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Review

Role of Halotolerant Plant Growth-Promoting Rhizobacteria in Mitigating Salinity Stress: Recent Advances and Possibilities

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Abstract: Soil salinity is one of the major abiotic constraints in agricultural ecosystems worldwide. High salinity levels have negative impacts on plant growth and yield, and affect soil physicochemical properties. Salinity also has adverse effects on the distribution and abundance of soil microorganisms. Salinity problems have previously been addressed in research, but most approaches, such as breeding for salt tolerant varieties and soil amelioration, are expensive and require years of efforts. Halotolerant plant growth-promoting rhizobacteria (HT-PGPR) secrete secondary metabolites, including osmoprotectants, exopolysaccharides, and volatile organic compounds. The importance of these compounds in promoting plant growth and reducing adverse effects under salinity stress has now been widely recognised. HT-PGPR are emerging as effective biological strategies for mitigating the harmful effects of high salinity; improving plant growth, development, and yield; and remediating degraded saline soils. This review describes the beneficial effects and growth-promoting mechanisms of various HT-PGPR, which are carried out by maintaining ion homeostasis, increasing nutrient availability, and the producing secondary metabolites, osmoprotectants, growth hormones, and volatile organic compounds. Exploring suitable HT-PGPR and applications in agriculture production systems can play a crucial role in reducing the adverse impacts of salinity stress and sustainable crop productivity.

Keywords: exopolysaccharides; osmoprotectants; growth hormones; soil microbes; volatile organic compounds

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1. Introduction

Food insecurity is a growing problem globally, owing to population growth, changing climates, and declining agricultural land, which threaten sustainable agriculture [1,2]. By 2070, the world population is expected to rise from 8 billion to 10 billion people [3]. This will require more farmland to meet the increasing food demand, but environmental factors including rising temperatures, erratic rainfall patterns, drought and soil salinity already limit land suitable for agricultural production [4]. Soil salinization is a major contributor to the degradation of agricultural land and reductions in crop productivity, with salinity affecting over 800 million hectares of land or 6% of the total worldwide land area [5]. Crop growth is impeded by salinity due to the toxicity of certain ions, nutrient imbalances, and osmotic stress [6], and low levels of organic matter in the soil, all of which can amplify the unfavourable effects of salinization [7,8]. The replacement of the ions responsible for salinity, either chemically or through the addition of organic materials has been effective in the amelioration of saline soils [9]. The productivity of such saline soils can therefore be increased through the adoption of new sustainable approaches, such as the use of inorganic or organic soil amendments and salt-resistant crop varieties [10].

Based on their responses to saline conditions, plants can be separated into two categories, glycophytes and halophytes, with the majority of plant species being glycophytes, and therefore relatively intolerant to salinity [11,12]. Halophytes, salt tolerant species, have evolved specialised strategies for survival in these conditions, such as root and shoot salt exclusion, ion compartmenting into various organs, and the synthesis of compatible solutes. The metabolic capacity of plants to respond to salt stress can also be enhanced by microbial interactions [13]. Research has shown many instances where microorganism-based plant biotechnology has proven to be more effective than traditional plant breeding or genetic modification techniques, and even soil amelioration approaches in alleviating soil constraints [14]. Microbes such as halotolerant plant growth-promoting rhizobacteria (HT-PGPR) can use a wide range of metabolic and genetic strategies to assist plants in mitigating the effects of salt stress and other abiotic stresses caused by harsh environmental conditions [15,16]. HT-PGPR are able to produce a wide range of secondary metabolites that aid in plant protection and assist in maintaining growth under saline environments, for both the symbiotic plant and bacteria species [17,18]. Most of these metabolites are only formed under abiotic stress conditions and enable the plant to survive in extreme climatic conditions, by acting on vital survival mechanisms including ion transport systems and uptake of osmoprotectants (Figure 1) [19]. Associated organic compounds have recently been shown to support plants in better adapting to saline conditions [20]. This review focuses on the important roles of HT-PGPR and their secondary metabolites, which could be used as next-generation bioinoculants for salt-affected agroecosystems.

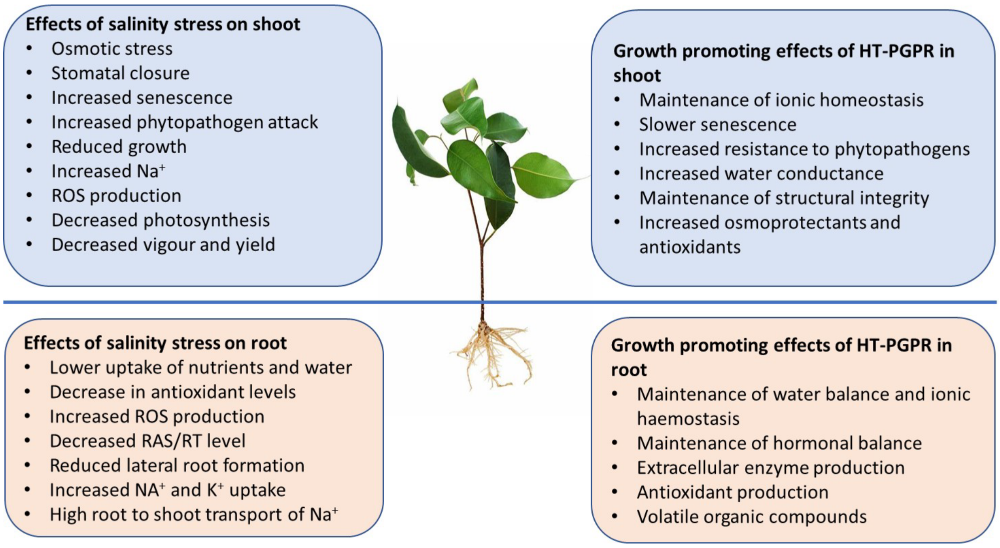

Figure 1. Effects of salinity stress and associated tolerance mechanisms induced by halotolerant plant growth-promoting rhizobacteria (HT-PGPR) in both plant roots and shoots.

2. HT-PGPR: Diversity and Their Effect on Crop Production

The use of HT-PGPR has recently emerged as a viable solution to issues associated with increasing soil salinity in agricultural lands [21]. These halophilic and halotolerant microorganisms are already adapted to thrive in salty environments [22] and through symbiotic relationships with associated plant species, they can influence host plant survival, root development, and growth (Figure 2) [23]. HT-PGPR can not only recognise and react to signal molecules secreted by plant roots, but also secrete a diverse range of signalling molecules that influence plant behaviour. These microbes also synthesis beneficial molecules including siderophores, phytohormones, volatile organic compounds (VOCs), exopolysaccharides (EPS), and other metabolites, along with solubilising nutrients such as phosphorus (P), zinc (Zn), and potassium (K) (Figure 2) [14,15]. These metabolites can assist plants through a wide range of biochemical, physiological, and molecular responses, including preserving ionic homeostasis through Na^+/K^+ transporters, enhancing water capacity, and activating *SOS* (*Salt-Overly Sensitive*) genes [24,25], together with acting as osmoprotectants, antioxidants, and compatible solutes. This three-tiered interwoven action–cumulation association between HT-PGPR and plant salt stress responses includes the existence of the bacteria itself in hyperosmotic conditions, the induction of salt-resistance in crops, and the improvement of soil quality [26] (Figure 1). Crop salt stress has been found to be reduced by several HT-PGPR species, including *Azospirillum*, *Arhrobacter*, *Burkholderia*, *Alcaligenes*, *Bacillus*, *Enterobacter*, *Klebsiella*, *Microbacterium*, *Streptomyces*, *Pseudomonas*, *Pantoea*, and *Rhizobium* [27]. These species may occur naturally around crop species or can be isolated from native halophytic plants.

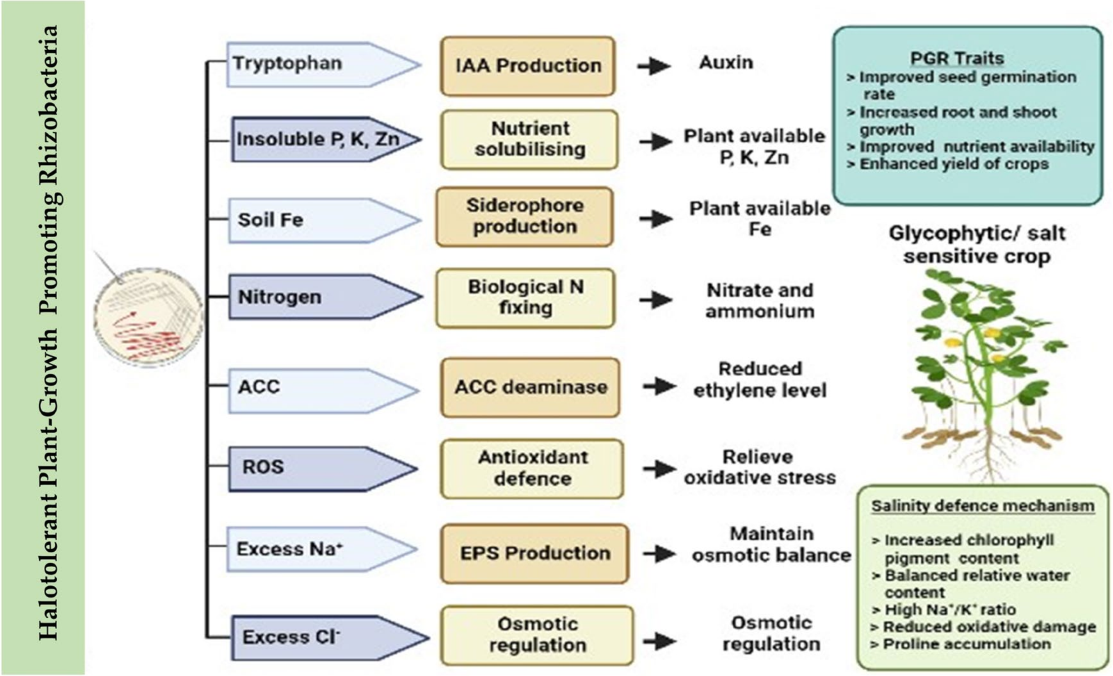

Figure 2. Effect of HT-PGPR on plant growth and salinity tolerance in glycophytic plants. The plate shown includes potential HT-PGPR isolated from native halophytes and consists of rhizobacteria and endophytes. Beneficial effects are shown in blue boxes, the underlying processes in orange boxes, and benefits plants in the last column.

Wheat inoculated with HT-PGPR *Enterobacter cloacae*, *Pseudomonas putida*, *Pseudomonas fluorescens*, and *Serratia ficaria*, then cultivated in naturally saline fields (ECe = 15 dSm^{-1}), had increased germination rates, percentage, and index by 51%, 43%, and 123%, respectively, in comparison to the nontreated controls, along with increased yield [28]. Another study found that the shoot and root fresh and dry biomass weights of *Brassica juncea*, cultivated in saline conditions (ECe = 12 dSm^{-1}), significantly increased after inoculation with salt-tolerant *Pseudomonas azotoformans* JMM15 and *Pseudomonas argentinensis* HMM57 strains [29]. Additionally, an F-11 halotolerant *Staphylococcus jettensis* F1 increased the dry biomass of *Zea mays* by a factor of three when plants were grown under 200 mM saline stress [30]. *Pseudomonas putida* performed best among strains tested under high salinity (15 dSm^{-1}), increasing plant height by 52%, root length by 60%, grain output by 76%, 100-grain weight by 19%, and straw yield by 67%, in wheat compared to the uninoculated crop [31]. Although it has been shown that HT-PGPR may improve crop production (in salt-affected soil) and reduce salinity stress, there is still much to learn about the interactions and processes that take place between plants and microorganisms under multidimensional stresses like salinity.

3. HT-PGPR and Their Effects in Mitigating Salt Stress in Crops

HT-PGPR provide plants with resistance to salt stress through several key processes. One such process is the regulation of the salt overly sensitive (*SOS*) pathway, which is involved in salt influx/efflux across membranes, through metabolites and associated gene expression patterns. It has been shown that the *SOS1* gene is directly regulated by metabolites such as EPS, VOCs, and suitable solutes (i.e., proline, glycine betaines, and trehalose) [25], which also direct stress regulation in *SOS* genes [3], *HKT1* transporter (high-affinity K) expression [32], and other genes implicated in the reduction in salt stress, i.e., ethylene biosynthesis and antioxidant protein encoding genes [33,34]. Examples of the beneficial effects of HT-PGPR, along with how they help plants cope with saline conditions in different plants, are reviewed and presented in Table 1. The following sections further discuss the importance and beneficial aspects of HT-PGPR, how metabolites are biosynthesised or promoted by HT-PGPR, and the role of these mechanisms in improving plant salinity tolerance.

Table 1. Effects of inoculating plant species with various halotolerant plant growth-promoting rhizobacteria (HT-PGPR) species. Table summarises genes involved, mechanisms to increase salt tolerance, and actual effects observed in different plants.

Plant Species	HT-PGPR Species	Gene/s Involved	Mechanism to Mitigate Stress	Effect Observed	References
Arabidopsis thaliana L.	*Bacillus oryzicola* YC7007	*RD22, KIN1, RD29B, RD20, RD22*, and *ERD1*	Stem and the root of the seedlings released stress-related genes	Enhanced plant tolerance to salt stress	[35]
	Pseudomonas putida PS01	*APX2* and *GLYI7*	*APX2* and *GLYI7* genes were downregulated	ABA signalling, jasmonic acid production route, ROS scavenging, detoxification	[36]
	Pseudomonas knackmussii MLR6	*NHX1, HKT1, SOS2, SOS3, SAG13*, and *PR1*	Enhanced stomatal conductance, transpiration rate, chlorophyll, and carotenoid levels	Reduced electrolyte leakage and priming ROS accumulation increasing cell membrane stability	[37]
	Bacillus amyloliquefaciens SQR9	*NHX1* and *NHX7*	Involved in reducing GSH biosynthesis	Reduced ion toxicity by sequestering Na$^+$ into vacuoles and releasing Na$^+$ from the cell	[38]
	Burkholderia phytofirmans PsJN	Upregulation of *RD29A* and *GLYI7*, and downregulation of *LOX2*	Enhancement of proline and transcription of genes related to abscisic acid signalling and downregulated gene *Lipoxygenase 2*	Abscisic acid signalling, ROS reduction, detoxifying, jasmonate synthesis, and ion transport	[39]
	Paenibacillus yonginensis DCY84^T	*AtRSA1, AtVQ9* and *AtWRKY8*	Upregulated salt-stress genes	Promoted more resistance to salinity, drought, and aluminium stresses	[40,41]
	Enterobacter sp. EJ01	*DREB2b, RD29A, RD29B, RAB18, P5CS1, P5CS2, MPK3*, and *MPK6*	Upregulated salt-stress genes	Promoted more resistance to salinity and enhanced plant growth	[42]
	Bacillus subtilis GB03	*HKT1*	Down- and upregulates HKT1 in roots and shoots, respectively	Decreased total plant Na$^+$ accumulation	[23]

Table 1. *Cont.*

Plant Species	HT-PGPR Species	Gene/s Involved	Mechanism to Mitigate Stress	Effect Observed	References
Bacopa monneri L.	*Dietzia natronolimnaea* STR1	*SOS1, SOS4, TaST, TaNHX1, TaHAK, and TaHKT1*	Reduction in ABA-signalling, upregulated *TaABARE* and *TaOPR1*	Abscisic acid signalling, ROS scavenging, antioxidant enzyme activity, enhanced ion transporter expression, high K^+/Na^+ ratio	[24]
	Bacillus pumilus STR2, *Exiguobacterium oxidotolerens* STR36	-	Mixture of plant growth-promoting traits under primary and secondary saline condition	Produced higher yield, high proline/lipid content peroxidation	[2]
Cicer arietinum L.	*Planococcus rifietoensis* (RT4) and *Halomonas variabilis* (HT1)	-	Biofilm and exopolysaccharides production	Improved crop growth, soil aggregation, and soil fertility	[43]
Glycine max L.	*Arthrobacter woluwensis* AK1	-	Reduced endogenous ABA and controlled antioxidant activity	Mitigated salinity stress and increased plant growth	[44]
	Microbacterium oxydans, *Arthrobacter woluwensis*, *Arthrobacter aurescens*, *Bacillus aryabhattai*, and *Bacillus megaterium*	-	Increased production of IAA, GA, siderophores, and phosphate solubilisation	Increased antioxidant enzymes and K absorption; reduced Na^+ in plant tissue; phytohormone	[45]
	Pseudomonas simiae AU	*P5CS*, *PPO* and *HKT1*	Downregulated *HKT1*, *LOX*, *PPO*, and *P5CS* genes	Increased chlorophyll, phosphate solubilisation, IAA, and siderophores; decreased root surface in saline	[46]
	Pseudomonas sp. strain AK-1	*HTK1*	Improve K^+/Na^+ ratio and Exopolysaccharide production binds free Na^+ from soil	Increased shoot/root length and decreased Na^+/K^+ ratio	[33]
	Pseudomonas simiae AU	*VSP2*	Increase vegetative storage protein (VSP), gamma-glutamyl hydrolase (GGH), and RuBisCo proteins	Reduced Na, increased K and P in soybean seedling roots, high proline and chlorophyll content	[47]
Helianthus annuus L.	*Pseudomonas libanensis* TR1	-	ACC-deaminase and exopolysaccharide production	Ni and Na^+ accumulation potential increased along with plant growth.	[48]
	Pseudomonas spp.	-	Upregulating of ACC deaminase	Improved P and K contents, and K^+/Na^+ ratio in shoot	[49]

Table 1. *Cont.*

Plant Species	HT-PGPR Species	Gene/s Involved	Mechanism to Mitigate Stress	Effect Observed	References
Hordeum vulgare L.	*Bacillus mojavensis*, *B. pumilus* and *Pseudomonas fluorescens*	*S1* and *S3*	ACC deaminase, IAA, and proline production	Reduced plant Na concentration, stimulated root growth, improved water and nutrient absorption	[50]
	B. aryabhattai MS3	*BZ8*, *SOS1*, *GIG*, and *NHX1*	Increased salt stress resistance and accumulation	Adaptation of plant under saline condition	[51]
	Bacillus amyloliquefaciens SN13	*DHN*	Upregulated salt stress-responsive genes and protein-related genes	Lipid peroxidation and electrolyte leakage reduced; increased rice biomass, water content, proline, and total soluble sugar	[52]
	Bacillus megaterium ST2-1	-	IAA production	Stimulated the growth of rice roots and dry biomass	[53]
	Pseudomonas pseudoalcaligenes ST1, *Bacillus pumilus* ST2	*EU440977* and *FJ840535*	Accumulation of proline decrease with inoculation, antioxidative activity	Enhanced plant growth by ROS scavenging and higher accumulation of osmoprotectant	[54]
Puccinellia tenuiflora L.	*Bacillus subtilis* (GB03)	-	Upregulated *PtHKT1;5* and *PtSOS1* genes, downregulated *PtHKT2;1*	Na homeostasis modulation, exclusive K+ absorption	[55]
Solanum lycopersicum L.	*Leclercia adecarboxylata* MO1	-	ACC deaminase and IAA production	Increased soluble sugars: organic glucose, sucrose, fructose, malic, amino acid, and proline	[56]
	Sphingobacterium sp. BHU-AV3	-	Reduction in ROS concentration in plant	Enhanced antioxidant activities and energy metabolism	[57]
	Enterobacter sp. EJ01	*DREB2b*, *RD29A*, *RD29B*, and *RAB18*	Downregulated *P5CS1* and *P5CS2*, and upregulated *MPK3* and *MPK6*	Biosynthesis, defence pathway modulation, salt response	[42]
	Pseudomonas putida UW4	Toc GTPase	Toc GTPase genes were upregulated and reduction in ACC deaminase	Increased shoot length and chlorophyll concentration	[58]
Trifolium repens L.	*Bacillus subtilis* (GB03)	-	Reduced shoot and root Na^+, improving K^+/Na^+ ratio	Decreased Na^+, increased chlorophyll, leaf osmotic potential, cell membrane integrity	[59]

Table 1. *Cont.*

Plant Species	HT-PGPR Species	Gene/s Involved	Mechanism to Mitigate Stress	Effect Observed	References
Triticum aestivum L.	*Pseudomonas aeruginosa* GI-1, and *Burkholderia gladioli* GI-6	-	P solubilisation, catalase activity, IAA production, N assimilation, and siderophores production	Encouraged growth and yield and improve soil fertility	[60,61]
	Arthrobacter nitroguajacolicus	-	Upregulated 152 genes whereas 5 genes were downregulated	Amplified ACC, IAA, siderophore, and phosphate solubility. ROS detoxification, Na^+ homeostasis, abiotic stress	[62]
	Serratia marcescens CDP-13	-	Increased salt tolerance in plant	ACC deaminase, phosphate solubilisation, siderophore, indole acetic acid, N fixation, and ammonia synthesis	[63]
	Pseodomonas sp and *Enterobacter cloacae* (R-10)	*B-22* and *S-49*	K and Zn solubilisation for identifying antifungal activity	Enhanced K^+ uptake, dry matter of wheat	[64]
	Hallobacillus sp. SL3 *Bacillus halodenitrificans* PU62	*acdS*	IAA production and siderophore production, phosphate solubilising, and siderophore production	Increased root elongation and dry weight	[65]
Zea mays L.	*Serratia liquefaciens* KM4	Upregulation of stress-related genes (*APX*, *CAT*, *SOD*, *RBCS*, *RBCL*, *H^+-PPase*, *HKT1*, and *NHX1*)	Regulating redox potential and stress-related gene expression	Higher leaf gas exchange, osmoregulation, antioxidative defence mechanisms, and nutrient uptake boosted maize growth and biomass production	[66]
	Azospirillum lipoferum, *Azospillum* sp., *Azotobacter chroococcum*, *Azotobacter* sp., and *Bacillus* sp.	-	Exopolysaccharide inoculation in the soil	Increased root and shoot dry weights, chlorophyll and carotenoids, restricted Na and Cl uptake, and increased shoot N, P, and K	[67]
Abelmoschus esculentus L.	*Enterobacter* sp. UPMR18	*X55749*	ROS pathway upgradation and enhancement in antioxidant enzyme activities	Higher germination, growth, and chlorophyll improved salt tolerance	[68]

4. Plant Growth-Promoting Mechanisms by HT-PGPR

4.1. HT-PGPR Mediated Increased Availability of Soil Nutrients

Reduced bioavailability of nutrients due to altered physicochemical properties is a common problem of salinity stress [69–71]. The composition and level of salinity, the concentration of nutrients, and environmental conditions all have an impact on the interaction between mineral nutrition and salinity [72]. Continuous applications of chemical fertilisers can be a temporary solution to address these issues, but pose environmental risks, reduces soil health, and, paradoxically, can increase soil salinity [73]. Therefore, the use of beneficial microorganisms to enhance nutrient bioavailability, rather than chemical amendments, is potentially a more environmentally friendly and sustainable approach to crop production [74].

Nitrogen (N) is necessary for plant growth and productivity, as it is primarily involved in the synthesis of enzymes, proteins, RNA, and DNA within plant cells [75]. High chloride (Cl^-) content, and therefore uptake in saline soils, can greatly diminish the uptake of N and sulphur (S) by plants [70]. The ability of HT-PGPR to increase essential soil nutrient bioavailability is possible through a wide range of action mechanisms. N is abundant in the air, but plants can only absorb it in the form of nitrate (NO_3^-) or ammonium (NH_4^+) [76]. N-fixing bacteria, such as *Pseudozyma rugulosa*, *Cryptococcus flavus*, and *Pseudozyma antarctica* can convert atmospheric N into plant-available NO_3^- or NH_4^+, especially under saline conditions, through a loose symbiosis mechanism also known as biological nitrogen fixation [77–79]. Typically limited to bacteria, it has also been shown that a soil-isolated yeast strain, *Candida tropicalis*, possesses an intriguing and remarkable ability to fix N [80], as well as the NH_4^+-producing yeast *Meyerozyma* [81,82]. These N-fixing bacteria, known as rhizobacteria, live as free-living ectorhizospheric or endophytic symbiotics on plant roots [83]. These rhizobacteria are able to fix atmospheric N into ammonia due to the presence of *FixABX* genes, which are necessary for free-living bacteria, and *Nif* genes, which encode the production of nitrogenase enzymes that reduce atmospheric N into ammonia [84]. Under saline stress, the host plants are then able to directly absorb the fixed plant-available N, relieving some of the stress on the plant caused by salinity-induced N deficiencies [85].

P is essential in many biochemical processes and a component of nucleic acids, nucleotide coenzymes, and metabolic intermediates [86]. Plants under severe salt stress often have a deficiency in P [87], owing to competition with Na^+ ions for membrane-transporter binding sites. When applied to soil, HT-PGPR with phosphate-solubilising capabilities, known as phosphate-solubilising bacteria (PSB), can significantly aid in raising soil P availabilities. PSBs have been shown to increase yields up to 50% without increasing the need for P fertilisers [88]. To meet the needs of plants, PSBs dissolve and absorb insoluble phosphate (Pi) to make it available for plant uptake. Two distinct types of PSBs can be identified by examining their P-dissolving patterns, (i) those that secrete organic acid to dissolve Pi compounds, and (ii) those that secrete phosphatase to enzymatically mineralise Pi compounds. By lowering soil pH and creating a P-offering micro-area around the plant rhizosphere, applications of both types of PSBs increase the plant's access to P, and boost the efficiency of other beneficial microorganisms such as *Rhizobium* and *Trichoderma* [89]. The PSBs secretes low-molecular-weight organic acids, such as gluconic acid, citric acid, succinic acid, propionic acid, and lactic acid, as by-products of sugar metabolism in root exudates, which aid in the digestion and assimilation of nutritionally important ionic compounds [90].

HT-PGPR are also able to solubilise organic K and Zn in the soil, using organic acid secretions and a resulting change in soil pH [46,79]. Rhizobacteria can also increase soil Fe bioavailability by synthesising siderophores, which are low-molecular-weight (0.5–1 kDa) compounds with functional groups of hydroximates and catechol's, which have a high affinity for ferric ions and a reversible binding mechanism [91,92]. Plants can then easily access the bacterial siderophore–Fe complexes that have formed, absorbing them via chelate destruction, direct uptake, or even hypothesised ligand exchanges [93]. Plant-made siderophores (phytosiderophores) may initiate the ligand exchange reaction between the bacterial siderophores and the Fe-containing complex, allowing the plants to take up the transferred Fe [94].

4.2. HT-PGPR Mediation Increase Availability of Indole-3-Acetic Acid

Indole-3-acetic acid (IAA) is a key plant hormone, important for seed germination, improved root and leaf growth, and reduction in adverse effects of salinity to plant production [95]. Exogenous production of phytohormones is not limited to only plants, in fact, many HT-PGPR have the ability to produce IAA, making them perfect bioinoculants to increase symbiotic plant IAA levels, which would improve plant growth under salinity stress [68,71,96]. HT-PGPR are able to use L-tryptophan, found in root exudates, as a precursor in the production of exogenous bacterial IAA [97], with the amount of IAA produced being altered by environmental conditions such as pH, temperature, osmotic stress, and carbon limitation [98]. The hydrolysis of IAA conjugates has also been hypothesised to result in IAA formation. Inducible adenylate cyclase is produced by *Pseudomonas*, *Bacillus*, *Klebsiella*, *Azospirillum*, *Enterobacter*, and *Serratia* [99]. Root-associated bacteria that produce

IAA may also aid in nodule formation and stimulate the expansion of root system by means of the development of lateral roots [100]. The exogenous IAA synthesised by HT-PGPR helps maintain a healthy ratio of endogenous IAA in the roots, promoting root growth and development, increasing root mass and size, encouraging root exudations, and forming lateral roots, allowing the plant to make greater soil contact. In high salt environments, plant root systems can therefore be improved with symbiotic HT-PGPR relationships, increasing capacity for nutrient exchanges, water uptake, and growth [101–103]. This, in turn, can help plant leaves continue to grow, keeping photosynthetic rates and yields relatively unchanged. Table 2 gives examples of isolated IAA-producing microbes that have significantly increased shoot length and weight (fresh and dry), root length and weight (fresh and dry), and germination rates of salt-sensitive crop seeds grown under saline conditions. In addition, control plants showed either slight improvements or no effects from the selected microbes [93,104,105].

Table 2. Indole-3-acetic acid producing halotolerant plant growth-promoting rhizobacteria (HT-PGPR) and their role in plants.

HT-PGPR	Crop	Role in Plants	Reference
Streptomyces fradiae NKZ-259	Tomato	Increases root and shoot length	[1]
Stenotrophomonas maltophilia AVO63	Avocado	Protection against white root rot	[106]
Pseudomonas entomophila PE3	Sunflower	Antioxidant, hydroxyl-scavenging; reduction in Na^+ accumulation	[107]
Arthrobacter pascens ZZ21	Forest soil	Enhanced plant growth and remediate fluoranthene-contaminated soil	[108]
Rhizobium sp. MRP1	Pea	Produce HCN, ammonia and EPS	[109]
Paenibacillus xylanexedens (PD-R6) and *Enterobacter cloacae* (PD-P6)	Date palm	Enhances nutrient uptake in roots and improves plant growth	[110]
Burkholderia cepacia 0057	Maize	Enhancement of disease control	[111]
Bradyrhizobium japonicum	Wheat	Improved growth and yield	[112]
Bacillus tequilensis SI 319, *Pseudomonas lini* SI 287, *P. frederiksbergensis* SI 307, and *Brevibacterium frigoritolerans* SI 433	Soil sample	Increased plant growth	[113]
Bacillus sp. PSB10	Chickpea	Reduced uptake of chromium	[114]
Pseudomonas putida LWPZF	Katsura	Improved plant growth and contained anti-heavy-metal properties	[115]

4.3. HT-PGPR Modulations of Ethylene

A key phytohormone that acts as a stress signal is ethylene, and at low concentrations triggers a number of defence mechanisms that help plants manage biotic and abiotic stresses [116]. The second peak of ethylene synthesis, also called stress ethylene, occurs only under conditions of prolonged and extreme stress. Roots are negatively impacted by stress ethylene as their development is stunted, which in turn affects root function, vegetative growth, and, ultimately, productivity and yield [87,117,118]. Plants produce ethylene from its precursor, 1-aminocyclopropane-1-carboxylic acid (ACC), which is oxidised by the enzyme ACC oxidase. Through the production of the enzyme ACC deaminase (ACC-D), some HT-PGPR with the *AcdS* genes can convert ACC found in root exudates into ammonia and ketobutyrate. As a result, the by-products are used by the rhizobacteria as their sole source of C and N [119]. In stressed plants, HT-PGPR and ACC-D activity of at least 20 nmol mg^{-1} h^{-1} can dramatically reduce the total pool level of ethylene precursors, and may diminish the second peak of ethylene production by as much as 90% [120]. The subsequent drop in ethylene concentration improves plant resistance to stress, restoring root function and allowing it to flourish despite adverse conditions [121]. Ethylene also interacts with other phytohormones either by manipulating gene expression or by affecting transcription factors [122], therefore the fine-tuning of ethylene levels may be a pathway to increased salt tolerance.

4.4. HT-PGPR Improves Osmoprotectants, Compatible Solutes, and Ion Homeostasis

The optimal operation of a plant's physiological and metabolic functions depends on water homeostasis. Excessive salt accumulation in soil disrupts a plant cell's ability to absorb water, and causes ionic toxicity and osmotic stress (Cl^- and Na^+ accumulation), which in turn prevents plant growth and development [123]. Numerous vital physiological processes, such as stem and root growth, photosynthesis and transpiration, cell structure maturation, hormonal status, nutrient uptake, and enzyme activity are therefore disrupted by the abundance of ions and hypertonic conditions [124,125]. To adapt to saline conditions, HT-PGPR mutually partnered with plants, will produce metabolites with low molecular weights that are recognised as relevant solutes, or osmoprotectant substances, which then aid in plant stress reduction, maintain high turgor pressure, and equalise ion efflux across the plasma membrane (Figure 3) [126]. To help plants with their water shortage, these substances also regulate stomatal opening, transpiration rate, and hydraulic conductivity [127,128]. Among the many suitable solutes produced by HT-PGPR, glycine betaine, carnitine, and especially proline, a reactive oxygen species (ROS) scavenger, are vital to plants [129,130]. Through processes like those shown in Figure 2, rhizobacteria help plants recover from abiotic stress by either acquiring these molecules from the surroundings or de novo production, depending on the stress level. Proline synthesis in particular is upregulated by plants during osmotic stress [131], as well as in response to HT-PGPR [17], enhancing control of cytosolic pH and maintain cell protein structures [132]. Most bacteria require the combined enzyme activity of glutamyl phosphate reductase, glutamyl kinase, and 1-1-pyrroline-5-carboxylate reductase to synthesise proline, with genes *ProB*, *ProA*, and *ProC* inducing this catalytic reaction [129,133]. Proline dehydrogenase enzyme activity has been shown to increase under salinity stress, leading to N-fixing bacteria showing higher proline metabolism [134,135]. Under saline circumstances, an HT-PGPR (*Bacillus fortis* strain SSB21) was involved in improved growth, increased chlorophyll and protein levels, and water use efficiency, due to increased proline synthesis [136]. Inoculation of *Mentha arvensis* with HT-PGPR from the genera *Exiguobacterium*, *Bacillus*, and *Halomonas*, also had a greater foliar proline concentration, compared to control plants [2].

Inoculating salt-sensitive plants with HT-PGPR can help to maintain ion homeostasis (K^+/Na^+), promote osmolyte accumulation, and increase nutrient (P, N, K, Mg, and Ca) bioavailability, which confers resistance against the negative consequences of salinity. Under 300 mM salt stress, the injection of salt-resistant *Paenibacillus yonginensis* DCY84T onto ginseng seeds resulted in increased levels of proline, polyamine, and total soluble sugars. Additionally, the treatment improved the nutritional availability of salt-stressed plants, ABA production, chlorophyll content, and the stimulation of stress-responsive genes [137]. Another suitable solute, glycine betaine (GB), accumulates in the cytosol of plants to counteract the effects of salt stress by reducing osmotic stress and preserving plant cell integrity as a whole [138,139]. When administered exogenously, GB improved salt tolerance in soybean, as evidenced by lower Na^+ concentrations and increased catalase (CAT) and superoxide dismutase (SOD) activity in treated plants [140]. In *Bacillus subtilis*, GB production is initiated by the activity of two enzymes, (i) a precursor molecule, choline, an intermediary chemical GB aldehyde, is oxidised by type III alcohol dehydrogenase, and (ii) an end product called GB aldehyde dehydrogenase [129,141,142]. The generation of GB in transgenic plants often involves the choline oxidase enzyme from *Arthrobacter globiformis*, which turns choline into GB [143]. Increased concentrations of GB were seen in maize after being injected with HT-PGPR *Bacillus subtilis* HL3RS14, with plants under salt stress growing quicker [144]. Similarly, *Acacia gerrardii* infected with *Bacillus subtilis* BERA71 produced more GB and osmolyte under saline conditions [145].

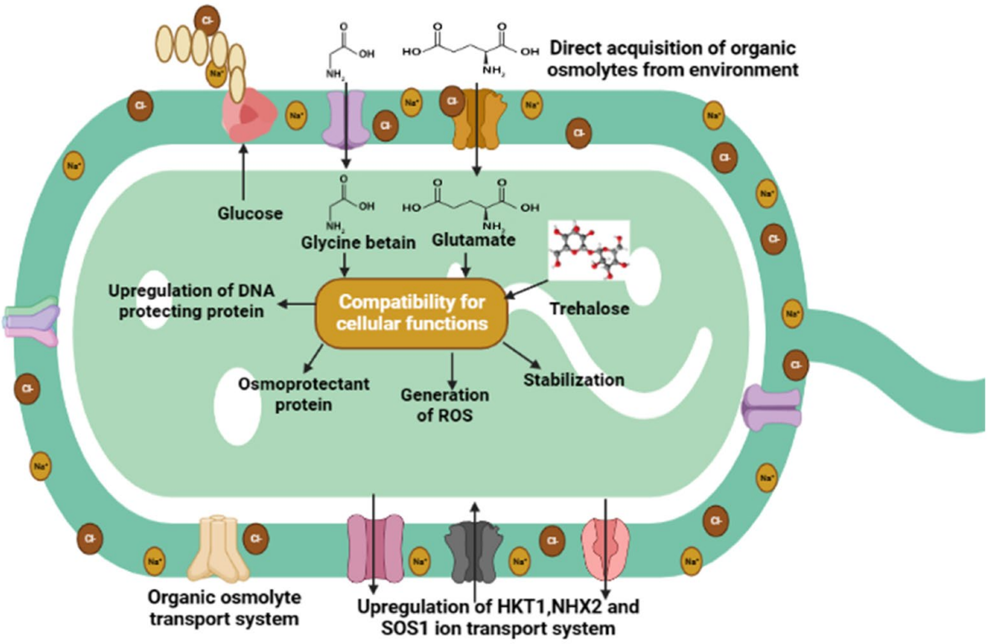

Figure 3. Model of osmoprotectants and compatible solutes produced by halotolerant plant growth-promoting rhizobacteria (HT-PGPR), their cellular locations, and functions.

On exposure to salt stress, ectoine (1,4,5,6-tetrahydro2-methyl-4-pyrimidinecarboxylic acid), another osmolyte, accumulates in the cytoplasm of plants [146]. Three enzymes, L-ectoine synthase, L-2,4-diaminobutyric acid aminotransferase, and L-2,4-diaminobutyric acid acetyltransferase, are involved in the synthesis of ectoine in bacteria, activated by *EctB*, *EctA*, and *EctC* genes [147]. In HT-PGPR, ectoine production quantity is inversely correlated with the rise in intracellular osmotic strain caused by various factors, such as salt stress [148]. In an experiment, it was discovered that ectoine, which was isolated from the halophilic *Chromohalobacter salexigens* KT989776, improved flax seed germination and decreased salt accumulation, phenoloxidase, and peroxidase activities in crops [149]. Trehalose, nonreducing disaccharides with two glucose moieties linked by α-1,1-glycosidic linkages, is another osmoprotectant used by HT-PGPR [150]. Trehalose cannot be produced by plants; however, HTPGPR play a significant role in supporting plants under salt stress by forming this osmoprotectant. Trehalose synthase, Alpha-trehalose-phosphate synthase, and Trehalose-6-phosphate phosphatase are a few of the enzymes that are included in trehalose production in HT-PGPR and are encoded by the *OtsAB* genes [151]. Most bacteria use the *TreS* and *TreY/TreZ* pathways to synthesise trehalose and tolerate the effects of salt stress, with trehalose levels increased during salinity and drought stress, similar to many other osmoprotectants [152,153]. *Azospirillum brasilence*, with the trehalose biosynthesis gene overexpressed, was used to inoculate maize, which then had increased root and leaf biomass, and increased ability to withstand osmotic stress. Similarly, when *Rhizobium etli* with trehalose-6-phosphate synthase overexpression, was inoculated into *Phaseolus vulagris*, plants showed osmotic stress resistance, higher number of nodules, and increased plant biomass [154]. Osmolyte accumulation and synthesis by HT-PGPR is therefore one of the critical processes that contribute to the reduction in multiple stress components caused by salinity. To decrease agricultural losses, salt-resistant transgenic crops may be created by genetically manipulating the genes from HT-PGPR that produce secondary metabolites [152].

4.5. Production of Exopolysaccharides and Volatile Organic Compounds by HT-PGPR

Exopolysaccharides (EPS) are often generated by HT-PGPR metabolites. Under salinity conditions, EPS production alone accounts for 40–90% of the weight of the bacterial extracellular matrix [108,155]. EPS facilitate microbial adhesion to plant roots, aid in biofilm formation to prevent cells from drying out due to salt stress, and increases the movement of bacteria that are connected to plant roots [156–158]. The phase of bacterial development, the composition of the medium, and exposure to environmental stresses, such as salt and dehydration, all affect EPS production [159,160]. Additionally, it has been shown that EPS have strong antioxidant properties and give bacteria resistance to ROS-dependent cell death. For example, the endophytic bacteria *Gluconacetobacter diazotrophicus* was shown in vitro and during rice plant colonisation, to be protected against oxidative destruction by EPS [161]. Similarly, the multilayer antioxidant activity of EPS generated by the halotolerant endophyte *Glutamicibacter halophytocola* KLBMP 5180 was studied to mitigate the destruction caused by salt stress on crops [162]. Another activity of EPS is soil aggregation and enhancing root-adhering soil through the formation of a sheath around roots, which increases water availability and nutrient (P, N, Fe, and K) accumulation from the soil [69,163]. Exopolysaccharides EX01 enhanced rice growth and improved osmotic stress tolerance through the increased expression of the HKT1/K^+ transporter, minimising Na^+ inflow and therefore reducing ionic toxicity in plants [23].

By regulating important plant metabolic processes and maintaining soil physicochemical properties, EPS-producing bacteria may also help increase crop production under saline conditions [43,164]. In addition to these well-recognised functions, bacterial EPS are also associated with cellular sensing and rhizosphere recognition, the protection of plants from phytopathogens, and act as a carbon source under nutrient-deficient settings [165,166]. In a severely salinized field (EC > 10 dS/m), Tiwari et al. [166] reported that inoculation with EPS-producing *Pseudomonas* sp. increased the yield of sunflower. Analysis also showed a decrease in the prevalence of charcoal rot virus in *Macrophomina phaseolina* under salinity soil after HT-PGPR inoculation. Salt-tolerant bacteria such as *Bacillus insolitus*, *Bacillus amyloliquefaciens*, *Pseudomonas syringae*, and *Microbacterium* spp. may improve wheat growth by preventing Na^+ input into the stele of plants under salinity stress [167]. Mung beans treated with EPS-producing *Bacillus drentensis* and *Enterobacter cloacae*, under salt stress, showed increased availability of nutrients and water absorption in plants due to biofilm formation in the root zone [168]. Similarly, *Pantoea alhagi* NX-11, an EPS-producing endophyte, inoculation increased the salt resistance of rice plantlets by enhancing antioxidant activity, leading to greater development when compared to those plantings inoculated with EPS mutant NX-11eps [169]. In salty environments, maize treated with EPS-producing *Azotobacter chrococcum* strains C5 and C9 had reduced salt stress through increased K^+/Na^+ ratio, chlorophyll content, ion absorption (K, Na, Mg, Ca), and accumulation of polyphenols and proline [170], while an EPS-based *Alcaligenes* sp. bioformulation was especially effective in decreasing osmotic stress in rice [171]. In general, studies indicate that EPS generated by HT-PGPR play significant roles in assisting plants minimise salt stress effects and may be utilised as bioinoculants to enhance soil quality, rhizosphere colonisation, and nutrient uptake under saline conditions. EPS could also be used as a bioinoculant amendment to help protect the HT-PGPR microbes from the initial stress encountered when first introduced into saline soils.

When exposed to salinity or other environmental stresses, HT-PGPR produce volatile organic compounds (VOCs) less than 300 Da molecular weight, with lipophilic natures and a low boiling points [172,173]. Numerous microbial volatiles have been documented, and most have the potential to enhance the overall growth of crops [174]. VOCs are often employed as markers to identify individual bacterial species in ecosystems, and to determine how these communities interact [175]. Plant hormones expansin, gibberellin, auxin, ethylene, and cytokinin were affected by the 1,3-propanediol and VOC albuterol generated by *Bacillus subtilis* SYST2, demonstrating the impact these compounds can have on plant regulation [176]. The most researched bacterial VOCs include dimethyl disulfide, geosmin, acetoin, and 2,3-butanediol, which aid in composting, auxin homeostasis, sulphur nutrition, cell growth, inducing systemic and drought resistance in crops, and soil formation processes [177–180]. Alcohols, aldehydes, and ketones were found to be the most common VOCs released by six different *Bacillus* strains [181]. In Arabidopsis, most VOCs promote lateral root development and primary root growth, with shoot and root biomass increases seen due to VOCs generated by root-associated *Microbacterium* spp. Just a short interaction with bacterial VOCs can promote plant development, indicating that these compounds may be used to prepare crops without subjecting them to direct or prolonged bacterial exposure. Additionally, it was shown that the VOC-mediated crop development proliferation was tissue-dependent and only caused a biomass increase in crops that were exposed to VOCs through their roots [182]. Under 150 mM salt stress, quinoline and 4-nitroguaiacol, two bacterial VOCs generated by salt-resistant *Pseudomonas simiae*, and a VOC-producing HT-PGPR *Paraburkholderia phytofirmans* PsJN, not only alleviated salt stress, but also stimulated Arabidopsis development in an extreme salinity environment [183].

The control of the HKT1/K^+ transporter, which prevents Na^+ inflow under salt stress, has been demonstrated to be related to the synthesis of VOCs [23], with VOC-generating *Bacillus subtilis* increasing the salt-resistance of Arabidopsis by suppressing the *HKT1* gene expression. *Alcaligenes faecalis* JBCS1294 produces a combination of three bacterial VOCs (propionic acid, benzoic acid, and butyric acid) [184], which in Arabidopsis stimulated plant development and promoted salt-resistance by regulating ionic transporters and hormonal pathways. Systematic investigation of microbial VOCs suggests that these substances could have previously unknown biological activities and ecological implications [174]. Though VOCs have significant contributions to plant stress tolerance pathways, including ion acquisition and controlling growth hormones, there is still much to learn about these metabolites, their direct functions, and their ability to help plants under stress. More research on microbial VOCs that help crops manage adverse environmental effects could lead to the creation of new agricultural bioinoculants.

5. Future Prospects

Increasing soil salinity significantly impacts agricultural productivity and presents a risk to food security. The use of HT-PGPR has shown preliminary effectiveness in increasing the salinity tolerance of crops through a range of mechanisms (Figure 4). Further studies are needed to understand how different HT-PGPR interact with plants, both in physiologically stressful and unstressed settings [185]. An emerging mapping approach known as “interactomics” is using bioinformatics tools to examine the interactions between biomolecules, including enzymes and proteins from rhizobacteria, and plant cells, to identify the communication channels between both partners under saline conditions [186]. As demonstrated in this review, it is possible to alter the phytomicrobiome surrounding plants via the decoding of feedback signals and interactions between microbes and plants. The in-depth study of the relationships between plant stress responses, microbiome assemblages, and signalling molecules is crucial for the future development of salt stress “smart agriculture” [187]. It will also be necessary to overcome the disadvantages of bioformulations, such as their short shelf life and inability to function in an abiotic stress environment. To enhance the quality of bioformulations for stressed agroecosystems, it may be possible to provide elements that reduce stress by using additives or metabolites to draw in microbes. In new formulations, HT-PGPR may be combined with osmoprotectants or cell-protectants to assist the microbes to progress beyond the initial stress and adapt to the environment. Fluorescent pseudomonads were more tolerant of salt after the exogenous addition of proline and glycine betaine to the growth media [188]. As a result, this may also be used to produce bioinoculants for saline soils. Therefore, by employing various HT-PGPR or their metabolites, novel bioformulations may be created to enhance crop production and increase the quality of saline soils (Figures 4 and 5). In addition to helping prepare microbes and plants against stress such as salinity, altering gene elicitors that induce salt-stress responses and promote the creation of biofilms may also serve to save the newly added bacterium from the initial shock, as HT-PGPR that develop biofilms can protect plants and stimulate their development in salinity conditions [189]. Utilising HT-PGPR to increase saline soil productivity and quality may also have a significant impact on microbial diversity, nutrient availability, water activity, soil organic matter, pH, and EC. These cutting-edge formulas have the potential to not only protect and boost crop yields, but also help restore stressed and damaged agroecosystems.

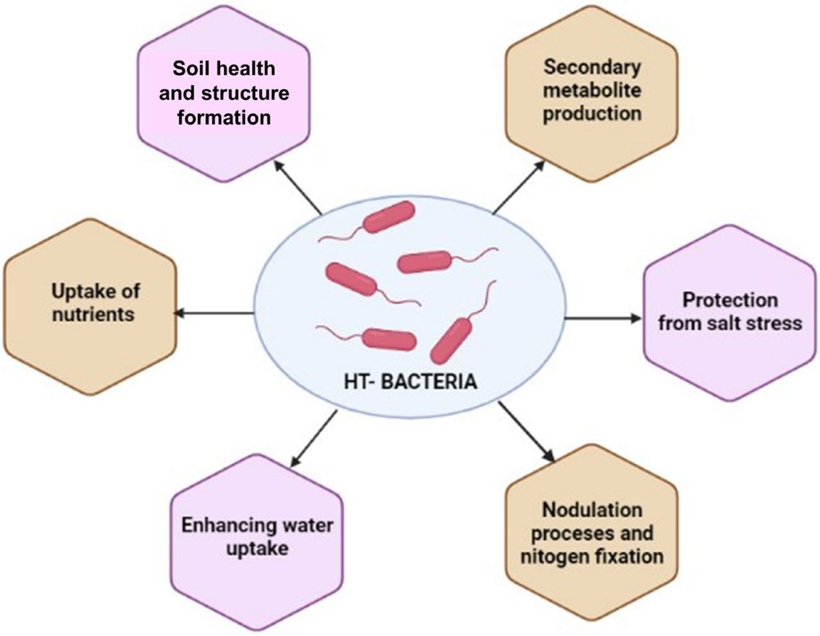

Figure 4. Advantages of biofilm production by HT-PGPR in making saline soil suitable for crop production.

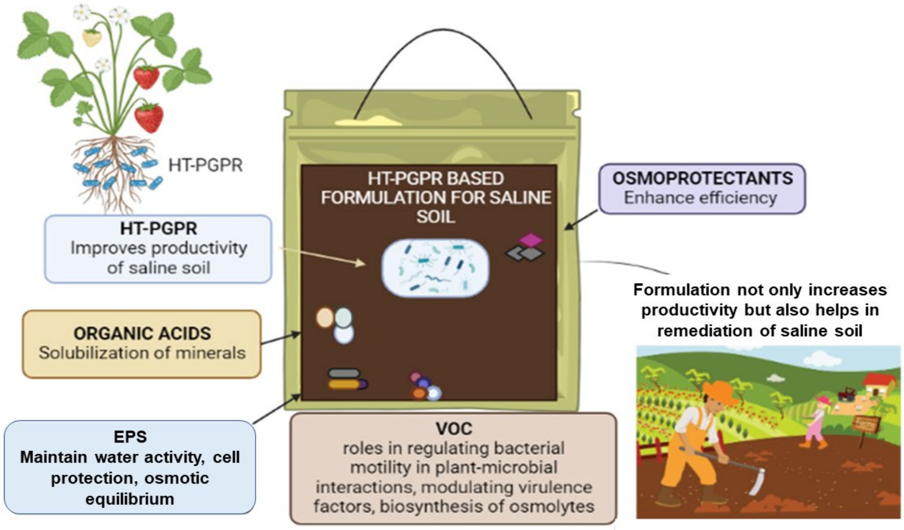

Figure 5. Benefits of HT-PGPR to alleviate salinity stress. The HT-PGPR improve crop productivity by improving organic acids; producing osmoprotectants, exopolysaccharides (EPS), and volatile organic compounds (VOCs); and remediating saline soils.

6. Conclusions

In addition to acting as a potential probiotic for plants impacted by salt, HT-PGPR can also help saline soils regain their natural balance. These bacteria are a useful tool for achieving the goals of sustainable farming due to their capacity to grow and encourage symbiotic plant growth in challenging environments. The beneficial effects on improving crop productivity from HT-PGPR includes the production of organic acids, osmoprotectants, EPS and VOCs, and balancing ion homeostasis, as illustrated in Figure 5. There is still much research to be conducted on halotolerant microbiota composition, structure, and metabolites. Nevertheless, as described in this review, HT-PGPR offer a new and exciting avenue in sustainable agriculture and food security. Further research will yield additional insights for developing future bioformulations that will contribute to the remediation of challenging growing environments.

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