The PGPR Mechanisms of Salt Stress Adaptation and Plant Growth Promotion

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Abstract: Worldwide crop productivity hampers severely due to the adverse effects of salinity. Global warming causes a rapid escalation of the salt-affected area, and new agricultural land is affected through saltwater intrusion. The ever-growing human population impulses to utilize the saline area for crop cultivation to ensure food security. Salinity resistance crops could be a promising substitute but with minor success because inappropriate tactics on saline soil management resulted in unsatisfactory yield. Salt-tolerant plant growth-promoting rhizobacteria (ST-PGPR) is considered an alternate way towards enhancing crop growth in saline ecosystems. It is reported that PGPR is enabled to produce exopolysaccharides which lead to biofilm formation and generate osmoprotectants and antioxidant enzymes that can significantly contribute to stimulating plant growth in the saline ecosystem. In addition, several plant growth-promoting characteristics of PGPR such as the acquisition of essential nutrients and upsurge hormone production could enhance plant growth simultaneously. In this review, we will explore the survival mechanisms of ST-PGPR and their influence on plant growth promotion in saline ecosystems.

Keywords: salinity; PGPR; mechanism; crop; growth

1. Introduction

Soil salinity is considered a major abiotic threat to agricultural production around the world [1]. Salinity is documented as a severe climatic menace affecting almost one billion hectares of land globally [2]. This cruel ecological anxiety causes an annual estimated economical loss in crop production is about USD 27.3 billion [3,4]. Furthermore, the risk of salinization at different latitudes is increasing due to the global warming scenarios and therefore a special attempt is required to obtain the maximum agricultural output from a saline ecosystem [5]. Annually 2500–5000 km² of crop production is lost due to salinity since it occupies more than 20% of the world-irrigated land [6]. Improper irrigation practices are expected to affect approximately 50% of the irrigated areas in the world following an annual expansion of up to 500,000 ha. These realities are an indicator of extreme global risk in achieving food security [7]. Lack of rainfall and increase in temperatures in most agricultural regions are the consequences of climate change which may lead to more arid and semi-arid zones [8,9]. To meet the rising food demand, the manipulation of saline areas for agricultural production is the way forward. Thus, coping with salinity is the ultimate
target for rising food production [10]. Renovation of salt-affected lands for successful crop cultivation through effective management practices is the challenge that needs to be highlighted. Physical removals of salts from the soil surface or chemical application are expensive as well as have an adverse environmental impact and would be difficult to apply in huge areas for soil retrieval purposes. In this case, the manipulation of soil beneficial soil microorganisms in stress-prone areas is an important concern. Microbial inoculants could improve plant health in saline-affected soils by ameliorating salt stress, supporting plant growth, and controlling diseases [11–13]. Several studies have confirmed the positive effects of soil beneficial microbes that could increase plants’ tolerance toward adverse salinity stresses [14,15]. Moreover, several studies are proving the hypothesis that PGPR facilitates plants’ continuing crop production in stressed soil through exopolysaccharides production and biofilm formation, which facilitates bacterial aggregation and forms a protective cover to get rid of adverse climatic conditions [16]. Bacterial production of osmoprotectants, antioxidant enzymes, and volatile organic compounds can trigger bacterial survival under high osmotic conditions. Through the production of the ACC deaminase enzyme, these bacteria help slow down ethylene production and accelerate bacterial survival under saline conditions. Due to their unique mechanism to withstand under saline state, they consistently assist the plants to grow through the production of various traits related to plant growth, such as the production of growth hormone, fixation of atmospheric nitrogen, and solubilizing of inorganic phosphate. This updated information of review will be helpful outlines to explore the mechanisms of PGPR to alleviate salt stress in plants.

2. Soil Salinization

Soil salinity denotes the excess amount of soluble salt in the root zone of plants. Due to the elevated osmotic pressure, salinity affects plant growth by restricting the uptake of water and essential plant elements [17]. The accretion of available salts such as sodium (Na\(^+\)), calcium (Ca\(^{2+}\)), potassium (K\(^+\)), magnesium (Mg\(^{2+}\)), chloride (Cl\(^-\)), sulfate (SO\(_4^{2-}\)), carbonate (CO\(_3^{2-}\)), bicarbonate (HCO\(_3^-\)) is considered as soil salinization. Moreover, weathering of minerals is also the cause of salt deposition. In addition, anthropogenic factors such as irrigation of the crop with salt waters, poor cultural practices, and low precipitation are other causes of soil salinization. The frequent use of different inorganic fertilizers and amendments of soil with gypsum, composts, and manures also contributes to developing soil salinization [18].

3. Effect of Salinity on Plants

Worldwide salinity is considered the main abiotic stress, troubling the coastal agricultural system [9]. Soil salinity considerably affects the humid and sub-humid rice-cultivating zone where the rate of sea-level rise is projected to surge, thus having a dramatic effect on crop production, especially salt-sensitive rice genotypes, which could be lost 50% of yield [19–21]. The crop response to salinity depends on several factors (i) the climatic conditions (ii) stress intensity and (iii) the tolerance level of the genotype [22]. Salinity negatively affects rice stand establishment, panicles, tillers, spikelets, individual grain size, and crop maturity [23]. Other crops such as wheat, sorghum, and cowpea are mostly susceptible to salinity at vegetative and early reproductive stages [24]. The osmotic stress and ionic toxicity are the primary causes of secondary oxidative stress in plants under salinity stress [25,26].

The toxicity of salinity in plants often occurs through (i) osmotic imbalance (ii) toxicity of ions (iii) oxidative stress following disruption of the photosystem, and other physiological disparities [27]. The ions Na\(^+\) and Cl\(^-\) are the causes of plant cell damage at both osmotic and ionic levels, which accumulate in the chloroplasts at a high concentration under salinity stress, consequently damaging thylakoid membranes [28]. In all rice genotypes, K\(^+\) concentrations decreased with the rise of salinity concentration, thus hindering the photosynthetic rate by altering the ultra-structure of the organelles and various pigment concentrations, including connected enzymes and stomatal regulations [29].
4. Role of PGPR for Salt Stress Reduction

Plant growth-promoting rhizobacteria (PGPR), are a group of rhizospheric bacteria, first defined by Kloepper and Schroth [30], a zone where the plant roots are available and essential macro and micronutrients are extracted resulting from higher microbial activities [26]. PGPR takes part in (i) nutrient mobilization in soil (ii) production of plant growth regulators (iii) controlling phytopathogenic attack (iv) induced systemic resistance (v) improvement of soil structure and (vi) polluted soil remediation [31,32]. The application of these beneficial microbes to the soil–plant system is well studied and proven under stressed soil [33]. A salt-tolerant bacterial strain *Staphylococcus xylosus* ST-1 caused a 25% growth increment of seedling at 100 mM NaCl over control [34]. In another study, the osmotic balance of the cells was changed by *Bacillus mojavensis* VKAK1 through changing plant water relations [35]. *Azospirillum* AZ19 strain inoculation in wheat plants originated from saline or non-salinated conditions and showed increased grain yield [36]. Habib et al. [37] showed that isolates UPMR7 (*Bacillus* sp.), UPMR17 (*Citrobacter* sp.), and UPMR18 can resist high NaCl concentration (up to 6%), which helps their survivability in a saline environment. Some of the potential salt-tolerant bacteria associated with different crops were shown in Table 1.

Table 1. The salt-tolerant bacteria with its mechanisms of salt-stress reduction in different crops.

| Name of the Bacteria                  | Plant Species       | Major Mechanism                                                                 | Reference |
|--------------------------------------|---------------------|---------------------------------------------------------------------------------|-----------|
| *Bacillus megaterium* A12            | *Lycopersicon esculentum* | The upregulation of PIP aquaporin expression                                     | [38]      |
| *Bacillus subtilis* GB03              | *Arabidopsis thaliana* | The upregulation of the sodium transporter HKT1                                 | [39]      |
| *Pseudomonas syringae* S5, *Pseudomonas fluorescens* S20, *Enterobacter aerogenes* S14, | *Zea mays* | ACC deaminase enzyme production                                                  | [40]      |
| *Pseudomonas fluorescens* TDK1        | *Arachis hypogaea*   | ACC deaminase production                                                       | [41]      |
| *Enterobacter* sp. EJ01               | *Lycopersicum esculentum* *Arabidopsis thaliana* | The regulation of salt stress responsive genes such as DREB2b, RD29A, RD29B, and RAB18. The upregulation of proline biosynthetic genes (i.e., P5CS1 and P5CS2) and of genes related to priming processes (i.e., MPK3 and MPK6) | [42]      |
| *Pseudomonas syringae* Mk1; *Pseudomonas fluorescens* Mk20 and *Pseudomonas fluorescens* Mk25 | *Vigna radiata* | Auxin production, ACC deaminase production                                      | [43]      |
| *Brachybacterium saurusitrense* JG-06, *Brevibacterium casei* JG-08 | *Arachis hypogaea* | Reduced oxidative stress through high proline and low MDA content in plants      | [44]      |
| *Pseudomonas* sp. PMDZnCd 2003        | *Oryza sativa*       | Indole-3-acetic acids (IAA) production, nitrogen fixation, and phosphate solubilization. | [45]      |
| *Alcaligenes* sp. SB1-ACC2 and *Ochrobactrum* sp. SB2-ACC2 | *Oryza sativa*       | Production of ACC Deaminase enzyme production                                  | [46]      |
| *Azospirillum* sp.                    | *Brassica napus*      | Regulation of antioxidant enzymes                                              | [47]      |
| *Streptomyces* sp. PGPA39             | *Solanum lycopersicum* | Production of ACC Deaminase,                                                    | [48]      |
| *Serratia* sp. SL-12                  | *Triticum aestivum*   | Accumulation of osmolytes such as total soluble sugar and total protein content  | [49]      |
| *Dietzia natronolimnaea* STR1         | *Triticum aestivum*   | ABA-signaling cascade, as TaABARE and TaOPR1 were upregulated                   | [50]      |
| Name of the Bacteria               | Plant Species  | Major Mechanism                                                                 | Reference |
|-----------------------------------|----------------|---------------------------------------------------------------------------------|-----------|
| *Azospirillum lipoferum* FK1       | *Cicer arietinum* | Modulating osmolytes, antioxidant machinery and stress-related genes expression. | [51]      |
| *Pseudomonas fluorescens* PGU2-79, WBO-3, WKZ1-93 and WB1-7 | *Triticum aestivum,* | ACC deaminase production                                                        | [52]      |
| *Pseudomonas fluorescens* B10, B2-10, B2-11 and B4-6 | *Hordeum vulgare* | ACC deaminase production                                                        | [53]      |
| *Pseudomonas* PS01                | *Arabidopsis thaliana* | Upregulation of LOX2                                                            | [54]      |
| *Aneurinbacillus aneurinilyticus* ACC02 and *Paenibacillus* sp. ACC06 | *Phaseolus vulgaris* | ACC deaminase activity                                                          | [55]      |
| *Burkholderia cenocepacia* CR318  | *Zea mays*      | Phosphate and potassium solubilization and antimicrobial activity                | [56]      |
| *Ochrobactrum* sp. NBRISH6        | *Zea mays*      | Ion homeostasis                                                                 | [57]      |
| *Bacillus* sp. NBRI YN4.4         | *Zea mays*      | Improves photosynthetic pigments, soluble sugar content, enhances soil enzymes. | [58]      |
| *Aeromonas* sp. SAL-17 and SAL-21 | *Triticum aestivum* | Acyl homoserine lactone                                                        | [59]      |
| *Bacillus atrophaeus* BR5, OR15, and RB13 | *Arabidopsis thaliana,* *Triticum aestivum* | Increase proline, TSS, Antioxidant enzyme, decrease MDA | [60]      |
| *Bacillus paramycoides* HB6J2, *Bacillus amyloliquefaciens* HB8P1 and *Bacillus pumilus* HB4N3 | - | HCN production, phosphate solubilization, IAA and ammonia production | [61]      |
| *Azospirillum lipoferum* SP2, *Bacillus coagulans* NCAIM B.01123, *Bacillus circulance* NCAIMB.02324, and *Bacillus subtilis* MF497446 | *Triticum aestivum* | Reduced the uptake of Na⁺ resulted in an increment in superoxide dismutase (SOD), catalase (CAT), and peroxidase (POX) activities that lessened oxidative damage and improved the nutrient uptake (N, P, and K) of deficiently irrigated wheat plants under soil salinity. | [62]      |
| *Enterobacter cloacae* PM23       | *Zea mays*      | Enhanced radical scavenging capacity, relative water content, soluble sugars, proteins, total phenolic, and flavonoid content | [63]      |

Soil bacteria are less tolerant to salinity than root-associated bacteria. In the rhizosphere, salinity stress is higher due to the higher uptake of water by the plant roots [64]. PGPR strains such as *P. chlororaphis* TSAU13, *P. extremorientalis* TSAU20, *P. putida* TSAU1, and *P. fluorescens* WCS356, can withstand up to 3% of NaCl [65]. The salinity stress on photosynthesis, essential nutrients, and antioxidant enzymes of basil plants was reduced through inoculation with *Pseudomonas* sp. and *Bacillus lentus*. Inoculation of *Azosprillium brasilense* NH, a halotolerant strain in wheat, enhanced germination and plant growth in salinated soil [66]. Abbaspoor et al. [67] also recorded that *P. fluorescens* 153 and *P. putida* 108 inoculations to wheat plants improved growth, grain yield, and 1000-grain weight. Stimulation of plant growth using salt-tolerant strains, *Exiguobacterium oxidotolerans* STR36 and *Bacillus pumilus* STR2 was noticed by Bharti et al. [68]. Vivekanandan et al. [69] inoculated five halo-tolerant bacterial strains on wheat seedlings at 80, 160, and 320 mM of NaCl, resulting in a considerable increase in biomass and root length compared with un-inoculated controls. *Halobacillus* sp. S13 and *Bacillus halodenitrificans* PU62 inoculation in wheat seedlings showed more than a 90% increase in dry biomass compared with uninoculated wheat plants at 320 mM of NaCl resulting in a remarkable decline in the toxic effects of NaCl.
5. Mechanisms of Plant Growth Promotion by PGPR under Saline Conditions

In saline conditions, plant growth could be hastened by PGPR by facilitating resource acquisition (nitrogen, phosphorus, potassium) and moderating plant hormone levels through producing ACC deaminase enzyme or indirectly by producing exopolysaccharides and biofilm, osmoprotectants, antioxidant enzymes, and volatile organic compounds (VOCs). All these properties help bacteria to survive and stimulate plant growth under saline conditions [70].

5.1. Nitrogen Fixation

In agricultural production, nitrogen is the major nutrient that has a remarkable effect on plant growth. The free-living and symbiotic bacteria in nature can fix atmospheric N\(_2\) in salt stress conditions and contribute to plant growth. A nitrogen-fixing salt-tolerant bacterium, *Swaminathan halotolerant* PA51T, isolated from wild rice associated with the mangrove ecosystem [71] has the potential to fix atmospheric nitrogen. Five salt-tolerant strains of rhizobium (L-19, L-68, L-292, L-304, and L-335) isolated from saline soils were inoculated to lentil plants (*Lens culinaris*) under saline conditions. Among the isolated strains L-19 and L-304 produced higher nodulation, yield, and nitrogen fixation in lentils [72].

Silini-Cherif et al. [73] identified a nitrogen-fixing bacterium named *Pantoea agglomerans* Ima2 from the wheat rhizosphere, which can tolerate a salinity level of 100 to 400 mM, and its application increased IAA production, siderophore formation, and solubilization of phosphates. Kumar et al. [74] isolated *Mesorhizobium loti* MTCC2379 and MTCC2381 from acacia, a salt-tolerant strain showing efficient nitrogenase activity under salt stress conditions. The symbiosis of rhizobium–legume is the most essential system of nitrogen fixation. Some rhizobia could tolerate up to 1.8 M of NaCl concentration. With the morphological and metabolic changes along with structural modifications, these salt-tolerant rhizobia cope with and adapt to salt stress. Under salt stress conditions, some of the rhizobia can form a successful symbiosis with legumes [75].

5.2. Phosphate Solubilization

High salinity reduces the uptake of available phosphorus (P) by plant roots due to sorption processes to the soil colloid. P solubilizing bacteria even in stress conditions could solubilize fixed and applied P in soil [76]. Chookietwattana et al. [77] have found *Bacillus megaterium* A12 as the efficient halotolerant phosphate solubilizing bacteria. Son et al. [78] identified *Pantoea agglomerans* R-42, a phosphate solubilizing bacterium from a salt-stressed environment. The soybean (*Glycine max*) seeds inoculated with halo-tolerant phosphate solubilizing bacteria significantly increased germination percentage and germination index, especially within 30 and 90 mM NaCl concentrations. Hence, it was suggested that the salt-tolerant phosphate solubilizing bacteria might be useful to reclaim the salt stress toxicity in plants.

5.3. Plant Growth Regulators

The indole-3-acetic acid (IAA), commonly known as the auxins, are important hormones in plants regulated by PGPR that help to promote plant root development and alter root architecture [79,80]. Nakbanpote et al. [45] demonstrated that the production of IAA by *Pseudomonas* sp. PDMZnCd2003 was not affected by salinity stress at 4–16 dS m\(^{-1}\). The auxin signaling plays a significant role in restructuring plant roots [81,82]. The halophyte strains of *Brevibacterium halotolerans* DSM8802, *Bacillus subtilis* h-g, *Brachybacterium saurasthreense* JG06, and *Pseudomonas* sp. JG010 can accelerate plant growth by producing indole acetic acid (IAA) [83–85]. Similarly, Shultana et al. [86] identified a promising strain, UPMRB9 (*Bacillus tequilensis*) based on the measurement of its IAA production showed a significant growth enhancement of three rice varieties in saline conditions.
5.4. ACC Deaminase Enzyme Production

The PGPR can produce ACC (1-aminocyclopropane-1-carboxylate) deaminase; thus, it can lower the ACC level in salt-stressed plants and reduce the quantity of ethylene synthesis in plants. Several studies reported that ACC deaminase-producing PGPR could help plants survive against salinity stress through the reduction of ethylene levels [87,88]. A number of PGPR genera, namely Bacillus, Burkholderia, Azospirillum, Pseudomonas, and Rhizobium are commonly known to synthesize ACC-deaminase enzyme [89–91]. Several reports showed that under axenic conditions, ACC deaminase-producing bacteria trigger plant growth [92,93]. The salt-tolerant and ACC deaminase-producing bacterium augment root development through the increased surface area for better water and nutrient accumulation [94]. Salt-tolerant bacteria associated with ACC deaminase production are shown in Table 2.

Table 2. ACC deaminase-producing salt-tolerant bacteria.

| Name of the Bacteria | Plant Species | Reference |
|----------------------|---------------|-----------|
| Pseudomonas syringae S5, Pseudomonas fluorescens S20 | Zea mays | [40] |
| Enterobacter aerogenes S14 | | |
| Raoultella planticola Rs-2 | Gossypium hirsutum | [95] |
| Pseudomonas fluorescens EU647703.1 | Brassica napus | [96] |
| Enterobacter cloacae AJS-15 | Aerwa javanica | [97] |
| Bacillus mojavensis K78 | Triticum aestivum | [98] |
| Pseudomonas migulae 8R6 and Pseudomonas sp. UW4 | Camelina sativa | [99] |
| Bacillus megaterium NMp082 | Medicago spp.; Arabidopsis thaliana | [100] |
| Bacillus cereus KP027636.1, Serratia odorifera NR037110.1, Lelliottia amnigena KM114915.1, Arthrobacter arilaitensis CP012750.1, Pseudomonas putida GQ2008822.1 | Triticum aestivum | [101] |
| Enterobacter sp. PR 14 | - | [102] |
| B. safensis HB-5 | Cicer arietinum | [103] |
| Enterobacter cloacae ZNP-4 | Triticum aestivum | [104] |
| Enterobacter ludwigii B30 | Cynodon dactylon | [105] |

5.5. Exo-Polysaccharide Production

Bacterial exo-polysaccharide production is recognized as a strategy for the existence under saline conditions reported by several researchers [106–108] where at high salt levels bacteria can retain a mini assembly to hold water level around the cells. Exopolysaccharides (EPSs) help to enable bacterial survival from inhospitable conditions [88] through chelating sodium ion (Figure 1) and reduce its availability for plants [109]. Bacterial polysaccharides are considered as a diverse range of macromolecules which includes peptidoglycan, lipopolysaccharides, capsules, and exopolysaccharides which are water-soluble acids, participate in the host–pathogen interaction and also the components of the structural cell wall (e.g., peptidoglycan) and facilitate the bacterium to survive in unfavorable environments [110,111]. These compounds were recognized as biologically active substances that promote the growth of bacteria and other plant species and also help their adhesion to surfaces and prevent desiccation [110]. The bacterial cells could discharge extra-cellular polysaccharides (EPS) into the atmosphere. EPS is environmentally important since it affects the microbial diversity and carbon cycle [112].
Exopolysaccharides (EPS) influence the formation of rhizosheath around the plant roots [113]. The micro-organisms that live in the proximity of plant roots can synthesize or release EPS in soil. The EPS-synthesizing rhizobacteria take part in the aggregation of soil and rhizosheath (biofilm) formation around the roots of the plants [113,114].

EPS functioned as a blockade within cells and the neighboring environment and thus plays a shielding role against dehydration, UV radiations, and salinity [115]. EPS enhances the retention of water and dispersion of carbon in the bacterial community. Recent findings showed that salinity tolerance of *Suaeda fruticose* markedly increased by the inoculation of *Glutamicibacter* sp. MK847981 and *Pseudomonas* sp. MK087034 through sinking the concentration of Na\(^+\) and increasing K\(^+\), consequently increasing the ratio of K\(^+\)/Na\(^+\) [116]. The content of Na\(^+\) in soybean was reduced because of the application of EPS-releasing bacterial strains in salinized soil. The progressive increase in mineral contents along with the reduction in Na\(^+\) and Cl\(^-\) concentrations in maize were noticed through bacterial inoculation in saline soil. Vivas et al. [117] informed that *Bacillus* sp. inoculated lettuce plants showed higher N, P, and K concentrations under stress conditions which were increased by 5, 70, and 50%, respectively, compared with control.

Under the saline condition, uptake of Na\(^+\) restricts by wheat roots through EPS-producing bacteria since EPS can alter the microenvironment and protects bacteria from desiccation [118]. In addition, EPS-producing rhizobium strain inoculation to plant roots improved soil properties [119]. Exopolysaccharide linkages help to bind microorganisms together growing in the free planktonic state. Microbial EPS are rich in monosaccharides such as glucose, fructose, mannose, xylose, etc., that serve as a signal for root colonization [120]. In addition, the major functional groups in bacterial EPS such as hydroxyl, carboxyl, phosphate, sulfhydryl, and amino groups are the prime factors chelating Na\(^+\) under saline soil conditions, thereby reducing the exposure of plants to the salt ions [121].

### 5.6. Exopolysaccharides and Biofilm Formation

Bacterial biofilm formation is closely linked with EPS production, which essentially contributes to bacterial colonization around plant roots [122]. The PGPR in soil participates
in removing contaminants and toxicants from soil and water [34,123]. EPS-driven biofilm protects bacteria embedded with the EPS layer from uncongenial conditions such as the presence of salinity, antibiotics, and radiations [124]. Several studies showed that microbial biofilms attached to roots significantly enhance soil fertility [120]. The salt-tolerant PGPR is enabled to synthesize biofilm containing extracellular polysaccharides with high water holding capacity [125]. Apart from increasing the effective root colonization, the bacteria also have the competitive advantage of osmo-tolerance under salt stress. Previously, a study proved that root colonization and plant growth-promoting activities of PGPR did not interfere with salinity [126]. The production of exopolysaccharides, biofilm formation and accumulation of intracellular osmolytes govern the osmo-tolerance of PGPR. Ashraf et al. [127] found that the inoculation of EPS producing bacterial strains to the roots of wheat plants in salt-affected soils provides a “blanket salt-tolerant cover”. Bacterial species that enable the production of exopolysaccharide and biofilm are shown in Table 3.

Table 3. The exopolysaccharide and biofilm producing salt-tolerant bacteria.

| Name of the Bacteria | Plant Species | Reference |
|----------------------|---------------|-----------|
| *Halomonas variabilis* (HT1) and *Planococcus rifetensis* (RT4) | *Cicer arietinum* | [106] |
| *Pseudomonas fluorescens*, *Bacillus amyloliquefaciens* and *Bacillus polymyxa* | - | [127] |
| *Bacillus amyloliquefaciens* MAS4, *Bacillus insolitus* MAS10 and MAS26, *Pseudomonas syringae* MAS129, *Microbacterium* sp MAS133. | *Triticum aestivum* | [128] |
| *Shewanella putrefaciens* (isolates No.603) | - | [129] |
| *Bacillus iodinum* RS16, and *Bacillus aryabhattai* RS341 | *Capsicum annuum* | [130] |
| *Bacillus* sp. SKU5, *Burkholderia cepacia* (SKU6), *Microbacterium* sp. (SKU9), *Enterobacter* sp. (SKU9), and *Paenibacillus macerans* (SKU10) | *Triticum aestivum* | [131–133] |
| *Pseudomonas aeruginosa* (Pa2), *Proteus penneri* (Pp1), and *Alcaligenes faecalis* (AF3) | *Zea mays* | [134] |
| *Bacillus tequilensis* UPMRB9, *Bacillus aryabhattai* UPMRE6 | *Oryza sativa* | [135] |

**6. Salinity Tolerance of *Bacillus* sp.**

The gram-positive bacteria *Bacillus* is widely familiar with rhizobacteria. Some important member of a genus under *Bacillus* includes *B. licheniformis* HSW-16, *B. amyloliquefaciens* SN13, *B. megaterium* A12, *B. subtilis* SU47, and *B. pumilus* HB4N3 are reported for plant growth, and stress management [61,131,133,136,137]. The PGPR, *Bacillus subtilis* 93,151 inoculated transgenic *Arabidopsis thaliana* showed enhanced proline synthesis with proBA genes that can upsurge the plant’s salinity tolerance [138]. Root hydraulic conductivity of maize plants was increased by the inoculation of *Bacillus megaterium* compared to the uninoculated plants under 2.59 dSm\(^{-1}\) of salinity. Wheat seed treated with *B. aquimaris* SU8 strains increased higher shoot biomass, and NPK accumulation through the higher synthesis of total soluble sugars, reducing sugars, and Na reduction in leaves under 5.2 dSm\(^{-1}\) of salinity in field conditions [139]. Inoculation of *B. subtilis* BERAl to chickpea plants improved the upregulation of antioxidant systems through the reduction of ROS and increased nutrient absorption [140,141]. Improved systemic acquired resistance (SAR) in wheat by the inoculation of strain *B. licheniformis* HSW-16 exhibited enhanced ammonium assimilation, nitrogen fixation, and phosphate and potassium uptake under saline conditions [137].
7. Osmoprotectants

Osmoprotectants, commonly known as a compatible solute, traveled from producers to consumers. The osmotic adjustment of bacterial cells largely depends on various kinds of osmoprotectants required for bacterial cells for osmotic adjustment and thus cells can be protected against high temperature, oxygen radicals, and desiccation [142]. Proline, glycine betaine (GB), proline betaine, and choline, a precursor of glycine betaine, stimulates bacterial growth and nitrogen fixation when added to media of elevated osmotic strength and proline overproduction also enhances osmo-tolerance [143,144]. Among the compatible solutes, glycine betaine plays a protective function under saline condition [115]. Glycine betaine is electrically neutral and dipolar at physiological pH. The essential role of GB in salinity stress is the stabilization of RuBisCO, protection of photosynthetic apparatus, foraging of reactive oxygen species (ROS), and osmotic adjustment [144]. It is widely accepted that GB at low concentrations protect nucleic acids, lipids and proteins and also performed as pools of nitrogen and carbon sources [145]. Only a few microorganisms secrete GB that can be transported actively and accumulate osmoprotectant [146].

The bacterial membrane is penetrable to water but creates an active blockade for various solutes in the medium and metabolites in the cytoplasm. To cope with osmotic stresses, the cells gather organic solutes under hyperosmotic conditions and releases under hypoosmotic conditions. The amino acids (e.g., proline and glutamate), the amino acid derivatives (peptides and N-acetylated amino acids), sugars (e.g., trehalose and sucrose), amines (e.g., carnitine, glycine betaine), tetrahydropyrimidines and K⁺ [147] comprises compatible solutes. These compatible solutes originate by de novo synthesis (synthesis of complex molecules from simple molecules) or shifted with the major cellular system without interference. In rhizobial cells, the accretion of poly-b-hydroxyl butyrate usually acts as a defensive measure during elevated salinity stress [75]. Paul and Nair [126] observed the de novo synthesis of osmolyte by PGPR strain, Pseudomonas fluorescens MSP-393 such as alanine, serine, glycine, glutamic acid, threonine, and aspartic acid in their cytosol. The correct folding of polypeptides supported by compatible solutes under denaturing conditions both in vivo and in vitro consequently stabilizes proteins [148].

8. Induced Antioxidative Activity

In saline conditions, the antioxidant activities could be altered through the generation of ROS as a form of the hydroxyl radical (OH⁻), superoxide radical (O²⁻), and hydrogen peroxide (H₂O₂). ROS damages plant cells’ DNA, proteins, and lipids [149]. The strains B. subtilis BERA71 produces different antioxidant enzymes such as SOD, POX, and CAT as well as non-enzymatic antioxidants such as tocopherol, ascorbate peroxidase (APX), ascorbate, and glutathione which take parts in scavenging cycle [140]. An improvement of salinity tolerance in potato plants (Solanum tuberosum) is due to inoculation of Bacillus pumilus DH-11 and B. firmus str. 40, ACC deaminase producer and phosphate solubilizers, respectively [150]. Higher antioxidant enzymes in bacteria inoculated canola plants were also reported by Neshat et al. [151] who determined the higher production of SOD, POD, and CAT with the inoculation of Enterobacter sp. S16-3 and Pseudomonas sp. C16-20 under salt stress conditions. This is because of the accelerated photosynthetic rate, higher accumulation of proline, improved expression of mRNA, and the activities of antioxidant enzymes. Likewise, Kim et al. [42] testified an IAA and ACC deaminase producer Enterobacter sp. EJ01 strain inoculation shows an increase in dry weight and plant height of tomato and augmentation of ROS detoxifying enzyme in aerial plant tissue under salt stress.

9. Volatile Organic Compounds (VOCs)

A complex blend of volatiles could be released by PGPR [152,153]. Volatiles are organic compounds at room temperature that contains a high vapor pressure. The VOCs have odors or scents, derivatives of various nitrogen and sulfur-containing compounds such as phenylpropanoids, terpenoids, and fatty acids [154]. The PGPR-generated VOCs, change physical and chemical properties in plants and consequently enhance plant salinity
tolerance [155]. The PGPR strain *Bacillus subtilis* GB03 mediated VOCs confers salt tolerance and plant growth promotion in *Arabidopsis thaliana* through recirculation and reduction of Na\(^+\) levels in the entire plant under saline conditions through buildup HKT1, a high-affinity potassium transporter that facilitates Na\(^+\) transportation, expression upregulated in shoots and downregulated in roots [39].

10. Molecular Mechanisms and Gene Expression of PGPR in Response to Salinity Stress

A higher concentration of NaCl stimulates bacteria towards showing an expression of a specific gene, which is denoted as a set of proteins produced in higher amounts in response to stress [126,156]. In the bioinformatics era, proteomics is considered a suitable tactic for disclosing the vibrant expressions of whole cells proteins and their interactions. Large numbers of specific proteins have been reported, which shows an increase in their level of expression. To identify and elucidate the genes responding to relative physiological actions, differentially displayed proteins could be used as nutrient transport, metabolism, and responses to stress, chemotaxis, motility, sporulation, and biosynthesis of teichuronic acid [157]. Diby et al. [158] confirmed that many genes are responsive to salt stress in a PGPR strain, *Pseudomonas pseudoalcaligenes* MSP-538. Under salt shock conditions, peptide mass fingerprinting analysis of *P. fluorescens* MSP-393 exposed various stress-related proteins [159]. A bacterium, *Bacillus subtilis* JH642, responsive to salt stress expressed the induction of upregulated 123 genes and downregulated 101 genes by the transcriptional profiling at 1.2 M NaCl [160]. Under salinity stress, *Escherichia coli* MC4100 has been shown to produce multiple up-regulated genes involved in the process of cellular metabolism, amino acid biosynthesis, and transportation [161]. A salt-responsive protein K\(^+\) uptake kup/trkD was highly expressed in response to salt stress [162]. Previously, the involvement of non-coding RNA Yfr1 for salt sensing was explored [163]. Paul [164] has recently reviewed the mechanisms of salt stress adaptions in rhizobacteria.

A stress-related PGPR responsive protein named a chaperone is known to bind particularly denatured proteins and prevent degradation [165]. In another study, it was declared that in eubacteria and eukaryotic organelles, numerous enzyme-folding functions were regulated by chaperonin 60 [166]. Again, Holland et al. [167] reported that the seedlings of *N. tabacum* showed resistance against prolonged darkness, salt, and cold due to the buildup of chaperonin 60.

In rice plants, the differential expression of thioredoxin proteins was observed with *P. fluorescens* KH-1. The tolerance of methionine sulfoxide and H\(_2\)O\(_2\) was noticed in *Saccharomyces* train EMY63 because of the expression of *Arabidopsis thioredoxin* [168]. The protein 10i showed high homology to the enzyme glutamine synthetase, which is required for osmolyte distribution and played a significant role in glutamate synthesis, a prominent osmolyte in bacteria [169].

The induced proteins 26i and 42i were found to be associated with membrane proteins, and it could also be corroborated with the high root-colonization potential of the strain even in salinated soils [106]. Protein 41i is a survival protein (SurE), essential for the survival of osmotic stress (2.5 M NaCl) in bacteria [170]. Kandasamy et al. [171] assumed an essential role of the GSTs gene for its overexpression which might be involved in the ISR for protecting cells from oxidative damage.

11. Knowledge Gaps and Future Prospects

Many unrevealed areas exist on the performance of these beneficial microbes in stressed soil and also concerning their interactions with the host plant. In-depth studies are required to know the role of abiotic factors in changing the activity of rhizobacteria and managing plant–microbe interactions, concerning their compliance to stress environments. There are a few recommendations for future work:

i. Identification of genetic and environmental factors responsible for higher bacterial EPS synthesis under salt stress conditions.
ii. Identification of stress-responsive proteins involved in signaling, gene expression, and metabolism during plant–microbe interaction under salt stress conditions.

iii. The mutual sharing of osmoprotectants and antioxidant enzymes of PGPR and plants for maximum plant–microbe interactions under salt stress conditions.

iv. Evaluation of crop performance inoculated with salt-tolerant PGPR in actual saline ecosystems is a prerequisite to observing the consistent field performance of the potential salt-tolerant PGPR.

12. Conclusions

Worldwide, there is a rising demand for the cultivation of crops in saline-affected areas by taking into account compatible, ecologically sound, and environmentally friendly tactics. The development of stress-tolerant crops is a desirable option but considered a long-drawn and expensive process, whereas soil manipulation, using microbial strains to alleviate plant stress recognized as a low-cost and environment-friendly option that could be achieved in a shorter time frame. The PGPR mechanisms of osmo-tolerance offer multiple advantages to plants cultivated in salinized soils. The salt-affected areas are expected to utilize for increasing crop productivity through a proper understanding of PGPR mechanisms on salt tolerance. This review has shown and suggested the function of salt-resistant plant growth-promoting microorganisms as an environmentally friendly and more economical to improve crop production in saline-affected areas. In the future, extensive research needs to be emphasized in this area, particularly on the field performance of potential microorganisms as a source of bio-fertilizers in stressed soil.

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