Chapter 4
Use of Plant Growth-Promoting Rhizobacteria to Alleviate Salinity Stress in Plants

Dilfuza Egamberdieva and Ben Lugtenberg

Introduction

Salinization is recognized as the main threat to environmental resources in many countries and affects almost one billion hectares worldwide (Munns and Tester 2008; FAO Land and Nutrition Management Service 2008). Major factors increasing salinity include irrigation of cultivated lands with saline water, poor cultural practices, and low precipitation. Almost 300 million hectares in the world are irrigated. Irrigated agriculture consumes about 90 % of the total water withdrawal to produce 36 % of the global food (Rengasamy 2006; ICID 2009). It has been estimated that inappropriate irrigation/drainage practices affect approximately fifty percent of the global irrigated areas, with an annual increase of up to 500,000 ha. These facts represent a serious threat to sustainable food production and to our natural resources (Ondrasek et al. 2009).

Natural salinity is the result of long-term natural accumulation of salts in the soil or in surface water. Secondary (anthropogenic) salinity results from irrigation and is widely responsible for increasing the concentration of dissolved salts in the soil profile to a level that impairs plant growth and that will result in abandoning agricultural land (Munns 2005; Egamberdiyeva et al. 2007; Manchanda and Garg 2008). Many of the most cultivated and widely used crops (cereals, horticultural crops, etc.) in human/animal nutrition are susceptible to salt stress (>4 dS m^{-1}), and their productivity is considerably reduced due to improper nutrition of the

D. Egamberdieva (✉)
Department of Microbiology and Biotechnology, Faculty of Biology and Soil Sciences,
National University of Uzbekistan, University Street 1, Tashkent, Uzbekistan100174,
e-mail: egamberdieva@yahoo.com

B. Lugtenberg
Institute of Biology, Sylvius Laboratory, Leiden University, PO BOX 9505 2300 RA,
Leiden, The Netherlands
e-mail: Ben.Lugtenberg@gmail.com

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plant (Chinnusamy et al. 2005; Mantri et al. 2012). Salinity and drought also strongly influence many other properties and processes of living organisms (Ondrasek et al. 2009).

Climate change may lead to even more saline landscapes in many non-irrigated regions since it is accompanied by less rainfall and higher temperatures in most agricultural regions. It will result in a change toward again a more arid climate, which is conducive to salt accumulation (Othman et al. 2006). Limiting crop losses due to salinity and drought is a major area of concern to cope with the background of increasing food requirements (Shanker and Venkateswarlu 2011). In a meeting in October 2012, the World Food Security Committee addressed the effects of climate change on food security and invited world leaders (1) to integrate food security and climate change concerns, (2) to increase resilience of food systems to climate change, and (3) to develop agricultural strategies that take into account the need to respond to climate change and to safeguard food security (CFS 2012). Novel agricultural technologies are required to improve food production in saline and dry soils (Wehrheim and Martius 2008). Many scientists have attempted to develop salt-tolerant crops through breeding, but these efforts have met with limited success due to the genetically and physiologically complexity of the salt tolerance trait (Flowers 2004; Araus et al. 2008; Dwivedi et al. 2010).

Promising measures for improving plant health in salinated soils are the use of microbial inoculants, which can ameliorate salt stress, promote plant growth (Lugtenberg et al. 2013a), and control diseases (Lugtenberg and Kamilova 2004; Lugtenberg and Kamilova 2009; Mayak et al. 2004; Lugtenberg et al. 2013b; Egamberdieva et al. 2008; Pliego et al. 2011). The utilization of root-associated bacteria that interact with plants by mitigating stress opens a new advanced technology for combating salinity. Many studies have demonstrated that the use of beneficial microbes can enhance a plant's resistance to adverse environmental stresses, e.g., drought, salinity, nutrient deficiency, and heavy metal contamination. Such inoculants contribute to the development of sustainable agriculture under stressed conditions (Glick et al. 2007; Dodd and Perez-Alfocea 2012; Berg et al. 2013).

The inoculation of seeds of various crop plants, such as tomato, pepper, canola, bean, and lettuce, with PGPR can result in increased root and shoot growth, dry weight, fruit and seed yield and in enhanced tolerance of plants to salt stress (Glick et al. 1997; Mayak et al. 2004; Yildirim and Taylor 2005; Barassi et al. 2006; Egamberdieva et al. 2013a). According to Creus et al. (2004), PGPR may alter plant–water relationships and show enhanced osmotic adjustment.

In the present chapter, we will review the current status of our understanding of the action of PGPR in crop cultivation under conditions of abiotic stress. We will start with studies about the effect of salt stress on plant growth and physiology, followed by the role of plant growth-promoting rhizobacteria in alleviating salt stress in plants and end with the main mechanisms involved in improvement of plant tolerance to salt stress caused by these microbes.

Effects of Soil Salinity on Plant Growth and Physiology

Seed germination and early seedling growth are the most salt-sensitive plant growth stages under environmental stresses, because the seedling root is in direct contact with soil and is affected by many soil changes, including salt stress (Rahman et al. 2000; Jamil et al. 2006). Many studies have demonstrated that salinity inhibits seed germination of various crops such as wheat (Egamberdieva 2009), faba bean (Rabie and Almadini 2005), rice (Xu et al. 2011), maize (Khodarahmpour et al. 2012), and soybean (Essa 2002). Moreover, Jamil et al. (2006) observed significant reductions in germination percentage, in germination rate, and in seedling root and shoot lengths of cabbage, sugar beet, paniculate amaranth, and pak-choi.

In our previous work, we observed that increasing salt content reduced the shoot length (50 %) and root length (7 %) of bean seedling grown in a gnotobiotic sand system in a growth cabinet (Egamberdieva 2011). These observations are in line with earlier reports about ground nut (Mensah et al. 2006), and chickpea (Al-Mutawa 2003), for which was reported that increased salinity leads to decreased root length. A similar result was observed by Demir and Arif (2003), who reported that the root growth of safflower was more inhibited by salinity than shoot growth. Ashraf (2004) and Razmjoo et al. (2008) found that high salt causes a significant reduction in the growth of shoot and root as well as in the essential oil content of *Ammolei majus*, *Hyoscyamus niger*, and *Matricaria chamomile*. Salinity also decreases photosynthesis, stomatal conductance, chlorophyll content, and mineral uptake of basil (*Ocimum basilicum*) (Golpayegani and Tilebeni 2011).

Several explanations for these effects have been proposed, such as disturbance of the hormonal balance (Prakash and Prathapasenan 1990), alteration of protein metabolism (Dantas et al. 2005), inhibition of the activity of enzymes involved in nucleic acid metabolism (Arbona et al. 2005), and the loss of control on nutrient uptake. These effects are assumed to be caused by the osmotic effect (Shirokova et al. 2000) and the ion toxicity of salt (Munns 2002; Tavakkoli et al. 2011).

The inhibition of root growth by salinity may be caused by a reduction in water uptake and an unbalanced nutrient uptake by the seedling (Dolatabadian et al. 2011). In addition, Atak et al. (2006) and Neamatollahi et al. (2009) pointed out that higher saline concentrations may reduce the germination percentage due to increased osmotic pressure. Abundance of Na^+ and Cl^- ions can lead to a reduction in accessibility and uptake of some elements such as N, P, K, and Mg by the plant (Heidari and Jamshid 2010). In another study, Xiong and Zhu (2002) reported that salinity induces inhibition of phytohormone synthesis and maturation of cell walls.

Most legumes are sensitive to salinity. Soil salinity particularly disturbs the symbiotic interaction between legumes and *Rhizobium* bacteria. These bacteria form root nodules in which they fix atmospheric nitrogen through the nitrogenase complex and make it available to the plant (Quispel 1988). Soil salinity reduces N_2 fixation and nitrogenase activity of several legumes such as soybean (*Glycine max*)

(Singleton and Bohlool 1984), common bean (*Phaseolus vulgaris*), and faba bean (*Vicia faba*) (Rabie et al. 2005).

Only a few agronomical legumes can grow in salt-affected soils (Ashraf and McNeilly 2004). *Galega offfcinalis* L (goat's rue, French lilac) might be a good candidate to cultivate in salt-affected soils because they are perennial, deep rooted, and grow fast after initial establishment. We have observed that *G. officinalis* plants inoculated with their rhizobial symbiont *Rhizobium galegae* suffer from retarded growth and impaired nodulation when grown under 75 mM NaCl conditions (Fig. 4.1). Salt stress also decreased the number of *Rhizobium* cells able of colonize *G. officinalis* root tips (Egamberdieva et al. 2013a).

An explanation for the reduction in symbiotic legume growth might be that the salt stress causes a failure of the infection and nodulation process. For example, according to Bouhmouch et al. (2005), salt inhibits the absorption of Ca^{2+} ions, which causes reduction in the growth of roots, root tips, and root hairs, thereby decreasing sites for potential rhizobial infection and further nodule development.

Fig. 4.1 Effect of 50 mM NaCl on growth of goat's rue plants (*Galega officinalis* L.). The effects of the treatment of *G. officinalis* with NaCl solutions were evaluated after plants were grown for eight weeks in lowly fertilized potting soil in the greenhouse. A salt concentration of 50 mM NaCl retarded significantly the growth of shoots and roots, as well as the nodulation of *G. officinalis* plants inoculated with *Rhizobium galegae*

Rhizobacteria in Saline Soils

Soil salinity not only inhibits plant growth and development, but also negatively affects the composition and activities of rhizosphere bacteria (Ofek et al. 2006). Nelson and Mele (2007) reported that sodium chloride affects the rhizosphere microbial community structure through its influence on the quantity and/or quality of root exudates. Also, increasing salinity decreases the diversity of *Pseudomonas* species associated with rice. *Pseudomonas* species found in saline soil include *P. aeruginosa, P. fluorescens*, *P. putida*, *P. stutzeri, P. mendocina, P. mallei,* and *P. diminuta* (Nagarajan et al. 2002). Non-saline soil favors the growth of the fluorescent *Pseudomonas* population, whereas in saline soil the dominant *Pseudomonas* subpopulation consists of *P. alcaligenes* and/or *P. pseudoalcaligenes*.

Loganathan and Nair (2004) isolated salt-tolerant, nitrogen-fixing bacteria from mangrove-associated wild rice and identified them as *Swaminathania salitolerans*. Tripathi et al. (2002) isolated and identified salt-tolerant rhizobacteria from rice roots, including *Serratia marcescens, P. aeruginosa*, *Alcaligenes xylosoxidans*, and *Ochrobactrum anthropi*.

Potential human pathogenic bacteria have been found in saline soils in a surprisingly high frequency. Egamberdieva et al. (2008) have isolated salt-tolerant rhizobacteria with high rhizosphere competence from wheat roots grown in salinated Uzbek desert soils. They observed that many of the root-associated bacteria are potential human pathogens, which were identified as *Alcaligenes faecalis*, *Acinetobacter* sp., *Enterobacter hormaechei, Pantoea agglomerans, P. aeruginosa*, *Bacillus cereus*, and *Staphylococcus saprophyticus*.

The presence of other human pathogens on plant roots in saline environments, such as *Salinivibrio*, *Halomonas*, *Chromohalobacter*, *Bacillus*, *Salinicoccus, Candida tropicalis, Alcaligenes faecalis, S. marcescens*, and *A. xylosoxidans*, was also reported (Tripathi et al. 2002; Sanchez-Porro et al. 2003; Bastos et al. 2004). Salt-tolerant *Mycobacterium phlei* strains were also found in association with roots of corn planted in saline soils of Uzbekistan (Egamberdieva 2011).

The presence of *P. aeruginosa* in the rhizosphere of wheat has been reported previously (Morales et al. 1996; Germida and Siciliano 2001). The consistent presence of *P. aeruginosa* in saline soils indicates a widespread incidence of this bacterium in the rhizosphere of plants growing in saline soil. Microorganisms compete for nutrients and niches in the plant rhizosphere. Exudates are thought not only to attract beneficial bacteria to colonize the roots, but also human pathogens which apparently have evolved to respond to the same signals (Roberts et al. 2000; Ji and Wilson 2002).

Morales et al. (1996) and Jablasone et al. (2005) reported that the survival and colonization of potentially pathogenic human-associated bacteria in the rhizosphere of plants are poor and that their persistence and colonization on plants are decreased by co-inoculation of pathogens with naturally occurring bacteria. We have also observed that the potential human pathogenic strains *B. cereus, S. saprophyticus, P. aeruginosa*, and *Acinetobacter* sp., isolated from roots of wheat plants growing in salinated soils, showed poor competitive colonization of the wheat rhizosphere when compared with *P. fluorescens* WCS365, an excellent root tip colonizer (Egamberdieva and Kucharova 2009). Since the potential pathogens were probably derived from manure used for fertilization, it is likely that the root-derived bacteria out compete the potential pathogens derived from humans and animals (Egamberdieva et al. 2011).

Egamberdieva and Kucharova (2009) have selected enhanced root tip colonizing bacteria from wheat grown in saline soil using an enrichment procedure described by Kamilova et al. (2005). The four selected strains were identified as *P. putida, P. extremorientalis, P. chlororaphis,* and *P. aureantiaca*, and since they do not belong to risk group 2 (Anonymous 1998), they are nonpathogenic. Those findings suggest that the screening procedure for the selection of enhanced root-colonizing rhizobacteria can select for environmentally save bacterial strains, which can be applied for plant growth promotion in salinated and stressed soil conditions. Moreover, they are likely to out compete potential pathogens of human and animal origin.

Plant Salt Stress Alleviation Using Plant Growth-Promoting Rhizobacteria

The rhizosphere is colonized more intensively by microorganisms than the other regions of the soil. These microbes can be beneficial, neutral, or pathogenic. Beneficial rhizobacteria can improve seed germination, root and shoot growth, nutrient uptake, and plant stress tolerance. Moreover, they are able to control various diseases. They are often referred to as plant growth-promoting rhizobacteria (PGPR) (Hiltner 1904; Lugtenberg et al. 2001; Compant et al. 2005; Arora et al. 2008; Lugtenberg and Kamilova 2009). A range of salt-tolerant rhizobacteria (e.g., *Rhizobium*, *Azospirillum, Pseudomonas*, *Flavobacterium*, *Arthrobacter*, and *Bacillus*) has so far shown beneficial interactions with plants in stressed environments (Egamberdieva and Islam 2008; Egamberdieva et al. 2011; Adesemoye et al. 2008).

The majority of cultivated plant species, especially widely grown horticultural and cereal crops, are susceptible to excessive concentrations of dissolved ions (e.g., >30 mM or >3.0 dS/m) in the rhizosphere (Ondrasek et al. 2009). For example, the yield of crops such as potato, corn, onion, and bean can be reduced by 50 % when the soil EC is increased to 5.0 dS/m (Horneck et al. 2007).

Earlier reports claim that salinity negatively affects soil bacterial activity by high osmotic strength and toxic effects by salts, but that salt-tolerant bacteria can survive and proliferate in the soil and in the rhizosphere in a harsh environment (Garcia and Hernandez 1996). Diby et al. (2005) observed that the population of the salt-tolerant *P. pseudoalcaligenes* strain MSP-538 did not change considerably with increasing salinity in the soil. Root-associated bacteria are more tolerant to salt stress than soil bacteria, since salinity stress is higher in the rhizosphere due to depletion of water by the plant root, resulting in an increase in both ionic strength and osmolality (Tripathi et al. 1998).

Several PGPR strains, such as *Serratia plymuthica* RR2-5-10, *S. rhizophila* e-p10, *P. fluorescens* SPB2145, *P. chlororaphis* TSAU 13, *P. putida* TSAU1, *P. extremorientalis* TSAU20, *P. fluorescens* PCL1751, and *P. aureofaciens* TSAU22, are salt tolerant up to at least 3 % NaCl and temperature resistant up to 40 °C (Egamberdieva and Kucharova 2009; Egamberdieva et al. 2011). Thus, it is likely that salt-tolerant PGPR strains are able to survive in the rhizosphere of plants due to their persistence and competitiveness under saline arid soil conditions (Mayak et al. 2004; Yasmin et al. 2007).

There are many reports on the improvement of plant growth, development, and nutrient uptake by salt-tolerant bacterial inoculants (Dodd and Perez-Alfocea 2012). An overview of ameliorative effects of PGPR on various plants mentioned in the literature is presented in Table 4.1. For example, Heidari et al. (2011) reported that plant growth, as well as auxin and protein contents of *Ociumum basilicm* inoculated with *Pseudomonas* sp. under conditions of drought stress increased. Golpayegani and Tilebeni (2011) observed that inoculation of basil with *Pseudomonas* sp. and *Bacillus lentus* alleviated the salinity effects on growth, photosynthesis, mineral content, and antioxidant enzymes. Dardanelli et al. (2008) observed that *Azospirillum brasilense* promoted root branching in bean seedling roots and increased secretion of flavonoids and lipochitooligosaccharides.

Inoculation of wheat with the halotolerant *A. brasilense* strain NH improved germination and growth of wheat under saline soil conditions (Nabti et al. 2010). Similar results were obtained by Abbaspoor et al. (2009) who reported increased plant growth, grain yield, and 1,000 grain weight of wheat by inoculation with *P. fluorescens* 153 and *P. putida* 108. In one of our studies, plant treatments with salt-tolerant strains, such as *P. chlororaphis* TSAU13 and *P. extremorientalis* TSAU20, increased shoot growth and dry weight of wheat at 50, 100, and 125 mM NaCl, compared to control plants (Figs. 4.2 and 4.3). The nutrient (N, P, K, and Mg) uptake of wheat was also increased by *Mycobacterium phlei* MbP18 and *Mycoplana bullata* MpB46 (Egamberdieva and Hoflich 2003).

According to Sivritepe et al. (2003), an increase in the potassium content in roots and shoots of plants grown under salt stress can reduce the negative effect of salinity on plant growth. A similar observation, namely that plants with a higher potassium content are more tolerance to salt stress, was reported by Kaya et al. (2003) for pepper and cucumber. *P. chlororaphis* TSAU13 and *P. extremorientalis* TSAU20 are able to stimulate root length (by 47 %) and dry weight (by 50 %) of bean (Egamberdieva 2011). Salinity did not inhibit the plant stimulating properties of salt-tolerant bacterial strains for wheat.

Hasnain and Sabri (1996) reported that inoculation of wheat with *Pseudomonas* sp. stimulated plant growth by reducing the uptake of toxic ions and increasing the auxin content. In another study, the PGPR strains *P. alcaligenes* PsA15, *P. chlororaphis* TSAU13, *P. extremorientalis* TSAU20, and *B. amyloliquefaciens* BcA12 significantly ($P < 0.05$) increased the length and dry weight of cotton roots and shoots in saline soil in comparison with the uninoculated control plants (Egamberdieva and Jabborova 2013). Similar results were reported by Yue et al. (2007) for *Klebsiella oxytoca* which, upon inoculation, was able to relieve salt

Table 4.1 Summary of the reported ameliorative effects of PGPR on crop plants under stress conditions

PGPR	Crop	Effects of inoculation	References
Achromobacter piechaudii	Tomato (*Lycopersicon esculentum*)	Fresh and dry weight	Mayak et al. (2004)
Pseudomonas fluorescens	Groundnut (*Arachis hypogaea* L.)	Plant growth, yield	Saravanakumar and Samiyappan (2007)
P. fluorescens	Maize (*Zea maize* L.)	Root elongation, fresh weight	Kausar and Shahzad (2006)
Pseudomonas sp.	Pea (*Pisum sativum*)	Plant growth, yield	Arshad et al. (2008)
Azospirillum, *Pseudomonas*, and *Mezorhizobium*	Chickpea (*Cicer arietinum* L.)	Plant growth, yield	Rokhzadi et al. (2008)
Azospirillum brasilense	Wheat (*Triticum durum* var. *waha*)	Germination, growth, spike length, stem height	Nabti et al. (2007)
Glomus clarum and *A. brasilense*	Bean (*Vicia faba*)	Plant growth, nodule number, protein content, N and P uptake, nitrogenase activity	Rabie and Almadini (2005)
Bacillus pumilus, Exiguobacterium oxidotolerans	Brahmi (*Bacopa monnieri*),	Plant weight, bacoside-A content	Bharti et al. (2013)
Pseudomonas putida, P. fluorescens,	Wheat (*Triticum aestivum*, L.)	Plant growth, grain yield, and 1000 grain weight	Abbaspoor et al. (2009)
Staphylococcus kloosii, Kocuria erythromyxa	Radish (*Raphanus Sativus* l.)	Shoot/root fresh and dry weight, chlorophyll content	Yildirim et al. (2008)
Bacillus megaterium	Maize (*Zea maize* L.)	Root growth, necrotic leaf area, leaf relative water content	Marulanda et al. (2010)
Pseudomonas pseudoalcaligenes, B. pumilus	Rice (*Oryza sativa*)	Shoot biomass, glycine betaine-like quaternary compounds	Jha et al. (2010)
A. brasilense	Bean (*Phaseolus vulgaris*)	Root branching, increased secretion of flavonoid and lipochitooligosaccharide	Dardanelli et al. (2008)
Pseudomonas sp.	Wheat (*Triticum aestivum*, L.)	Root/shoot growth, reducing toxic ions uptake	Hasnain and Sabri (1996)

(continued)

Table 4.1 (continued)

PGPR	Crop	Effects of inoculation	References
Pseudomonas sp., *Bacillus lentus*	Basil (*Ociumum basilicm*)	Improved growth, photosynthesis, mineral content and antioxidant enzymes	Golpayegani and Tilebeni (2011)
Pseudomonas extremorientalis	Milk thistle (*Silybum marianum*)	Root, shoot length and fresh weight	Egamberdieva et al. (2013b)
Pseudomonas sp.	Basil (*Ociumum basilicm*)	Plant growth, auxin and protein contents	Heidari et al. (2011)
Bradyrhizobium japonicum	Soybean (*Glycine max*)	Plant growth, number of nodules, grain yield and protein content	Egamberdieva et al. (2004)
Pseudomonas alcaligenes, P. chlororaphis, *Bacillus amyloliquefaciens*	Cotton (*Gossypium hirsutum*)	Root/shoot length, dry weight	Egamberdieva and Jabborova (2013)
Klebsiella oxytoca	Cotton (*Gossypium hirsutum*)	Root/shoot length, dry weight	Yue et al. (2007)
P. extremorientalis, *P. chlororaphis*	Bean (*Vicia faba*)	Root/shoot growth, dry weight	Egamberdieva (2011)
Bacillus megaterium	Maize (*Zea maize* L.)	Higher root hydraulic conductance	Marulanda et al. (2010)
P. mendocina and Mycorrhizal fungi	Lettuce (*Lactuca sativa*)	Plant growth, glomalin-related soil protein (GRSP)	Kohler et al. (2010)
S. plymuthica, S. rhizophila, *P. fluorescens*	Cucumber (*Cucumis sativus*)	Root shoot length, dry weight, fruit yield	Egamberdieva et al. (2011)
P. extremorientalis, *P. trivialis* and *Rhizobium galegae*	Goat's rue (*G. officinalis* L.)	Root/shoot length, dry weight, nodule number, N uptake	Egamberdieva et al. (2013a)
Rhizobium tropici and *Paenibacillus polymyxa*,	Common bean (*Phaseolus vulgaris* L.)	Plant growth, nitrogen content, nodule number	Figueiredo et al. (2008)
Serratia sp. and *Rhizobium* sp.	Lettuce (*Lactuca sativa*)	Plant growth, N, P and K uptake, chlorophyll content, antioxidant enzymes	Han and Lee (2005)
A. brasilense and *Glomus clarum*	Faba bean (*Vicia faba*)	Plant growth, N and P uptake, nodule number, protein content and nitrogenase enzymes	Rabie and Almadini (2005)

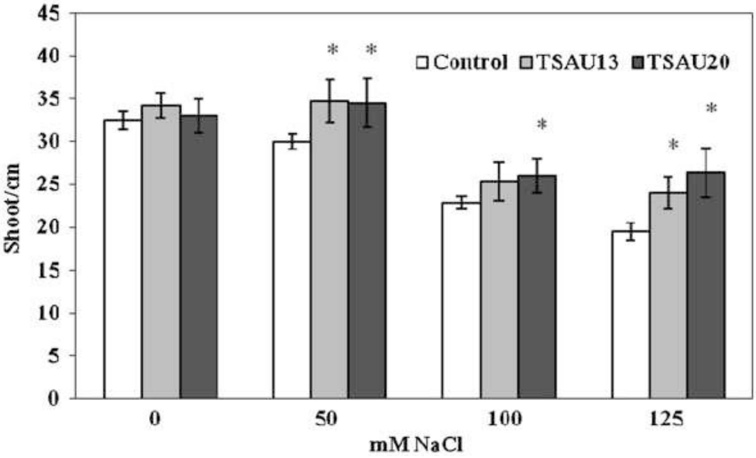

Fig. 4.2 Effect of *P. chlororaphis* TSAU13 and *P. extremorientalis* TSAU20 on shoot growth of wheat under salinated soil. Pot experiments, NaCl concentrations are 50, 100, 125 mM

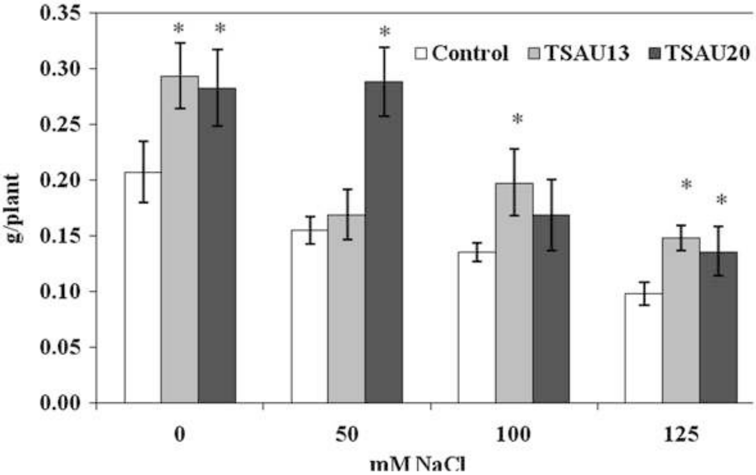

Fig. 4.3 Effect of *P. chlororaphis* TSAU13 and *P. extremorientalis* TSAU20 on dry weight of wheat in salinated soil. Pot experiments, NaCl concentrations are 50, 100, 125 mM

stress and promote the growth of cotton seedlings in salinated soil. Moreover, plant height and dry weight of cotton increased by 14.9 and 26.9 %, respectively.

Rabie and Almadini (2005) reported that inoculation of bean with the AMF (arbuscular mycorrhizal fungus) *Glomus clarum* and the bacterium *Azospirillum brasilense* significantly increased plant growth, nodule number, protein content, and nitrogen and phosphorus uptake in comparison with uninoculated plants and also improved plant stress tolerance. Yildirim et al. (2008) studied the ameliorative effect of *Staphylococcus kloosii* strain EY37 and *Kocuria erythromyxa* strain EY43 on radish growing in saline soil. They observed that bacterial inoculants significantly increased shoot/root dry weight, leaf number per plant, relative water content of the leaf, and chlorophyll content of radish fruit. Bharti et al. (2013) observed that salt-tolerant *Bacillus pumilus* and *Exiguobacterium oxidotolerans* stimulated plant growth and bacoside-A content of brahmi (*Bacopa monnieri*).

In all reports presented above, the bacterial inoculant strains were isolated from the rhizosphere of plants naturally growing in saline soils. We observed that for the application of bacteria in salinated soils, there is no strict need to isolate these bacteria from plants grown in salinated soil. In our study (Egamberdieva et al. 2011), *S. plymuthica* strain RR2-5-10, *S. rhizophila* strain e-p10, and *P. fluorescens* strain SPB2145, all isolated from regions with a moderate to cold climate and non-saline soil, were able to increase cucumber growth and yield in salinated soil of Uzbekistan. These results are consistent with observations showing that the rhizosphere is characterized by changing osmotic conditions, and that its microbial inhabitants can adapt to increased osmolarity, for example by producing osmoprotective substances (Miller and Wood 1996).

Rhizobium–Legume Symbiosis Improved by PGPR

Under saline conditions, the symbiosis of legumes with *Rhizobium* spp. can be improved by co-inoculation with PGPR (Valverde et al. 2005; Yadegari and Rahmani 2010). Dual inoculation with *Rhizobium* and PGPR result in an increase in the total nodule number of pigeon pea (*Cajanus cajan*) compared to inoculation with *Rhizobium* alone (Tilak et al. 2006).

We have investigated whether the PGPR strains *P. extremorientalis* TSAU20 and *P. trivialis* 3Re27 have the ability to alleviate salinity stress in *G. officinalis* L (goat's rue). In comparison with plants inoculated with *R. galegae* alone, co-inoculation of both unstressed and salt-stressed goat's rue with *Rhizobium galegae* HAMBI 1141 and either *P. trivialis* 3Re27 or *P. extremorientalis* TSAU20 significantly improved root and shoot growth as well as nodulation of the plants. This was the case in both gnotobiotic sand and low-fertilized potting soil. The nitrogen content of the co-inoculated plant roots was significantly increased at both 50 and 75 mM NaCl in potting soil (Fig. 4.4) (Egamberdieva et al. 2013a).

Figueiredo et al. (2008) studied the effect of *Rhizobium tropici,* when co-inoculated with *Paenibacillus polymyxa,* on growth, nitrogen content, and nodulation of the common bean (*Phaseolus vulgaris* L.) under conditions of drought stress. They observed that plants co-inoculated with both *R. tropici* and *P. polymyxa* showed improved plant growth, shoot dry matter, nodule dry matter, and N uptake as well as higher nodule numbers than those inoculated with *R. tropici* alone.

Rokhzadi et al. (2008) showed that the combined inoculation of *Azotobacter, Azospirillum*, *Pseudomonas*, and *Mezorhizobium* resulted in promotion of the grain yield and biomass in chickpea. Han and Lee (2005) observed that inoculation of non-legume lettuce with *Serratia* sp. and *Rhizobium* sp. alleviated the negative

H_2O, 50 mM NaCl, 75 mM NaCl

Rhizobium galegae

H_2O, 50 mM NaCl, 75 mM NaCl

R. galegae + *Pseudomonas trivialis* 3re27

Fig. 4.4 Effect of the salt-tolerant bacterium *Pseudomonas trivialis* 3re27 on the growth of *Galega officinalis* inoculated with *Rhizobium galegae* R1141

effects of salinity on the plant. The inoculation resulted in increased plant growth and N, P, and K uptake. Also, stomatal conductance, chlorophyll content, and the activities of antioxidant enzymes such as ascorbate peroxidase and glutathione reductase increased.

Rabie and Almadini (2005) examined tripartite interactions among a bacterium (*A. brasilens*), an AMF (*G. clarum*), and a legume plant (*Vicia faba*) under increased NaCl levels in pot cultures. Significant positive effects of inoculation were found in the plants with respect to salinity tolerance, mycorrhizal dependence, phosphorus level, phosphatase enzymes, nodule number, nitrogen uptake, protein content, and nitrogenase activity. Based on these findings, the authors suggested that bacterial–AMF–legume tripartite symbioses could be a new approach for increasing the salinity tolerance of legume plants.

The studies mentioned above indicate that PGPR are able to alleviate salt stress in leguminous plants, whereas more nodules might develop into nitrogen-fixing ones, thereby enabling the plant to obtain part of its nitrogen from the atmosphere. Co-inoculation techniques could be a new approach to increase the salt tolerance and yield of legumes used for the food and green manure production in salt-affected soils, providing a supply of biologically fixed N at low cost.

Mechanisms of Action by Which PGPR Alleviate Salt Stress

PGPR can use various mechanisms to stimulate plant growth and development, to protect plants from soilborne diseases, and to increase plant stress tolerance. These mechanisms include (1) the production of phytohormones, antifungal metabolites, and/or lytic enzymes, (2) increasing the availability of plant nutrients, (3) reduction in stress-induced ethylene production, and (4) induction of systemic resistance (Lugtenberg and Kamilova 2009; Pliego et al. 2011; Egamberdieva et al. 2013a; Penrose et al. 2001; Glick 2005).

Phytohormone Production

Phytohormones have a major role in plant growth development and in stress responses (Shaterian et al. 2005). They may enhance different cellular defence systems for the protection of plants from external adverse conditions (Bianco and Defez 2009). Salinity and drought stresses inhibit the production of auxins, gibberellins, and zeatin in the roots and leaves of plants (Sakhabutdinova et al. 2003; Figueiredo et al. 2008; Perez-Alfocea et al. 2010).

The decrease in hormone levels in the root system of plants results in a reduction in the germination percentage, and of plant growth and development (Werner and Finkelstein 1995; Sakhabutdinova et al. 2003). Salt stress reduces the supply of cytokinin from root to shoot (Naqvi and Ansari 1974) and also the recovery of diffusible auxin from maize coleoptile tips (Itai et al. 1968).

Salinity does not inhibit auxin production of salt-tolerant PGPR. Nabti et al. (2007) isolated the halotolerant *A. brasilense* strain NH which is able to produce auxin at a concentration of 200 mM NaCl. A similar observation was reported in our previous work in which the PGPR strains *S. plymuthica* RR2-5-10*, S. rhizophila* e-p10*, P. fluorescens* SPB2145, and *P. chlororaphis* TSAU13 were shown to produce auxin at 1.5 % NaCl (Egamberdieva et al. 2011; Egamberdieva 2012).

Root-colonizing bacteria which produce auxin under saline condition may supply additional auxin into the rhizosphere, which could help to maintain root growth under stress, and also can contribute to maintaining leaf growth (Albacete et al. 2008). In one of our studies, the inoculation of wheat with the individual auxin-producing bacterial strains *P. aureantiaca* TSAU22, *P. extremorientalis* TSAU6, and *P. extremorientalis* TSAU20 significantly increased seedling root growth up to 40 % and shoot growth up to 52 % at 100 mM NaCl compared to control plants (Egamberdieva 2009). Arkhipova et al. (2007) also observed increased root and shoot growth as well as cytokinin concentrations in plants by treatment with a cytokinin-producing *B. subtilis* strain.

In conclusion, PGPR can have multiple impacts on the phytohormone status, modifying root-to-shoot signalling and shoot hormone concentrations, which may improve growth, development, and physiological processes of plants under salt stress (Dodd et al. 2010).

Osmolites

Plants may protect themselves from drought and salt stress by accumulating compatible solutes such as sugars and amino acids to osmotically adjust themselves (Serraj and Sinclair 2002; Evelin et al. 2009). Jha et al. (2010) reported that paddy rice (*Oryza sativa* L.) inoculated with *P. pseudoalcaligenes* showed a significantly higher concentration of glycine betaine-like quaternary compounds and a higher shoot biomass under salinity conditions. Bano et al. (2013) observed that *A. lipoferum* increased accumulation of free amino acids and soluble sugars in maize, as compared to the control, under drought stress conditions.

Azospirillum inoculation leads to an increased content of proline (Kandowangko et al. 2009) and free amino acids in maize under drought stress conditions (Sandhya et al. 2010). Verbruggen and Hermans (2008) reported that the accumulation of proline is one of the best-known alterations induced by water and salt stress in plants. Kandowangko et al. (2009) observed that inoculation of corn with *Azospirillum* causes an increase in leaf proline content. Several PGPR strains, such as *Burkholderia* (Barka et al. 2006), *Arthrobacter*, and *Bacillus* (Sziderics et al. 2007), enhance proline synthesis in stressed plants, which helps in maintaining the cell water status, thereby helping the plant to cope with the salinity stress. Proline may enhance the activity of various enzymes, stabilizing the pH within the cell and maintaining antioxidant activity by scavenging reactive oxygen species (Verbruggen and Hermans 2008).

Ashraf (2004) observed that bacterial exopolysaccharides bind the Na^+ ion in the root, through which the plant's Na^+ accumulation decreases. In that way, bacteria may alleviate salt stress in plants. Sandhya et al. (2009) reported that exopolysaccharides produced by PGPR exhibit increased plant resistance to water stress. Kerepesi and Galiba (2000) indicated that the accumulation of sugars in salinity-stressed plants prevents the destruction of soluble proteins. Co-inoculation of *Phaseolus vulgaris* L. with *R. tropici* and the PGPR *Paenibacillus polymyxa* (which produces trehalose) increased plant growth, N content, and nodulation under drought stress (Figueiredo et al. 2008).

ACC Deaminase

The hormone ethylene is involved in the plant developmental cycle, and it may be stimulatory or inhibitory, depending upon its concentration (Penrose et al. 2001). Ethylene has previously been found to be an inhibitor of plant root elongation in several different systems (Glick 2005). The production of ethylene in plants is highly dependent on the endogenous levels of 1-aminocyclopropane-1-carboxylate (ACC). The enzyme ACC deaminase is present in many rhizosphere bacteria (Glick 2010). Such bacteria can take up ACC from the plant root and convert it into a-ketobutyrate and ammonia. This results in the decrease in ACC levels and therefore also in ethylene levels in the plant and in decreased plant stress (Bianco and Defez 2009; Pliego et al. 2011).

PGPR containing the enzyme ACC deaminase decrease the ethylene level, enhance the survival of some seedlings, and improve root growth and development in various plants such as tomato, pepper, and bean under stressed conditions (Glick et al. 1998; Mayak et al. 2004; Nadeem et al. 2009). We have previously reported that PGPR strain *P. trivialis* 3Re27 is able to utilize ACC as its sole N source, indicating that it contains ACC deaminase. This observation suggests that the presence of ACC deaminase leads to an increase in salt tolerance and a stimulation of shoot and root growth of goat's rue in salinated soil (Egamberdieva et al. 2013a).

ACC deaminase-producing *Achromobacter piechaudii* strain ARV8 confers 'induced systemic tolerance' (IST) against drought and salt stress in pepper and tomato (Mayak et al. 2004). Shahzad et al. (2010) observed that rhizobacteria containing ACC deaminase increase the number of lateral roots, lateral root length, and root dry weight of chickpea seedlings and a direct correlation has been found between in vitro bacterial ACC deaminase activity and root growth (Shaharoona et al. 2006). Longer roots may take up relatively more water from deep soil under stress conditions, thus increasing the water use efficiency of the plants (Zahir et al. 2008).

In another study, *P. fluorescens* strain TDK1, which produces ACC deaminase, improved the plant growth parameters and the salt stress resistance of groundnut seedlings under saline condition as compared to plants inoculated with *Pseudomonas* strains lacking ACC deaminase activity (Saravanakumar and Samiyappan 2007). Similar results were observed by Kausar and Shahzad (2006), who reported that *P. fluorescens* containing ACC deaminase stimulated root growth of maize under saline conditions.

It is assumed that ACC exuded from the root will be degraded by ACC deaminase and that the products of hydrolyzed ACC will be used by root-colonizing bacteria. In that way, both plant and bacteria benefit from this process (Glick et al. 1998; Bianco and Defez 2012). In our opinion, a more likely and more efficient explanation is that the ACC deaminase-producing bacterium uses the needle of the type three secretion system to suck up plant sap containing ACC and deliver it in the bacterial cytoplasm where the enzyme ACC deaminase is located.

Root Colonization

Efficient colonization of the plant surface is the only option for bacterial soil inoculants to survive under adverse soil conditions and to compete with the better adapted native microflora in this highly competitive environment (Van Overbeek and Van Elsas 1997; Lugtenberg et al. 2001; Rekha et al. 2007; Lugtenberg and Kamilova 2009). The successful colonization of the rhizosphere by introduced beneficial bacteria also requires that these bacteria are well adapted to the rhizosphere and have some selective advantage over the numerous indigenous bacteria which have the potential to colonize that rhizosphere (Kawaguchi et al. 2002).

In one of our studies, the salt-tolerant bacterial strains *P. cholororaphis* TSAU13 and *P. extremorientalis* TSAU20 were able to colonize the rhizosphere of wheat under saline conditions up to 125 mM NaCl (Table 4.2). The colonization of *P. chlororaphis* TSAU13 was slightly inhibited, from 4.1 to 3.2 [Log (CFU)/cm of root tip], at 125 mM NaCl (Table 4.2). These results show that both bacterial

Table 4.2 Effect of salt stress on the colonization of bacterial strains *P. chlororaphis* TSAU13 and *P. extremorientalis* TSAU20 in the rhizosphere of wheat (Log CFU/cm of root tip), grown in a gnotobiotic sand system for 7 days

Bacteria	NaCl concentrations (mM)			
	0	50	100	125
P. chlororaphis TSAU13	4.1 ± 0.2	4.1 ± 0.3	4.0 ± 0.2	3.2 ± 0.2
P. extremorientalis TSAU20	4.6 ± 0.2	4.6 ± 0.1	4.4 ± 0.1	3.8 ± 0.2

strains are able to survive on the root of wheat under saline soil condition. Similarly, Diby et al. (2005) reported that the population of *P. pseudoalcaligenes* MSP-538 in rice root was not inhibited with increasing salinity. Paul and Nair (2008) also observed that the root colonization potential of the salt-tolerant strain *P. fluorescens* MSP-393 is not hampered by high salinity in the soil.

In our previous study, rifampicin-resistant mutants of the effective biocontrol strains *P. alcaligenes* PsA15, *P. chlororaphis* TSAU13, *P. extremorientalis* TSAU20, and *B. amyloliquefaciens* BcA12 were able to colonize the rhizosphere of cotton and persisted in saline soil (Egamberdieva and Jabborova 2013). Strain *P. extremorientalis* TSAU20, which was isolated as an enhanced wheat root colonizer (Egamberdieva and Kucharova 2009), showed high colonization ability in the rhizosphere of cotton, whereas *B. amyloliquefaciens* BcA12 had lower colonization ability. Bacterial motility could contribute to survival in the soil and the initial phase of colonization, where attachment and movement toward the root surface are important (Turnbull et al. 2001). *Pseudomonas* strains are motile and able to colonize the entire root system, in contrast to *Bacillus* which was unable to effectively colonize the rhizosphere of plants (Fukui et al. 1994).

Conclusion and Future Prospects

The present review indicates that soil salinity decreases germination, plant growth, plant development, and nutrient uptake. PGPR isolates are able to alleviate salt stress in plants, increase germination, shoot/root length, dry matter production, and yield in various agricultural and horticultural plants. Thus, PGPR can contribute significantly to solving the plant production problems caused by high salinity. Elucidation of the mechanisms of alleviation of salt stress and plant growth promotion by PGPR, such as stimulation of root growth by the production of phytohormones, decreasing ethylene levels by the enzyme ACC deaminase, production of osmoprotectants, and competition for nutrient and niches has provided a greater understanding of possible ways to open new doors for strategies which can improve the efficacy of PGPR agents. However, there is still a lot that is not understood regarding the functioning of these organisms under stressed soil conditions and also with respect to their interactions with the host plant. Knowledge of the mechanisms contributing to plant stress tolerance by PGPR as well as the constraints to their activity under severe conditions can facilitate a more effective use of bacterial inoculants. More detailed studies are needed on the role of abiotic factors in altering the activity of rhizobacteria and managing plant–microbe interactions, with respect to their adaptability to extreme environments. Aspects which have to be included in future research are (1) mechanisms involved in alleviation of salt stress in plants, (2) potential competition between PGPR strains and indigenous soil microflora in the rhizosphere of plants grown in stressed environments, and (3) induction of salt stress tolerance at plant tissue, cell, and molecular level.

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