Halo-tolerant plant growth promoting rhizobacteria for improving productivity and remediation of saline soils

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GRAPHICAL ABSTRACT
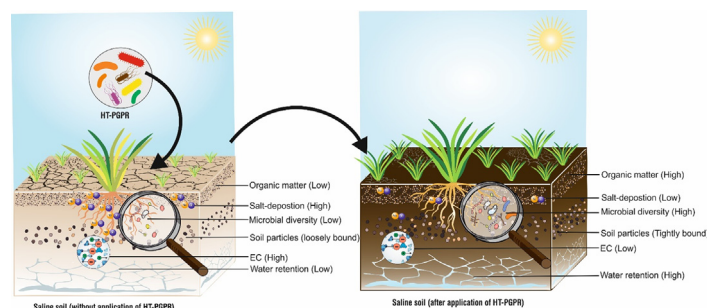
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ABSTRACT

Background: The collective impact of climate change and soil salinity is continuously increasing the degraded lands across the globe, bringing agricultural productivity and food security under stress. The high concentration of salts in saline soils impose osmotic, ionic, oxidative and water stress in plants. Biological solutions can be the most reliable and sustainable approach to ensure food security and limit the use of agro-chemicals.
Aim of Review: Halo-tolerant plant growth promoting rhizobacteria (HT-PGPR) are emerging as efficient biological tools to mitigate the toxic effects of high salt concentrations and improve the growth of plants, simultaneously remediating the degraded saline soils. The review explains the role of HT-PGPR in mitigating the salinity stress in plants through diverse mechanisms and concurrently leading to improvement of soil quality.
Key Scientific Concepts of Review: HT-PGPR are involved in alleviating the salinity stress in plants through a number of mechanisms evoking multipronged physiological, biochemical and molecular responses. These include changes in expression of defense-related proteins, exopolysaccharides synthesis, activation of antioxidant machinery, accumulation of osmolytes, maintaining the Na$^+$ kinetics and improving the levels of phytohormones and nutrient uptake in plants. The modification of signaling by HT-PGPR inoculation under stress conditions elicits induced systemic resistance in plants which further prepares them against salinity stress. The role of microbial-mechanisms in remediating the saline soil through structural and compositional improvements is also important. Development of novel bioinoculants for saline soils

based on the concepts presented in the review can be a sustainable approach in improving productivity of affected agro-ecosystems and simultaneously remediating them.

Introduction

Soil salinity has emerged as one of the biggest constraints influencing crop productivity around the globe. In the last few decades, anthropogenic activities have exacerbated the rate of soil salinization [1,2]. Saline soils are high in electrical conductivity (EC), low in water potential and excessive in amounts of ionic salts making survival of plant and other life forms difficult [3,4]. It is estimated that salinity has affected over 800 million hectares of agricultural land around the globe [5]. There are reports claiming that each year around 1–2% of fertile soils are being degraded worldwide due to salinity [6]. It has also been forecasted that in the next 35 years, about 50% of the land on earth will suffer due to various degrees of salinity [7]. Additionally, data indicates that in past few decades the annual cost of salt-induced land degradation in irrigated areas was estimated to be US$ 27.3 billion [8].

The presence of an excess amount of salt in soil shows cumulative and far- reaching effects on crops [9]. Salt stress triggers ionic imbalance in plants, causes nutrient deficiency, perturbations in carbon (C) and nitrogen (N) assimilatory pathways, lowered rate of photosynthesis, generation of reactive oxygen species (ROS), osmotic and oxidative stress, thereby retarding growth and yield of crops [10,11]. Salt stress also poses negative impacts on soil processes, pH, decomposition rate, nutrient composition, microbial biodiversity and water availability, leading to the prevalence of drought-like conditions [12,13]. According to Attia et al. [14] in several agro-ecosystems, particularly in arid and semi-arid regions, drought and salinity occur simultaneously resulting in overlapping symptoms of both the stresses in the plants. Physical methods of treatment of saline soils, that include flushing, leaching, scraping and chemical amendments e.g. addition of gypsum and lime, are not sustainable [4]. Soil flushing and scraping has achieved only a little success and has limited practical significance as the salt accumulation tends to resurface due to lowering of water table and the problem intensifies with course of time. Soil leaching although comparatively successful but requires relatively low soil moisture and low ground water level [15] making it difficult for agro-ecosystems. Another drawback of this method is that important nutrients applied to the soil may also leach out lowering their availability in the plant root zones [16]. Among chemical methods, addition of gypsum is most commonly used. However, gypsum is a non-renewable mineral and also results in low solubility or availability of nutrients such as phosphorus (P), copper (Cu), iron (Fe) and zinc (Zn) to the plants [17,18]. Apart from physical and chemical approaches, several other methods such as modification in breeding practices, shifting of crop calendars and introduction of genetically engineered salt-tolerant plant varieties have been evaluated for enhancement of crop productivity in salt-affected soils but have largely proved to be in-effective [19,20]. These methods are time-consuming, costly and above all, cause genetic erosion of indigenous species [21,22].

Application of halo-tolerant plant growth promoting rhizobacteria (HT-PGPR) has the potential of alleviating salt stress in plants through elicitation of several physiological and molecular mechanisms. This includes modification in root systems, inducing antioxidant machinery, production of exopolysaccharides (EPS) and siderophores, modulation of phytohormones, synthesis of osmolytes, uptake of minerals and control of phytopathogens [23–25]. Several species of halotolerant soil bacteria such as *Arthrobacter, Azospirillum, Alcaligenes Bacillus, Burkholderia, Enterobactor,*

Flavobacterium, Pseudomonas and *Rhizobium,* have been reported to ameliorate salt stress in crops [26,27]. Their use as bioinoculants is reported to increase soil organic matter, improve soil structure and water retention capacity. Apart from this, use of HT-PGPR in form of bioinoculants is an eco-friendly and sustainable method of improving productivity of saline agro-ecosystems [28]. In spite of overwhelming advantages the exact mechanisms of HT-PGPR in helping the plants are not precisely known. Hence it is important to find out the underlying molecular mechanisms of HT-PGPR involved in plant growth promotion. These findings can assist in ascertaining the role of HT-PGPR as efficient candidates for increasing production and remediation of saline soils.

HT-PGPR mediated salt tolerance in plants

The intrinsic metabolic and genetic properties of the HT-PGPR have a direct role in lessening the harmful effects of salt stress in plants [6]. However, intriguing interactions happening in between HT-PGPR and plants under stress conditions are still a matter of further research. Probably, mitigation of salt stress by HT-PGPR may involve a three-tier entwined action cum association i.e. survival of bacteria itself under hyperosmotic environment, induction of salt tolerance events in plants and improvisation of soil quality through various mechanisms. Fig. 1 explains the mechanisms of salt-stress mitigation in plants inoculated with HT-PGPR. In last few years, research confirmed that the presence of HT-PGPR can modulate the expression of several genes responsible for the amelioration of salinity stress in plants (Table 1). The major aspect of salt stress-tolerance in plants mediated by HT-PGPR involves the generation of responsive machinery to pool out the toxicity and establishing an osmotic equilibrium state to avoid desiccation and flaccidity in plant's cells. HT-PGPR constrict the uptake of Na^+ by changing the composition of the cell wall/ cell membrane, which increases the electrogenic Na^+/H^+ ionic-porters along with increased expression of salt overly sensitive (SOS) genes and NHX transporters in plants [29,44]. In a study it was shown that HT-PGPR *Bacillus subtilis* reduced the absorption of Na^+ by *Arabidopsis thaliana* roots through down-regulation of high-affinity K^+ transporter (HKT1) in salt-affected conditions [41]. Yasmin et al. [45] revealed that inoculation of salt-stressed soybean plants with *Pseudomonas pseudoalcaligenes* triggered synthesis of key defense enzymes that reduced the Na^+ concentration in roots and shoots simultaneously balancing the cellular condition by increasing intracellular K^+ levels. Similarly, *Pseudomonas koreensis* strain AK-1 reduced Na^+ and elevated K^+ levels in *Glycine* max L. Merrill [46]. Treatment of HT-PGPR, *Burkholderia phytofirmans* PsJN modified the expression patterns of ion-homeostasis related genes including Arabidopsis K + Transporter 1*(AKT1),* High-Affinity K + Transporter 1*(HKT1),* Sodium Hydrogen Exchanger 2 (*NHX2*), and *SOS1* in salt-sensitive *A. thaliana* plants [29]. The upregulation of *PtHKT1;5* and *PtSOS1* and downregulation of *PtHKT2;1* in *B. subtilis* GB03 inoculated plants reduced uptake of Na^+ in halophyte grass *Puccinellia tenuiflora* [37]. The use of strain GB03 in improving drought tolerance in ryegrass [47] and salt tolerance in wheat [48], white clove [49] and *Codonopsis pilosula* [50] elucidates the involvement of some common genes and traits in mitigating both the intermingled abiotic stresses. Volatile organic compounds (VOCs) produced by HT-PGPR can trigger induction of HKT1 in shoots and reduction of HKT1 in roots, hence limiting Na + entry
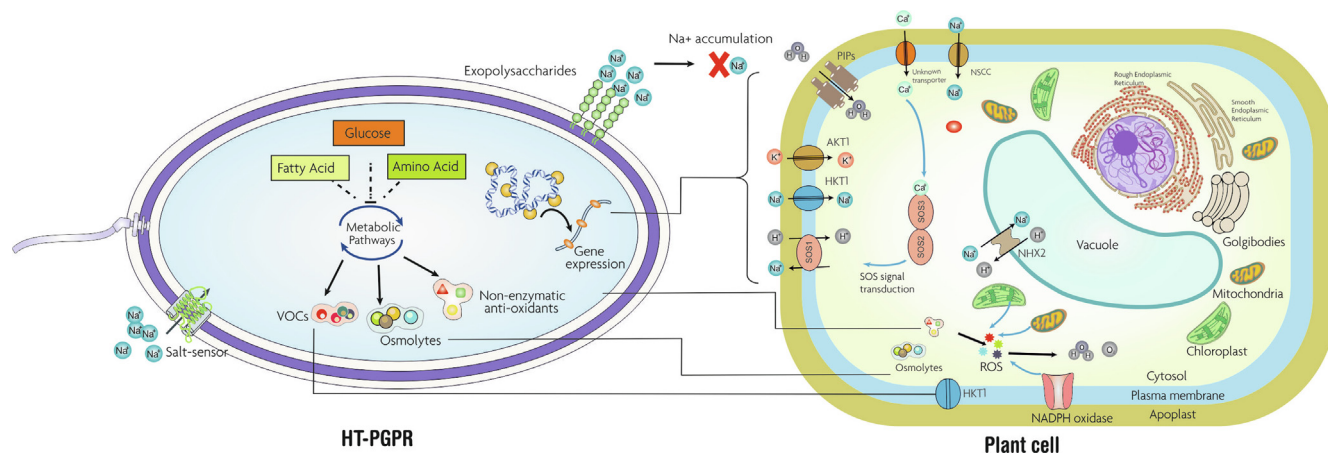
Fig. 1. Metabolic and genetic properties of HT-PGPR involved in salt tolerance in plants. Metabolic and genetic properties of the HT-PGPR have a direct role in the amelioration of salt-stress in plants. They can regulate the expression of ion transporters/channels such as high-affinity K+ transporter (HKT1), Arabidopsis K+ Transporter 1 (AKT1), Sodium Hydrogen Exchanger 2 (NHX2), weakly voltage-dependent nonselective cation channel (NSCC), and plasma membrane intrinsic proteins (PIPs) that collectively take part in ion homeostasis and osmatic balance in plants. All of these channels/transporters can mediate Na^+ and K^+ influx into plant cells and help a suitable K+: Na+ ratio in the cytoplasm which prevents cellular damage and nutrient deficiency. The presence of HT-PGPR can also modulate the Salt Overly Sensitive (SOS1) pathways. Compatible osmolytes produced by HT-PGPR can be uptaken by plant cells to reduce the osmotic potential and stabilize proteins and cellular structures from salt stress. Volatile organic compounds (VOCs) produced by HT-PGPR can also trigger the induction of HKT1 in shoots and reduction of HKT1 in roots that limit Na^+ entry into roots and facilitating shoot-to-root Na+ recirculation. Apart from these, non-enzymatic anti-oxidants produced by HT-PGPR can control the formation of ROS in plant cells. Excretion of exopolysaccharides (EPS) facilitate binding of Na+ in roots cells and prevents their translocation to leaves thus acting as a physical barrier around the roots.

into roots and facilitating shoot-to-root Na + recirculation [51] Inoculation with HT-PGPR *Dietzia natronolimnaea* up-regulated HKT antiporters in salt-stressed wheat plants [33]. Similarly, upregulation of HKT family antiporters has also been reported in wheat inoculated with *Serratia* sp. Sl-12 [52], *Arthrobacter nitroguajacolicus* [39] and maize plants treated with *Bacillus amyloliquefaciens* SQR9 [36] under salinity stress. Detailing the response to salinity stress in wheat by the inoculation of *Enterobacter cloacae* - SBP-8, Singh et al. [53] reported upregulation of defense related proteins by 2065%, photosynthesis related proteins by 792% and ion transport associated proteins by 765%. The upregulated ion-transporter proteins included malate transporter, and ROS-responsive calcium channel proteins to cope up the toxic ion influx and maintain ion homeostasis. The study also showed that bacterial inoculation upregulated expression of proteins involved in strengthening of cell wall and membrane integrity to prevent cellular damage and lateral diffusion of molecules in the endodermis. Similar mechanism of tolerance has also been reported in durum wheat when inoculated with HT-PGPR under drought and heat stress resulting in better adaption by the plants [54,55]. This again suggests the correlation in between salinity and drought stresses along with common mechanisms at molecular level to combat them by the help of HT-PGPR.

Apart from the direct exclusion of the salts from cells/roots/shoots, HT-PGPR also help the plant in accumulating low molecular weight osmolytes (soluble sugars, amino acids, quaternary amines, polyols and tetrahydropyrimidines) for maintaining ionic equilibrium in the cytoplasm under salinity stress [56]. It has been found that instead of synthesizing *de novo*, plants prefer uptake of osmolytes liberated by HT-PGPR when exposed to high salt conditions [57,28]. Osmotic accumulation is found to be negatively correlated with cellular osmotic potential. Due to increased concentration of osmolytes in cells under osmotic and water stresses the osmotic potential becomes negative and causes endosmosis of water which thereby maintains the turgor pressure and integrity of cells [58]. After the stress is over, osmolytes help in repairing the endodermis and cortical cell layers of plants and act as source of nitrogen and energy [59,60]. *Bacillus fortis* SSB21 was reported to increase biosynthesis of proline and upregulation of stress- related genes *CAPIP2, CaKR1, CaOSM1,* and *CAChi2* in capsicum under saline conditions [5]. Inoculation of HT-PGPR strains, *Acinetobacter* sp. (Br3),

Pseudomonas putida (Br18) and *Curtobacterium* sp. (Br20) in *Sulla carnosa*, enhanced chlorophyll content, photosynthetic activity, total soluble sugars and antioxidant activities under saline stress [61]. With varying salt concentrations, transcription of genes responsible for osmoprotectants synthesis may express differentially in some HT-PGPR. For example, in *B. amyloliquefaciens* FZB42 trehalose and proline synthesis were found to be differentially expressed at 0 mM and 100 mM NaCl concentrations facilitating stress adaption in *A. thaliana* [62]. Among the class of transcription factors (TFs), WRKY induces several adaption responses in plants against abiotic stresses [63,64]. Safdarian et al. [39] reported the role of WRKY TFs in mitigating salinity and drought stress through modulation of osmotic balance, scavenging of ROS and triggering of stress related genes. The study also proved that inoculation of wheat with *A. nitroguajacolicus* had higher WRKY28 gene expression and promoted growth of the plants under salinity stress.

Along with ionic imbalance, long term exposure of salinity generates water deficit conditions which affect plant growth. The growth of plants is majorly affected in the osmotic phase due to decrease in the soil water potential and the mitigation requires changes at molecular, cellular and physiological levels. HT-PGPR are reported to increase the expression of genes for aquaporins (AQPs) thereby, channeling the uptake of water by plants in saline and associated drought stress [65]. HT-PGPR such as *Azospirillum brasilense, Pantoea agglomerans*, and *Bacillus megaterium* were found to induce the expression of *PIP2, ZmPIP1-1*, and *HvPIP2-1* genes involved in AQPs synthesis. The up-regulation of these genes stimulates water uptake and maintains desired water potential [66,67]. Uptake of water by *Chenopodium quinoa* was improved when inoculated with HT-PGPR *Enterobacter sp*. MN17 and *Bacillus sp*. MN54 [68]. An increase in water availability was reported in mung bean when inoculated with *Bacillus drentensis P16* and *E. cloacae* P6 under saline conditions [69]. Apart from channeling the uptake of water, PIP1 subgroup of aquaporin TaAQP8 has been reported to confer salinity mitigation in transgenic tobacco through K^+/Na^+ ion homeostasis, retaining calcium content, reducing H_2O_2 accumulation, membrane damage and stimulation of antioxidant systems [70].
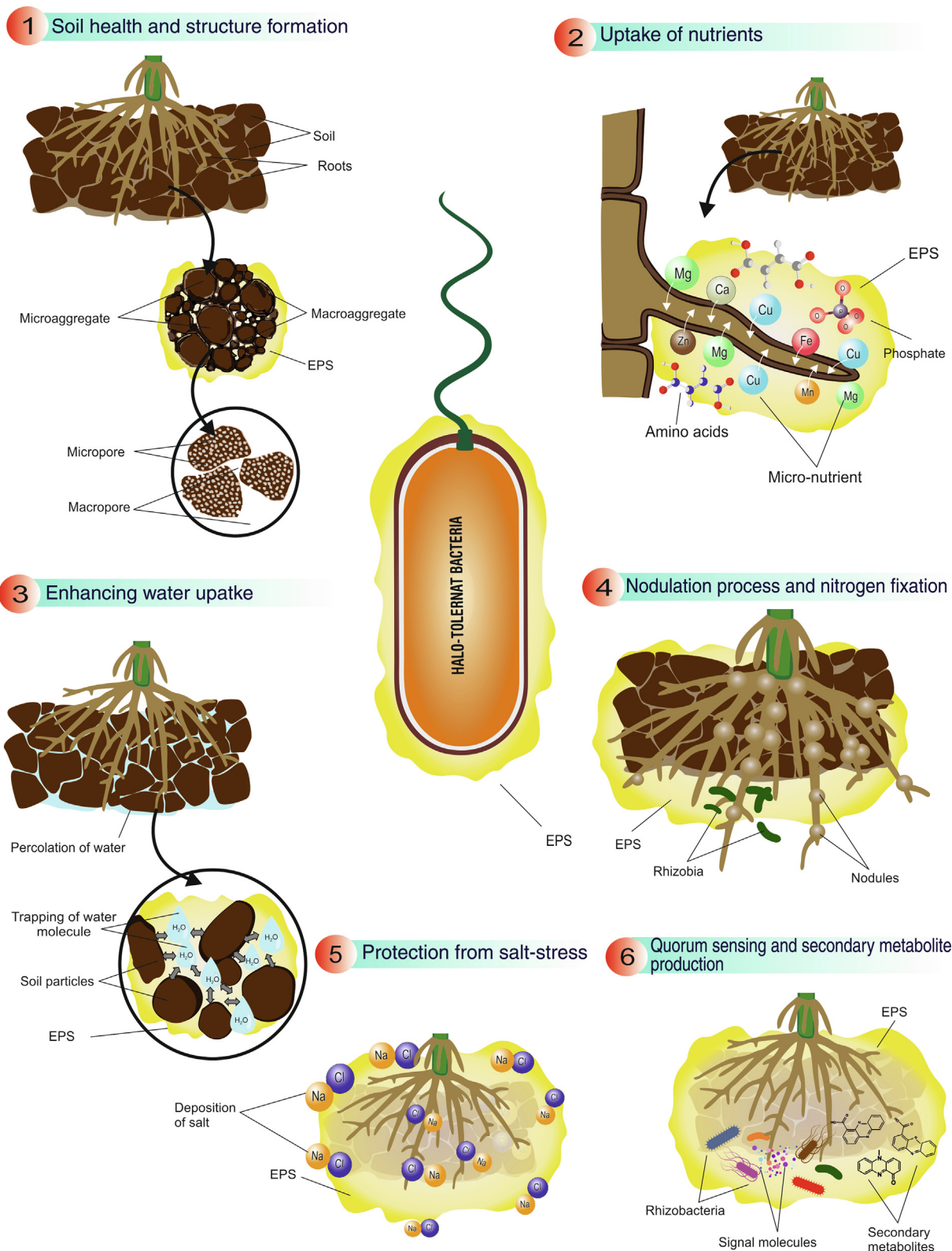
Production of natural polysaccharides or EPS during unfavorable conditions is a well-known characteristic of HT-PGPR. EPS produced by HT-PGPR help in the formation of a watery-nutrient

Table 1
PGPR mediated expression of genes detected in plants responsible for amelioration of salinity stress.

S. No	Plant species	Involved PGPR	Stress responsive gene	Function	Reference
1.	*Arabidopsis thaliana*	*Burkholderia phytofirmans* PsJN	Transcription of *RD29A, RD29B, APX2* and *GLYI7* Downregulation of *LOX2* Expression pattern of *AKT1, NHX2, SOS1* and *HKT1*	Proline accumulation, abscisic acid signaling, ROS scavenging, detoxification, jasmonic acid biosynthesis pathway, ion homeostasis	[29]
2.	*Glycine* max	*Pseudomonas simiae* strain AU	Upregulation of *POX, CAT, VSP* and *NR* Downregulation of *HKTI, LOX, PPO* and *P5CS*	Production of antioxidant enzymes such as peroxidase, catalase and also vegetative storage protein, nitrite reductase	[30]
3.	*Abelmoschus esculentus*	*Enterobacter* sp. UPMR18	Upregulation of *CAT, APX, GR* and *DHAR*	Reactive oxygen species (ROS) pathway, production of antioxidant enzymes such as peroxidase, catalase	[31]
4.	*A. thaliana*	*Pseudomonas putida* PS01	Upregulation of *LOX2* Downregulation of *APX2* and *GLY17* No changes in expression of *RD29A* and *RD29B*	Jasmonic acid synthesis pathway, ROS scavenging activity, detoxification, abscisic acid (ABA) signaling	[32]
5.	Wheat	*Bacillus safensis* W10	Upregulation of expansins, endotransglucosylase/hydrolase, sulphur rich thionin, S adenosylmethinoine secarboxylase precursor and metallothionines Downregulation of Flavonone hydroxylase, oxalate oxidase, protein phosphatase	Alleviation of salt stress	[21]
6.	Wheat	*Dietzia natronolimnaea* STR1	Upregulation of *TaABARE* and *TaOPR1* Enhanced expression of *TaST, APX, MnSOD, CAT, POD, GPX, GR* Tissue-specific responses of *TaNHX1, TaHAK, TaHKT1, ABARE* and *TaOPR1*	Abscisic acid signaling, reactive oxygen species scavenging, antioxidant enzyme activity, increased expression of ion transporters, maintenance of high K+/Na + ratio	[33]
7.	*A. thaliana*	*Enterobacter* spp. EJ01	Increased expression of DREB2b, RD29A, RD29B and RAB18 Expression of *P5CS1, P5CS2, MPK3* and *MPK6*	Proline biosynthesis, regulation of defense pathways and salt responses	[34]
8.	*Solanum lycopersicum*	*Bacillus megaterium*	Expression of *MT2* and *GR1*	Metallothionein Glutathione reductase enzyme synthesis	[35]
9..	*G.* max	*Bacillus firmus* SW5	Upregulation of *GmVSP, GmPHD2, GmbZIP62, GmWRKY54, GmOLPb* and *CHS* Expression of *APX, CAT, Fe-SOD* and *POD*	Antioxidant enzyme production, tolerance to salinity, flavonoid biosynthetic pathway	[24]
10.	*Zea mays* L.	*Bacillus amyloliquefaciens* SQR9	Upregulation of RBCS, RBCL, H+-PPase, HKT1, NHX1, NHX2 and NHX3 Downregulation of NCED	Photosynthesis, Na + export and sequestration	[36]
11.	*Puccinellia tenuiflora*	*Bacillus subtilis* (GB03)	Upregulation of *PtHKT1;5* and *PtSOS1* Downregulation of *PtHKT2;1*	Modulation of Na + homeostasis	[37]
12.	*S. lycopersicum*	*P. putida* UW4	Expression of Toc GTPase	Regulation of chloroplast import apparatus components	[38]
13.	Wheat	*Arthrobacter nitroguajacolicus*	Upregulation of *AA0618700, AA0359620, APX, GPX* Expression of *AA0410390, AA1982260, AA0412840* and *AA1872340*	Plant cell wall biosynthesis, phenylpropanoid biosynthetic pathway, glutathione-ascorbate cycle, modulation of celular osmotic balance, ROS scavenging activity	[39]
14.	*Oryza sativa*	*B. amyloliquefaciens* SN13	Upregulation of *NADP-Me2, EREBP, SOSI, BADH* and *SERK1* Repression of *GIG* and *SAPK4* NADP-Me2, EREBP, SOSI, BADH and SERK1 Accumulation of *MAPK5*	Na+/H+ antiporter system, plant growth and development, abiotic stress response, oxidative decarboxylation of L-malate, Ion homeostasis	[40]
15.	*A. thaliana*	*B. subtilis* GB03	Expression of *HKT1*	Na + import in roots	[41]
16.	*A. thaliana*	*Paenibacillus yonginensis* DCY84T	Expression of *AtRSA1, AtVQ9* and *AtWRKY8*, AtERD15, AtRAB18, and AtLT178	Detoxification of reactive oxygen species, Na+ homeostasis, responses to abiotic stress	[42]
17.	*O. sativa*	Root-associated plant growth-promoting rhizobacteria (PGPR)	Expression of *RAB18*	Intracellular protein transport	[43]

rich layer around the root surface, known as rhizosheath [71]. There is evidence that rhizosheath serves as physical barrier against deposition of ionic salts and also acts as an active site of nutrient cycling, cation uptake, symbiotic association, nodulation and maintaining osmotic equilibrium in root region of plants exposed to high salt concentrations [72–74]. EPS are found to be useful in soil aggregate formation, humification, increase in water retention, quorum sensing, nodulation and establishing microbial diversity in saline soils (Fig. 2). Isfahani et al. [75] elucidated the combined action of silicon nanoparticles, bacterial EPS and bacterial inoculum on growth of *Solanum lycopersicum* L. grown under various salinity levels (0.3, 2, 4, 6, and 8 dS m^{-1}). The combination was found to increase the root length/ shoot length, fresh weight and dry weight of the plant (upto 8 dS m^{-1} salinity level) in com-

parison to control. HT-PGPR namely *Bacillus aryabhattai*, *Achromobacter denitrificans* and *Ochrobactrum intermedium* have been reported to have significant role in increasing productivity of rice under salinity stress (200 mM NaCl) by production of high amounts of EPS along with efficient nitrogen fixation and phosphate solubilization, thus facilitating nutrients to the plant under adverse conditions [76]. EPS produced by *Pseudomonas fluorescens* D11, DR7, *Enterobacter hormaechei* DR16 enhanced the colonization of bacteria in root hairs and promoted the growth of foxtail millet under drought stress. The authors also reported increased soil/root tissue ratio due to higher adhesion of soils caused by gel-like nature of EPS [77]. Endophytic and rhizospheric isolates *Halomonas, Bacillus*, *Virgibacillus* and *Zhihengiluella* from the halophytic species *Salicornia rubra, Sarcocornia utahensis*, and *Allenrolfea occidentalis*

against oxidative stress caused by ROS during salt stress [79,80]. SOD has been reported as key antioxidant enzyme and first line of defense to mitigate abiotic stresses for scavenging H_2O_2, reducing Haber–Weiss reaction and hydroxyl ion formation [81]. Enzymes CAT, APX (ascorbate peroxidase) and POD (peroxidase) act as the second line of defense found to mitigate the products of SOD [82]. Inoculation of plants with anti-oxidant enzymes producing HT-PGPR exhibited higher expression of *APX, CAT, SOD* genes under salt stress which attenuated the risks of cellular damage due to ROS in plants [24]. Inoculation of HT-PGPR (*B. megaterium* UPMR2 and *Enterobacter* sp. UPMR18) enhanced the levels of SOD, APX, and CAT and triggered the regulation of genes involved in ROS pathway (CAT, APX, GR, and DHAR) in okra plants under salinity stress [31]. Priming of *Panax ginseng* with salt-tolerant *Paenibacillus yonginensis* DCY84[T] facilitated the expression of various antioxidant genes such as *PgAPX* and *PgCAT,* increasing the plant tolerance against salinity stress [83]. Along with enzymatic ROS scavenging, HT-PGPR also produce non-enzymatic antioxidants such as ascorbate (AsA), carotenoids, tocopherols, glutathione (GSH) and phenolics which act as defense molecules for the plant under saline conditions [84]. HT-endophyte *Pseudomonas stutzeri* ISE12 isolated from halophyte *Salicornia europaea* upon inoculation to *Brassica napus* L. triggered antioxidant system and rearrangement of plant cell wall, consecutively inducing the tolerance in plants [85]. Inoculation of cowpea with HT-PGPR *Bradyrhizobium* and *Pseudomonas graminis* showed the accumulation of AsA and GSH and helped plants survival under salt stress [86].

Solubilization of inaccessible form of soil minerals into bioavailable form is a noted activity of HT-PGPR. HT-PGPR employ a vast array of mechanisms including production of low molecular weight organic acids, chelating agents and ion exchange for solubilization of P, Zn and potassium (K) in saline soil [87,88]. Minimizing the rhizospheric competition in nutrient scant stressed soils, some microbes through penetration or nodulation establish themselves as endophytes and in turn benefit the plant by assimilating nutrients and increasing survival/ adaption rate [89]. P is an important macronutrient required in large quantities by the plant i.e. ~ 0.2%- 0.8% [90]. But the enhanced level of salt in soil messes up with the availability of P to plants. In alkaline and calcareous soils, lime reacts with P forming strong calcium phosphate compounds, thereby exacerbating the chelation by plants [91]. Thus, along with phosphatic fertilizers application of phosphate solubilizing microorganisms (PSMs) are gaining attention. Bacterial isolates from saline mangrove swamps exhibited the property to solubilize rock phosphate with maximum chelation of 97% by *Oceanobacillus picturae* [87]. HT-PGPR such as *Vibrio, Arthrobacter, Bacillus, Azospirillum, O. picturae,* and *Phyllobacterium* are reported to increase the P uptake by plants in saline soils [92,6]. Apart from the macro-nutrients, availability of Fe is another challenge, limiting the growth and productivity of crops. Chelation of Fe is mainly governed by the pH of the soil system. Under saline conditions, higher content of bicarbonates inactivates the soluble Fe and thus, the uptake (of Fe by plants) is reduced. Saline soils tend to have pH more than 6.5 which causes oxidation of soluble ferrous to insoluble ferric oxide [93]. Siderophore production by HT-PGPR fulfill the demand of Fe in crops grown under salinity stress [94,95]. Mukherjee et al. [96] reported the role of siderophore production by *Halomonas sp.* in chelating Fe and growth promotion of rice under salinity stress. Goswami et al. [97] noted that *Bacillus licheniformis* strain A2 isolated from rhizosphere of salt tolerant desert plant *Suaeda fruticosa* solubilized phosphate and produced siderophore contributing to increment in plant biomass and height when grown under salinity stress. Another issue faced by the plants under salt stress is the deficiency of N due to negative influence on population and distribution of microbes. Process of dinitrogen fixation can be hampered in presence of salinity unless and until

proper strains are not selected and inoculated [98]. A novel study determining the diversity of diazotrophic endophytes in salt tolerant plant *S. europaea* L (growing at 55 and 112 dS/ m salinity) highlighted the presence of wide range of efficient nitrogen fixing genera including *Curtobacterium, Microbacterium, Rhodococcus, Mycobacterium, Cellulomonas, Sanguibacter, Clavibacter, Cryocola/ Labedella, Frigoribacterium, Agreia, Herbiconiux,* and *Plantibacter* [99]. The study also reported that nitrogen fixing Actinobacteria have higher salinity tolerance abilityb than Proteobacteria which are often reported at lower salinity. Similarly, Jha et al. [100] reported novel diazotrophic spectra of HT-PGPR including *Brachybacterium saurashtrense* sp. nov., *Zhihengliuella* sp., *Brevibacterium casei, Haererehalobacter* sp.*, Halomonas* sp.*, Vibrio* sp.*, Cronobacter sakazakii, Pseudomonas* spp.*, Rhizobium radiobacter,* and *Mesorhizobium* sp. from the rhizosphere of extreme halophyte *Salicornia brachiate*. The isolates were found to be potent nitrogen fixers, efficient IAA (indole acetic acid) producers, phosphate solubilizers along with positive for 1-aminoacyclopropane 1-carboxylate (ACC) deaminase activity (ACCD). *Gordonia* sp., a HT- PGPR was reported positive for *nif*H gene and siderophore production, stimulating the growth of pearl millets under saline conditions [101]. The lesser explored extreme habitats should thus be explored to discover the potential strains of stress tolerant PGPR so as to utilize them in strained agro-ecosystems.

Modulation of phytohormones and accumulation of nutrients against the hyperosmotic and hypo-nutritive conditions is an important role of HT-PGPR to confer symbiotic association and promote growth and productivity of plants. Studies confirmed that under salt stress, expression of genes for auxin like compounds increase in HT-PGPR and compensate plant's requirement of growth hormone [102,89]. Apart from the improvement in growth, there is also evidence that phytohormones produced by HT-PGPR showed role in the exclusion of ionic salts. Rojas-Tapias et al. [103] reported improved K^+ uptake, Na^+ ion exclusion and plant growth promotion in maize upon inoculation with auxin producing *Azotobacter* C5 and C9 strains under salt stress. Priming the seeds of *Triticum durum* var. *waha* with potent IAA producing HT-PGPR *A. brasilense* NH along with the extract of Marine Alga *Ulva lactuca* served as a novel bioformulation and enhanced the growth parameters of plants under saline conditions [104]. Synthesis of IAA is transcriptionally related to soaring level of ethylene in plants via the expression of ACC synthase gene (producing ethylene) [105]. Ethylene increases salt tolerance in plants but at the expenditure of growth and productivity [106]. The first small peak of ethylene under abiotic stresses takes up ACC and initiates expression of genes responsible for defense mechanism, while second larger peak is majorly deleterious to plants causing leaf chlorosis abscission, and senescence [107]. Mitigating this second ethylene peak, HT-PGPR synthesize ACC deaminase (ACCD) enzyme for growth and development of stressed plants [108]. ACCD encoding gene acdS are found in halotolerant microbes functioning to convert ACC (precursor of ethylene) to ammonia, α-ketoglutaraldehyde and utilizing for energy and N source [109]. Concluding from the direct correlation between IAA and ethylene it can be suggested that HT-PGPR with combined property of IAA production and ACCD should be used for stress amelioration [110,111].

Under salt stress PGPR also modulate 'emergency hormone' abscisic acid (ABA) biosynthesis and ABA-mediated signaling pathways for growth elevation of plants. Relatively, inoculation of wheat plants with halotolerant strain *D. natronolimnaea* STR1 under salinity stress caused the up-regulation of TaABARE (ABA-responsive gene) and TaOPR1 (12-oxophytodienoate reductase 1) stimulating TaMYB and TaWRKY following the expression of salt-stress induced gene TaST [33]. *P. fluorescens* inoculation to rice plants under drought stress was found to be enhancing the intrinsic tolerance level of plant through elevated expression of ABA syn-

thetic genes, particularly at later reproductive stage [112]. The authors reported increased expression of *nced1*, an ABA biosynthesis gene in tomato plants, upon inoculation with bacteria. The increased ABA content helped in stomatal closure to prevent loss of water from plants in a water-deficit condition. Gibberellic acid (GA) is another class of phytohormones inducing the physiological responses, germination and plant growth promotion. Under salt stress the mitigation strategy by GA involves antioxidant activity, inhibiting lipid peroxidation, chlorophyll synthesis, elevated root-shoot length, photosynthetic activity and plant biomass [113]. Kang et al. [114] reported that inoculation of salt and drought stressed soybean plants with *P. putida* H2-3, elevated the production of gibberellins and helped in regulating the hormonal and stress physiology.

Cytokinin phytohormonal signaling events also impart osmotic balance and help plant acclimatize to salinity [115]. These purine derivatives are directly involved in root callus differentiation, root hair and embryo vasculature formation, increase in leaf area, chlorophyll synthesis, and nutrient signaling [116]. Although cytokinins are less studied in comparison to auxins but their role in salt stress tolerance is equally significant. Sandhya et al. [117] found that a quarter of pseudomonads that were isolated from plants growing in arid and semi-arid areas showed increased cytokinin production under osmotic stress conditions. Elucidating the role of cytokinins under saline stress, a hypothesis illustrates that may be limiting the root proliferation leads to reduced uptake of salts by plants, but the larger picture of cytokinin driven tolerance mechanism is still unknown [118].

Apart from governing the molecular and physical interactions in plants, PGPR also elicit induced systemic resistance/ tolerance (ISR/ IST) through signaling [119]. ISR is primarily governed by ethylene and jasmonic acid (JA) signaling and the complex transcriptome analysis reveals involvement of *MYB72*, β-glucosidase U42 (*BGLU42*) and *MYC2*, in rhizobacteria mediated ISR [120]. PGPR produce plethora of signaling molecules including volatile organic compounds (VOCs), quorum sensing molecules such as N-acyl homoserine lactone (AHL) and cyclodipeptides (CDPs) which are effective in induction of systemic resistance in plants [121–123]. The exogenous application of *N*-3-oxo-hexanoyl-homoserine lactone (3OC6-HSL) (molecule of AHL family) enhanced the salt tolerance in *Arabidopsis* and wheat plants. 3OC6-HSL was found to be increasing the root and shoot length, plant biomass, proline and chlorophyll content and reduced MDA (malondialdehyde) and Na^+ levels. The molecular mechanism revealed that 3OC6-HSL was up-regulating expression of salinity-tolerance genes including *COR15a, RD22, ADH* and *P5CS1* (ABA-dependent osmotic stress regulating genes), *ERD1* (ABA-independent pant signaling gene), and *SOS1, SOS2* and *SOS3* (salinity responsive genes) in both the plants [124]. Correlatively, red rice plants inoculated with *Gluconacetobacter diazotrophicus* under drought stress showed synthesis of AHL molecules by LuxI proteins (autoinducer proteins) which enhanced tolerance in plants through IST [125]. Also two stress marker genes, PR-1 (for salicylic acid SA pathway) and PR-10 (for JA/ ethylene pathway) were induced transcriptionally to activate ISR. Therefore, *G. diazotrophicus* strain Pal 5 was suggested as future bioinoculant to reduce the damages in plants due to abiotic stresses and AHL an elicitor of plant defense systems [126].

HT-PGPR as soil remediators

The presence of HT-PGPR in saline soil greatly influences soil quality and fertility parameters. Studies have confirmed that HT-PGPR improve nutrient status, soil structure, organic matter, pH, EC, and deposition of ionic salts in soil [127]. HT-PGPR mitigate ionic toxicity through cation bridging, hydrogen bonding, and anion adsorption [128]. There are reports where application of HT-PGPR has improved salt index of saline soil [129]. Mitigating the nutrient status, HT-PGPR improve N, C, P, Fe and Zn content of saline soils, thereby reviving the lost vegetative index and accelerating the agricultural sustainability. Under saline conditions the N content and population of nitrogen fixers are found to be decreasing. Thus, acting as an efficient reclamation strategy, the symbiotic and asymbiotic biological nitrogen fixation by salt tolerant microbes enhances the N content as well as improves fertility of soil [88,130,131]. The enrichment of saline soil using nitrogen fixing PGPR *Pseudomonas aeruginosa*, along with N compost stimulated the level of nitrogen as compared with un-inoculated control [132]. Revival of arid and saline soil by utlizing salt-tolerant rhizobia can help in improving the fertility and productivity of these stressed agro-ecosystems [133]. Hassan et al. [134] utilized root powder of a halophyte *Cenchrus ciliaris* as carrier to develop inoculant from HT-PGPR *Bacillus cereus, Pseudomonas moraviensis,* and *Stenotrophomonas maltophilia*. The developed bioinoculant when applied in field improved growth of wheat and simultaneously resulted in better texture, EC, pH and organic matter of saline-sodic soil. Along with N, HT-PGPR can stimulate the P, Zn and Fe content of saline soils. *P. moraviensis* reclaimed saline sodic soil by improving P, nitrate (NO_3^-), N and K content by almost 18–35% [135]. Increase in P content of saline soil was observed by inoculation with phosphate solubilizing *B. licheniformis* MH48 strain. Reduction in soil pH, EC and enhanced availability of macro-nutrients (NPK), micronutrients (Fe, Zn, Mn and Cu) and organic matter was reported when saline soil was inoculated with HT-PGPR and phosphogypsum [136].

Besides nutrition, aggregation is also an important soil quality which promotes water percolation, root penetration, aeration and micropore formation [137]. HT-PGPR improve soil structure and aggregation by production of EPS (in stress conditions) resulting in formation of microaggregates (<250 μm) and macroaggregates (greater than250 μm) thus entrapping nutrients and water molecules. Formation of coherent EPS-soil complex in protected environment against odds of salinity helps in protection of both the plants and HT-PGPR population in the rhizosphere [138,139]. Qurashi and Sabri [140]. concluded that significant increase in soil aggregation was found due to EPS producing PGPR *Planococcus rifietoensis* (RT4) and *Halomonas variabilis* (HT1). Acting as protective sponge, EPS in the biofilm complex also increase the water holding capacity of soil and improves the water activity in plants under stress conditions of salinity and drought [74]. Improvement in water holding capacity and aggregation of soil upon application of EPS extracted from *P. putida* GAP-P$_{45}$ under salt and drought stress was reported [128]. Similarly, Boukhelata et al. [141] testified that EPS produced by *Alcaligenes latus* absorbed 1000 times more water than its own dry weight, while water absorbing capacity of EPS from *P. aeruginosa* strain CMG1421 was 400 times [142] and that from *Rhizobium* sp. and *Paenibacillus* sp., 100 times more than the dry weight [143]. EPS is an excellent soil conditioner and can even be utilized as an additive for development of bioformulations [144].

Increase in salinity by more than 5% significantly lowers the population of bacteria and actinobacteria [145]. The exogenous application of HT-PGPR while improving the soil structure also participates in assimilating the organic matter and increasing the microbial interactions. The establishment of biofilm in soil aggregates or on root surface is characterized by high concentration of root exudates, signaling molecules, organic matter and water content. This complex acts as a dragging force in selecting and establishing microbial diversity. The primary content of biofilm (EPS) regulates the organic matter by serving as C source and coagulating soil particles thereby ensuring the formation of humic substances which are stable organic carbon forms [146]. Improvement of C
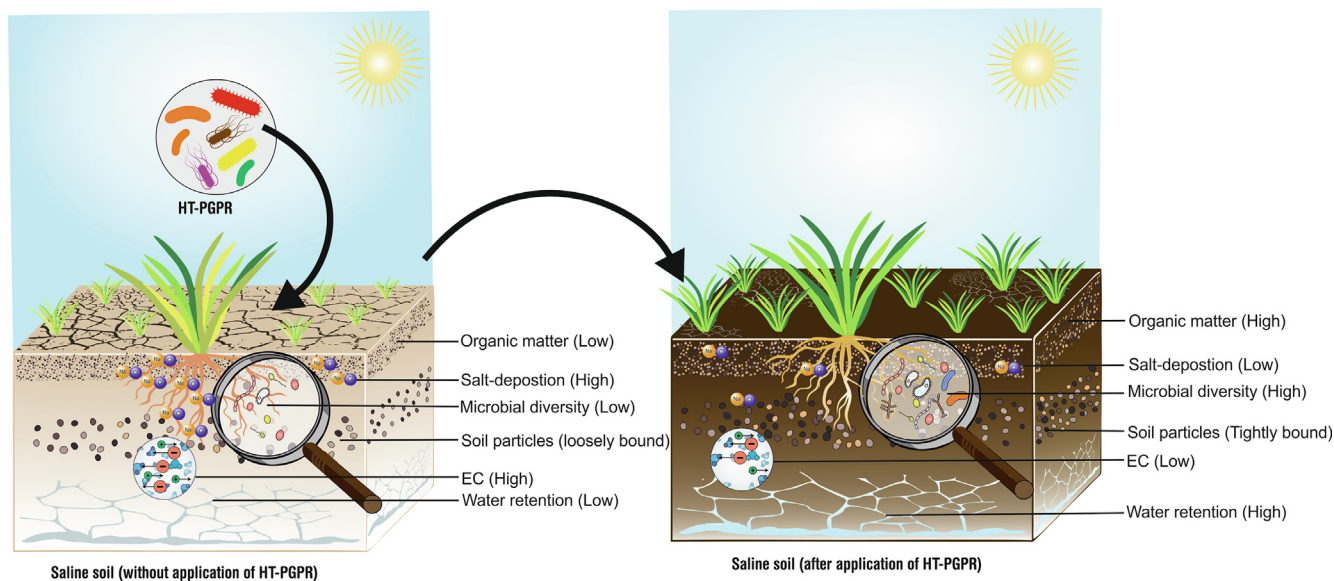
Fig. 3. Application of HT-PGPR showing rejuvenation of saline soil by different mechanisms for better productivity.

cycling in saline soil is reported when inoculated with PGPR [147]. Another mechanism of action reported by Lipińska et al. [148] highlights that bacterial inoculation increases the dehydrogenase activity which is suggested to be directly correlated with soil microbial biomass. Islam et al. [149] described increase in microbial biomass carbon and dehydrogenase activity in saline soil upon inoculation with HT-PGPR *B. cereus* Pb25. Research thus clearly shows the role and possible utilization of HT-PGPR in improving the quality of soils impacted with abiotic stresses such as salinity (Fig. 3).

Future prospects

Rapid increase in salinization of soil has not only affected agricultural production but also posed a threat to food security. Although still in its infancy, recent research shows that application of HT-PGPR has proven effective and a sustainable solution for the reclamation of saline soils. With the advancement of methodologies and techniques wide array of metabolites and genes (by PGPR) have been identified in response to salinity stress. However, further insights are required into the metabolome of the HT-PGPR during their interaction with plants both under physiologically stressed and non-stressed conditions [150]. 'Interactomics' is the emerging mapping technique involving bioinformatics tools to analyze the relationships between biomolecules such as proteins/enzymes from both plants and bacterial cells so as to determine the pathways involved in communication between both the partners under salt stress [151]. The decoding of the signaling and interactions between microbe-to-plant or plant-to-microbe can be used to modify the phytomicrobiome for the benefit of stressed plants. The connection between plant stress responses, signaling molecules and assemblages of microbiome can be further explored for development of stress 'smart agriculture' [152]. Limitations of bioformulations such as shelf-life and inability to perform in conditions prevalent under abiotic stresses have to be overcome. Inducing the stress ameliorating factors by adding additives or metabolites to attract the microbes can be explored to improve the quality of bioformulations for stressed agro-ecosystems. AHL can be used as one such elicitor for enhancing the plant–microbe communication and ensuring physiological, biochemical and

molecular changes to prevent salt-injury in crops [153]. Osmoprotectants or cell-protectants can also be added in the novel formulations, along with HT-PGPR, to help them overcome the initial stress and get acclimatized to the conditions. Exogenous application of glycine betaine and proline to culture medium resulted in enhanced salinity tolerance of fluorescent pseudomonads [154]. Hence this can also be utilized for development of bioinoculants for saline soils. Novel bioformulations can thus be developed by utilizing diverse HT-PGPR or their metabolites for improving productivity and quality of saline soils (Fig. 4). Amending gene elicitors inducing salt-stress responses and aiding in formation of biofilms can not only help in preparing the plant and microbe against stress like salinity, but also protect the introduced microbe from initial shock. Biofilm formation by HT-PGPR has already been reported in protection and growth promotion of plants in saline conditions [155]. Improvement of productivity and quality of saline soils utilizing HT-PGPR can play important role in improving the microbial diversity, soil organic matter, water activity, EC, pH and nutrient availability. Bioinoculants based on HT-PGPR can thus be of multiple utility. These novel formulations can not only protect and improve the crops' yields but also play crucial role in remediating stressed agro-ecosystems.

Conclusion

Switching from unsustainable traditional methods, microbiological approaches are emerging as the most significant biological tools to remediate and increase the productivity of saline soils. HT-PGPR have an array of mechanisms in their armor to manage and overcome the harmful impacts of soil-salinity. The application of these under-used but potential microorganisms to improve the productivity and instigate remediation of saline soils is required to be explored. Further research is needed to develop novel bioinoculants to tackle the menace of soil-salinity. To be a replicable and reliable technology, more scientific inputs will be required so as to understand the intricacies of the plant–microbe-microbe interactions under the complex stresses elicited due to soil salinity. This novel microbial technology needs to be explored further for improving crop-productivity and control the pandemic of soil salinity.
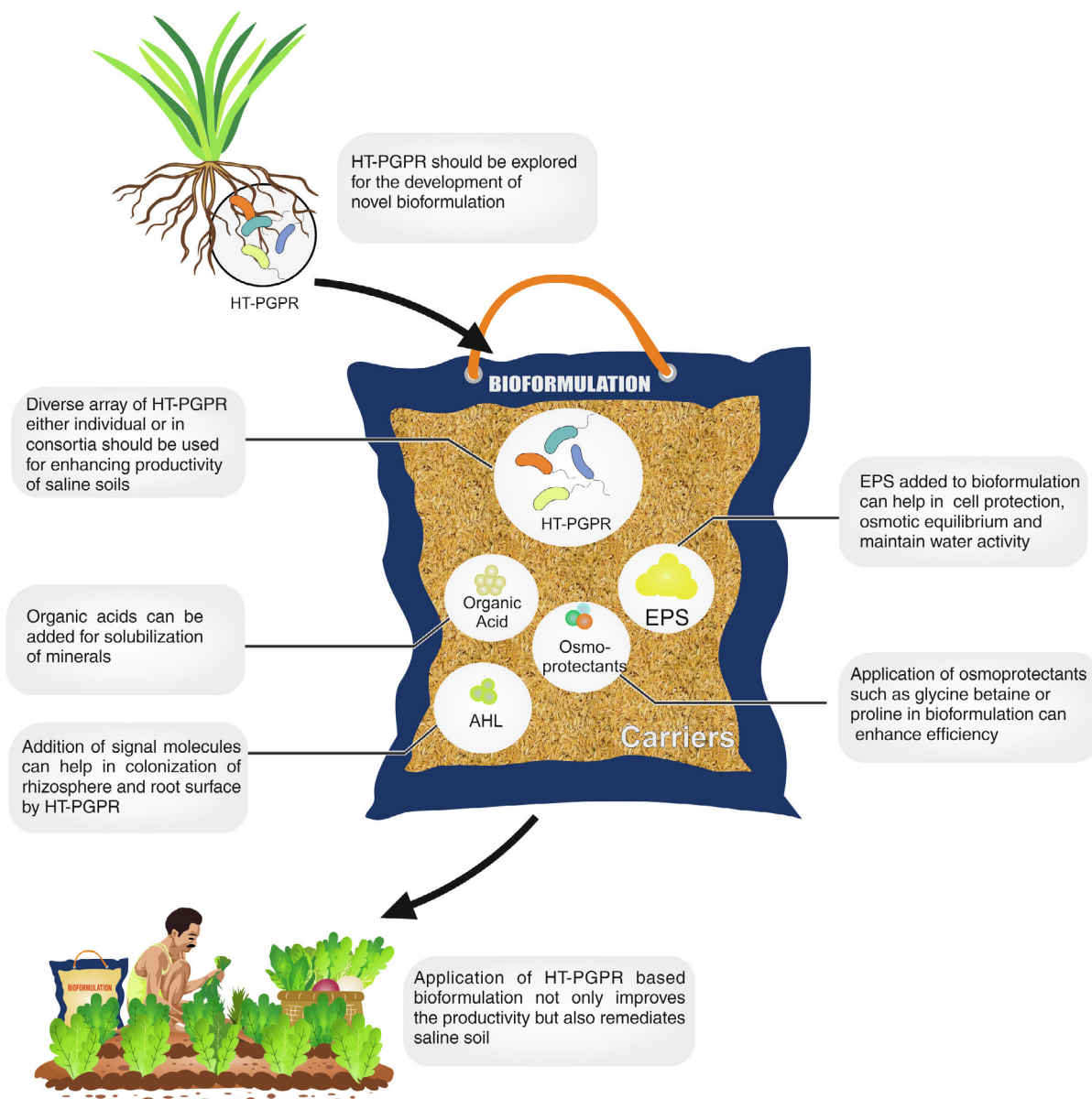
Fig. 4. HT-PGPR and their metabolites for development and application of novel bioformulation for saline soil.

Compliance with ethics requirements

This article does not contain any studies with human or animal subjects.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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