32 Plant Growth-Promoting Bacteria as an Alternative Strategy for the Amelioration of Salt-Stress Effects in Plants

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32.1 PLANT GROWTH-PROMOTING BACTERIA AND SALT TOLERANCE IN PLANTS

Plant growth-promoting bacteria (PGPB) represent a group of rhizospheric and/or endophytic bacteria that colonize interior or exterior of roots. Although most of these belong to the genera *Bacillus* and *Pseudomonas*, they may also belong to the *Microbacterium*, *Pantoea*, *Rhizobium*, *Burkholderia*, *Methylobacterium*, *Azospirillum*, *Poenibacillus*, *Micorococcus* and *Variovorax*. All of them could improve tolerance to host plants during abiotic stresses (Akram et al. 2016; Shahid et al. 2018; Abbas et al. 2019). Those bacteria could improve plant growth under normal conditions, as well as enhance tolerance against salinity stress by various mechanisms. Those mechanisms could be divided into two groups – direct and indirect mechanisms. Direct mechanisms represent improving the bioavailability of different mineral nutrients, such as iron (for siderophore production) and phosphorus

(phosphate solubilization), nitrogen fixation, production of different phytohormones (indole-acetic acids, auxins, ethylen). Among the indirect mechanisms are the activation of antioxidative defense, production of exopolysaccharides (EPS) and compatible osmolytes and the biosynthesis of volatile organic compounds (VOC) (Yang et al. 2009; Numan et al. 2018; Abbas et al. 2019). PGPB are able to activate “memory” defence in plants and induce response against salinity through microbe-associated molecular patterns. Such mechanisms, providing tolerance in stress conditions, are known as “induced systemic tolerance – IST” (Abbas et al. 2019). Interestingly, PGPB able to activate IST could be salt-tolerant, also, but this is not obligatory.

32.1.1 MECHANISMS OF PGPB-MEDIATED SALT-STRESS TOLERANCE

PGPB are able to use a plethora of mechanisms, which directly or indirectly ameliorate salt-stress effects in plants (Hashem et al. 2016; Egamberdieva et al. 2019). All these mechanisms act synergistically in order to cope with emerging stress, activating different protection mechanisms, such as antioxidative systems and osmoprotectants.

32.1.1.1 Synthesis of Plant Growth Regulators

Many PGPB have the ability to release phytohormones, such as gibberelic acids (GA), auxins (indole-3-acetic acid – IAA, dominantly), cytokinins (CK) and abscisic acid (ABA). Apart from these hormones, some PGPB strains could modulate plant hormone status by releasing metabolites as well as the enzymes, such as 1-aminocyclopropane-1-carboxylase (ACC) deaminase. Together these can play essential roles in ameliorating salt-stress effects in plants. Acting as specific regulators, these molecules are able to modulate plant metabolism and morphology.

32.1.1.1.1 Auxins

Many strains of PGPB can produce auxins, such as indole-3-butyric acid or indole-3-acetic acid (IAA), or their precursors (Martinez-Morales et al. 2003; Spaepen et al. 2007; Numan et al. 2018). IAA is the most important and the most investigated auxin, acting as a key player in many processes, like cell division, differentiation and extension, but also in gravitropic and phototropic responses (Korasick et al. 2013) and circadian rhythms (Vinterhalter et al. 2015). This hormone can be produced in the tryptophan-based pathway via the formation of indole-3-pyruvic acid or indole-3-acetamide (Vaishnav et al. 2016). It is interesting that plant root cells secrete tryptophan, produced in the phenylpropanoid pathway from chorismate, and secreted amino acid is taken up by microorganisms situated in the rhizosphere. Production of IAA by PGPB is one of the most common and widely studied bacterial signaling molecules involved in plant-microbe interaction. There is a lot of experimental data confirming the importance of IAA-producing PGPB in minimizing the deleterious effects of salinity on crop plants. Generally, plants inoculated with IAA-producing PGPB grow more main roots and laterals, due to the effects of the hormone on apical meristems. These changes increase plant access to soil nutrients (Manulis et al. 1994; Nicolas et al. 2004). In addition, inoculated plants have more leaves, as IAA is also the main auxin promoting shoot

growth (Malhotra and Srivastava 2009). All these effects of IAA-producing PRGP on plants are considered as adaptive responses to salinity (Vaishnav et al. 2016). Experiments on *Phaseolus vulgaris* exposed to 50 mM NaCl showed that application of *Azospirillum brasiliense* could alleviate the negative effects of stress, by encouraging higher branching of roots and activating the production of flavonoids (Dardanelli et al. 2008). Yao et al. (2010) showed that *Pseudomonas putida* was able to modulate production of IAA in plant tissues, increasing growth parameters in cotton plants. Some PGPB, like salt-tolerant *Streptomyces* isolates that produce IAA, were able to improve the root system of wheat plants exposed to salt stress (Sadeghi et al. 2012). *Bacillus amyloliquefaciens* SQR 9 was able to enhance salt-stress tolerance in maize seedlings exposed to 100 mM NaCl. Maize seedlings inoculated with that bacteria strain showed not only increased total chlorophyll and soluble sugar contents, but also enhanced glutathione content. In addition, SQR9 inoculation activates peroxidase (POD) and catalase (CAT) and reduced the ABA level induced by salinity. As a consequence of plant-microbe interaction, upregulation of many of the genes (*RBCS*, *RBCL*, *NCED*, *HKT1*, *NHX1*, *NHX2* and *NHX3*) involved in photosynthesis and metabolism has been observed (Chen et al. 2016; Ilangumaran and Smith 2017). In *Arabidopsis* and tomato (*Solanum lycopersicum*) plants, inoculation with *Enterobacter* sp. EJ01 (isolated from a halophyte) improved the tolerance of plants to salt stress (200 mM NaCl). In these plants, inoculation with EJ01 activated the expression of genes involved in dehydration, such as DRE-binding proteins DREB2b, LEA genes RAB18 and a gene involved in biosynthesis of proline – P5CS1 (Ilangumaran and Smith 2017). More recent experiments have shown that the salt-tolerant PGPB *Leclercia adecarboxylata* regulates sugar biosynthesis, the production of different organic acids and chlorophyll fluorescence in tomato under salt stress (Kang et al. 2019). Those effects are also accomplished via IAA.

32.1.1.1.2 Absciscic Acid

Although it has been proposed that many PGPB produce ABA *in vitro*, there are relatively few studies about the role of ABA in plant-microbe interactions. In addition, it is not clear whether ABA, produced by bacteria, can modulate ABA status in plants exposed to enhanced salinity (Dodd et al. 2010; Ilangumaran and Smith 2017). Some reports have shown that PGPB inhibit ABA production in salt-stressed plants, while others claim that bacteria enhance the accumulation of ABA, providing better conditions for plant survival under salt stress (Vaishnav et al. 2016). However, the experimental data show that PGPB modulate not only ABA biosynthesis, but also ABA-mediated signaling pathways. In wheat, inoculation with *Dietzia natronolimnaea* STR1 induced salinity tolerance in plants exposed to 150 mM NaCl, via modulation of an ABA-signaling cascade. Inoculation upregulates *TaABARE* (an ABA-responsive gene) and *TaOPR1* (the 12-oxophytodienoate reductase gene), which lead to the activation of TaMYB and TaWRKY, and finally upregulated the expression of the stress-related gene *TaST* (salt stress-induced). Inoculation of cucumber (*Cucumis sativus*) with *Burkholderia cepacia* SE4, *Promicromonospora* sp. SE188 and *Acinetobacter calcoaceticus* SE370 provided better performance (higher biomass) of plants grown at 120 mM NaCl. It was interesting that inoculated

plants had a lower ABA level compared with control (non-inoculated) plants, as well as an increased water potential and decreased electrolyte leakage. In addition, inoculation increased salicylic acid and gibberellin content (Kang et al. 2014). Inoculation of cotton (*Gossypium hirsutum*) seeds with *Pseudomonas putida* Rs-198 increased plant biomass and reduced ABA level. Non-inoculated plants showed a higher accumulation of ABA in leaves (Yao et al., 2010). Barnawal et al. (2017) observed that, in wheat plants, inoculation with *B. subtilis* LDR2 and *Arthrobacter protophormiae* SA3 increased ABA content under salt-stress conditions (100 mM NaCl). That effect was accomplished by upregulation of the *TaCTR1* (Serine/Threonine protein kinase – ethylene responsive) and *TaDRE2* (drought-responsive element) genes.

32.1.1.1.3 Gibberellin

There are a few data about the gibberellin-producing PGPB, especially about their role in acquiring salt-stress tolerance in plants. It is well known that some plants, inoculated with different *Rhizobium* strains (GA7 producers), have longer roots (Numan et al. 2018). Cassán et al. (2014) showed that inoculation of wheat and soybean with GA-producing *A. brasilense* enhanced plant growth.

32.1.1.1.4 Cytokinins

CK are a group of purine-derivates acting as plant hormones: they regulate many processes, like cell division, differentiation of root callus, shoot formation, chloroplast maturation and stomatal conductance in higher plants (Cassán et al. 2014). It is well known that plants maintain their totipotent stem cells in root and shoot meristems due to the action of CK (Howell et al. 2003; Leibfried et al. 2005). Although many experimental data have shown that increased growth of inoculated plants is correlated with cytokinin-producing PGPB (Nieto and Frankenberger 1991; Arkhipova et al. 2005), the role of bacterial CK in salt-stress tolerance is unknown. Egamberdieva (2019) showed that some *Pseudomans* strains (*P. aurantiaca* TSAU22, *P. extremorientalis* TSAU6 and *P. extremorientalis* SAU20) could increase plant growth as well as break salinity (100 mM NaCl) induced seed dormancy.

32.1.1.1.5 Ethylene

Ethylene, the only gaseous plant hormone, is known as a stress hormone. As stress increases the ethylene content in plants, the transcription of auxin response factors is inhibited leading to a perturbation in plant growth. Plants use the Yang cycle for ethylene biosynthesis, in which ACC, as the precursor, is converted into ethylene by the ACC oxidase enzyme (Yoon and Kieber 2013). Salinity stress induces the accumulation of ethylene, as well as its precursor ACC, in the leaves, which results in decreased photosynthesis and foliar senescence (Ghanem et al. 2008). Many PGPB are able to secrete ACC deaminase, an enzyme that restricts ethylene biosynthesis in plants. ACC deaminase converts ACC to ammonia and α -ketobutyrate and thereby decreases ethylene levels in plants. Many experimental data show that ACC deaminase-producing PGPB could provide tolerance to plants in saline soil. Thus, cucumber plants are able to grow in saline soil due to the stimulation effects of *Stenotrophomonas rhizophila* (Egamberdieva et al. 2011). Nadeem et al. (2009) reported that *Pseudomonas fluorescens* and *Enterobacter* spp. could improve the

yield of maize grown in a salt-affected soil. In addition, tomato seedlings, inoculated with *Pseudomonas putida* UW4, were able to grow in saline conditions (90 mM NaCl). Interestingly, these plants showed increased shoot growth after 6 weeks in saline conditions. In that case, the bacteria used for inoculation, although producing ACC deaminase, were able to up regulate the expression of *TocGTPase* gene. That gene coding is part of the chloroplast protein import apparatus, facilitating the import of proteins involved in stress response (Yan et al. 2014). Peanut tolerance to saline condition has been improved by inoculation with *Brachybacterium saurashtrense* (JG-06), *Brevibacterium casei* (JG-08) and *Haererohalobacter* (JG-11), ACC-producing PGPB (Shukla et al. 2012). Apart from its role in decreasing ethylene level in plants, preventing them from senescence, it has been found that ACC deaminase producing PGPB strains could have other effects on plants, such as the production of pigments under drought and salt stress, the biosynthesis of compatible solutes and the stabilization of membranes (Tiwari et al. 2018). In pea plants (*Pisum sativum* cv. Alderman), inoculated with *Variovorax paradoxus* 5C-2, under salt-stress conditions – 70 and 130 mM NaCl, there was an increased K^+/Na^+ ratio in shoots. This is very important for pea survival under saline conditions, as experimental data have shown that pea varieties have different sensitivity to salinity (Miljuš-Djukić et al. 2013). These strains could also have the effects on nodule formation in legume crops (Ahmad et al. 2011; Egamberdieva et al. 2019). PGPB that produce both ACC deaminase and auxin (IAA) have a great potential for plant protection from different stresses. Accumulation of IAA activates the enzyme ACC synthase, increasing the ACC level and subsequently ethylene level. The excess ACC could be destroyed by ACC-deaminase producing PGPB, allowing the promotion of plant growth under stress conditions mediated by IAA (Glick 2012; Ilangumaran and Smith 2017).

32.1.1.2 Volatile Organic Compounds

VOC play one of the crucial roles in plant-microorganism interactions. Due to high vapor pressure, these compounds can enter the atmosphere as vapors. VOC-producing PGPB are able to modulate many signaling pathways in plants, resulting in the promotion of growth and the activation of induced systemic resistance – ISR (Ryu et al. 2004; Zhang et al. 2008; Numan et al. 2018). Using a microarray, Zhang et al. (2007) showed that the VOC of *B. subtilis* GB03 in *A. thaliana* seedlings altered the expression of more than 600 genes. Under saline conditions, VOCs were able to upregulate the expression of HKT1 – the high affinity K^+ transporter, thus lowering accumulation of Na^+ in plant tissues (Zhang et al. 2008). *Pseudomonas simiae* AU, a VOC producing PGPB, was able to induce salt tolerance in soybean (*Glycine max*) exposed to high salinity (100 mM NaCl) by decreasing the accumulation of sodium cations in roots and increasing the accumulation of proline. Analysis of proteins revealed upregulation of different vegetative storage proteins involved in Na^+ homeostasis and the RuBisCO large subunit (Vaishnav et al. 2016). Ledger et al. (2016) showed that VOCs produced by *Paraburkholderia phytofirmans* PsJN induced salinity tolerance *in vitro* and in the soil. Also, all growth parameters, such as fresh weight, length of primary roots and rosette area were higher in Arabidopsis plants treated with VOCs comparing with non-inoculated plants (Ledger et al. 2016).

32.1.1.3 Exopolysaccharides

EPS or surface polysaccharides secreted by bacteria are responsible for bacterial attachment to root surfaces, soil particles as well as to other bacteria. Some of PGPB secrete EPS (Tewari and Arora 2014; Khan and Bano 2019). It is important that EPS could act as a barrier around plant roots, thus supporting plant growth under saline conditions (Vaishnav et al. 2016). Inoculation of chickpea (*Cicer arietinum* var. CM-98) with EPS-producing PGPB *Halomonas variabilis* HT1 and *Planococcus rifietoensis* RT4 resulted in increased plant growth at 200 mM NaCl (Qurashi and Sabri 2012). Yang et al. (2016) inoculated quinoa (*Chenopodium quinoa*) seeds with *Enterobacter* sp. MN17 and *Bacillus* sp. MN54 and showed plant survival under saline irrigation conditions (400 mM NaCl). Recently, it has been shown that salt-tolerant EPS producing *B. subtilis* subsp. *inaquosorum* and *Marinobacter lypoliticus* SM19 reduced drought and salinity stress effects in wheat (Atouei et al. 2019). In *A. thaliana*, EPS producing *Pseudomonas* sp. was able to upregulate the *LOX2* gene which encodes a lipoxygenase. This enzyme is a component of the jasmonic acid biosynthesis pathway (Chu et al. 2019).

Apart from exopolysaccharides, many PGPB produce lipo-chitooligosaccharides. These molecules are secreted by rhizobia as Nod-factors (NFs) and their secretion is induced by flavonoids present in root exudates. NFs, thus, initiate nodule formation (Ilangumaran and Smith 2017). Miransari and Smith (2009) reported that inoculation of soybean plants with *Bradyrhizobium japonicum* 532C enhanced nodulation and growth under mild salinity stress (36 mM and 61 mM NaCl).

32.1.1.4 Osmoprotectants

Salt stress is basically a two-component stress and plant growth and development are first affected by the osmotic impacts of salt stress. The accumulation of salt ions leads to a decrease in the osmotic balance in plants. Plants accumulate compatible osmolytes to improve plant-water relations and maintain cell structures protected from osmotic shock. Many PGPB also use this mechanism for protection against osmotic stress (Ilangumaran and Smith 2017). Choudhary et al. (2012) reported that many PGPB, such as *Burkholderia*, *Arthobacter*, *Bacillus* and *Pseudomonas*, are able to enhance proline levels in plants under abiotic stress. Some endophytic bacteria, producing ACC deaminase and IAA, are able to increase proline content in sweet pepper (*Capsicum annum*). Maize plants (*Zea mays*) inoculated with *Rhizobium* and *Pseudomonas* accumulated more proline comparing with control (non-inoculated) plants (Bano and Fatima 2009). According to the experimental data, it is evident that the accumulation of proline under abiotic stress is a result of the activation of the pyrroline-5-carboxylate synthase (*P5CS*) gene; thus, bacterial treatment activates the expression of *P5CS* gene (Kumari et al. 2015). Some PGPB also produce polyamines, such as spermidine (*Bacillus megaterium* BOFC15) and soluble sugars (trehalose). Many of PGPB have genes for the biosynthesis of trehalose (Qin et al. 2018; Shim et al. 2019).

32.1.1.5 Antioxidant Enzymes

Many reports have shown that inoculation of plants with PGPB reduced the oxidative stress in plants and its deleterious effects (Manaf and Zayed 2015; Islam et al. 2016).

PGPB strains are able to activate and even increase the concentration of antioxidative enzymes. Under saline conditions, the activity of soluble POD, superoxide dismutase, CAT and glutathione reductase has been increased by PGPB (Jha and Subramanian 2013; Sen and Chandrasekhar 2015; Ansari et al. 2019). Plant inoculation with *Azospirillum lipoferum* FKI induced an increasing level of antioxidant gene transcripts (El-Esawi et al. 2019). Kohler et al. (2009) reported that lettuce plants inoculated with PGPB showed increased activity of CAT under salinity stress. In *Jatropha* plants exposed to salt stress, Patel and Saraf (2013) observed an increased level of APX and CAT activity in leaves. Although many reports have claimed that plants inoculated with PGPB showed increased activities of antioxidative enzymes, the exact mechanism for enzyme activation remains unknown.

32.1.1.6 Nutrient Acquisition

Salinity can affect plant growth and productivity due to a limitation of nutrients in the soil. As salinity changes the pH of soil, some nutrients become less available for plants. PGPB are able to solubilize different nutrients making them available for plants. PGPB exert these effects by different mechanisms, such as siderophore production, increased phosphorous solubilization, organic and inorganic phosphate solubilization and non-symbiotic nitrogen fixation.

Siderophores are agents able to chelate iron and represent an important trait for the promotion of plant growth. Siderophores produced by different PGPB have high affinity for iron, thus preventing the proliferation of phytopathogens (Numan et al. 2018). Siderophores are secreted in the rhizosphere, so plant roots can uptake iron from them via two mechanisms – by chelate degradation or by direct uptake (Rajkumar et al. 2010). In saline soil, the availability of Fe^{3+} ions can be reduced due to changes in pH (Thomine and Lanquar 2011); plant inoculation with siderophore-producing PGPB can, therefore, help plants to overcome the nutrient stress caused by high salinity.

Phosphorus is a crucial macronutrient for plants. In organic form, it is present as inositol phosphates, phosphoesters, phosphodiesteres and phosphotriesters (Sindhu et al. 2010). A large part of the soil phosphorus pool is immobilized and unavailable for plants (Numan et al. 2018). PGPB can play an important role in the transformation of phosphorus, making it available for plants. Phosphate solubilizing bacteria belong to the genera *Bacillus*, *Pseudomonas*, *Brevibacterium*, *Serratia*, *Xanthomonas*, *Corynebacterium* and *Alcaligenes* (Sindhu et al. 2010). These bacteria are able to hydrolyze unavailable forms of phosphorus into more available forms. As salinity can cause the precipitation of available phosphorus, PGPB could solubilize precipitated forms, providing nutrients to plants under salinity stress.

PGPB have the ability to provide other nutrients to plants, such as nitrogen, potassium, sulfur and zinc (Vaishnav et al. 2016). Some PGPB can enhance the nodulation process, especially in saline soil, which is important because *Rhizobium* are often not effective for the induction of nodulation under saline conditions (Ahmad et al. 2011).

32.2 FUTURE PERSPECTIVES

In order to successfully use PGPB strains in the region affected by increased salinity the best way is to use halotolerant bacteria for plant and/or seed inoculation. These PGPB should be isolated from salt-affected soils, which make them able to colonize roots under salinity (Paul and Nair 2008; Vaishnav et al. 2016). Ramadoss et al. (2013) demonstrated that five PGPB halotolerant bacteria could ameliorate salt stress in wheat plants. In these experiments, they used 320 mM NaCl for inducing salt stress and observed that inoculation was able to increase root length by up to 71.7%. Apart from the use of halotolerant bacteria, it is speculated that is possible to use PGPB which are not halotolerant (tested in laboratory conditions with growing medium supplemented with NaCl) for the enhancement of plant growth under saline conditions. In that case it should be the use of bacterial cultures for seed inoculation, so called “seed priming”. In this way, PGPB could activate different mechanisms in plants, including ISR, making them more tolerant to salinity. Some plant seeds, inoculated with non-halotolerant PGPB, were able to germinate faster under salt stress, compared with non-inoculated control seeds.

The commercialization of PGPB strains is a complex process, which includes many stages – from isolation, screening and testing in laboratory conditions, up to testing in the field, estimating their efficacy and making adequate formulations. It is necessary also to test the viability of formula and industrial production, etc. (Bhattacharyya and Jha 2012; Vaishnav et al. 2016).

Many of the mechanisms of osmo-adaptation of PGPB still need to be elucidated; establishing these could have a big impact on the process of improvement of productivity in agriculturally important plants grown in saline agro-ecosystem (Paul 2013). Further work is also required to investigate the regulatory networks which provide salt (and other) stress tolerance to bacteria. Also, plant-microbe interaction, particularly under saline condition, should be deeper investigated. Although many mechanisms are well documented, the possible interaction among them is still controversial. A deeper analysis of the bacterial communities associated with plant roots, as well as examination of the dynamic changes of microbiomes under saline condition could provide valuable data.

It is very important that the research findings obtained under laboratory conditions be extended to field trials and in different geographical regions. Also important is that this research should be conducted on different plants, even on different cultivars, which is a major challenge. The major issue for the end-users is using developed bioinoculant formula on many different plants. Having in mind that PGPB are diverse, in respect to their plant-growth promoting effects, the recommendation is to use no single PGPB strains, but several strains or consortia. Using diverse microbes in consortia formulations is potentially a promising strategy for the alleviation not only of salinity (and other abiotic) stress in plants, but also biotic stress – phytopathogens (Egamberdieva et al. 2019).

PGPB used for enhancing the plant productivity in saline agro-ecosystem have the potential to help in achieving food security and improving global food production. Moreover, they can change the quality of soil and help in combating the adverse effects of climate change (Arora 2019).

32.3 CONCLUSION

Salt stress is still a major problem for agriculture, limiting the yield of many agriculturally important crops. Although plant-growth promoting bacteria, including halotolerant types, represent a promising tool for the alleviation of salt-stress effects on plants, a lot is yet to be explored, at the biochemical as well as at the molecular levels. Apart from helping plants, PGPB in saline agro-ecosystem have the potential to improve soil qualities, like soil fertility. These microorganisms, used as biocontrol agents, as a part of alternative green biotechnologies, should be extensively used in the future not only in saline soils, but also in other marginal soil types. Many issues, including problems with the formulation and production of final products, as well as potential legal and social impacts, should be further analyzed.

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