Halotolerant Plant Growth-Promoting Rhizobacteria in Mitigating Salinity Stress

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Contributor: Vikash Kumar , Nikhil Raghuvanshi , Abhay K. Pandey , Abhishek Kumar , Emily Thoday-Kennedy , Surya Kant

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. 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 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.

exopolysaccharides osmoprotectants growth hormones soil microbes volatile organic compounds

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].

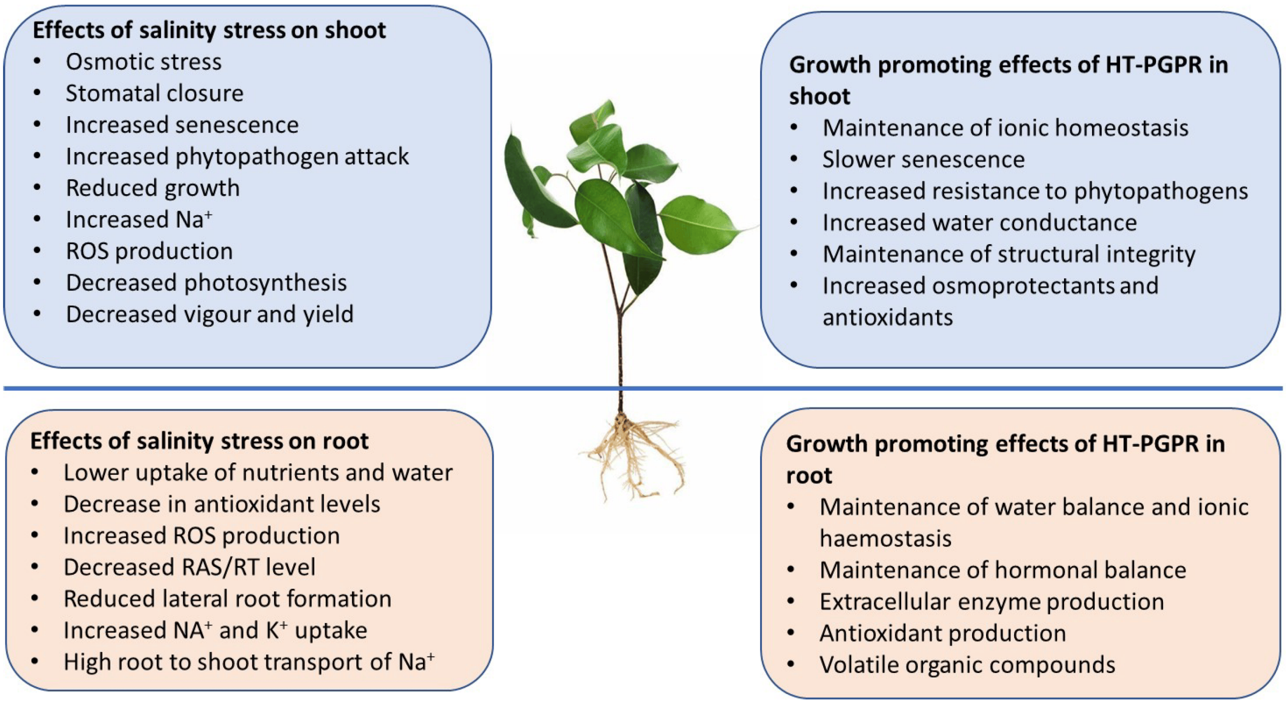

Figure 1. Effects of salinity stress and associated tolerance mechanisms induced by halotolerant plant growth-promoting rhizobacteria (HT-PGPR) in both plant roots and shoots.

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.

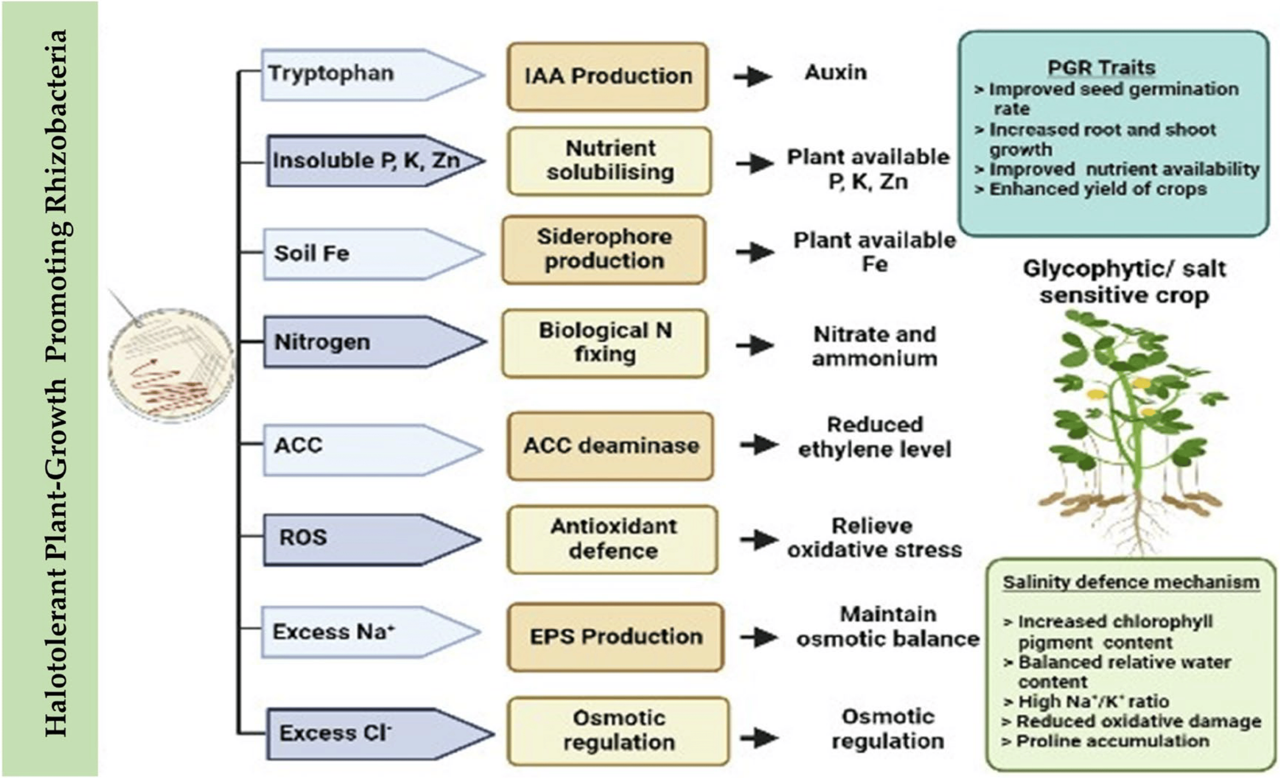

Figure 2. Effect of HT-PGPR on plant growth and salinity tolerance in glycophytic plants. The plate shown includes potential HT-PGPR isolated from native halophytes and consists of rhizobacteria and endophytes. Beneficial effects are shown in blue boxes, the underlying processes in orange boxes, and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

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	[37]

Plant Species	HT-PGPR Species	Gene/s Involved	Mechanism to Mitigate Stress	Effect Observed	References
				membrane stability	
	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]
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]

Plant Species	HT-PGPR Species	Gene/s Involved	Mechanism to Mitigate Stress	Effect Observed	References
Cicer arietinum L.	*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]
	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]

Plant Species	HT-PGPR Species	Gene/s Involved	Mechanism to Mitigate Stress	Effect Observed	References
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]
	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]
Hordeum vulgare L.	*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	Na homeostasis modulation,	[55]

Plant Species	HT-PGPR Species	Gene/s Involved	Mechanism to Mitigate Stress	Effect Observed	References
			PtSOS1 genes, downregulated *PtHKT2;1*	exclusive K+ absorption	
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]
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	[62]

Plant Species	HT-PGPR Species	Gene/s Involved	Mechanism to Mitigate Stress	Effect Observed	References
				detoxification, Na$^+$ homeostasis, abiotic stress	
	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]

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Related Techniques; Zaman, M., Shahid, S.A., Heng, L., Eds.; Springer International Publishing: Cham, Switzerland, 2018; pp. 43–53. ISBN 978-3-319-96190-3.

Plant Species	HT-PGPR Species	Gene/s Involved	Mechanism to Mitigate Stress	Effect Observed	References
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]

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8. Orhan, F. Alleviation of Salt Stress by Halotolerant and Halophilic Plant Growth-Promoting Bacteria in Wheat (Triticum aestivum). Braz. J. Microbiol. 2016, 47, 621.
9. Al-Yassin, A. Adverse Effects of Salinity on Citrus. A review paper. J. Cent Eur. Agric. 2004, 4, 263–272.
10. Egamberdieva, D.; Wirth, S.; Bellingrath-Kimura, S.D.; Mishra, J.; Arora, N.K. Salt-Tolerant Plant Growth Promoting Rhizobacteria for Enhancing Crop Productivity of Saline Soils. Front. Microbiol. 2019, 10, 2791.
11. Mishra, A.; Tanna, B. Halophytes: Potential Resources for Salt Stress Tolerance Genes and Promoters. Front. Plant Sci. 2017, 8, 829.
12. Rahman, M.M.; Mostofa, M.G.; Keya, S.S.; Siddiqui, M.N.; Ansary, M.M.U.; Das, A.K.; Rahman, M.A.; Tran, L.S.-P. Adaptive Mechanisms of Halophytes and Their Potential in Improving Salinity Tolerance in Plants. Int. J. Mol. Sci. 2021, 22, 10733.
13. Nguyen, H.M.; Sako, K.; Matsui, A.; Suzuki, Y.; Mostofa, M.G.; Ha, C.V.; Tanaka, M.; Tran, L.-S.P.; Habu, Y.; Seki, M. Ethanol Enhances High-Salinity Stress Tolerance by Detoxifying Reactive Oxygen Species in Arabidopsis thaliana and Rice. Front. Plant Sci. 2017, 8, 1001.
14. Dong, O.X.; Ronald, P.C. Genetic Engineering for Disease Resistance in Plants: Recent Progress and Future Perspectives. Plant Physiol. 2019, 180, 26–38.
15. Singh, R.; Singh, P.; Sharma, R. Microorganism as a Tool of Bioremediation Technology for Cleaning Environment: A Review. Proc. Int. Acad. Ecol. Environ. Sci. 2014, 4, 1–6.
16. Gopalakrishnan, S.; Sathya, A.; Vijayabharathi, R.; Varshney, R.K.; Gowda, C.L.L.; Krishnamurthy, L. Plant Growth Promoting Rhizobia: Challenges and Opportunities. 3 Biotech 2015, 5, 355–377.
17. Abbas, R.; Rasul, S.; Aslam, K.; Baber, M.; Shahid, M.; Mubeen, F.; Naqqash, T. Halotolerant PGPR: A Hope for Cultivation of Saline Soils. J. King Saud Univ. Sci. 2019, 31, 1195–1201.
18. Sharma, K.; Sharma, S.; Vaishnav, A.; Jain, R.; Singh, D.; Singh, H.B.; Goel, A.; Singh, S. Salt-Tolerant PGPR Strain Priestia Endophytica SK1 Promotes Fenugreek Growth under Salt Stress by Inducing Nitrogen Assimilation and Secondary Metabolites. J. Appl. Microbiol. 2022, 133, 2802–2813.

19. Egamberdieva, D.; Wirth, S.J.; Alqarawi, A.A.; Abd_Allah, E.F.; Hashem, A. Phytohormones and Beneficial Microbes: Essential Components for Plants to Balance Stress and Fitness. Front. Microbiol. 2017, 8, 2104.
20. Sunita, K.; Mishra, I.; Mishra, J.; Prakash, J.; Arora, N.K. Secondary Metabolites From Halotolerant Plant Growth Promoting Rhizobacteria for Ameliorating Salinity Stress in Plants. Front. Microbiol. 2020, 11, 567768.
21. Hernández-Canseco, J.; Bautista-Cruz, A.; Sánchez-Mendoza, S.; Aquino-Bolaños, T.; Sánchez-Medina, P.S. Plant Growth-Promoting Halobacteria and Their Ability to Protect Crops from Abiotic Stress: An Eco-Friendly Alternative for Saline Soils. Agronomy 2022, 12, 804.
22. Ruginescu, R.; Gomoiu, I.; Popescu, O.; Cojoc, R.; Neagu, S.; Lucaci, I.; Batrinescu-Moteau, C.; Enache, M. Bioprospecting for Novel Halophilic and Halotolerant Sources of Hydrolytic Enzymes in Brackish, Saline and Hypersaline Lakes of Romania. Microorganisms 2020, 8, 1903.
23. Zhang, H.; Kim, M.-S.; Sun, Y.; Dowd, S.E.; Shi, H.; Paré, P.W. Soil Bacteria Confer Plant Salt Tolerance by Tissue-Specific Regulation of the Sodium Transporter HKT1. Mol. Plant Microbe Interact. 2008, 21, 737–744.
24. Assaha, D.V.M.; Ueda, A.; Saneoka, H.; Al-Yahyai, R.; Yaish, M.W. The Role of Na+ and K+ Transporters in Salt Stress Adaptation in Glycophytes. Front. Physiol. 2017, 8, 509.
25. Pan, J.; Peng, F.; Xue, X.; You, Q.; Zhang, W.; Wang, T.; Huang, C. The Growth Promotion of Two Salt-Tolerant Plant Groups with PGPR Inoculation: A Meta-Analysis. Sustainability 2019, 11, 378.
26. Huang, X.-F.; Chaparro, J.M.; Reardon, K.F.; Zhang, R.; Shen, Q.; Vivanco, J.M. Rhizosphere Interactions: Root Exudates, Microbes, and Microbial Communities. Botany 2014, 92, 267–275.
27. Nadeem, S.M.; Zahir, Z.A.; Naveed, M.; Nawaz, S. Mitigation of Salinity-Induced Negative Impact on the Growth and Yield of Wheat by Plant Growth-Promoting Rhizobacteria in Naturally Saline Conditions. Ann. Microbiol. 2013, 63, 225–232.
28. Phour, M.; Sindhu, S.S. Amelioration of Salinity Stress and Growth Stimulation of Mustard (Brassica juncea L.) by Salt-Tolerant Pseudomonas Species. Appl. Soil Ecol. 2020, 149, 103518.
29. Aslam, F.; Ali, B. Halotolerant Bacterial Diversity Associated with Suaeda fruticosa (L.) Forssk. Improved Growth of Maize under Salinity Stress. Agronomy 2018, 8, 131.
30. Zahir, Z.A.; Ghani, U.; Naveed, M.; Nadeem, S.M.; Asghar, H.N. Comparative Effectiveness of Pseudomonas and Serratia Sp. Containing ACC-Deaminase for Improving Growth and Yield of Wheat (Triticum aestivum L.) under Salt-Stressed Conditions. Arch. Microbiol. 2009, 191, 415–424.
31. Kasotia, A.; Varma, A.; Tuteja, N.; Choudhary, D.K. Amelioration of Soybean Plant from Saline-Induced Condition by Exopolysaccharide Producing Pseudomonas-Mediated Expression of High

Affinity K + -Transporter (HKT1) Gene. Curr. Sci. 2016, 111, 1961–1967.

32. Kwon, S.-W.; Park, J.-Y.; Kim, J.-S.; Kang, J.-W.; Cho, Y.-H.; Lim, C.-K.; Parker, M.A.; Lee, G.-B. Phylogenetic Analysis of the Genera Bradyrhizobium, Mesorhizobium, Rhizobium and Sinorhizobium on the Basis of 16S RRNA Gene and Internally Transcribed Spacer Region Sequences. Int. J. Syst. Evol. Microbiol. 2005, 55, 263–270.
33. Kwon, Y.S.; Ryu, C.-M.; Lee, S.; Park, H.B.; Han, K.S.; Lee, J.H.; Lee, K.; Chung, W.S.; Jeong, M.-J.; Kim, H.K.; et al. Proteome Analysis of Arabidopsis Seedlings Exposed to Bacterial Volatiles. Planta 2010, 232, 1355–1370.
34. Baek, D.; Rokibuzzaman, M.; Khan, A.; Kim, M.C.; Park, H.J.; Yun, D.; Chung, Y.R. Plant-Growth Promoting Bacillus Oryzicola YC7007 Modulates Stress-Response Gene Expression and Provides Protection From Salt Stress. Front. Plant Sci. 2020, 10, 1646.
35. Chu, T.N.; Tran, B.T.H.; Van Bui, L.; Hoang, M.T.T. Plant Growth-Promoting Rhizobacterium Pseudomonas PS01 Induces Salt Tolerance in Arabidopsis thaliana. BMC Res. Notes 2019, 12, 11.
36. Rabhi, N.E.H.; Silini, A.; Cherif-Silini, H.; Yahiaoui, B.; Lekired, A.; Robineau, M.; Esmaeel, Q.; Jacquard, C.; Vaillant-Gaveau, N.; Clément, C.; et al. Pseudomonas Knackmussii MLR6, a Rhizospheric Strain Isolated from Halophyte, Enhances Salt Tolerance in Arabidopsis thaliana. J. Appl. Microbiol. 2018, 125, 1836–1851.
37. Chen, L.; Liu, Y.; Wu, G.; Veronican Njeri, K.; Shen, Q.; Zhang, N.; Zhang, R. Induced Maize Salt Tolerance by Rhizosphere Inoculation of Bacillus Amyloliquefaciens SQR9. Physiol. Plant 2016, 158, 34–44.
38. Pinedo, I.; Ledger, T.; Greve, M.; Poupin, M.J. Burkholderia Phytofirmans PsJN Induces Long-Term Metabolic and Transcriptional Changes Involved in Arabidopsis thaliana Salt Tolerance. Front. Plant Sci. 2015, 6, 466.
39. Sukweenadhi, J.; Kim, Y.-J.; Choi, E.-S.; Koh, S.-C.; Lee, S.-W.; Kim, Y.-J.; Yang, D.C. Paenibacillus Yonginensis DCY84T Induces Changes in Arabidopsis thaliana Gene Expression against Aluminum, Drought, and Salt Stress. Microbiol. Res. 2015, 172, 7–15.
40. Kim, Y.-J.; Sukweenadhi, J.; Seok, J.W.; Kang, C.H.; Choi, E.-S.; Subramaniyam, S.; Yang, D.C. Complete Genome Sequence of Paenibacillus Yonginensis DCY84T, a Novel Plant Symbiont That Promotes Growth via Induced Systemic Resistance. Stand. Genom. Sci. 2017, 12, 63.
41. Kim, K.; Jang, Y.-J.; Lee, S.-M.; Oh, B.-T.; Chae, J.-C.; Lee, K.-J. Alleviation of Salt Stress by Enterobacter Sp. EJ01 in Tomato and Arabidopsis Is Accompanied by Up-Regulation of Conserved Salinity Responsive Factors in Plants. Mol. Cells 2014, 37, 109–117.
42. Qurashi, A.W.; Sabri, A.N. Bacterial Exopolysaccharide and Biofilm Formation Stimulate Chickpea Growth and Soil Aggregation under Salt Stress. Braz. J. Microbiol. 2012, 43, 1183–1191.

43. Khan, M.A.; Asaf, S.; Khan, A.L.; Jan, R.; Kang, S.-M.; Kim, K.-M.; Lee, I.-J. Rhizobacteria AK1 Remediates the Toxic Effects of Salinity Stress via Regulation of Endogenous Phytohormones and Gene Expression in Soybean. Biochem. J. 2019, 476, 2393–2409.
44. Khan, M.A.; Asaf, S.; Khan, A.L.; Adhikari, A.; Jan, R.; Ali, S.; Imran, M.; Kim, K.-M.; Lee, I.-J. Halotolerant Rhizobacterial Strains Mitigate the Adverse Effects of NaCl Stress in Soybean Seedlings. Biomed. Res. Int. 2019, 2019, 9530963.
45. Vaishnav, A.; Kumari, S.; Jain, S.; Varma, A.; Tuteja, N.; Choudhary, D.K. PGPR-Mediated Expression of Salt Tolerance Gene in Soybean through Volatiles under Sodium Nitroprusside: PGPR-Mediated Amelioration of Soybean under Salt Stress. J. Basic Microbiol. 2016, 56, 1274–1288.
46. Vaishnav, A.; Kumari, S.; Jain, S.; Varma, A.; Choudhary, D.K. Putative Bacterial Volatile-Mediated Growth in Soybean (Glycine max L. Merrill) and Expression of Induced Proteins under Salt Stress. J. Appl. Microbiol. 2015, 119, 539–551.
47. Ma, Y.; Rajkumar, M.; Oliveira, R.S.; Zhang, C.; Freitas, H. Potential of Plant Beneficial Bacteria and Arbuscular Mycorrhizal Fungi in Phytoremediation of Metal-Contaminated Saline Soils. J. Hazard. Mater. 2019, 379, 120813.
48. Kiani, M.Z.; Ali, A.; Sultan, T.; Ahmad, R.; Hydar, S.I. Plant Growth Promoting Rhizobacteria Having 1-Aminocyclopropane-1-Carboxylic Acid Deaminase to Induce Salt Tolerance in Sunflower (Helianthus annus L.). Nat. Resour. 2015, 6, 391–397.
49. Mahmoud, M.B.; Hidri, R.; Talbi-Zribi, O.; Taamalli, W.; Abdelly, C.; Djébali, N. Auxin and Proline Producing Rhizobacteria Mitigate Salt-Induced Growth Inhibition of Barley Plants by Enhancing Water and Nutrient Status. S. Afr. J. Bot. 2020, 128, 209–217.
50. Sultana, S.; Paul, S.C.; Parveen, S.; Alam, S.; Rahman, N.; Jannat, B.; Hoque, S.; Rahman, M.T.; Karim, M.M. Isolation and Identification of Salt-Tolerant Plant-Growth-Promoting Rhizobacteria and Their Application for Rice Cultivation under Salt Stress. Can. J. Microbiol. 2020, 66, 144–160.
51. Chauhan, P.S.; Lata, C.; Tiwari, S.; Chauhan, A.S.; Mishra, S.K.; Agrawal, L.; Chakrabarty, D.; Nautiyal, C.S. Transcriptional Alterations Reveal Bacillus Amyloliquefaciens-Rice Cooperation under Salt Stress. Sci. Rep. 2019, 9, 11912.
52. Nghia, N.K.; Tien, T.T.M.; Oanh, N.T.K.; Nuong, N.H.K. Isolation and Characterization of Indole Acetic Acid Producing Halophilic Bacteria from Salt Affected Soil of Rice–Shrimp Farming System in the Mekong Delta, Vietnam. Agric. For. Fish. 2017, 6, 69.
53. Jha, Y.; Subramanian, R.B.; Patel, S. Combination of Endophytic and Rhizospheric Plant Growth Promoting Rhizobacteria in Oryza Sativa Shows Higher Accumulation of Osmoprotectant against Saline Stress. Acta Physiol. Plant 2011, 33, 797–802.

54. Niu, S.-Q.; Li, H.-R.; Paré, P.W.; Aziz, M.; Wang, S.-M.; Shi, H.; Li, J.; Han, Q.-Q.; Guo, S.-Q.; Li, J.; et al. Induced Growth Promotion and Higher Salt Tolerance in the Halophyte Grass Puccinellia Tenuiflora by Beneficial Rhizobacteria. Plant Soil 2016, 407, 217–230.
55. Kang, S.-M.; Shahzad, R.; Bilal, S.; Khan, A.L.; Park, Y.-G.; Lee, K.-E.; Asaf, S.; Khan, M.A.; Lee, I.-J. Indole-3-Acetic-Acid and ACC Deaminase Producing Leclercia Adecarboxylata MO1 Improves Solanum lycopersicum L. Growth and Salinity Stress Tolerance by Endogenous Secondary Metabolites Regulation. BMC Microbiol. 2019, 19, 80.
56. Vaishnav, A.; Singh, J.; Singh, P.; Rajput, R.S.; Singh, H.B.; Sarma, B.K. Sphingobacterium Sp. BHU-AV3 Induces Salt Tolerance in Tomato by Enhancing Antioxidant Activities and Energy Metabolism. Front. Microbiol. 2020, 11, 443.
57. Yan, J.; Smith, M.D.; Glick, B.R.; Liang, Y. Effects of ACC Deaminase Containing Rhizobacteria on Plant Growth and Expression of Toc GTPases in Tomato (Solanum lycopersicum) under Salt Stress. Botany 2014, 92, 775–781.
58. Han, Q.-Q.; Lü, X.-P.; Bai, J.-P.; Qiao, Y.; Paré, P.W.; Wang, S.-M.; Zhang, J.-L.; Wu, Y.-N.; Pang, X.-P.; Xu, W.-B.; et al. Beneficial Soil Bacterium Bacillus Subtilis (GB03) Augments Salt Tolerance of White Clover. Front. Plant Sci. 2014, 5, 525.
59. Shah, D.; Khan, M.S.; Aziz, S.; Ali, H.; Pecoraro, L. Molecular and Biochemical Characterization, Antimicrobial Activity, Stress Tolerance, and Plant Growth-Promoting Effect of Endophytic Bacteria Isolated from Wheat Varieties. Microorganisms 2021, 10, 21.
60. Vaishnav, A.; Kumar, R.; Singh, H.B.; Sarma, B.K. Extending the Benefits of PGPR to Bioremediation of Nitrile Pollution in Crop Lands for Enhancing Crop Productivity. Sci. Total Environ. 2022, 826, 154170.
61. Safdarian, M.; Askari, H.; Shariati, J.V.; Nematzadeh, G. Transcriptional Responses of Wheat Roots Inoculated with Arthrobacter Nitroguajacolicus to Salt Stress. Sci. Rep. 2019, 9, 1792.
62. Singh, R.P.; Jha, P.N. The Multifarious PGPR Serratia Marcescens CDP-13 Augments Induced Systemic Resistance and Enhanced Salinity Tolerance of Wheat (Triticum aestivum L.). PLoS ONE 2016, 11, e0155026.
63. Pirhadi, M.; Enayatizamir, N.; Motamedi, H.; Sorkheh, K. Screening of Salt Tolerant Sugarcane Endophytic Bacteria with Potassium and Zinc for Their Solubilizing and Antifungal Activity. Biosci. Biotech. Res. Comm. 2016, 9, 530–538.
64. Ramadoss, D.; Lakkineni, V.K.; Bose, P.; Ali, S.; Annapurna, K. Mitigation of Salt Stress in Wheat Seedlings by Halotolerant Bacteria Isolated from Saline Habitats. Springerplus 2013, 2, 6.
65. El-Esawi, M.A.; Alaraidh, I.A.; Alsahli, A.A.; Alzahrani, S.M.; Ali, H.M.; Alayafi, A.A.; Ahmad, M. Serratia Liquefaciens KM4 Improves Salt Stress Tolerance in Maize by Regulating Redox

Potential, Ion Homeostasis, Leaf Gas Exchange and Stress-Related Gene Expression. Int. J. Mol. Sci. 2018, 19, 3310.

66. Alla, M.M.N.; Hassan, N.M. A Possible Role for C4 Photosynthetic Enzymes in Tolerance of Zea mays to NaCl. Protoplasma 2012, 249, 1109–1117.
67. Habib, S.H.; Kausar, H.; Saud, H.M. Plant Growth-Promoting Rhizobacteria Enhance Salinity Stress Tolerance in Okra through ROS-Scavenging Enzymes. Biomed. Res. Int. 2016, 2016, 6284547.
68. Etesami, H.; Beattie, G.A. Mining Halophytes for Plant Growth-Promoting Halotolerant Bacteria to Enhance the Salinity Tolerance of Non-Halophytic Crops. Front. Microbiol. 2018, 9, 148.

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