Patel et al. (2010), in a study, showed that salinity reduces the P uptake by plant (*Acacia auriculiformis* A. Cunn. Ex Benth). In addition to forming insoluble cation-phosphorus compounds, decrease in the P uptake by plant under salinity stress can also be associated with the poor root development (Rawal and Kuligod 2014).

One of the ways to meet the P requirement of plants in saline or non-saline soils is to use chemical fertilizers; however, due to their limited resources, the increase in their cost, the environmental hazards resulting from their application, and the fixation of a large part of the P fertilizers consumed as insoluble forms for plant, attention to use of phosphate bio-fertilizers has been increasing in the past decades. It is well found that soil microorganisms (bacteria, fungi, actinomycetes, and even algae) interfere with some of the solubilizing processes of phosphate, which affect the transformation and maintenance of the status of P and ultimately its bioavailability for the plant (Richardson 2001; Sharma et al. 2013).

It is well known that various PGPR can increase the availability of nutrients to plant. For example, phosphate-solubilizing microorganisms (PSMs) provide P available to plants by different mechanisms (Sharma et al. 2013). There is evidence that soil phosphate-solubilizing bacteria (PSB) can solubilize and convert insoluble phosphorus into available forms to plant. Also, microbial biomass with absorption of soluble phosphorus prevents precipitation or fixation of P in the soil (Khan et al. 2007).

PSMs form a significant part of the population of soil microorganisms (Kucey et al. 1989). Bacteria and fungi account for the highest percentage of PSMs in soil; therefore they are divided into two groups of phosphate-solubilizing bacteria (PSB) and phosphate-solubilizing fungi (PSF) (Whitelaw et al. 1997). PSB can solubilize insoluble P compounds and release P from these compounds (Sharma et al. 2013). The most important types of PSB can be referred to *Enterobacter agglomerans*, *Bacillus circulans*, *B. subtilis*, *B. megaterium* var *phosphaticum*, *Pseudomonas putida*, *P. fluorescens*, *P. striata*, *Pantoea*, *Paenibacillus polymyxa*, *Rhizobium leguminosarum* bv. *trifolii*, *Xanthobacter agilis*, *Klebsiella*, and *Agrobacterium radiobacter*, and fungi *Aspergillus* and *Penicillium* are of the most important types of PSF (Sharma et al. 2013). It has been also reported that PSF produce more acids compared to PSB (Venkateswarlu et al. 1984) and are able to traverse long distances more easily than PSB and hence may be more important to P-solubilization in soils (Kucey 1983). Overall, due to having a higher population density, bacteria may be very effective at solubilizing phosphates compared to fungi.

The solubilization and mineralization of P in the rhizosphere is the most important mechanism of PGPR including PSB that provide plants with the nutrient. PSB play an important role in three main components of soil P cycles such as dissolution-precipitation, absorption and desorption (interactions between mineral surfaces and P), and mineralization-immobilization (transformation of organic P to inorganic P by biological transformations) (Gyaneshwar et al. 2002; Jones and Oburger 2011; Owen et al. 2015). PSB and their interactions with soil play a critical role in mediating the distribution of P between the soluble P reservoir in the soil solution and the total P of the soil through solubilization and mineralization reactions, the immobilization of P into the microbial biomass, or the formation of relatively available organic P and mineral forms. In general, PSB convert insoluble phosphate compounds into soluble forms by producing and releasing metabolites such as organic acids that, through their hydroxyl and carboxyl groups, chelate the cations (mainly calcium) bound to phosphate (Miller et al. 2010; Sagoe et al. 1998).

Some of the potential known mechanisms through which PSB could mobilize the soil P unavailable for plants include:

1. Acidification of rhizosphere medium by production of mineral acids and H^+ extrusion or NH_4^+ absorption (release of H^+ ions from the roots during the assimilation of $NH^+{}_4$) (Illmer and Schinner 1992).
2. Exchange reactions. In this process, the low molecular weight organic anions (e.g., succinic, citric, gluconic, α-ketogluconic, and oxalic acids) produced by PSB are exchanged for P on adsorption sites of soil (Chen et al. 2006; Jones and Oburger 2011; Zhang et al. 2014). The organic acids/organic anions (e.g., lactic acid, tartaric acid, aspartic acid, gluconic acid, oxalic acid, and citric acid) produced by PSB can also lower pH, compete with P for adsorption sites on the soil, and form soluble complexes with metal ions associated with insoluble P (Ca, Al, and Fe) (Sharma et al. 2013).
3. Releasing CO_2 during respiration. The formed carbonic acid caused by being dissolved CO_2 in water (present in the soil pores) can solubilize P by diminishing the mycorrhizosphere pH (Marschner 1995).
4. Stimulating the indirect dissolution of calcium phosphate (Ca-P) by removing and assimilating phosphate from the soil (sink theory) to re-establish the P equilibrium (Halvorson et al. 1990).
5. The release of chelating compounds (e.g., siderophores, enzymes, phenols, amino acids, sugars, and organic acid anions). These compounds reduce metals with variable oxidation states, which bound to phosphate, to a lower oxidation state, resulting in more soluble phosphate (Kim et al. 1997).
6. The secretion of extracellular alkaline and acid phosphatases or phytases (enzymatic hydrolysis), which convert organic phosphate into an inorganic form (Etesami and Maheshwari 2018; Franco-Correa et al. 2010; Gyaneshwar et al. 2002; Owen et al. 2015; Sharma et al. 2013).

It has been reported that the main mechanism for mineralization of organic P is the production of acid phosphatases (Khan et al. 2009; Sharma et al. 2013). Species of genera *Bacillus*, *Burkholderia*, *Enterobacter*, *Pseudomonas*, *Rhizobium*, *Serratia*, and *Staphylococcus* are the most important bacteria involved in P mineralization (Shedova et al. 2008).

Previous studies have shown that PSB have also other PGP traits (Etesami and Maheshwari 2018; Sharma et al. 2013). Based on scientific findings, plant growth-promoting bacteria (PGPB) probably have more than one mechanism for plant growth (Etesami and Maheshwari 2018). It has been shown that the increase in plant growth and yield was not associated with the application of PSB by increasing P uptake in plants (Poonguzhali et al. 2008). It is believed that PSMs, in fact, have potential for controlling plant pathogens as well as plant growth promotion through the production of siderophores, ACC deaminase, and IAA (Han and Lee 2006; Sharma et al. 2013). As an example, Gulati et al. (2010) reported that the phosphate-solubilizing strain BIHB723 belonging to *Acinetobacter* was capable of producing other PGP metabolites such as IAA, ACC deaminase, siderophore, and ammonia. In addition to solubilization of P in growth medium (rhizosphere), P absorption by the plant depends on root growth. The root system is especially important because it helps the plant to absorb water and nutrients (Etesami and Alikhani 2016a; Fageria and Moreira 2011). The absorption of P by plant is proportional to root density, so increasing rooting system increases the plant's ability to absorb P from soil (Grant et al. 2001). For example, Iqbal Hussain et al. (2013) stated that increased P uptake by plant could be due to increased root growth or root hair lengthening by specific microorganisms. It has been reported that low amounts of IAA result in prolonged initial roots, while high levels of IAA lead to an increase in the formation of lateral roots (Xie et al. 1996). Also, keeping the concentration of ethylene in low amounts can increase root growth. PSB with the ability to produce ACC deaminase can maintain the concentration of ethylene in low amounts through the hydrolysis of ethylene to ammonia and α-ketobutyrate (Pereira and Castro 2014). It seems that the combination of these mechanisms in PSB has the most effect on increasing plant growth indices under nutritional deficiency stress such as P (Etesami and Maheshwari 2018).

It has been found that the establishment and performance of PSMs are affected severely under environmental stresses including salinity (Johri et al. 1999). In other words, the solubilization ability of phosphate by PSMs decreases in the presence of salinity (decrease in the amount of inorganic P released by PSMs with increase in NaCl concentration) (Cherif-Silini et al. 2013; Sánchez-Porro et al. 2009; Srinivasan et al. 2012). However, it has been reported that the microorganisms (halotolerant microorganisms) isolated from saline environments or halophytes were able to maintain their ability in solubilizing phosphate in the presence of salinity (better performance of PSMs of salt-affected soils in releasing inorganic P from TCP (tricalcium phosphate) under salt stress conditions) (Etesami and Beattie 2018). It has been reported that PSB were also isolated from the stressed environments (Chen 2006; Etesami and Beattie 2018; Etesami and Maheshwari 2018). For example, the *Kushneria sinocarni*, a salt-loving strain, were isolated from salt lake sediments on the east coast of China and showed phosphate solubilization (Zhu et al. 2011). In another study, Srinivasan et al. (2012) showed that the amount of inorganic P released from TCP by the PSB strains (e.g., *Aerococcus* sp. strain PSBCRG1–1, *Pseudomonas aeruginosa* strain PSBI3–1, *Alteromonas* sp. PSBCRG, etc.) was found to increase with an increase in salt concentration up to 800 mM NaCl, whereas the reference strain (*P. striata*) showed a significant decrease in P-solubilization at NaCl concentrations. Phosphate-solubilizing salinity-resistant bacteria (e.g., *Klebsiella* sp., *Pseudomonas* sp., *P. stutzeri*, *Agrobacterium tumefaciens*, *Ochrobactrum anthropi*, *Halomonas elongata*, *H. eurihalina*, *H. sinaiensis*, *H. halmophila*, *H. ilicicola*, *H. indalina*, *H. variabilis*, *H. xinjiangensis*, *H. taeheungii, Zhihengliuella* sp., *Vibrio alginolyticus*, *Brevibacterium casei*, *Marinococcus halophilus, Halobacillus trueperi*, *Nesterenkonia halobia*, *Oceanobacillus picturae*, *Virgibacillus olivae*, *Chromohalobacter marismortui*, *Haererehalobacter* sp., *Cronobacter sakazakii*, and *Chromohalobacter salexigens* (Jha et al. 2012; Mapelli et al. 2013; Sharma et al. 2016) were also isolated from halophytes such as *Arthrocnemum indicum*, *Salicornia strobilacea*, and *Salicornia brachiate*. These bacteria were also able to supply the plant P and thus the growth of the plant under saline conditions. For example, following the inoculation of *Solanum lycopersicum* plant with phosphate-solubilizing *Achromobacter piechaudii*, the amount of plant P increased under salinity stress (Mayak et al. 2004a). In another study, the content of P in leaves of salinity-stressed wheat inoculated with phosphate-solubilizing *B. aquimaris* was significantly enhanced in a field experiment (Upadhyay and Singh 2015). A screen of the mangrove *Avicennia marina* rhizosphere identified 129 bacterial strains with the ability to solubilize rock phosphate up to 97% (El-Tarabily and Youssef 2010). Phosphate-solubilizing bacteria isolated from halophytes (e.g., *Arthrobacter*, *Bacillus*, *Azospirillum*, *Vibrio*, *Phyllobacterium*, and *Oceanobacillus picturae*) were able to solubilize $Ca_3(PO4)_2$, $AlPO_4$, and $FePO_4$ (Banerjee et al. 2010; Bashan et al. 2000; El-Tarabily and Youssef 2010; Yasmin and Bano 2011) and increase P content in both host plants and nonhost plants (halophytes and glycophytes) under salinity stress. In addition, when the oilseed halophyte *Salicornia bigelovii* was inoculated with phosphate-solubilizing halotolerant bacteria (i.e., *Vibrio*, *Azospirillum*, *Bacillus*, and *Phyllobacterium*), content of P in foliage also increased over non-inoculated plants (Bashan et al. 2000).

As mentioned above, in addition to bacteria, ability of solubilizing insoluble phosphate compounds in fungi has been well proven, constituting about 0.1–0.5% of total fungal populations (Kucey 1983). It is well known that the mycorrhizal association increases host nutrient acquisition, particularly P (Smith and Read 2010). In one study, the effects of AM fungi *Glomus intraradices* and *Gigaspora margarita* on *Plantago lanceolata* in poor soils showed that these fungi could increase the absorption of nutrients such as N, P, and K, but the effectiveness of each fungus was different (Veresoglou et al. 2011). The effect of mycorrhizal fungi on increasing P absorption by plant is one of the most important effects of these fungi. Mycorrhizal fungi extend beyond the root-depleted zone and play an important role in exploring and extracting P outside the root-depleted zone. In addition, other auxiliary mechanisms have been proposed for P uptake by mycorrhizal fungi. Mycorrhizal hyphae have a lower Km than the roots of plants. As a result, the minimum concentration or threshold concentration for fungal hyphae fungi is lower than roots of plant. Mycorrhizal hyphae have the ability to access microsites. These fungi can access the inorganic and organic P forms that are inaccessible to non-mycorrhizal plants (Zwetsloot et al. 2016). By secreting organic acids, which mobilize inorganic P from rock phosphate and phosphatase enzymes, fungi such as *Aspergillus* and *Penicillium* spp. and AM fungi belonging to the phylum Glomeromycota *Rhizophagus intraradices* and *Funneliformis mosseae* (Krüger et al. 2012) were able to increase the P availability and consequently enhance P uptake in diverse crop plants (Barrow and Osuna 2002; Cozzolino et al. 2013; Koide and Kabir 2000; Owen et al. 2015; Richardson and Simpson 2011; Smith et al. 2011; Vassilev et al. 1996; Williams et al. 2013). These fungi can also increase immobile nutrient absorption potential such as PO_4^{3-}, as a slowly diffusing ion, by forming an extensive mycelial network within the soil (Owen et al. 2015) that extends the plant's effective absorption surfaces beyond the nutrient-depleted zone that develops around the root caused by direct root uptake processes (Porcel et al. 2012). Fungal hyphae, which are functionally analogous to fine root hairs, also support a microbial community (Andrade et al. 1998) with a high potential in mineralizing and solubilizing recalcitrant nutrient complexes which are then transported to the plant via the mycelial network (Owen et al. 2015; Toljander et al. 2007).

Phosphate-solubilizing fungi have also been isolated from saline environments. For an example, PSF such as *Aspergillus* sp. PSFNRH-2, isolated from salt-affected soils, showed significant increase in P-solubilization with increase in NaCl concentration up to 1.0 M than the reference strain irrespective of NaCl concentrations (Srinivasan et al. 2012). According to previous studies (Al-Karaki 2000; Giri et al. 2003; Hirrel and Gerdemann 1980; Ojala et al. 1983; Pond et al. 1984; Poss et al. 1985), the improved growth of mycorrhizal plants was primarily related to mycorrhiza-mediated enhancement of host plant P nutrition (as the most important strategy of salinity stress tolerance in AM-colonized plants) in saline conditions. It has been reported that AM fungus moderates the negative effects of Na^+ and Cl^- on salinity-stressed plant by increasing the availability of P of the plant (Pfetffer and Bloss 1988; Poss et al. 1985) and maintaining vacuolar membrane integrity, which prevents these ions from interfering in growth metabolic pathways (Cantrell and Linderman 2001) and facilitates compartmentalization within vacuoles and selective ion intake (Rinaldelli and Mancuso 1996). The above findings can be interpreted as evidence of the salinity-resistant phosphate-solubilizing fungi and PGPR's ability to solubilize insoluble P compounds under salinity stress.

5.5 PGPR and AM Fungi-Mediated Increase of K Availability Under Salinity Stress

Potassium (K) is one of the essential macronutrients of plants and is the most abundant nutrient in plants after N. This nutrient is considered as a key parameter of soil fertility and plant growth as without adequate K, the plants will have poorly developed roots, grow slowly, produce small seeds, and have lower yields (Parmar and Sindhu 2013). Potassium plays a very important role in photosynthesis, cell division and growth, protein production, quantity and quality of products, and increased plant resistance to diseases and pests (Saber and Zanati 1984). Potassium is also required to activate over 80 different enzymes responsible for such plant and animal processes as energy metabolism, starch synthesis, nitrate reduction, photosynthesis, and sugar degradation. Without adequate amounts of K, water is lost from the cells, and the plant cells weaken and start to wilt. Potassium-deficient plants will have poorly developed cell walls with lower levels of stored protein and starch, and they become an easy meal for sucking insects and an easy target for invasion by fungal spores (Meena et al. 2014, 2015).

More than 90% of K in the soil exists in the form of insoluble rocks and silicate minerals (Etesami et al. 2017; Parmar and Sindhu 2013). Most of the K is unavailable for plant uptake. Muscovite, orthoclase, biotite, feldspar, illite, and mica are of the most important minerals including K, and the major amounts of K are present in the soil as a fixed form which is not directly taken up by plant. Plants obtain K from K originated from the addition of chemical fertilizers and/or K present in soil (Sparks and Huang 1985). Most soils have relatively high amounts of total K, but their available K is relatively low. Potassium is present in several forms in the soil, including mineral K (more than 90–98% of soil K), non-exchangeable K (approximately 1–10% of soil K), exchangeable K, and dissolved or solution K. Among different forms of K, its available (water-soluble K) and exchangeable forms are available for the use of plants, and the rest of the forms are almost non-available for the use of plants (Sparks and Huang 1985). Plants absorb K mainly in the form of K^+ and from the soil solution. The amount of K of soil solution is very variable and is typically between 1 and 10 mg/kg. The clay minerals contain a large amount of K, and often there is a positive correlation between available K (water-soluble K) and the amount of clay minerals in the soil (Sparks and Huang 1985). Non-exchangeable K plays a significant role in plant nutrition under intensive cultivation conditions, especially in cases where exchangeable K is less than the plant's adequacy limit (Mc Lean and Watson 1985). When soluble and exchangeable K of the soil decreases to less than the plant's adequacy limit, non-exchangeable K can be released from the layers of clay minerals (Tributh et al. 1987). The amount of K released in these conditions is influenced by the amount and type of K-bearing minerals such as muscovite, potassium feldspar, and vermiculite (Steffens and Sparks 1997). Many studies have shown that the release of non-exchangeable form and structural unavailable forms of K compounds in to soil solution can significantly contribute to the amount of K absorbed by the plant (Snapp et al. 1995).

In addition to imbalanced fertilizer application, the introduction of high-yielding crop varieties/hybrids, and the progressive intensification of agriculture, which deplete K reserve of soils at a faster rate (Parmar and Sindhu 2013), soil salinity has also caused K deficiency to be one of the major constraints in crop production. Sodium-induced K^+ deficiency has been implicated in various crops (Botella et al. 1997). It has been reported that salinity (Na^+ ions) affects K uptake by plant and prevents its absorption (Barea et al. 2005; Colla et al. 2008; Rawal and Kuligod 2014) by interfering with various transporters (competing with K for binding sites essential for various cellular functions) in the root plasma membrane, K^+-selective ion channels (Wild 1988). Na^+-induced decrease of K uptake has been attributed to the competitive intracellular influx of both ions (Cerda et al. 1995). The greater absorption of sodium by plant in saline soils leads to increasing Na^+/K^+ ratio in plant, disrupting various metabolic processes such as protein synthesis in the cytoplasm (Tester and Davenport 2003). As mentioned above, K has many roles in plant metabolism such as activating a range of enzymes. The high levels of Na or high Na/K ratios can not only substitute for K role in activating enzymes but can also disrupt various enzymatic processes in the cytoplasm (Bhandal and Malik 1988). Therefore, maintenance of adequate levels of K^+ is essential for plant survival in saline habitats (Botella et al. 1997). Providing K for salinity-stressed plants can partly reduce the negative effects of sodium on the plants. The K absorbed by the plants can influence the ionic balance of the cytoplasm or Na efflux from plants (Bach Allen and Cunningham 1983).

There are several ways to increase K solubilization and release K from K-bearing minerals, but the use of soil microorganisms can be a good complement to plant nutrition due to its ease of use and low cost (Etesami et al. 2017). The ability of roots of plants and microorganisms in the weathering of minerals and significant alterations in mineralogy has been reported in the past (Etesami et al. 2017; Nabiollahy et al. 2006). Biochemical processes that are involved in weathering of minerals mainly occur in the presence of soil microorganisms and are affected by soil microorganisms. Several studies have reported the effects of biological processes and secreted materials of the roots of plants and microorganisms on weathering of minerals in rhizosphere environment (Arocena et al. 2012; Wu et al. 2008).

Among the microorganisms of soil, AM fungi and bacteria are of great importance in terms of K availability to plants. It has been reported that some beneficial soil bacteria including potassium-solubilizing bacteria (KSB) (i.e., *Acidithiobacillus ferrooxidans*, *Enterobacter hormaechei*, *Arthrobacter* sp., *Pseudomonas* spp., *P. aeruginosa Paenibacillus* sp., *P. mucilaginosus*, *P. frequentans*, *P. glucanolyticus*, *Aminobacter*, *Sphingomonas*, *Burkholderia*, *Bacillus mucilaginosus*, *Bacillus edaphicus*, and *B. circulans*) could solubilize the insoluble K to soluble forms of K by various mechanisms including production of organic acids (i.e., succinic, citric, gluconic, α-ketogluconic and oxalic, lactic, propionic, glycolic, malonic, succinic, fumaric, and tartaric acids), which enhance the chelation of cations (e.g., Si and Al) bound to K and help for acidolysis of surrounding environment of microbes or directly dissolve rock K, and inorganic acids, acidolysis, polysaccharides, complexolysis, chelation, polysaccharides, and exchange reactions (Etesami et al. 2017; Meena et al. 2014; Parmar and Sindhu 2013; Uroz et al. 2009). Potasium-solubilizing bacteria also contribute directly to the growth of plants directly by increasing the solubilization of insoluble K compounds through increasing rooting system and improving symbiosis-mutually beneficial relationships with host plant at different stages of growth (Etesami et al. 2017). Johnston and Krauss (1998) showed that if the root density in the soil is low, the concentration of K in the soil solution should be so high that the root can easily absorb K. The PSB with production ability of IAA and ACC deaminase can also increase plant access to K by increasing the root system of plant under nutrient deficiency conditions (Etesami et al. 2017). Previous studies have also shown that these bacteria could exert beneficial effects on growth of crop plants (Badr et al. 2006; Basak and Biswas 2009, 2010; Han and Lee 2006; Nadeem et al. 2007; Sheng 2005; Sheng and He 2006). Nadeem et al. (2007) reported that plants inoculated with ACC deaminase-producing bacteria had higher growth and higher K^+/Na^+ and chlorophyll than non-inoculated plants in saline conditions. Mayak et al. (2004a) also reported that the absorption of P and K in tomato shoot increased under salinity stress by inoculation of *Achromobacter piechaudii* RV8.

In addition to KSB, mycorrhizal fungi can increase the plant growth and yield and absorption of nutrients (i.e., K) by increasing the absorption surfaces of plant roots (Meena et al. 2014). Fungi such as *Funneliformis mosseae*, *Aspergillus terreus*, *A. niger*, *Penicillium* sp., and *Rhizoglomus intraradices* can increase the K level in soil solution through the release of H^+, CO_2 and the production of organic acids/organic acid anions (e.g., citrate, malate, and oxalate), which solubilize K from insoluble K-bearing minerals such as feldspar and potassium aluminum silicates (Meena et al. 2014; Prajapati et al. 2012; Sangeeth et al. 2012; Sieverding et al. 2015; Wu et al. 2005). These fungi also influence K mobilization through mycelial transport (Rashid et al. 2016). It has been reported that AM fungi can also provide plants with K under salinity stress (Giri et al. 2007; Mohammad et al. 2003; Ojala et al. 1983; Porcel et al. 2012). For example, Giri et al. (2007), Colla et al. (2008), and Zuccarini and Okurowska (2008) showed that AM plants had a higher concentration of K in root and shoot tissues than non-AM plants under salinity stress. Higher K^+ accumulation by AM plants may help in maintaining a high K^+/Na^+ ratio, thus preventing the disruption of various enzymatic processes and inhibition of protein synthesis under salt stress conditions (Porcel et al. 2012). The above studies show that application of K-solubilizing microorganisms as bio-fertilizer for agriculture improvement can reduce the use of agrochemicals and support eco-friendly crop production in salt-affected soils. At the present time, there is a little information on salinity-resistant K-solubilizing microorganisms (KSMs). So, it is required to evaluate salinity-resistant microorganisms isolated from halophyte plants and saline environments in terms of solubilizing K-bearing minerals in the future.

5.6 PGPR and AM Fungi-Mediated Increase of Micronutrients Availability Under Salinity Stress

Most of the micronutrients are poorly available in saline-sodic soils, and plant growth is highly depressed on such types of soils (Yousfi et al. 2007). Plant growth on these soils is affected concurrently by salinity and micronutrients deficiency.

Iron (Fe), as a micronutrient, is needed by all kind of living organisms. This nutrient is a component of many enzymes which are involved in diverse biochemical processes including respiration, photosynthesis, and N_2 fixation (Kobayashi and Nishizawa 2012). Fe deficiency depressed nodule mass and particularly leghemoglobin content, number of bacteroids, and nitrogenase activity (Garcia et al. 2015; Tang et al. 1990). Fe predominantly exists in nature in ferric (Fe^{3+})

form. Plants absorb iron as ferrous (Fe^{2+}) form, which is oxidized to Fe^{3+}, thereby forming insoluble compounds and leaving a very low amount of iron for microbial or plant assimilation (Ma 2005). In general, the availability of Fe is very low in calcareous and saline-sodic soils throughout the world (Rabhi et al. 2007).

Microorganisms including PGPR can increase the availability of micronutrients for plants through various mechanisms, such as soil pH reduction and the production of chelating agents (Miransari 2013). PGPR can produce chelating agents in iron deficiency conditions, which are called siderophores. Siderophores are small, high-affinity Fe(III)-chelating compounds that can scavenge iron. These iron-siderophore complexes can be easily accessible to plants (Kloepper et al. 1980). The other theory about the supply of iron via siderophores is the ligand exchange. The iron provided through bacterial siderophores can interact with plant siderophores (phytosiderophores) in the reaction of ligand exchange, and eventually iron is absorbed through phytosiderophores (Latour et al. 2009). Siderophore-producing PGPR were able to fulfill iron requirement for normal growth of iron-starved tomato plants (Grobelak and Hiller 2017; Pii et al. 2015; Radzki et al. 2013; Scavino and Pedraza 2013). It is noteworthy that halotolerant PGPR (e.g., *Brachybacterium saurashtrense* sp., *Serratia marcescens, Acinetobacter, Pseudomonas* sp., *P. stutzeri*, *P. putida*, *Microbacterium*, *Streptomyces* sp., *S. umbrinus*, *S. griseoplanus*, *S. exfoliatus*, *S. avidinii*, *S. europaeiscabiei*, *Bacillus* sp., *B. cereus*, *B. pumilus*, *B. simplex*, *B. mycoides*, *Serratia plymuthica*, *Microbacterium* sp., *M. oxydans*, *Rhodococcus* sp., *R. equi*, *R. erythropolis*, *Micrococcus luteus*, *Nocardia* sp., *Agrobacterium tumefaciens*, *Zhihengliuella* sp., *Brachybacterium* sp., *Vibrio alginolyticus*, *Brevibacterium casei*, *Cronobacter sakazakii*, *P. pseudoalcaligenes*, *Haererehalobacter* sp., and *Halomonas* sp.) isolated from halophytes such as *Salicornia brachiate*, *Aster tripolium* L., and *Prosopis strombulifera* had a significant ability to produce siderophore that may also be used in saline soils (Etesami and Beattie 2018; Gontia et al. 2011; Jha et al. 2012; Sgroy et al. 2009; Szymańska et al. 2016). The potential evaluation of siderophore-producing salinity-resistant PGPR isolated from halophytes in terms of increasing the availability of other micronutrients (e.g., Zn, Mn, Cu, etc.) is also suggested for future research (Etesami and Beattie 2018).

It has been shown that some PGPR can increase the manganese (Mn) availability for plant. For example, PGPR such as *Bacillus*, *Pseudomonas*, and *Geobacter* can reduce Mn^{4+} to Mn^{2+}, which is a metabolically useful form of Mn for plants (Osorio Vega 2007). These bacteria affect the availability of Mn in soil mainly due to their effect on plant growth and thus root secretion (Etesami and Maheshwari 2018). Increasing root secretions caused by bacterial activity leads, in turn, to supply of electron (through decomposition of carbohydrate compounds in root exudates) and protons (through the proton-secretion system of root cells) needed to reduce MnO_2 to Mn^{2+}. In addition, PGPR can produce different chelating agents such as phenolic compounds and organic acids that form soluble complexes with Mn, Fe, and other micronutrients, preventing the precipitation of these micronutrients. The effects of soil microorganisms on the availability of Cu and Zn in soil are directly affected by the production of various compounds such as phenolic compounds and carboxylic acids or indirectly affected by plant growth and as a result of root exudates (Iqbal et al. 2010).

The role of mycorrhizal fungi in increasing the absorption of nutrients is important only in the ecosystems that have nutrient deficiency (Cardoso and Kuyper 2006). Enhanced acquisition of Zn, Cu, and Fe by mycorrhizal plants has been reported (Al-Karaki 2000; Al-Karaki and Clark 1998; Marschner and Dell 1994). The extensive mycelial system of the fungi can absorb nutrients such as N, P, K, Zn, Cu, and Fe. The nutrients absorbed by the fungi are not exclusive to the fungi, and some of them are transmitted to the plant (Cardoso and Kuyper 2006). Clark and Zeto (1996) showed that the use of AM fungi increased the Fe concentration in corn shoots. In addition, symbiosis of mycorrhiza increased Fe concentration in the sorghum plant (Caris et al. 1998). Zn availability is limited due to the low mobility and partial availability of this element in soil. Also, the absorption surface is an important parameter that affects the bioavailability of Zn. Therefore, increasing the absorption surface through colonization of arbuscular mycorrhizal fungi may have a special importance on Zn uptake in comparison with other plant nutrient elements (Hajiboland et al. 2009). Root colonization by AM fungi increases Zn absorption in root length unit due to increased root absorption surface caused by growth of fungal hyphae (Gao et al. 2007). In general, the above studies show that salinity-resistant microorganisms can increase the availability of micronutrients to salinity-stressed plants by the production of organic acids and chelating agents, increasing the rooting system of the plant (i.e., by production of IAA and ACC deaminase) and thus increasing the root exudates (Etesami et al. 2015a, b; Etesami and Maheshwari 2018).

5.7 Conclusions

Water and soil salinity is one of the most important agricultural problems in arid and semiarid regions. Utilization of soil halotolerant microorganisms is one of the strategies to deal with this stress. Since use of chemical fertilizers in salt-affected soils increases the salinity of the soil twice, and the application of chemical fertilizers is not common, or is carried out at the minimum, the use of halotolerant PGP microorganisms can reduce some limitations in the production of crop plants in saline soils. However, their application as bio-fertilizer in field conditions requires more research. A better understanding on the interaction of halotolerant bacteria and AM fungi when applied under field conditions is required. The clarification of the mechanisms used by halotolerant PGP microorganisms in improving the availability of micro- and macronutrients under salinity stress may help in the development of innovative and cost-effective management practices for improving the fertility and crop production capacity of salt-affected soils.

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