



Halotolerant Plant Growth Promoting Rhizobacteria: A Futuristic Direction to Salt Stress Tolerance

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Abstract

Salinity is one of the most devastating abiotic stresses known to affect all the major processes such as germination, photosynthesis, water relations, nutrient uptake, reproduction, etc., affecting the growth and yield of the majority of the plants. High salinity-induced decrease in water potential causing osmotic stress and accumulation of salt-induced oxidative damage are major causes for the limitation in plant growth, productivity and cell death in the majority of plants. Employment of Plant Growth Promoting Bacteria (PGPB) is a well-studied alternative for the protection of plants from salinity stress-induced detrimental effects. Since rhizospheric bacterial communities have a direct influence on the physiology and development of plants, identification and characterization of plant beneficial microbes are important. Halotolerant Plant Growth Promoting Rhizobacteria (PGPR) are beneficial microbes that colonize internal and external parts of the plant roots and play a pivotal role in improving plant growth and alleviating the adverse effects of salinity stress. They influence the physiology and development of plants by producing various plant growth-promoting traits that have a direct effect on the growth and stress tolerance of plants. Efforts are taken to identify and characterize the PGPR from different rhizosphere zones and prepare the consortia for agricultural applications thereby reducing the usage of synthetic fertilizers and agrochemicals. In the current chapter, we describe the general effects of salinity stress in plants, highlighting the importance of employment of PGPR either in isolation or consortia for the

preparation of bioformulations for agricultural applications and improvement of salinity tolerance.

Keywords

Exopolysaccharides • Osmolytes • Phytohormones • Plant growth promoting rhizobacteria • Salinity stress

Abbreviations

ABA	Abscisic acid
ACC	1-Aminocyclopropane-1-carboxylic acid
IAA	Indole-3-acetic acid
PGPB	Plant growth promoting bacteria
PGPR	Plant growth promoting rhizobacteria
ROS	Reactive oxygen species

1 Introduction

An increase in soil salinity is one of the adverse abiotic stress conditions that occur through natural and anthropogenic reasons. Accumulation of water-soluble salts in the soil is the main cause of soil salinization, having a strong impact on agricultural productivity and environmental health (Rahman et al. 2021). Soil salinity changes the fertile land to unproductive land, ultimately resulting in loss of crop productivity and economical loss. The high salt accumulation in the soils can be due to low precipitation, weathering of native rocks, geological deposits, ground water with high salt, poor agricultural practices, evapotranspiration and lack of rainfall to flush the salts (Parihar et al. 2015; Hanin et al. 2016). The soils having an electrical conductivity of the saturation soil extract of more than 4 deciSiemens/meter (dS/m^{-1}) at 25 °C are considered saline soils. However, the limit can be lowered to 2 dS m^{-1} for the fruits and ornamental plants which can be seriously affected by the salinity range of 2–4 dS m^{-1} . Compared to normal soil, saline soils show an excessive

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amount of ionic salts, higher electrical conductivity and lower water potential. Although sodium and chloride are the dominant ions present in saline soils, chlorides and sulphates of sodium, calcium and magnesium are also commonly present. The irrigation water contains calcium, magnesium and sodium and upon water evaporation, calcium and magnesium often precipitate into carbonates leaving sodium in the soil. Accumulation of sodium and chloride in the soil restricts the nutrient-ion activities and generates external osmotic potential restricting the influx of water into the roots thereby resulting in water deficit in plants (Acosta-Matos et al. 2017). Salinity stress is known to adversely affect crop productivity by reducing the net cultivable area, especially in arid and semiarid areas all over the world (Singh and Roychoudhury 2021). High salinity is known to cause ion toxicity, oxidative stress and alteration of metabolism leading to reduced growth, development and crop productivity (Parihar et al. 2015). The situation warrants the development of sustainable methods to increase the productivity of saline soils without causing any damage to the environment (Guzmán et al. 2021). Although breeding for salt-tolerant plants and the development of transgenic plants with salt tolerance capacity can be the solution, the approaches are cumbersome and time-consuming. Under these circumstances, microbes with the potential for plant growth promotion seem to be a viable option. Soil being a reservoir for diverse microorganisms such as bacteria, fungi and archaea is known to host microbes that have the inherent capacity to tolerate high concentrations of salt in soil and possess plant growth-promoting traits. These salt-tolerant microbes particularly bacteria are important for promoting the growth and improving crop productivity in arid and semiarid regions (Egamberdieva et al. 2019). Additionally, several of the bacteria colonize the plant roots and are involved in imparting beneficial effects to the plants. These bacteria are termed Plant Growth Promoting Rhizobacteria (PGPR).

Extensive studies have been performed on the bacteria belonging to the genera, *Acetobacter*, *Achromobacter*, *Acinetobacter*, *Alcaligenes*, *Arthrobacter*, *Azoarcus*, *Azotobacter*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Exiguobacterium*, *Gluconacetobacter*, *Methylobacterium*, *Microbacterium*, *Ochromobacter*, *Paenibacillus*, *Pantoea*, *Pseudomonas*, *Rhodococcus*, *Staphylococcus*, *Serratia*, *Stenotrophomonas* and *Streptococcus* for their plant growth-promoting traits (Babalola 2010; Dodd and Perez-Alfocea 2012; Chauhan et al. 2015; Egamberdieva et al. 2019). Additionally, since many species of the phytomicrobiome are non-culturable, metagenomics approaches were utilized to decipher the variation in the composition of the microbiome genotype wise (Hirsch and Mauchline 2012; Wintermans et al. 2016). Researchers have used either a single bacterium or a consortium of bacteria under controlled laboratory conditions, greenhouse and field conditions for

analysing plant growth promotion in plants (Chauhan et al. 2015). The PGPR strains have also been utilized for commercial agriculture. The ability of the plant growth promoting bacteria to colonize the plant roots and their efficient release of stimulants are critical determinants for evaluating the suitability of utilizing the plant growth promoting bacteria as inoculants for crop improvement and increased productivity under salinity stress conditions. Additionally, research also indicated that the plants efficiently control the composition of the rhizomicrobiome by producing root exudates of varying compositions (Chaparro et al. 2012; Trabelsi and Mhamdi 2013; Zhang et al. 2017). The root exudates as a source of reduced carbon serve as signals to attract specific microbes, favouring their growth, modulate the expression of several genes and induce the cell to cell signaling by quorum sensing (Meneses et al. 2011; Alquéres et al. 2013; Beauregard et al. 2013; Massalha et al. 2017; Smith et al. 2017). In the current chapter, the general effects of salinity stress in plants are briefly outlined with a major focus on highlighting the importance of employment of halotolerant PGPR either in isolation or consortia for agricultural applications and improvement of salinity tolerance.

2 Salt Stress in Glycophytes

Based on the plant's ability to grow and survive under saline environments, they are classified as glycophytes (salt-sensitive) and halophytes (salt-tolerant). Among the angiosperms, while a majority of the crop species are glycophytes whose growth is compromised under saline stress conditions, halophytic plants survive, reproduce and complete their life cycle under high saline soils since they are endowed with varied mechanisms to tolerate salinity (Flowers et al. 1977; Mishra and Tanna 2017; Chen et al. 2018). Salt stress in glycophytic plants affects morphological, physiological and biochemical functions seriously affecting their growth and development at every stage of their life cycle. Salinity stress seriously affects germination, photosynthesis, water relations, nutrient balance, growth and development of crops leading to increased oxidative damage and a drastic reduction in yield (Parihar et al. 2015). Salinity stress in glycophytic plants seriously affects photosynthesis, increases the production of reactive oxygen species thereby causing damage to DNA, membrane lipids and proteins triggering cell death. The decrease in photosynthesis during salinity stress is mainly due to a decrease in chlorophyll content, reduced photosystem II efficiency and electron transport rate (Acosta-Matos et al. 2017).

High salinity in the soil is known to inhibit plant growth either by reducing its ability to take up water, causing water deficit or dehydration in cells or causing excess

accumulation of ions resulting in ionic stress (Tester and Davenport 2003; Munns and Tester 2008). The net movement of the water is zero when the salt concentration in the soil is equal to that of the plant, however, the higher salt concentration in the soil leads to movement of water from the plant to the soil causing physiological drought and cellular dehydration (Munns and Tester 2008). While physiological drought imposed by high salinity does not lead to a build-up of either Na^+ or Cl^- ions, whereas the physiological and metabolic processes that are affected are similar to drought stress-affected plants. Contrary to this, ionic stress induced by excess accumulation of Na^+ or Cl^- ions during salinity stress causes oxidative stress leading to damage and cell death. While Na^+ is a non-essential element in the majority of the plants, its intracellular accumulation during salinity stress interferes with K^+ uptake leading to stomatal regulation disturbance causing water loss through transpiration. Compared to Na^+ ions, Cl^- ions are essential for the regulation of turgor pressure, pH and enzyme activities in the plant cell cytoplasm. Accumulation of Cl^- ions cause disturbance in the production of chlorophyll and cause chlorine toxicity symptoms (Tavakkoli et al. 2011; Parihar et al. 2015). Salinity stress-induced excess accumulation of Na^+ in plants causes ionic stress leading to disturbances in K^+ ion efflux thereby causing an imbalance in cellular homeostasis and oxidative stress (Tester and Davenport 2003; Munns and Tester 2008). High salinity-induced accumulation of Na^+ or Cl^- leads to a decrease in uptake of essential nutrients such as phosphorus (P), potassium (K^+), nitrogen (N) and calcium (Ca^{+2}) (Zhu 2001). While maintenance of high tissue and cytosolic K^+/Na^+ ratios are required for salt tolerance, salinity stress-induced Na^+ accumulation in the cytoplasm leads to K^+ ion efflux from both leaf and root cells leading to activation of K^+ outward rectifier channels (GORK, guard cell outward rectifying K^+ channel) for exclusion of K^+ ions (Wang et al. 2009; Demidchik et al. 2014; Shabala and Pottinson 2014). The ability of the plants to retain intracellular K^+ ions is a very important feature for salt stress tolerance since K^+ is an essential nutrient important for many enzymatic reactions and participates in a plethora of plant physiological functions (Ahmad and Maathius 2014; Assaha et al. 2017).

Since the accumulation of high levels of Na^+ ions is detrimental for plants, regulating Na^+ transport in leaves of glycophytic plants is very crucial for salt tolerance. Plant roots exposed to salt in the soil activate several signaling cascades restricting Na^+ influx into the roots and reducing its translocation. While halophytes compartmentalize the Na^+ ions effectively into the vacuoles, the majority of the glycophytic plants succumb to death due to overaccumulation of Na^+ ions in the cytoplasm (Bartels and Dinakar 2013). The reduced influx and increased efflux along with sequestration of Na^+ ions into the vacuole are the major

determinants of plants aiding in acclimation or tolerance to salinity stress. Salinity stress-induced accumulation of compatible osmolytes and increased antioxidants to scavenge the reactive oxygen species leading to a decrease in oxidative stress are considered important strategies to combat salinity stress by plants (Bartels and Dinakar 2013; Flowers et al. 2015; Acosta-Motos et al. 2017; Liang et al. 2018). The uptake of Na^+ from the soil by the roots is reported to occur through high-affinity K^+ transporters (HKTs), K^+ channels, *Arabidopsis* K^+ transporter (AKT1), high-affinity K^+ uptake transporter (AKT1), cyclic nucleotide-gated channels (CNGCs) and glutamate receptors (GLRs) (Tester and Davenport 2003; Hanin et al. 2016; Assaha et al. 2017). Additionally, SOS1, a plasma membrane-localized Na^+/H^+ antiporter is known to transport Na^+ from root to shoot in both glycophytes and halophytes under salinity stress conditions (Munns and Tester 2008; Shabala 2013; Foster and Miklavcic 2019; Gupta et al. 2021). High salt in the soil favours the absorption of Na^+ by the roots which moves through the xylem with the aid of transporters and reaches the shoot and the leaf blades (Munns and Tester 2008). Hence, downregulation of the genes coding for Na^+ influx transporters may be required to limit the Na^+ uptake by the roots in glycophytic plants. Although glycophytic plants can withstand mild salinity stress by operating various stress tolerance mechanisms, increased salinity accelerates oxidative damage resulting in cell death.

3 Mitigation of Salinity Stress by Halotolerant Plant Growth Promoting Rhizobacteria

Salt tolerance mechanisms in plants are intricate and complex requiring the operation of multiple metabolic pathways and activation of a network of genes. Although salt tolerance in crops can be attained by conventional breeding approaches and genetic engineering, long-duration along with high costs for generating breeding varieties and public acceptance of the genetically modified crops are major concerns (Egamberdieva et al. 2019; Bakka and Challabathula 2020). Under these circumstances, the usage of beneficial microorganisms for stress amelioration is gaining importance for salinity stress management in plants. PGPR are rhizospheric or endophytic bacteria capable of colonizing either in the interior or exterior parts of plant roots imparting plant beneficial effects and mitigation of salt stress. Although PGPR constitutes only around 2–5% of the rhizospheric bacteria, reports suggest that they can be effectively used under nutrient deficiency conditions as a replacement for chemical fertilizers aiding in the improvement of soil fertility (Grover et al. 2021). In recent years,

usage of halophilic/halotolerant PGPR has gained importance, since they are environment friendly and their inoculation to glycophytic crops species has shown remarkable improvement in stress tolerance and increased productivity (Egamberdieva et al. 2019). Halotolerant PGPR has the inherent ability to tolerate high amounts of salts and is found in areas such as coastal dunes, saline deserts, hypersaline lakes, salt marshes, and inland salt seas. Although they are usually isolated from the high saline environment, they do not require high salt for their growth (Bremer and Kramer 2019). One of the adaptive strategies employed by halotolerant bacteria to survive in high salt conditions is the maintenance of lower intracellular levels of ions along with the accumulation of compatible solutes to balance the osmotic level inside the cytoplasm than the outer medium (Bremer and Kramer 2019). Along with this, the halotolerant PGPR have evolved several mechanisms to protect the cellular integrity thereby coping with salinity stress conditions. Accumulation of compatible solutes, activation of different salt efflux systems, reduced generation of ROS, limitation in oxidative damage is some of the mechanisms they operate to withstand high salinity stress (Egamberdieva et al. 2019). The halotolerant PGPR employs diverse mechanisms such as the production of phytohormones, possessing ACC deaminase activity, production of exopolysaccharides, and osmolytes which are directly or indirectly involved in the amelioration of salt stress in crop plants (Egamberdieva et al. 2016; Mishra et al. 2021). Additionally, activation of plant defence responses and antioxidant enzymes is observed in PGPR inoculated plants during salinity stress conditions to protect plant cells from oxidative stress. The list of plant growth promoting bacteria and their beneficial effects on plants in modulating the expression of plant genes and their involvement in salinity tolerance is shown recently by Mishra et al. (2021). The changes that are observed in the aerial and underground plant organs upon inoculation with PGPR under salinity stress conditions is shown in Fig. 1.

4 Attributes of Halotolerant Plant Growth Promoting Rhizobacteria

4.1 Production of Phytohormones

4.1.1 Indole-3-Acetic Acid

Halotolerant PGPR is known to produce a variety of phytohormones such as auxins, gibberellins, cytokinins and abscisic acid for plant growth, development and increased salt stress tolerance (Dodd et al. 2010; Dodd and Perez-Alfocea 2012). Among the auxins, indole-3-acetic acid (IAA) produced by the bacteria stimulates root growth and cell division not only under normal conditions but also under salt stress conditions. Halotolerant PGPR such as

Azotobacter, *Arthrobacter*, *Azospirillum*, *Pseudomonas*, *Stenotrophomonas* and *Rahnella* are known to produce IAA under salt stress conditions (Piccoli et al. 2011; Egamberdieva et al. 2018). During tryptophan-dependent IAA synthesis, the PGPR utilizes the tryptophan released from the root exudates and converts them into IAA (Backer et al. 2018a, b). The IAA produced by the PGPR acts like a signaling molecule to trigger auxin signaling in plant roots along with causing induction in the expression of phytohormone related genes, defence genes and antioxidant genes resulting in increased auxin signaling, production of longer roots, increased root biomass and enhancement in plant growth and development (Hong et al. 1991; Spaepen et al. 2014; Ruzzi and Aroca 2015; Lorente et al. 2016). Although L-tryptophan has been identified as the main precursor for IAA biosynthesis, tryptophan independent mechanisms of IAA biosynthesis also exist possibly by using other small molecules produced from the root exudates (Myo et al. 2019). Identification and characterization of intermediates of IAA biosynthesis from bacteria and plants revealed the existence of significant similarity in the biosynthesis of IAA by tryptophan-dependent pathways in PGPR and plants (Spaepen et al. 2007; Spaepen and Vanderleyden 2011). Protection from salt stress-induced yield loss has been reported in different crops species such as tomato, cotton, and wheat by the inoculation of IAA producing PGPR such as *Pseudomonas putida*, *Streptomyces* sp., *Leclercia adencarboxylata* MO1 and *Azospirillum* sp. (Egamberdieva et al. 2008, 2019; Yao et al. 2010; Piccoli et al. 2011; Sadeghi et al. 2012; Kang et al. 2019).

4.1.2 Gibberellins

Gibberellins are a group of hormones that are known to stimulate seed germination with multiple growth attributing functions in plants. Gibberellins regulate reproductive organ formation and development, cell division and elongation, promote ripening of fruits, stimulate hypocotyl extension and stem growth (Plackett and Wilson 2016; Urbanova and Leubner-Metzger 2016). Many gibberellin producing bacteria such as *Acinetobacter calcoaceticus*, *Bacillus pumilus*, *Bacillus licheniformis*, *Azospirillum* sp., etc., have been isolated and their ability to induce endogenous gibberellin biosynthesis thereby promoting plant growth was reported (Bottini et al. 2004; Kang et al. 2009). Although a significant increase in the production of gibberellins was observed in the shoots of tomato, cucumber, radish and red pepper plants inoculated with PGPR strains *Bacillus cereus* MJ-1, *Leifsonia soli* SE134 and *Promicromonospora* sp. SE188, the mechanism of bacterial mediated synthesis of gibberellins in plants and their role in conferring salt tolerance to inoculated plants is not clearly understood (Joo et al. 2005; Kang et al. 2012, 2014).

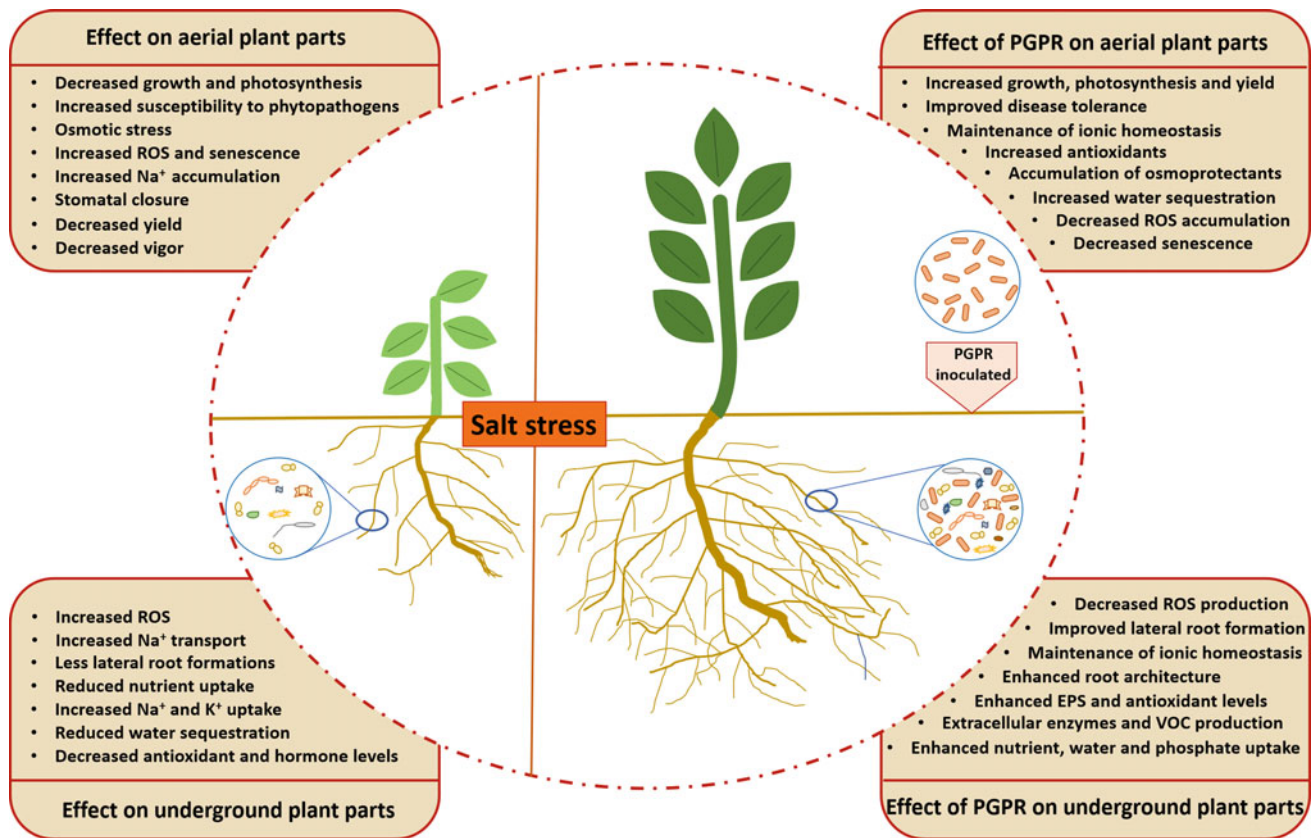


Fig. 1 Schematic representation of the effect of PGPR inoculation in aerial and underground plant organs of glycophytic plants under salinity stress conditions. The changes that are observed in PGPR inoculated and uninoculated glycophytic plants during salinity stress are shown

4.1.3 Cytokinins

Cytokinins which are involved in cell proliferation and differentiation in plants are known to be produced by PGPRs. Compared to auxins, although the role and functions of bacterially synthesized cytokinins were not studied in detail, reports suggested that PGPR effectively produce cytokinins which may be important for plant growth and development under normal and stress conditions. The PGPR—*Pseudomonas entomophila*, *Pseudomonas stutzeri*, *Pseudomonas putida*, *Pseudomonas syringae* and *Pseudomonas monteilli* isolated from the rhizosphere of *Pennisetum glaucum*, *Helianthus annuus* and *Zea mays* plants produced cytokinins not only under normal conditions but also under osmotic stress conditions (Sandhya et al. 2010b). Increased cytokinin levels in the shoot and root tissues of *Platycladus orientalis* and *Arabidopsis thaliana* plants upon inoculation with cytokinin producing PGPR strains *Bacillus subtilis* and *Bacillus megaterium* were observed suggesting the importance of bacterially synthesized cytokinin for inducing cytokinin synthesis along with plant growth promotion (Ortiz-Castro et al. 2008; Liu et al. 2013). Several halotolerant bacteria such as *Arthrobacter* sp., *Bacillus* sp., *Halomonas* sp., *Azospirillum* sp. and *Pseudomonas* sp. are known

to produce cytokinins and promote cell division leading to growth in plants (Egamberdieva et al. 2019). Furthermore, organic volatiles emitted by PGPR *Bacillus subtilis* SYST2 led to increased cytokinin content and increased expression of cytokinin biosynthesis genes in tomato plants indicating the involvement of PGPR for increased synthesis of cytokinins in plants (Tahir et al. 2017). Although PGPR are known to synthesize cytokinins directly, they are also known to employ different mechanisms to induce cytokinin levels in plants to promote plant growth, however, the detailed underlying mechanisms of PGPR induced cytokinin mediated stress tolerance in plants is not clearly understood.

4.1.4 Abscisic Acid

Abscisic acid (ABA) is a stress hormone specifically synthesized in plants that are exposed to abiotic stress conditions such as salt, drought, cold, etc. It is the central regulator of abiotic stress tolerance mechanisms and is known to activate stress tolerance genes coordinating an array of functions for the growth and development of plants. Several of the halotolerant PGPR such as *Proteus mirabilis*, *Bacillus megaterium*, *Bacillus licheniformis*, *Pseudomonas fluorescens*, *Achromobacter xylosoxidans*, *Azospirillum*

brasilense and *Azospirillum lipoferum*, are known to synthesize ABA (Karadeniz et al. 2006; Forchetti et al. 2007; Cohen et al. 2009; Salomon et al. 2014). Inoculation of these bacteria in the majority of the instances showed increased ABA levels in plants correlating with stress tolerance (Salomon et al. 2014; Cohen et al. 2015). Although the role of PGPR synthesized ABA in plants and its influence on the growth and development of plants under salt stress conditions is not clearly understood, modulation in ABA synthesis and ABA-dependent signaling pathways in plants upon PGPR inoculation contribute to the stress tolerance and enhanced plant growth under salt stress conditions is shown in few studies (Yao et al. 2010; Bharti et al. 2016; Barnawal et al. 2017). Inoculation of halotolerant PGPR *Dietzia natronolimnaea* STR1 to wheat plants showed upregulation of ABA-responsive genes and induced salinity tolerance suggesting the bacterial mediated modulation of ABA responses in plants (Bharti et al. 2016). Additionally, the expression of salt overly sensitive (SOS) pathway genes and ion transporter genes were also modulated in inoculated plants indicating the upregulation of salt tolerance mechanisms and enhanced protection against salt stress (Bharti et al. 2016).

4.1.5 ACC Deaminase Activity

The presence of ACC deaminase activity is one of the key characteristics that is observed in halotolerant PGPR for decreasing endogenous ethylene levels in plant cells thereby improving their plant growth. Stress induces the expression of 1-aminocyclopropane-1-carboxylic acid synthase (ACC synthase) genes which upon translation catalyzes the conversion of S-adenosylmethionine to ACC leading to ethylene accumulation in plants. Although ethylene as a plant hormone is implicated in the regulation of various plant physiological processes, stress-induced ethylene production and accumulation promotes senescence and is detrimental for plant growth and development wherein it serves as an indicator for plants' sensitivity towards stress (Glick 2014; Müller and Munné-Bosch 2015). Abiotic and biotic stresses cause a substantial increase in ethylene levels causing adverse effects on the growth of the plants (Dubois et al. 2018). Halotolerant PGPR with ACC deaminase activity hydrolyzes ACC to ammonia and α -ketobutyrate, significantly decreasing the ethylene levels in the plants (Gamalero and Glick 2015; Singh et al. 2015a, b; Gupta and Pandey 2019). The produced ammonia and α -ketobutyrate are utilized by the bacteria as nitrogen and carbon sources (Glick 2014). Inoculation of ACC deaminase producing bacteria *Stenotrophomonas maltophilia* SBP9 to wheat plants stimulated the plant growth under salinity stress conditions and augmented the resistance against abiotic and biotic stresses (Singh and Jha 2017). In another study, the improvement in growth along with other physiological properties was

observed in plants inoculated with ACC deaminase enzyme-producing PGPR *Pseudomonas fluorescens* and *P. migulae* strains under salt stress (Egamberdieva et al. 2011; Ali et al. 2014). ACC deaminase producing PGPR such as *Variovorax paradoxus* 5C-2, *Bacillus amyloliquefaciens* SQR9, *Arthrobacter* sp., *Brevibacterium* sp., *Gracilibacillus* sp., *Virgibacillus* sp., *Salinicoccus* sp., *Pseudomonas* sp., *Pseudomonas fluorescens*, *Exiguobacterium* sp., *Alcaligenes* sp., *Bacillus* sp. and *Ochrobactrum* sp. induced salt tolerance and stimulated the growth in tomato, rice, maize and pea plants under salt stress conditions suggesting the efficacy of PGPR with ACC deaminase activity for the amelioration of salt stress responses and phytoremediation in crop plants (Bal et al. 2013; Ali et al. 2014; Wang et al. 2016; Habib et al. 2016; Aslam and Ali 2018; Kang et al. 2019).

4.2 Exopolysaccharides

While exopolysaccharide production is considered as one of the characteristic features of rhizobacteria, the amount of production and its composition varies in different halotolerant PGPR inhabiting different ecological niches. Exopolysaccharide production by the bacteria is considered as a protection mechanism employed to survive under environmental stress conditions such as salinity, temperature, heavy metals or pollution (Morcillo and Manzanera 2021). Many halotolerant PGPR secrete exopolysaccharides that form biofilms promoting cell to cell aggregation facilitating the rhizobacterial anchorage and adhesion to root surfaces. Exopolysaccharides are formed with either homo or heteropolysaccharides binding to the surface of the cell and play an important role in nutrient acquisition, formation of hydrophilic biofilms, water transport to the roots and regulation of soil aggregation favouring the growth of plants under salt stress conditions (Dar et al. 2021; Morcillo and Manzanera 2021). The exopolysaccharides produced by the halotolerant PGPR form rhizo-sheaths, a physical barrier around the host plant roots complexing with the Na^+ ions decreasing their availability to the inoculated roots thereby decreasing Na^+ toxicity under salt stress conditions. Exopolysaccharides of halotolerant PGPR such as *Pseudomonas* sp. AK1, *Bradyrhizobium japonicum* and *Bacillus subtilis* have the potential to bind to Na^+ ions limiting their uptake by the roots of soybean thereby maintaining normal growth under salinity stress conditions by maintaining K^+/Na^+ balance (Han and Lee 2005; Kasotia et al. 2016). Inoculation of exopolysaccharide producing PGPR *Bacillus subtilis* to *Arabidopsis thaliana* significantly decreased the influx of Na^+ ions to the roots by downregulating the expression of HKT1/ K^+ transporter (Zhang et al. 2008). *Helianthus annuus* plants inoculated with exopolysaccharide

producing *Pseudomonas aeruginosa* showed enhanced salt stress tolerance along with increased growth, development and yield (Tewari and Arora 2014). In another study, increased plant growth and improved soil stability are observed in Chickpea plants inoculated with the exopolysaccharide producing halotolerant PGPR *Halomonas variabilis* (HT1) and *P. rifietoensis* (RT4) suggesting the importance of PGPR secreted exopolysaccharides for plant salinity tolerance (Qurashi and Sabri 2012; Dar et al. 2021).

4.3 Osmoprotectants

Halotolerant PGPR exposed to salt stress conditions accumulate osmoprotectants such as proline, trehalose, polyamines and glycine betaine in their cytosol to maintain osmotic balance inside the cell. While secretion of root exudates attracts the halotolerant PGPR to colonize the root surface and other internal tissues, the osmolytes secreted by halotolerant PGPR are absorbed by the plant roots thereby helping in the osmotic adjustment of plants during salinity stress (Chandran et al. 2021). Although salinity-induced accumulation of osmolytes is also observed in plants, the bacterial osmolytes mimic the plant metabolites during the plant–microbe interaction and the response in bacteria is quicker (Ilangumaran and Smith 2017). Salt stress-induced accumulation of osmolytes such as proline, glycine betaine, polyamines, quaternary ammonium compounds and other amino acids are reported in many plant species inoculated with halotolerant PGPR (Sandhya et al. 2010a; Wang et al. 2016). The accumulation of these metabolites in the cytoplasm of the plant cell renders osmotic adjustment and protects the macromolecules such as proteins, nucleic acids and lipids from oxidative damage during salinity stress conditions (Parihar et al. 2015; Acosta-Motos et al. 2017). Inoculation of PGPR such as *Burkholderia*, *Arthrobacter*, *Bacillus*, *Rhizobium* and *Pseudomonas* are reported to increase the proline content in plants during salinity stress (Bano and Fathima 2009; Choudhary 2012). Increased proline accumulation along with reduced ROS generation, reduced lipid peroxidation and upregulation of stress-responsive genes is observed in *Capsicum* plants inoculated with PGPR *Bacillus fortis* SSB21 (Yasin et al. 2018). While exogenous application of glycine betaine in salt-stressed soybean plants improved salt tolerance along with increased antioxidant enzyme activities and decreased intracellular Na^+ levels, inoculation of halotolerant PGPR *Bacillus* HL3RS14 and *Bacillus subtilis* BERA71 increased the accumulation of glycine betaine in plants and protected the plants from salinity stress-induced oxidative damage (Malekzadeh 2015; Hashem et al. 2016a, b; Mukhtar et al. 2020). Maize plants inoculated with *Azospirillum brasilense* harbouring a yeast trehalose biosynthesis gene showed

higher trehalose levels along with an increase in leaf and root biomass (Rodríguez-Salazar et al. 2009). These kinds of studies signify the importance of osmolytes for increased stress tolerance.

4.4 Antioxidant Enzymes

The Reactive Oxygen Species (ROS) are continuously produced in different organelles as metabolic by-products during normal conditions in plant cells. Under salt stress conditions, the production of ROS such as hydrogen peroxide, hydroxyl ion, superoxide ions and singlet ions is aggravated posing a threat of oxidative damage (Sharma et al. 2012). Increased ROS causes oxidative stress leading to damage to nucleic acids, proteins and lipids finally resulting in cell death (Apel and Hirt 2004; Gill and Tuteja 2010; Hasanuzzaman et al. 2020). Management of ROS in plant cells although is efficiently done by antioxidant systems comprising of enzymatic (superoxide dismutase, catalase, peroxidase, glutathione reductase, etc.) and non-enzymatic components (ascorbate, glutathione, carotenoids, flavonoids, etc.) to protect the cells from oxidative damage, salinity stress-induced aggravation in ROS causes inactivation of antioxidant systems leading to cell damage (Miller et al. 2010). Inoculation of halotolerant PGPR to plants is reported to increase the potential of plants to produce more antioxidant enzymes during salinity stress conditions. Higher amounts of antioxidant enzymes such as superoxide dismutase, catalase, peroxidase and glutathione reductase were reported in plants inoculated with halotolerant PGPR (Islam et al. 2016; Ha-Tran et al. 2021). Soybean plants inoculated with PGPR *Bacillus firmus* SW5 showed increased expression of genes encoding antioxidant enzymes suggesting better protection from salinity stress-mediated injury (El-Esawi et al. 2018). The *Abelmoschus esculentus* plants inoculated with *Bacillus megaterium* UPMR2 and *Enterobacter* sp. UPMR18 showed improvement in germination rate and increased growth correlating with decreased ROS levels and increased superoxide dismutase, catalase and ascorbate peroxidase activities (Habib et al. 2016).

4.5 Siderophores

The halotolerant PGPR possess specialized strategies to overcome iron (Fe) limitation by using chelators called siderophores which can extract Fe from Fe^{3+} complexes in soil aiding in the supply of usable iron to the plants (Ferreira et al. 2019). Since Fe is an essential micronutrient important for photosynthesis, respiration and chlorophyll biosynthesis in plants and salinity stress is known to reduce the availability of Fe due to lower release of iron-chelating

compounds, the halotolerant PGPR chelates the Fe and provides the nutrient to the plants for their survival under stress conditions (Abbas et al. 2015; Chakraborty et al. 2016; Ferchichi et al. 2016). The secretion of siderophores by halotolerant PGPR is considered as an alternative strategy for Fe uptake by plants facilitating improved nutrition along with inhibition of phytopathogens under salt stress conditions. While the bacterial genera *Bacillus*, *Burkholderia*, *Enterobacter* and *Grimontella* are known to produce high siderophores, improvement of salinity tolerance in plants such as alfalfa, corn, wheat and mungbean has been observed upon inoculation with siderophore producing halotolerant PGPR (Ramadoss et al. 2013; Singh et al. 2015a, b; Souza and Ambrosini 2015; Zhu et al. 2020).

4.6 Other Mechanisms

Phosphate solubilization is another important plant growth promoting trait possessed by halotolerant PGPR. Since the majority of the phosphorous in the native soils will be in an insoluble form, strategies for increasing the bioavailability of phosphorous in the usable form for plants are required. Phosphorus in plants is a macronutrient that plays a vital role in the growth and development of plants for improving photosynthesis, root growth, cell division, flower and seed formation, resistance to plant diseases, etc. Being the second most important macronutrient, it is also an essential component of nucleic acids, enzymes, nucleotides and phospholipids (Souza and Ambrosini 2015). Often the phosphorous fertilizers are sprayed onto the crops to protect them from deficiency symptoms, however, continuous usage negatively affects the soil pH, soil structure and microbiome. Utilization of plant growth promoting bacteria with phosphate solubilization potential is an alternative way for supplementing phosphorous to the plants thereby improving crop productivity. The halotolerant PGPR are known to solubilize inorganic soil phosphates, through the production of organic acids particularly gluconic and carboxylic acids, and hydroxyl ions (Rodríguez et al. 2006; Sharma et al. 2013; Anand et al. 2016). The bacteria belonging to the genera *Bacillus*, *Rhodococcus*, *Arthrobacter*, *Serratia*, *Chryseobacterium*, *Gordonia*, *Phyllobacterium* and *Delftia* are known to produce acids such as citric acid, gluconic acid, lactic acid, succinic acid and propionic acids to solubilize inorganic phosphates and supply phosphorous to the plants (Chen et al. 2006). Roots and rhizospheric soil are reservoirs for phosphate solubilizing bacteria. The rhizosphere of the rice plants dominated by the genera *Burkholderia*, *Cedecea*, *Cronobacter*, *Enterobacter*, *Pantoea* and *Pseudomonas* showed phosphate solubilization potential leading to improved plant growth (Costa et al. 2013; Granada et al. 2013; Souza et al. 2013, 2014). The halotolerant PGPR are

also known to release a wide variety of secondary metabolites and volatile organic compounds for improvement of plant growth and salt stress tolerance. The PGPR are reported to produce polyamines that induce polyamine biosynthesis in host plants resulting in increased photosynthesis, growth and biomass under stress conditions and producing HCN as biocontrol for controlling the pathogenic microbes in the rhizosphere (Kumar et al. 2015; Backer et al. 2018a, b). The volatile organic compounds released by the PGPR *Bacillus subtilis* promoted the biosynthesis of choline and glycine betaine in host plants along with inhibition of Na⁺ ion transport to root cells resulting in improved salt stress tolerance (Zhang et al. 2008; Timmusk et al. 2014; Backer et al. 2018a, b; Lopes et al. 2021).

5 Methods of Inoculation of Halotolerant PGPR to Plants

Although a majority of the halotolerant PGPR show high potential for plant growth promotion and salinity stress amelioration under laboratory conditions, the favourable responses are often not observed under field conditions mainly due to the inoculation methods used and due to variations in soil and fluctuations in external environmental factors such as light and temperature (Lopes et al. 2021). Although carbon, nitrogen, organic matter content, water availability and pH are the main factors determining the growth of the microorganisms, the soil type, the geographical location and seasonality also play a crucial role in the establishment and survival of halotolerant PGPR on the rhizospheric zone (Bossio et al. 1998; Drenovsky et al. 2004; Garcia-Pausas and Paterson 2011; Kristin and Miranda 2013). Alterations in the soil conditions are known to modify the microbiome diversity. While low soil moisture content is detrimental to the growth of bacteria, high soil moisture content generally observed during flooding reduces oxygen availability resulting in the decrease of microbial biodiversity (Gouda et al. 2018). Increasing the efficacy of the bacteria to colonize the soil, root or seed is an effective way to establish PGPR-plant connection to observe a bacterial mediated increase in the growth of plants under salinity stress conditions. The compatibility of the bacterial strain to the roots of the host plants along with the stability of the bacteria in the soil is critical for establishing effective colonization thereby having a consistent growth performance of the plants (Egamberdieva et al. 2018; Lopes et al. 2021). While microbial inoculants are mainly inoculated onto seeds, soil, roots and leaves, improvement of the plant—PGPR interaction and evaluating the responses of PGPR to changing environmental conditions are important to have efficient bacterial inoculation to see the desired plant growth promoting effect (Callaghan 2016) (Fig. 2b).

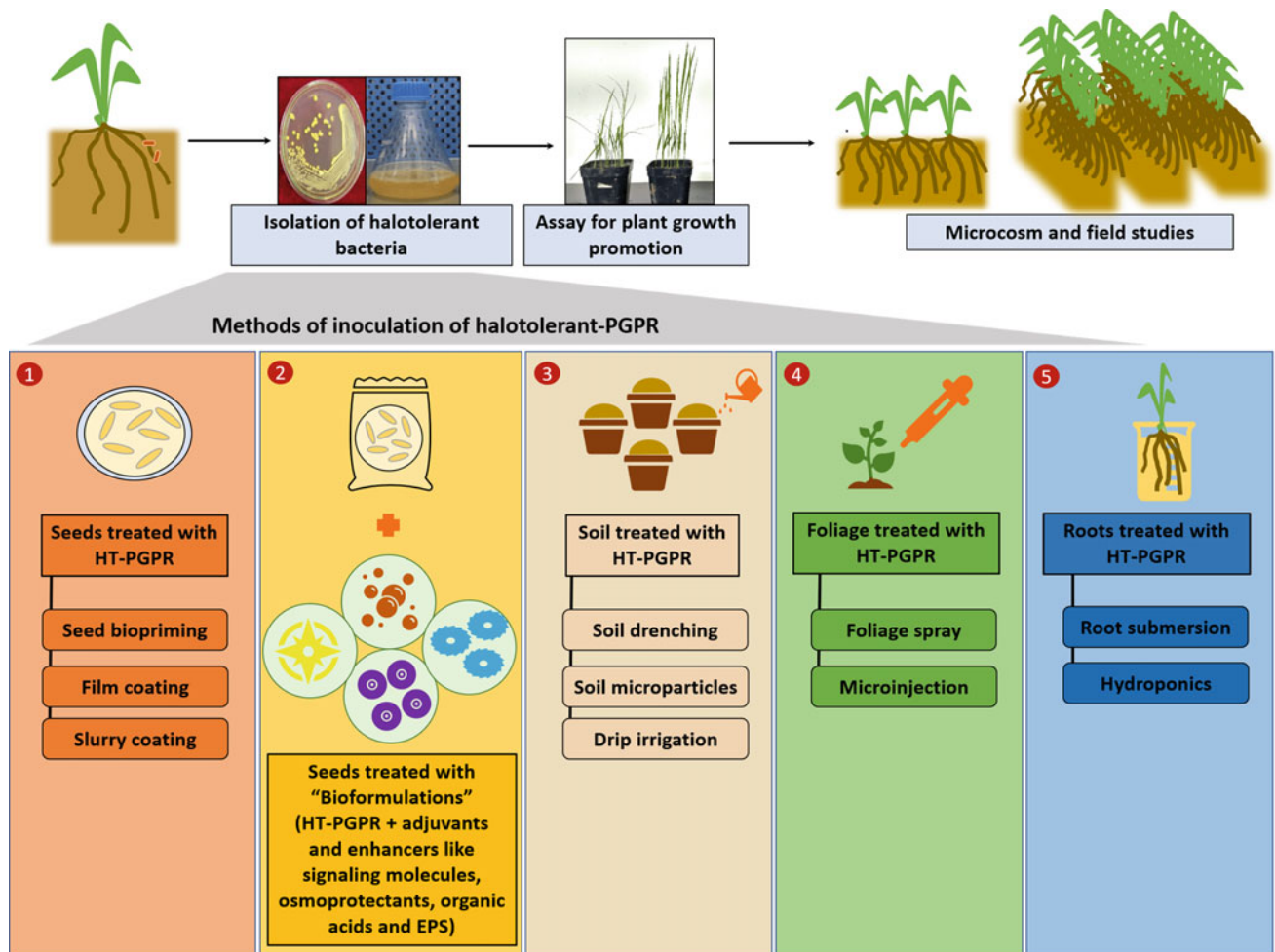


Fig. 2 Diagrammatic representation of different methods of halotolerant PGPR inoculation in plants. **a** Depiction of different steps such as isolation of halotolerant bacteria from rhizosphere combined with lab

and field studies for analysing plant growth promotion. **b** Different methods of inoculation of halotolerant PGPR to seeds, leaves and roots of glycophytic plants

Since salinity stress induces serious changes in the composition of the rhizospheric environment, different methods such as inoculation of the halotolerant PGPR to seeds, soil amendments by directly adding the inoculum onto soil and dipping of the roots in the PGPR suspension before transplanting are employed to ensure efficient inoculation of the bacteria to the plants thereby increasing the efficiency of bacteria for survival and colonization (Mahmood et al. 2016). Since the method of PGPR inoculation determines the survival efficacy of the bacteria, several methods such as seed priming with PGPR, seed priming with bioformulations, soil drenching, foliar application and root dipping were developed to increase the colonization efficiency of the PGPR to the plant tissues (Fig. 2b). Several modifications of every method have also been evaluated and standardized. Different methods employed for the efficient inoculation of halotolerant PGPR are shown in Fig. 2.

Inoculation of the halotolerant PGPR to seeds is an efficient method since it delivers the microorganisms to soil and ensures efficient root colonization (Philippot et al. 2013). Different methods of seed inoculation such as (i) Seed biopriming, involving immersion of the seeds in the PGPR microbial suspension for a definite period followed by drying, initiates the physiological processes inside the cell thereby ensuring colonization of PGPR (Taylor and Harman 1990) (ii) Film coating, involving the coating of the PGPR inoculum in a film as a thin layer on the seed surface complexing with methylcellulose, paraffin oils and polysaccharide materials is used to increase the adherence capacity of the PGPR to roots (iii) Slurry coating, involving inoculation of PGPR to the surface of the seeds by using carriers such as peat (Fig. 2b1). However, the survival of the inoculum in the seed is stronger and efficient in the bio-primed seeds, than film coating and slurry coating inoculums

(Callaghan 2016). Biopriming of the seeds of maize with different strains of *Azotobacter* and *Azospirillum* showed a significant increase in growth, development and yield (Sharifi 2011). Inoculation of *Rhizobia* and *Bacillus* species to the seeds of *Oryza sativa* and *Cicer arietinum* L. plants resulted in increased biomass production (Ullah et al. 2017; Khan et al. 2019).

Decoding the signaling components and the metabolites involved in plant-PGPR interaction during salt stress conditions is important to modify the Phyto microbiome for increasing the colonization potential of the bacteria. The bioformulations with the signaling molecules like AHL (N-acyl homoserine lactone) which is a known elicitor of plant-microbe interactions evokes biochemical and molecular changes to avert salinity-induced injuries in plants (Zhou et al. 2017). The external application of osmoprotectants like glycine betaine and proline along with halotolerant PGPR to the seeds helps in the initial acclimatization of the bacterial inoculants to the salinity stress (Arif and Ghoul 2018). Exopolysaccharides and organic acids are used as adjuvants for maintenance of osmotic equilibrium, water activity, cell protection and better mineral solubilization, respectively (Sunita et al. 2020, Fig. 2b).

Soil inoculation is done by either drenching the soil in PGPR solution or by incorporating PGPR into soil mixed with a substrate in the form of microcapsules. This method provides an advantage over other methods by increasing the PGPR density over indigenous soil microbiota. Soil inoculations with microcapsules lead to a gradual release of inoculum offering a higher probability for root colonization and viability (Hernandez-Montiel et al. 2017, Fig. 2b3). Foliar PGPR inoculation usually involves spraying of PGPR solution on foliar regions of the plant and the interaction between plant leaf surface and microorganism leads to improved growth and yield in plants (Efthimiadou et al. 2020). Foliar microinjection of PGPR is also practised, however, the foliar spray is found to be a superior method (Basha et al. 2006, Fig. 2b4). Root inoculation involves a submersion of seedling roots for a definite period in PGPR solution, thereby improving root colonization of bacteria. In rice plants, the root inoculation was found to be more effective than the seed inoculation method resulting in increased panicle length and plant height (Ullah et al. 2017, Fig. 2b5). In soybean, tomato and cucumber plants, hydroponics has been used to provide the roots with a continuous source of PGPR inoculum wherein inoculated plants showed a remarkable increase in yields respectively (Gagnè et al. 1993; Gül et al. 2013; Yasmin et al. 2020). Inoculation of *Burkholderia phytofirmans* PsJN to the roots of *Vitis vinifera* increased the plant's tolerance to low-temperature stress, modified the carbohydrate levels in leaves and increased plants growth (Fernandez et al. 2012).

6 Usage of Halotolerant PGPR as an Alternative to Chemical Fertilizers

Increased population growth demanding for higher agricultural productivity, nutrient deficiency in soils and abiotic stress factors causing a serious decline in crop productivity are the major factors that created a demand for chemical fertilizers in agriculture applications worldwide (Scagliola et al. 2021). Excessive usage and application of chemical fertilizers in agricultural fields were found to be a serious threat to soil quality causing pollution to the environment and having significant detrimental effects on human health (Zhang et al. 2018; Scagliola et al. 2021). Additionally, the depletion of nutrients and soil biodiversity that occurs due to the application of chemical fertilizers on agricultural soils has created an urgent need to recycle the available organic resources and alternative sources such as beneficial rhizospheric microbes for improving plant growth under stress conditions and restoring the soil fertility. Soil is heterogeneous with innumerable microorganisms such as bacteria and fungi interacting with others and each other through symbiosis, antagonism, mutualism, parasitism and saprophytism. The halotolerant PGPR are considered as suitable candidates either in isolation or in consortia to improve the plant growth directly by producing plant growth promoting traits, by enhancing the nutrient bioavailability to the roots and indirectly helping the host plants by restricting the growth of phytopathogenic organisms near to rhizosphere and activating systemic resistance against plant pathogens (Maras-toni et al. 2019; Kolega et al. 2020). The halotolerant PGPR is known to colonize in the rhizosphere or the interior of the plant and act like biofertilizers aiding in increasing the availability of nutrients and production of siderophores for iron uptake. Research has convincingly demonstrated that inoculating plants with halotolerant PGPR or treating plants with the signaling compounds released by the PGPR stimulates plant growth even under high salinity stress conditions (Backer et al. 2018a, b).

Halotolerant PGPR is equipped with a plethora of mechanisms to cope up with salinity stress in the soil and provide benefit to host plants. These halotolerant PGPR can be applied to the agricultural fields as bioinoculants or multifunctional PGPR-based formulations to improve crop productivity not only under optimal conditions but also under salinity stress conditions. Application of halotolerant PGPR like *Bacillus subtilis*, *Bacillus amyloliquefaciens* NBRISN13, *Enterobacter* sp., *Lysinibacillus* sp., *Pseudomonas strain* 002 and *S. sciuri* SAT-17 to rice, wheat and maize plants promoted plant growth, decreased intracellular ROS levels by increasing the antioxidant enzyme activities, increased osmolyte accumulation and modulated the expression of salt stress-responsive genes during salinity

stress (Upadhyay and Singh 2015; Singh and Jha 2016; Nautiyal et al. 2013; Zerrouk et al. 2016; Rima et al. 2018; Sarkar et al. 2018; Damodaran et al. 2019). Further, *Azospirillum*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Flavobacterium*, *Pseudomonas*, *Rhizobium*, *Frankia*, *Klebsiella*, *Clostridium*, *Serratia* and *Streptomyces* are known to increase agricultural productivity under salinity stress conditions (Abhilash et al. 2016; Oosten et al. 2017; Gouda et al. 2018). Research findings highlight the importance of phytohormones, phosphate solubilization potential, siderophore production, ACC deaminase activity, production of osmoprotectants and modulation in antioxidant defences as key elements for ameliorating the salinity stress responses in halotolerant PGPR inoculated crop species (Egamberdieva et al. 2019; Kumar Arora et al. 2020; Shilev 2020). Usage of halotolerant PGPR as a whole or preparation of bioinoculants or bioformulations not only improves the crop growth and productivity but also helps the plants survive under high salinity conditions. Hence, the halotolerant PGPR can be considered as an alternative to chemical fertilizers due to various growth promoting attributes under salinity stress conditions and environment-friendly nature.

7 Commercialization

The interaction of the PGPR with plant roots and its effect on the plant growth promotion is a complex process involving several steps such as root exudation followed by attachment, colonization by the PGPR, the release of phytohormones, release of volatile organic compounds by the PGPR and finally influencing the growth of the plant. Any microbe if identified as a potential PGPR through isolation and characterization should colonize and show the plant growth promoting traits. Although many of the halotolerant PGPR have been isolated from different rhizospheric zones and characterized for their plant growth promoting traits, many of the bacteria fail to colonize the root system under field conditions and hence they cannot be exploited for commercial purposes. However, they may be important for plant growth promotion and restoration of soil fertility by employing unexplored and uncharacterized mechanisms. Single PGPR, consortia of PGPR or the signal molecules can be exploited for commercialization and can be used for enhancing agricultural productivity. The process involves PGPR isolation, screening, laboratory pot tests, field trials, development of formulation, formulation testing, product registration and availability in the market (Backer et al. 2018a, b, Fig. 2a).

Halotolerant PGPR can be isolated from the rhizospheric zones of the salt-tolerant plants and their characterization is done based on biochemical and molecular characteristics

(Bakka and Challabathula 2020; Taj and Challabathula 2021). Further, they are screened for the presence of plant growth promoting traits and growth inhibition of plant pathogens. While the biochemical characterization is done based on Bergey's manual of determinative bacteriology, DNA and RNA-based homology testings are mostly used for molecular characterization. The cultivable bacteria with high plant growth promoting activity are selected and are tested under laboratory and field conditions for preparing the consortia (Backer et al. 2018a, b). For the isolation of potential signal compounds also referred to as biostimulants, the entire PGPR culture supernatant tested positive for plant growth promotion will be fractionated by HPLC and the individual active compounds are isolated, purified and subjected to mass spectrometry for identification. Formulations are done with either consortium comprising of multiple PGPR isolates or by using a single PGPR isolate (Backer et al. 2018a, b; Scagliola et al. 2021). To minimize the loss of bioactivity of the PGPR in formulations and for even distribution, stickers/binders such as corn flour, carboxymethyl cellulose; surfactants such as Tween 80; desiccants such as silica gel and anhydrous sodium sulphate; dispersants like microcrystalline cellulose; thickeners like xanthan gum; stabilizers such as lactose and sodium benzoate; and UV protectants are added (Schisler et al. 2004; Callaghan 2016; Backer et al. 2018a, b; Egamberdieva et al. 2019). Although recent studies indicated biochar as the promising carrier material for PGPR inoculations mainly due to its porosity and nutrient content and its feasibility to be applied as seed coatings replacing peat-based inoculants (Backer et al. 2018a, b), due to variations in biological, physical and chemical properties of the produced biochar, it can harm soil fertility and growth of microbes and plants (Nguyen et al. 2017; Wang et al. 2017). The formulations can be liquid-based, talc-based, saw-dust-based, fly ash-based, encapsulation-based and peat-based with specific advantages and disadvantages upon inoculation onto different plant species (Gopalakrishnan et al. 2016). Liquid-based formulations can be sprayed onto the seeds before sowing or seeds can be drenched in the inoculum. Isolation of halotolerant PGPR that can sustain plant growth under salinity stress conditions in laboratory and field conditions is cumbersome. Further, isolating the halotolerant PGPR with high efficacy, multiple benefits, long shelf life and high root colonization rate is achievable. However, preparation of the formulations that can be applied on the field with a high success rate combined with commercialization requires a strong research link between the public and private funded universities, research organizations with private industries to observe augmentation in the production of crops under salinity conditions.

8 Conclusion

High salinity poses a serious threat to agricultural systems worldwide and inoculation of halotolerant PGPR has shown increased salinity stress tolerance along with growth promotion in not only model plants but also in many agriculturally important crop species. Compared to the usage of fertilizers and pesticides for plant growth promotion and removal of pests which were reported to have negative effects on the soil and environment, inoculation of halotolerant PGPR as bioinoculants is an environment friendly approach. Additionally, the halotolerant PGPR were reported to replenish the fertility of the soil and protect the plants from pathogens. Over the past few years, many halotolerant PGPR with plant beneficial effects have been isolated from different rhizospheric zones and were efficiently characterized. However, the significant effects were always observed under laboratory conditions and their suitability to be used as bioinoculants under field conditions is questionable. At this juncture, steps are necessary for the isolated and well-characterized halotolerant PGPR to be used as products for commercial agriculture particularly for mitigating the salinity stress in plants. Since stressor-specific and non-specific responses are observed in plants exposed to abiotic stress conditions, the bioformulations with a single bacterium, consortia of bacteria or the signal molecules should be custom-made for their usage for saline soils to observe the improvement of salt tolerance in plants. Isolation of new halotolerant bacterial strains with potent plant growth promoting traits, improvements in inoculation technologies for increasing the efficiency of inoculum along with the survival of the bacteria and preparation of novel bioformulations are key to combat the challenges of crop growth and productivity in saline soils.

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