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Review

Roles of plant growth-promoting rhizobacteria (PGPR) in stimulating salinity stress defense in plants: A review

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Abstract: To date, soil salinity becomes a huge obstacle for food production worldwide since salt stress in plants is one of the major factors limiting agricultural productivity. It is estimated that a significant loss of crops (20%–50%) would be due to drought and salinity. To embark upon this harsh situation, numerous strategies such as plant breeding, plant genetic engineering, and a large variety of agricultural practices including the applications of plant growth-promoting rhizobacteria (PGPR) and seed biopriming technique have been developed to improve plant defense system against salt stress, resulting in higher crop yields to meet human's increasing food demand in the future. In the present review, we update and discuss the advantageous roles of beneficial PGPR as green bioinoculants in mitigating the burden of high saline conditions on morphological parameters and on physio-biochemical attributes of plant crops via diverse mechanisms. In addition, the applications of PGPR as a useful tool in seed biopriming technique are also updated and discussed since this approach exhibits promising potentials in improving seed vigor, rapid seed germination, and seedling growth uniformity, Furthermore, the controversial findings regarding the fluctuation of antioxidants and osmolytes in PGPR-treated plants are also pointed out and discussed.

Keywords: PGPR; salt stress; salinity; abiotic stress; ACC deaminase; seed priming; IAA

1. Introduction

Soil salinization caused by saline irrigation regimes [1], by water scarcity [2], and by the rise in sea level due to global warming [3]. Another potential source causing soil salinity comes from compost fertilizer since the raw materials for composting operations are food waste and municipal organic waste that contain large quantities of NaCl [4]. Salinity not only hampers crop productivity, but also threatens the sustainability of agro-ecosystems worldwide. The osmotic stress caused by high salinity is originated from the reduction in the solute potential of soil solution. The reduced solute potential, in turn, leads to the decrease in hydraulic conductance and then in water and solute uptake by plants [5]. This conducts the prevalence of drought-like conditions and makes drought and salinity occur simultaneously in various agricultural systems [6]. Salinity stress also imposes nutrients deficiencies by interfering directly with ion transporters in the root plasma membrane (e.g., K^+-selective ion channels) [7], and by inhibiting root growth [8–10]. Due to the rising severity of salinity on global food production, numerous strategies have been offered to

cope with the increasing challenging soil conditions. Along with plant breeding [11], plant genetic engineering [12], and genetic transformation [13], agricultural practices have dramatically contributed to the improvement of plant tolerance to salinity stress. The bacterization of plant crops with PGPR and the implementation of these useful rhizobacteria in seed biopriming have demonstrated their beneficial properties in enhancing plant growth and development, and in augmenting plant salt stress tolerance through different mechanisms. PGPR aid to alleviate salinity stress in plants by boosting water absorption capability, by enhancing essential nutrients uptake, and by accumulating osmolytes (e.g., proline and glutamate) and antioxidant enzymes in plant tissues [11,14]. On the other hands, the conventional agricultural practices depend profoundly on chemical fertilizers and pesticides which cause soil pollution, decrease soil microorganism diversity, thereby destabilizing the balance in the ecosystem. Fortunately, beneficial microorganisms can play a main role to deal with the increasing environmental challenges since they are involved in the decomposition of organic matters, the cycling of nutrient elements, and the conversion of energy in the ecosystem [15]. In all types of salinity, sodium chloride (NaCl) is the most soluble and widespread salt [16] and Na^+ is the primary cause of ion-specific damage for many plants, especially for graminaceous crops [17]. Consequently, to narrow down the scope of this review, we focus mainly on the negative effects of Na^+ ion on plants, although high concentrations of Cl^- anion are also toxic to plants. In this point of view, three terms "salt", "saline", and "Na^+" were used interchangeably in the review to indicate the salinity.

2. Adverse effects of salinity on plants

2.1. Na^+ accumulation, nutrients uptake inhibition and plant growth reduction

Under salt stress, Na^+ is accumulated at higher concentrations in plant tissues, causing changes in Na^+/K^+ ratio and the inhibitions of essential nutrient uptake *[14,18,19]*. This could be attributed to the competition between the similar ionic radii of Na^+ and K^+ in soils *[20]*, causing the dysfunctional ionic selectivity of the cell membranes. In the review of Manishankar et al. *[21]*, high Na^+ concentration in soil can change soil texture, resulting in the decrease in soil porosity. This leads to the reduction of soil aeration and water conductance. Also according to Manishankar et al. *[21]*, the zones of low water potential caused by high salt deposition in the soil make difficult for the roots to uptake water and nutrients. With 35 mM NaCl treatment, the Na^+ concentrations in strawberry leaves and roots were 3.4-fold higher than those in the control plants *[19]*. Moreover, salt stress also caused the critical reduction in the fruit yield with 35% yield loss for the variety Camarosa and 45% for the variety Oso Grande *[19]*. At 150 mM NaCl, a tremendous increase (50.4-fold) in the Na^+ content in the roots of *Broussonetia papyrifera*, a woody plant used in paper industry, was recorded, in harmony with the decrease of K^+ (25.6%), Ca^{2+} (23.3%), Mg^{2+} (21.4%), P^{3+} (8.4%) contents, and the increase in Na^+/K^+ ratio as compared to the control plants (1.48 vs. 0.02) *[22]*. However, an upsurge of Na^+ content was found in the leaves of the canola plants (*Brassica napus* L.), with approximately 4-fold greater than that in the roots *[18]*. Na^+ content in the common bean leaves (*Phaseolus vulgaris*) was 5–7–fold higher than that in the control plant leaves, whereas the K^+ content was decreased by 32–35% relative to the control plants *[23]*. Na^+ content in the salt treated-chickpea leaves (*Cicer arietinum*) was 3.2-fold higher than that in the control plants, leading changes in Na^+/K^+ ratio from 0.31 in the non-saline condition to 2.24 in the saline condition, and the N, K, Ca, Mg concentrations were decreased by 54%, 55%, 60% and 55%, respectively as compared to the control leaves *[24]*.

In general, phytotoxicity caused by high salt concentrations was found under *in vitro* and greenhouse conditions and the toxic symptoms increase correlatively with the increase in NaCl treatments. High salinity significantly affects plant growth, resulting in the decrease in germination rate, in fresh and dry matters, in photosynthetic pigments, in essential nutrients uptake, and most importantly, in the loss of ultimate crop yields. In contrast, a

significant increase in antioxidant enzymes, osmoregulators, lipid peroxidation, membrane damage, ROS contents, Na^+ uptake, and Na^+/K^+ ratio was obviously observed with the increasing NaCl concentrations *[25]*. The shoot and root dry matters of 35 mM NaCl-treated strawberry plants (*Fragaria x ananassa* Duch) was 45.8% and 58.6% lower than those in the control plants, respectively *[19]*. Salt stress adversely impacted all plant growth stages, causing the reduction in fruit yield (FY) (227 vs. 415 g/plant), fruit weight (FW) (8.4 vs. 9.6 g/fruit), number of fruits per plant (NF) (27 vs. 43), and water-soluble dry matter (SDM) (6.6% vs. 8.4%) of stressed plants relative to the unstressed plants. The root dry weight (RDW) of common bean decreased by 59–61% and the final yield lost by 27–30% under 200 mM NaCl *[23]*. Similarly, at 200 mM NaCl concentration, salt stress impacted 38% shoot dry weight and 50% root dry weight of chickpea (*Cicer arietinum*, cv. Giza 1) compared to the control plants *[24]*. Regarding nutritional values, although moderate saline stress can enhance glucosinolates and antioxidants contents in broccoli (*Brassica oleracea* L. var. italica cv. Marathon) *[26]* and the contents of lycopene, β-carotene, vitamin C and overall phenolic compounds of tomato fruits *[27]*, high salinity concentrations markedly reduced protein, fat, and crude fiber contents of wheat grains *[28]*. Moreover, the fruit size of tomato *[29]* and the fruit weight of pepper *[30]*, which are major determinants of price and marketable characteristics, were strongly reduced with the increase of saline levels.

2.2. Impairment of physio-biochemical attributes

2.2.1. Reduced photosynthetic pigments.

Salinity stress can cause an unrepairable damage to the photosynthetic apparatus at any development stage of plant's life as it alters the chloroplasts structure, degrades chloroplast envelope, and triggers chloroplast protrusions [31]. Numerous studies indicated that high salinity led to a serious degradation of chlorophyll (Chl) and carotenoids (Car) in salt-stressed plants, however, the degrees of reduction in these photosynthetic pigments depended largely on plant species, plant age, NaCl concentrations and the duration of salt stress exposure. Specifically, only 9%, 11%, 13% and 14% reduction in the total Chl were determined in the rice (*Oryza sativa* L.), soybean (*Glycine max*), maize (*Zea mays* L.), and cucumber (*Cucumis sativus*) seedlings, respectively in the studies of Khan et al. (2016) [32], Kang et al. (2014 b) [33], Li and Jiang (2017) [34], and Kang et al. (2014 a) [35], respectively. However, contrary to these studies, the reduced contents of total Chl were tremendously varied from 22% in oat (*Avena sativa*) seedlings, 41% in tomato (*Solanum lycopersicum* L.) seedlings, 42% in tomato (*Solanum lycopersicum* L.) plants, 44% in tomato (*Solanum lycopersicum* L.) plants, 50% in peanut (*Arachis hypogaea*) seedlings, 56% in rice (*Oryza sativa* L.) seedlings to 61% in rapeseed (*Brassica napus* L.) plants in the reports of Sapre et al. (2018) [36], Akram et al. (2019) [37], Orozco-Mosqueda et al. (2019) [38], Vaishnav et al. (2020) [39], Alexander et al. (2020) [40], Sarkar et al. (2018) [41], and Cheng et al. (2012) [18], respectively. Concerning Car content, under salt detriment, a 16% decrease in ginseng plantlets, a 19% decrease in mung bean plants, and a 49% decrease in tomato seedings were reported by Sukweenadhi et al. (2018) [42], Shahid et al. (2021) [25], and Akram et al. (2019) [37], respectively. In addition, NaCl toxicity also declined net photosynthetic rate, stomatal conductance, and transpiration rate in stressed plants [43].

2.2.2. Increased lipid peroxidation

Lipids are essential components of cell membranes that are responsible for structure maintenance and cell functions control [44]. ROS are generated from several life processes and an excess of ROS can damage cell, tissues and organs [45]. Lipids are primary targets of ROS attack (e.g., oxygen free radicals) and the free radicals oxidation of polyunsaturated fatty acids is called lipid peroxidation [46]. As a byproduct of lipid peroxidation, malonaldehyde (MDA) has been largely used as an important indicator to evaluate the extent of damaging effects caused by ROS associated with oxidative stress that act on membrane lipids to reduce membrane stability [47]. The MDA content was tremendously increased from 36% in ginseng root plantlets [42], 39% in maize [34], 47% in peanut [40],

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70% in chickpea [24], 131% in oat [36], 153% in mung bean [25] and 300% in rice seedlings [48], indicating an extensive damage to cell membrane integrity and/or membrane permeability [49].

2.3. Increased accumulation of ROS and elevated production of antioxidant enzymes, non-enzymatic antioxidants, and osmolytes

On the one hand, ROS function as signaling molecules to mediate a wide range of important biological processes during plant growth and development such as seed germination [50], cell differentiation [51], root primary growth [52], and stem cell activities [53]. On the other hand, an elevated accumulation of ROS in plant tissues also causes oxidative damage to protein, DNA, lipids, and Chl biosynthesis [54,55]. Salinity stress brings about an excessive accumulation of ROS including superoxide anion ($O_2^{\bullet -}$), hydrogen peroxide (H_2O_2), singlet oxygen ($^1O_2$), and hydroxyl radicals ($^\bullet OH$), which disturb cellular redox homeostasis and lead to oxidative stress [56]. ROS homeostasis, therefore, is essential to maintain a delicate balance for plant growth, especially under environmentally adverse conditions. To deal with salinity-derived oxidative stress, plants possess enzymatic defense system that synthesizes an arsenal of antioxidant enzymes such as superoxide dismutase (SOD, EC 1.15.1.1), peroxidase (POD, EC 1.11.1.7), catalase (CAT, EC 1.11.1.6), ascorbate peroxidase (APX, EC 1.11.1.11), monodehydroascorbate reductase (MDHAR, EC 1.6.5.4), dehydroascorbate reductase (DHAR, EC 1.8.5.1), and glutathione reductase (GR, EC 1.6.4.2), along with non-enzymatic antioxidants, namely, glutathione (GSH), Car, ascorbic acid (AsA), and polyphenols (PP) [57]. The antioxidant enzymes conduct the scavenging activity by breaking down and removing free radicals and the non-enzymatic antioxidants perform their scavenging functions by interrupting free radical chain reactions [58]. Furthermore, the synthesis and accumulation of osmoregulators, namely, proline (Pro), glycine betaine, choline, O-sulphate, sugars and polyols, are also common responses executed by plants to provide osmotic adjustments and to protect cell membrane integrity [59]. In plants, Pro is synthesized by either glutamate pathway or orinithine pathway [60] and is accumulated in cytosol and vacuole during stressful conditions. Under non-stress conditions, Pro only accounts for less than 5% of the total pool of free amino acids in plants. However, under various stresses, the Pro concentration might increase up to 80% of the total amino acid pool, indicating its vital roles in ROS homeostasis and water balance in plants [61]. Pro was found to exhibit protective roles against damages caused by $^1O_2$ or $^\bullet OH$ [62]. Ethylene (C_2H_4), a small volatile phytohormone in higher plants, is involved in all stages of plant growth and development, from seed germination to fruit ripening [63]. Furthermore, ethylene has been considered as a stress hormone since it participates in plant stress responses to various types of stresses such as wounding [64], salinity [65], drought [66], etc. Although a small amount of ethylene, which is immediately produced after the onset of a stress, can initiate the systemic resistance in plants, the excess ethylene from the second ethylene peak may bring about the inhibition of plant growth or even lead to cell death [67].

3. Plant growth-promoting rhizobacteria

3.1. Key criteria for being applicable PGPR and their current studies in promoting plant salt stress tolerance.

The close alliance among soil, plant, and microbes exists during the entire life cycle of plants promotes plant development, induces systemic resistance in the host plant against pathogens and mitigates salinity stress [68]. PGPR have been widely used for decades to control insects pests [69], plant diseases [70], to promote plant growth [71], to manage nutrient [72], and to alleviate abiotic stress [73]. The ameliorative functions of PGPR are involved in three aspects, including the ability to survive under hyperosmotic conditions, to aid plant tolerate better to elevated salinity, and to improve soil quality [74]. Regarding the roles of PGPR in promoting plant salinity tolerance, PGPR exhibit their beneficial traits in mitigating the toxic effects of high salt concentrations on morphological, physiological, and biochemical processes of plants, resulting in the significant rescue of yield losses

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caused by salinity stress. According to Fouda et al. [75], the application of PGPB could ameliorate the negative impacts of salinity via two main mechanisms as follows: (1) PGPR activate stress response systems in the host plants soon after the exposure of the plants to stress, and (2) PGPR synthesize antistress biochemicals such as antioxidant enzymes, non-enzymatic antioxidants and osmoregulators that are responsible for the removal of ROS [76]. Furthermore, PGPR can also mitigate salt stress symptoms by producing Na^+-binding exopolysaccharides (EPS), by improving ion homeostasis, by decreasing ethylene levels through enzyme ACC deaminase, and by synthesizing phytohormones [77–79].

3.1.1. ACC deaminase-producing PGPR and other plant growth promoting attributes.

Enzyme ACC deaminase [EC 4.1.99.4] catalyzes the cleavage of 1-aminocyclopropane-1-carboxylate (ACC), an intermediate precursor of ethylene in higher plants, to produce α-ketobutyrate and ammonia [80]. A proper amount of ethylene derived from the existing pool of ACC, or so called the small peak of ethylene in the biphasic ethylene response model described by Glick et al. [81] and Pierik et al. [82], is thought to be beneficial to plants in activating plant defensive responses to stress stimuli (e.g., temperature extremes, drought or flooding, insect pest damages, phytopathogens, and mechanical wounding, etc.) [83]. However, an excess ethylene, also called stress ethylene or the larger peak of ethylene in the biphasic model, may cause harmful effects (e.g., chlorosis, abscission, and senescence) on plant growth [84], even lead to dead when being present at high concentrations in plant tissues [85]. Although PGPR possess many different mechanisms to maintain plant growth under salinity detriment, the production of ACC deaminase is extremely important in reducing the elevated levels of ethylene, thereby indirectly support plant growth. The ACC deaminase-producing PGPR that live on plant surfaces or colonize in the plant tissues function as a sink for ACC [18] and the use of ACC as a nitrogen source is beneficial to plant health since nitrogen (N) uptake is always suppressed under salt conditions [86]. Up to now, a plethora of PGPR that have been recently studied to evaluate their beneficial traits in mitigating salinity stress on plants. The PGPR, namely, *Pseudomonas putida* UW4 [18], *Arthrobacter protophormiae* [87], *Enterobacter* sp. EJ01 [88], *Enterobacter* sp. UPMR18 [89], *Zhihengliuella halotolerans*, *Bacillus gibsonii*, *Halomonas* sp. [90], *Chryseobacterium gleum* sp. SUK [91], *Pseudomonas fluorescens* 002 [92], *Microbacterium oleivorans* KNUC7074, *Brevibacterium iodinum* KNUC7183, and *Rhizobium massiliae* KNUC7586 [93], *Stenotrophomonas maltophilia* SBP-9 [94], *Enterobacter* sp. P23 [41], *Burkholderia* sp. MTCC 12259 [48], *Paenibacillus yonginensis* DCY84 [42], *Bacillus pumilus* strain FAB10 [43], *Pantoea agglomerans* [95], *Aneurinibacillus aneurinilyticus* and *Paenibacillus* sp. [80], *Leclercia adecarboxylata* MO1 [96], *Pseudomonas argentinensis* and *Pseudomonas azotoformans* [97], *Bacillus subtilis* (NBRI 28B), *B. subtilis* (NBRI 33 N), *Bacillus safensis* (NBRI 12 M) [98], *Bacillus megaterium* NRCB001, *B. subtilis* subsp. *subtilis* NRCB002, *B. subtilis* NRCB003 [99], and *Kosakonia sacchari* [25] can produce ACC deaminase, as well as other important products such as indole-3-acetic acid (IAA), siderophore (Sid), EPS, and Pro. In addition, the PGPR can also conduct biofilm forming, N fixation, phosphate (P) solubilization, hydrogen cyanide (HCN) and antifungal enzymes production [91]. The capability of PGPR for moderating salinity could be an indispensable trait to improve plant growth and salt tolerance [100], reflecting via the elevated amounts of ACC deaminase, IAA, EPS, GSH and Pro produced by PGPR during salt exposure to protect themselves against the damaging effects of high saline. For instance, at 500 mM NaCl concentration, *Sphingomonas* sp. LK11 produced more GSH and Pro to counteract the detrimental effects of salinity imposed on its growth [100]. Similarly, the productions of ACC deaminase and Pro by the halotolerant PGPR *Burkholderia* sp. MTCC 12259 were highly correlated with the increasing NaCl concentrations in the medium broth, in which ACC deaminase reached the highest at 600 mM NaCl, while the highest Pro level was obtained at 1000 mM NaCl [48]. This result was in accordance with the report of Ilyas et al. [101] when the Pro produced by a consortium consisting of *Bacillus* sp. (KF719179), *Azospirillum brasilense* (KJ194586), *Azospirillum lipoferum* (KJ434039), and *Pseudomonas stutzeri* (KJ685889) reached the maximum value at the

highest NaCl concentration (10%, w/v). Also, the productions of ROS-quenching enzymes SOD, CAT, POD, PPO and osmolyte Pro in *Enterobacter* sp. P23 were increased with the increase in NaCl concentrations [41]. The levels of IAA, Sid, and ACC deaminase produced by *K. sacchari* strain MSK1 were increased with the increasing NaCl concentrations and reached the highest levels at the highest NaCl concentration (400 mM) [25]. Recently, Misra and Chauhan [98] found that two *B. subtilis* strains NBRI 28B, NBRI 33N, and *B. safensis* NBRI 12 M increased the production of ACC deaminase, biofilm, EPS, and Alginate (Alg) in proportion to the increasing NaCl concentrations in nutrient broth. This finding was in corroboration with the previous study of Mukherjee et al. [102], in which *Halomonas* sp. Exo1 could tolerate up to 20% (w/v) salt concentration and its EPS yield was directly proportional to the increasing NaCl.

3.1.2. Improvements of growth parameters, nutrients uptake, and photosynthetic pigments in PGPR-inoculated plants under non-stress conditions

The halotolerant bacterium *Enterobacter* sp. strain P23 isolated from India's rice fields possesses the abilities to exhibit high ACC deaminase activity, to solubilize phosphate, to produce IAA, Sid, and HCN [41]. In non-tress conditions, the P23-inoculated rice seedlings showed better morphological parameters, namely SL, RL, SFW, SDW, RFW, and RDW, higher Chl content than those in the non-inoculated rice seedlings. This result was consistent with numerous other studies where the PGPR-inoculated plants grew better than the non-inoculated plants in non-stress environments. Specifically, the values of SFW, RFW, SDW, RDW, Chl a, Chl b, Car, and N, P, and K concentrations in S20-inoculated maize seedlings were increased by 2%, 6%, 5%, 2%, 4%, 7%, 2%, 16%, 43%, 2%, respectively as compared to the control seedlings [103]. Also, in *Chryseobacterium gleum* sp. SUK + feather lysate inoculum (FLI)-inoculated wheat seedlings, the increase in total Chl, and amino acids contents was 24% and 13%, respectively [91]. Likewise, the increase in SL, RL, SFW, RFW, total Chl was noticed in *L. adecarboxylata*-inoculated tomato plants with 22%, 16%, 28%, 51% and 13%, respectively higher than those in the control plants [96]. The same trend was found in the studies of Li and Jiang [34], Khan et al. [32], Sapre et al. [36], Sarkar et al. [41], Akram et al. [37], and Alexander et al [40]. The increase in total Chl was widely observed in various studies. However, the extent to which these pigments increased depends on PGPR, NaCl treatments, plant species. For instance, only a 5% Chl increase in maize seedling bacterized by *B. aquimaris* DY-3 was noticed by Li and Jiang (2017) [34], whereas 12% increase in *P. putida* H-2-3-inoculated soybean seedlings [33], 17% in *S. maltophilia* BJ01-peanut seedlings [40], 29% in *K. sacchari*-treated mung bean seedlings [25], 41% in *Bacillus megaterium* BMA12-bacterized tomato seedlings [37], 46% in *B. pupilus*-inoculated rice seedlings [32], and 60% in *A. brasilense*-treated white clover plants [49].

Nevertheless, in some exception cases, the applications of PGPR under normal conditions would not always promote plant growth and yield. Instead, the PGPR even exhibited negative effects on eggplant and tomato plants growth as shown in the study of Abd El-Azeem et al. [14] and Vaishnav et al., respectively [39]. Specifically, the SFW, SDW and yield of eggplant were decreased by 8%, 9%, 12%, respectively after being inoculated with *X. autotrophicus* BM13, or decreased by 12%, 21%, 30%, respectively when inoculated with *Bacillus brevis* FK2 [14], and the SL of *Sphingobacterium* BHU-AV3-inoculated tomato was reduced by 11% as compared to the control tomato plants. Likewise, the SL, RL and total plant fresh weight (TPFW) in the *C. gleum*-inoculated wheat plants were decreased by 16%, 36%, and 13%, respectively relative to the control [91]. The data in these previous reports were in accordance with our preliminary data (unpublished data) as the SFW and RFW of the *Curtobacterium* sp. C1-inoculated Arabidopsis plants were lower than those in the uninoculated plants.

Although the suppressive impacts of PGPR on plant growth and yield are scarcely recorded under non-stress conditions, this should be taken into consideration prior to PGPR bacterization practices. Furthermore, the response of plant variety to PGPR is genotype-

dependent as shown in the report of Nawaz et al. [104] where the salt tolerant wheat genotype Aas-11 responded positively to *B.* and *E. aurantiacum*, whereas the salt sensitive wheat genotype Galaxy-13 responded better to *P. fluorescence*. In this regard, we should agree that the interactions between host plants and microbes are complicated and not always a win-win situation. In addition, the adaptation of plant species to PGPR might markedly vary from case to case.

3.1.3. Improvements of growth parameters, nutrients uptake, and photosynthesis in PGPR-inoculated plants under salinity conditions

Although PGPR can promote plant growth and improve nutrients uptake, as well as stimulate the synthesis of photosynthetic pigments in non-stress environments, their ameliorative roles in plant defense responses are fully expressed till plant crops endure harsh environmental conditions. In the study of Sarkar et al. [48], the inoculation of rice seeds with *Enterobacter* sp. strain P23 promoted higher germination percentage (76% ± 7.03 vs. 48% ± 4.78), and higher seedling vigor index (SVI) (881.6 ± 67 vs. 57.5 ± 12.6) as compared to the non-inoculated seeds. Under salt conditions, the Pro peaked its highest level, and the antioxidant enzymes SOD, CAT, POD, PPO, and MDA exhibited their highest activities in uninoculated rice seedlings. The activities of these enzymes in P23-inoculated seedlings, however, were significantly reduced relative to those in the non-inoculated seedlings. The productions of ethylene in non-inoculated seedlings and P23 AcdS mutant-inoculated seedlings were comparable, consistent with the study of Cheng et al. [18], while ethylene in the WT P23 strain-treated plants was lower, indicating that the WT P23 succeeded in decreasing stress ethylene production. In the reports of Awad et al. [105] and Abd El-Ghany and Attia [106], they found that the bacterization of maize (*Zea mays* L.) plants and faba bean (*Vicia faba* cv. Giza3) seeds with *Azotobacter chroococcum*, an EPS-producing bacterium, had the decreased Na^+ and Cl^- concentrations and the increased N, P, and K concentrations in their plant tissues. PP, known as potent antioxidants, can eliminate radical species (e.g., $^1O_2$, $O_2^{\bullet-}$, OH^-, H_2O_2), thus preventing the propagation of oxidative chain reactions [107]. In the study of Hichem et al. [108], the amounts of total PP including phenolic acids, flavonoids, anthocyanins and proanthocyanidins increased accordingly with the increased salinity in young and mature maize leaves and the elevated concentrations of these phenolic compounds had an inverse correlation with H_2O_2 content and lipid peroxidation in leaves, indicating the scavenging activity of endogenous phenolic compounds against free radicals [109]. The total PP in the leaves of *Azotobacter chroococcum*-inoculated maize seedlings were always higher than those in the non-inoculated maize seedlings, regardless of salt concentrations [110]. Moreover, the total PP reached the highest level at the highest NaCl concentration (5.85 g NaCl/kg soil). Abd_Allah et al. [24], who evaluated the effects of endophytic *B. subtilis* (BERA71) on mitigating saline soil stress in chickpea plants (*Cicer arietinum* cv. Giza 1), found that the *B. subtilis* (BERA71)-inoculated chickpea plants yielded higher plant biomass, achieved higher photosynthetic pigments, while reduced ROS levels, and lipid peroxidation compared to the non-inoculated seedlings. The positive correlation between proline accumulation and salt stress adaptation has been widely recognized. However, the results are still controversial, and more investigations should be conducted to thoroughly explain the underlying mechanisms that regulate antioxidants and osmolytes production.

Regarding nutrient acquisition, the PGPB helped to decrease sodium accumulation, whereas enhanced the acquisitions of nitrogen (N), calcium (Ca), magnesium (Mg), and potassium (P) contents in the chickpea plants [24]. The increased uptake of Mg^{2+} induced by *B. subtilis* and *B. pumilus* inoculations were associated with the elevated photosynthetic pigment contents since Mg^{2+} is the major component of Chl [32,111]. Accordingly, the expression level of *Cab2*, the gene encoding a Chl a/b protein in Arabidopsis plant, was downregulated in Mg-deficient plants before any obvious symptom of chlorophyll deficiency appears [112]. However, Abd_Allah and his colleagues [24] did not investigate the mechanisms that enhanced the uptake of essential nutrients in their study. Therefore, it is

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unclear whether the increased nutrient acquisition in the *B. subtilis*-inoculated chickpea plants is due to the modulation of root architecture [113,114], the mobilization of phosphate in the soil [115,116], or the nitrogen fixation [117,118] induced by *B. subtilis*. Similarly, Khan et al. [32] noticed the limited uptake of Na^+ in *B. pumilus*-inoculated paddy plants relative to the control plants, but the mechanism that suppressed Na^+ uptake was not thoroughly investigated yet. In contrast, an extensive accumulation of Na^+ was observed in the shoots of *Bacillus*-inoculated halophyte *Arthrocnemum macrostachyum* relative to the control plant at high NaCl concentration (1030 mM) [119]. Up to now, a plenty of studies recognize the roles of PGPB in increasing K^+/Na^+ ratio, in activating K^+-Na^+ selectivity, in maintaining photosynthetic pigments, in enhancing nutrient uptakes, thereby alleviating salt stress in saline environments [32]. However, more studies are needed to clearly elucidate the mechanisms underlying these phenomena.

Table 1. Ameliorative effects of PGPR on plant growth and physio-biochemical parameters under salinity conditions.

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PGPR	Treatments	Growth parameters and yield	Phyto-hormones	Photosyn-thetic pigments	Lipid peroxidation (MDA)	Antioxidant enzymes	Non-enzymatic antioxidants	Osmolytes (Proline)	Nutrient contents	Sources
B. brevis FK2, *E. aerogenes* BM10, and *X. autotrophi-cus* BM13. The eggplant seed-lings inoculated with individual bac-terium.	0 mM NaCl + Uninoculated									Abd El-Azeem et al. (2012)
	0, 25, 50 mM NaCl + FK2	**(0 mM NaCl)** ↑ 17% RDW, ↓ 12% SFW, ↓ 21% SDW, ↓ 30 Y **(25, 50 mM NaCl)** ↓ 33%, ↓ 59% SFW ↓ 44%, ↓ 67% SDW ↓ 42%, ↓ 77% Y ↓ 9%, ↓ 27% RDW	N/A						**(0 mM NaCl)** In shoot: ↓ 30% Na^+ Na^+/K^+ ratio ~ 0.46 **(25, 50 mM NaCl)** ↑ 4% Na^+, ↑ 114% Na^+ Na^+/K^+ ratio ~ 1.2, 3.6	
	0, 25, 50 mM NaCl + BM10	**(0 mM NaCl)** ↑ 5% SFW, 2% SDW, ↑ 73% RDW, ↓ 9% Y **(25, 50 mM NaCl)** ↓ 34%, ↓ 47% SFW ↓ 47%, ↓ 60% SDW ↓ 12%, ↓ 20% RDW ↓ 39%, ↓ 72% Y							**(0, 25, 50 mM NaCl)** In shoot: ↑ 0% Na^+, ↑ 72% Na^+, ↑ 113% Na^+ Na^+/K^+ ratio ~ 0.5, 1.8, 3.2	
	0, 25, 50 mM NaCl + BM13	**(0, 25, 50 mM NaCl)** ↓ 8%, ↓ 30%, ↓ 51% SFW ↓ 9%, ↓ 47%, ↓ 61% SDW ↓ 12%, ↓ 62%, ↓ 72% Y							**(0 mM NaCl)** In shoot: ↓ 12% Na^+ Na^+/K^+ ratio ~ 0.46 **(25, 50 mM NaCl)** ↑ 117% Na^+, ↑ 139% Na^+ Na^+/K^+ ratio ~ 2.1, 3.5	

B. cepacia SE4, *Promicromono-spora* SE188, and *A. calcoaceticus* SE370. 7-day old tomato-plants inoculated with PGPR, 120 mM NaCl for 7 days.	0 mM NaCl + Uninoculated									
	120 mM NaCl + Uninoculated	↓ 17% SFW ↓ 25% SDW	↑ 255% ABA, ↑ 194% SA	↓ 14% total Chl	N/A	↑ 86% CAT ↑ 213% POD ↑ 456% PPO	↑ 79% PP	N/A	In shoot: ↑ 740% Na^+, ↓ 4% K^+ Na^+/K^+ ratio ~ 0.28	Kang et al. (2014) a
	120 mM NaCl + SE4	↓ 11% SFW ↓ 8% SDW	↑ 10% ABA ↑ 367% SA	Unchanged total Chl		↑ 27% CAT ↑ 163% POD ↑ 333% PPO	↑ 45% PP		In shoot: ↑ 297% Na^+ ↑ 17% K^+ Na^+/K^+ ratio ~ 0.11	
	120 mM NaCl + SE118	↓ 13% SFW ↓ 6% SDW	↑ 6% ABA ↑ 217% SA	Unchanged total Chl		↑ 23% CAT ↑ 131% POD ↑ 322% PPO	↑ 35% PP			
	120 mM NaCl + SE370	↓ 10% SFW ↓ 9% SDW	↑ 23% ABA, ↑ 261% SA	Unchanged total Chl		↑ 46% CAT ↑ 156% POD ↑ 322% PPO	↑ 52% PP			
P. putida H-2-3. 21-day-old soybean seedlings inoculated with *P. putida*, 120 mM NaCl for 10 days.	0 mM NaCl + Uninoculated									
	120 mM NaCl + Uninoculated	↓ 18% SL ↓ 12% TPFW	↑ 33% ABA ↑ 114% SA ↓ 11% JA	↓ 11% total Chl	N/A	↑ 301% SOD	↓ 23% total PP	N/A	In whole plant: ↑ 86% Na^+, ↑ 55% P	Kang et al. (2014) b
	0 mM NaCl + *P. putida*	↑ 17% SL ↑ 8% TPFW	↑ 18% ABA ↑ 29% SA ↓ 25% JA	↑ 12% total Chl		↑ 2% SOD	Unchanged total PP		In whole plant: ↓ 17% Na^+, ↑ 22% P	
	120 mM NaCl + *P. putida*	↓ 9% SL, Unchanged TPFW	↓ 6% ABA ↓ 26% SA ↑ 54% JA	↓ 7% total Chl		↑ 4% SOD	↑ 4% total PP		In whole plant: ↑ 45% Na^+, ↑ 30% P	

B. pumilus. 14-day-old rice seedlings inoculated with *B. pumilus*, 10 ppm Boron, 150 mM NaCl, and 10 ppm Boron + 150 mM NaCl, 8 weeks.	0mM NaCl + Uninoculated									Khan et al. (2016)
	0 mM NaCl + *B. pumilus*	↑ 22% SFW		↑ 46% total Chl		↑ 22% SOD ↑ 20% POD ↑ 73% CAT		↑ 7%	In shoot: ↓ 54% Na^+, ↑ 57% K^+, ↑ 76% Mg^{2+}, ↑ 18% Ca^{2+}, Na^+/K^+ ratio ~ 0.27	
	10 ppm Boron + Uninoculated	Unchanged SFW		↓ 18% total Chl		↑ 274% SOD ↑ 212% POD ↑ 204% CAT		↑ 41%	In shoot: ↓ 23% Na^+, ↑ 7% K^+, ↑ 5% Mg^{2+}, ↑ 0% Ca^{2+}, Na^+/K^+ ratio ~ 0.67	
	10 ppm Boron + Inoculated	↑ 18% SFW		↑ 59% total Chl		↑ 400% SOD ↑ 272% POD ↑ 254% CAT		↑ 74%	In shoot: ↓ 31% Na^+, ↑ 61% K^+, ↑ 67% Mg^{2+}, ↑ 18% Ca^{2+}, Na^+/K^+ ratio ~ 0.4	
	150 mM NaCl + Uninoculated	↓ 10% SFW		↓ 9% total Chl		↑ 248% SOD ↑ 168% POD ↑ 204% CAT		↑ 56%	In shoot: ↑ 458% Na^+, ↓ 50% K^+, ↓ 38% Mg^{2+}, ↓ 76% Ca^{2+}, Na^+/K^+ ratio ~ 10.4	
	150 mM NaCl + *B. pumilus*	↑ 11% SFW		↑ 86% total Chl		↑ 348% SOD ↑ 220% POD ↑ 273% CAT		↑ 83%	In shoot: ↑ 185% Na^+, ↑ 24% Mg^{2+}, ↓ 7% K^+, ↓ 18% Ca^{2+}, Na^+/K^+ ratio ~3	
	10 ppm Boron + 150 mM NaCl + Uninoculated	↓ 10% SFW		↓ 23% total Chl		↑ 300% SOD ↑ 388% POD ↑ 377% CAT		↑ 146%	In shoot: ↑ 531% Na^+, ↓ 32% K^+, ↓ 33% Mg^{2+}, ↓ 27% Ca^{2+}, Na^+/K^+ ratio ~ 8.6	
	10 ppm Boron + 150 mM	↑ 3% SFW		↓ 5% total Chl		↑ 322% SOD ↑ 316% POD ↑ 254% CAT		↑ 85%	In shoot: ↑ 115% Na^+, ↓ 11% K^+, ↓ 5% Mg^{2+}, ↓ 4% Ca^{2+}, Na^+/K^+ ratio ~ 2.2	

	NaCl + *B. pumilus*									
C. gleum SUK. Wheat plantlets inoculated with *C. gleum*, 100 mM NaCl at 48h of intervals, 30 days.	0 mM NaCl + Uninoculated									Bhise et al. (2017)
	100 mM NaCl + Uninoculated	↓ 41% SL, ↓ 46% RL, ↓ 16% TPFW		↓ 36% total Chl			↑ 80% FLA	↑ 31%	In shoot: ↑ 128% Na^+, ↓ 30% K^+, Na^+/K^+ ratio ~ 0.12	
	0 mM NaCl + SUK + FLI	↓ 13% SL, ↓ 14% RL, ↓ 0% TPFW		↑ 18% total Chl			↑ 96% FLA	↑ 48%	N/A	
	100 mM NaCl + SUK + FLI	↓ 9% SL, ↓ 9% RL, ↑ 19% TPFW		↑ 5% total Chl			↑ 147% FLA	↑ 63%	In shoot: ↑ 61% Na^+, ↓ 19% K^+, Na^+/K^+ ratio ~ 0.08	
	0 mM NaCl + SUK	↓ 16% SL, 36% RL, 13% TPFW		↓ 11% total Chl			↑ 57% FLA	↑ 25%	N/A	
	100 mM NaCl + SUK	↓ 19% SL, ↓ 9% RL, ↓ 6% TPFW		↓ 23% total Chl			↑ 84% FLA	↑ 47%	In shoot: ↑ 67% Na^+, ↓ 19% K^+, Na^+/K^+ ratio 0.08	
B. aquimaris DY-3. Three-day old maize seedlings were inoculated with DY-3	0 mM NaCl + Uninoculated									Li and Jiang (2017)
	1% (w/v) NaCl + Uninoculated	↓ 34% TPDW		↓ 13% total Chl	↑ 39%	↑ 21% SOD ↑ 16% POD ↑18% CAT ↑ 23% APX	↑ 22% PHE	↑ 36%	N/A	
	0% NaCl + DY-3	↑ 12% TPDW		↑ 5% total Chl	↓ 8%	↑ 13% SOD ↑ 9% CAT ↑ 9% APX ↓ 12% POD	↑ 11% PHE	↑ 24%		

	1% (w/v) NaCl + DY-3	↓ 13% TPDW		↓ 9% total Chl	↑ 26%	↑ 53% SOD ↑ 42% CAT ↑ 65% APX ↓ 2% POD	↑ 67% PHE	↑ 77%		
Klebsiella IG3. Oat seedlings inoculated with IG3	0 mM NaCl + Uninoculated									Sapre et al. (2018)
	100 mM NaCl + Uninoculated	↓ 22% SL, ↓ 31% SFW, ↓ 29% RFW, ↓ 18% RL	↓ 6% IAA	↓ 22% total Chl	In shoot: ↑ 135% In root: ↑ 231%	↑ 353% SOD ↑ 540% POD		↑ 230%		
	0 mM NaCl + IG3	↑ 3% SL, ↑ 3% SFW, ↑ 1% RFW, ↑ 13% RL	↑ 41% IAA	↑ 4% total Chl	In shoot: ↑ 3% In root: ↑ 18%	↑ 0% SOD ↑ 2% POD		↑ 42%		
	100 mM NaCl + IG3	↓ 10% SL, ↓ 18% SFW, ↓ 16% RFW, ↓ 2% RL	↑ 67% IAA	↓ 13% total Chl	In shoot: ↑ 27% In root: ↑ 45%	↑ 96% SOD ↑ 286% POD		↑ 155%		
P. yonginensis DCY84. Root seedlings of ginseng inoculated with *P. yonginensis* DCY84	Short period of stress (3 days of 300 mM NaCl exposure)									Sukweenadhi et al. (2018)
	0 mM NaCl + Uninoculated								In shoot: Na^+/K^+ ratio ~ 13 In root: Na^+/K^+ ratio ~ 11	
	0 mM NaCl + DCY84	↑ 15% SFW, ↑ 5% RFW		↑ 3% Chl a ↑ 2% Chl b ↑ 2% Car	Unchanged	↑ 62% APX ↑ 40% POD ↑ 114% CAT		↑ 253%	In shoot: Na^+/K^+ ratio ~15 In root: Na^+/K^+ ratio ~11	
	300 mM NaCl + Uninoculated	↓ 13% SFW, ↓ 9% RFW		↓ 15% Chl a ↓ 13% Chl b ↓ 16% Car	↑ 29%	↑ 55% POD ↑ 0% APX ↓ 14% CAT		↑ 20%	In shoot: Na^+/K^+ ratio ~6.4 In root: Na^+/K^+ ratio ~ 7	
	300 mM NaCl + DCY84	↑ 12% SFW, ↑ 0% RFW		↑ 3% Chl a ↓ 2% Chl b ↓ 9% Car	↑ 21%	↑ 54% APX ↑ 80% POD ↑ 114% CAT		↑ 233%	In shoot: Na^+/K^+ ratio ~8.2 In root: Na^+/K^+ ratio ~9.8	
	Long period of stress (12 days of 300 mM NaCl exposure)									

	0 mM NaCl + Uninoculated								In shoot: Na^+/K^+ ratio ~ 7.2; In root: Na^+/K^+ ratio ~ 9.9	
	0 mM NaCl + DCY84	↑ 17% SFW, 1% RFW	N/A	↑ 3% Chl a ↑ 2% Chl b ↓ 2% Car	Unchanged	↑ 45% APX ↑ 100% POD ↑ 143% CAT	N/A	↑ 300%	In shoot: Na^+/K^+ ratio ~ 7.8, In root: Na^+/K^+ ratio ~ 11	
	300 mM NaCl + Uninocu-lated	↓ 18% SFW, 22% RFW		↓ 53% Chl a ↓ 66% Chl b ↓ 57% Car	↑ 36%	↓ 31% APX ↓ 33% POD ↓ 71% CAT		↑ 13%	In shoot: Na^+/K^+ ratio ~ 4.4, In root: Na^+/K^+ ratio ~ 3.8	
	300 mM NaCl + DCY84	↑ 12% SFW, ↓ 3% RFW		↓ 3% Chl a ↓ 11% Chl b ↓ 7% Car	↑ 14%	↑ 90% APX ↑ 317% POD ↑ 343% CAT		↑ 287%	In shoot: Na^+/K^+ ratio ~ 6.5, In root: Na^+/K^+ ratio ~ 7.7	
B. megaterium A12 (BMA12). Ten-day old tomato seedlings inoculated with BMA12	0 mM NaCl + Uninoculated									Akram et al. (2019)
	200 mM NaCl + Uninoculated	↓ 37% PH, ↓ 50% RL, ↓ 59% TPFW, ↓ 54% TPDW, ↓ 35% TLA	↓ 32% IAA ↓ 43% GA4 ↑ 100% C_2H_4, ↑ 82% ABA	↓ 32% Chl a ↓ 40% Chl b ↓ 41% total Chl ↓ 49% Car	N/A	↑ 24% SOD ↑ 27% CAT ↓ 24% APX ↓ 24% POD ↓ 57% PPO	↑ 74% GSH, ↑ 228% ASC	N/A	N/A	
	0 mM NaCl + BMA12	↑ 23% PH, ↑ 37% RL, ↑ 28% TPFW, ↑ 40% TPDW, ↑ 25% TLA	↑ 53% IAA, ↑ 170% GA4 ↓ 16% C_2H_4, ↓ 14% ABA	↑ 53% Chl a, ↑ 14% Chl b, ↑ 41% total Chl ↑ 35% Car		↑ 86% SOD ↑ 54% CAT ↑ 34% APX ↑ 37% POD ↑ 55% PPO	↑ 17% GSH ↑ 5% ASC			
	2000 mM NaCl + BMA12	↓ 13% PH, ↓ 28% RL, ↓ 33% TPFW, ↓ 35% TPDW, ↓ 21% TLA	↑ 0% IAA ↑ 11% C_2H_4 ↑186%	↑ 5% Chl a ↓ 17% Chl b, ↓ 4% total Chl,		↑ 213% SOD ↑ 91% CAT ↑ 78% APX ↑ 18% POD	↑ 252% GSH ↑ 100% ASC			

			ABA, ↑ 86% GA4	↓ 24% Car		↓ 10% PPO				
Pseudomonas (wild-type UW4 and mutant strains). Seven-day old tomato plants inoculated with UW4.	0 mM NaCl + Uninoculated									Orozco-Mosqueda et al. (2019)
	200 mM NaCl + Uninoculated	↓ 56% RL, ↓ 37% SL, ↓ 37% TPDW	N/A	↓ 42% total Chl	N/A					
	200 mM NaCl + WT UW4	↑ 16% RL, ↑ 3% SL, ↑ 25% TPDW		↑ 31% total Chl						
	200 mM NaCl + acdS-mutant	↓ 33% RL, ↓ 9% SL, ↓ 17% TPDW		↓ 25% total Chl						
	200 mM NaCl + treS- mutant	↓ 39% RL, ↓ 31% SL, ↓ 8% TPDW		↓ 13% total Chl						
	200 mM NaCl + acdS-/treS- double mutant	↓ 58% RL, ↓ 37% SL, ↓ 35% TPDW		↓ 56% total Chl						
	200 mM NaCl + OxtreS	↑ 45% RL, ↑ 3% SL, ↑ 54% TPDW		↑ 61% total Chl						
S. maltophilia BJ01. Seven-day old peanut seedlings inoculated with BJ01	0 mM NaCl + Uninoculated									Alexander et al. (2020)
	0 mM NaCl + BJ01	↑ 4% SL, ↑ 11% TPFW, ↓ 15% RL	↑ 19% auxin	↑ 11% Chl a, ↑ 0% Chl b, ↑ 17% total Chl	↓ 26%	N/A		↓ 32 %	N/A	
	100 mM NaCl + Uninoculated	↑ 9% RL, ↓ 45% TPFW, ↓ 39% SL	↑ 16% auxin	↓ 56% Chl a, ↓ 42% Chl b, ↓ 50%	↑ 47%			↑ 1355%		

				total Chl					
	100 mM NaCl + BJ01	↓ 26% SL, ↓ 3% RL, ↓ 26% TPFW	↑ 29% auxin	↓ 11% Chl a, ↓ 34% Chl b, ↓ 23% total Chl	↑ 16%		↑ 1173%		

Abbreviation in the Table 1: ABA, Abscisic acid; *A. calcoaceticus, Acinetobacter calcoaceticus; A. aneurinilyticus, Aneurinibacillus aneurinilyticus;* APX, Ascorbate peroxidase; ASC, Ascorbate; *B. aquimaris, Bacillus aquimaris*; *B. brevis, Bacillus brevis*; *B. cepacia, Burkholdera cepacia*; *B. megaterium, Bacillus megaterium; B. pumilus, Bacillus pumilus;* C_2H_4, ethylene; Car, Carotenoids; CAT, Catalase; *C. gleum, Chryseobacterium gleum;* Chl, Chlorophyll; *E. aerogenes*, *Enterobacter aerogenes*; FLA, Flavonoids; FLI, Feather lysate inoculum; GA4, Gibberellins 4; GSH, Glutathione; IAA, Indole-3-acetic acid; JA, Jasmonates; MDA, Malondialdehyde; N/A, Not available; *P. fluorescence, Pseudomonas fluorescence;* PH, Plant height; PHE, Phenols; POD, Peroxidase; PP, Polyphenol; *P. putida, Pseudomonas putida;* PPO, Polyphenol oxidase; Pro, Proline; *P. yonginensis, Paenibacillus yonginensis*; RDW, Root dry weight; RFW, Root fresh weight; RL, Root length; SA, Salicylic acid; SDW, Shoot dry weight; SFW, Shoot fresh weight; SL, Shoot length; *S. maltophilia, Stenotrophomonas maltophilia;* SOD, Superoxide dismutase; TLA, Total leaves area per plant; TPDW, Total plant dry weight; TPFW, Total plant fresh weight; *X. autotrophicus, Xanthobacter autotrophicus*; Y, Yield.

3.1.4. Improvements of growth parameters, nutrients uptake, and photosynthesis in PGPR-primed seeds and their respective seedlings under salinity conditions

Seed is a dramatically important component of agricultural production since it is considered the primary determinant in establishing a fruitful crop. Moreover, seed germination is one of the first and the most critical stages of the plant's life cycle [120]. The uniformity of seed germination is one of the fundamental criteria that is used to evaluate seed vigor [121]. In the era of climate change, seeds always suffer from the environmental challenges that may cause the reduction in seed germination rate and/or the dysfunction of seedlings, resulting in a decrease in ultimate crop yields. Seed biopriming with living PGPR inoculum stimulates a speed and uniformity of gemination, assures a rapid, uniform, and high establishment of crops, thereby improving yield and fruit/grain quality in various harsh conditions [122].

In the study of Cheng et al. [18], the ACC deaminase-producing *P. putida* UW4 was used as a tool for seed biopriming to investigate its ameliorative effects on the primed canola seeds against salt toxicity. Under 250 mM NaCl treatment, the shoot fresh weight (SFW) and shoot dry weight (SDW) of *P. putida* UW 4-inoculated canola plants (*Brassica napus* L.) were 1.7-fold higher than those of untreated plants. However, the *P. putida* ACC deaminase (AcdS) minus mutant-inoculated canola plants did not show significant difference in SFW and SDW relative to the untreated plants, indicating the critical role of a functional ACC deaminase enzyme in plant growth under salinity stress. The proteins involved in photosynthesis in the WT *P. putida* UW4 plants were downregulated, however, to a lesser extent as compared to that in the uninoculated plants or in the *P. putida* AcdS plants, resulting in the higher chlorophyll contents relative to the uninoculated plants. Surprisingly, both AcdS and WT *P. putida* plants could accumulate large amount of NaCl in their shoots with 3.7–7-fold higher than that in the uninoculated plants, respectively while being able to maintain their normal growth. This could be partly explained by the increase cell permeability caused by IAA that was produced by the WT *P. putida* and the AcdS mutant. This finding is intriguing and controversial since numerous other studies recognized the decreased Na^+ uptake in PGPR-bacterized plants [32,34,91,103].

Under non-stress conditions, the germination rates of two endangered fir plant species *Abies hickelii* and *Abies religiosa* were highly stimulated by a combination of 12 h-hydropriming with PGPR biopriming, resulting an improved germination rate up to 91% of *P. fluorescens* JUV8-primed *A. hickelli* seeds vs. 28% of unprimed control and up to 68% of *B. subtilis* BsUV-primed *A. religiosa* seeds vs. 32% of unprimed control [123]. Similarly, the germination rate of isolate Ac26-primed wheat seeds was increased to 93.3% and the vigor index was 2830.7, much higher than those of the unprimed control with 53.3% and 1097.5, respectively [124]. The subsequent development of primed plants was also better than the unprimed plants, suggesting the lasting impacts of PGPR treatment on physio-biochemical attributes of the treated plants [123,124].

Under salt conditions, seed biopriming using PGPR not only enhances germination rates, also promotes morphological and biochemical parameters in respective primed seedlings. Sarkar et al. (2018) [48] found that the germination of rice seeds (*Oryza sativa* cv. Swarnamasuri) was tremendously suppressed at 185 mM NaCl concentration with only 50% germinated seeds, while that value of the *Burkholderia*-primed seeds was approximately 85%. In their another study, Sarkar et al. (2018) [41] primed the rice seeds (*Oryza sativa* cv. Ratna) with *Enterobacter* sp. P23 and achieved greater germination rate (76% vs. 48%), as well as seedling vigor index (881.6 vs. 57.6) relative to the unprimed seeds. Subsequently, the growth and development of the respective primed rice seedlings were better than the unprimed control, representing via greater SFW, RFW, SDW, RDW, SL, RL, amylase, protease, auxin, Chl values [41,48]. In the study of Zhu et al. (2020) [99], the treatment with 130 mM NaCl severely affected the germination rate of the non-primed alfalfa seeds (*Medicago sativa* L.) in comparison with the primed seeds. Specifically, the gemination rate of the non-primed seeds reduced to 29% versus 32% of *B. megaterium* NRCB001-primed seeds, 42% of *B. subtilis* NRCB002, and 40% of *B. subtilis* NRCB003. Also in Zhu et al. [99],

the vegetative parameters such as PH, RL, NL, TLA, TPDW of primed seedlings were always higher than those of unprimed seedlings and the MDA content in their leaves were lower, suggesting a less injured cellular membrane in the primed alfalfa grass.

Regarding the synergy between different PGPR and/or between the microbes and chemicals, the synergistic effects of a consortium (*A. aneurinilyticus* + *Paenibacillus* sp.) were observed via the maximum physio-morphology parameters of primed French bean seedlings (*Phaseolus vulgaris*) in comparison to uninoculated- or individual *A. aneurinilyticus* and *Paenibacillus*-primed seedlings [80]. Two volatile organic compounds (VOCs), namely 4-nitroguaiacol and quinoline derived from *Pseudomonas simiae* exhibited their ability to induce soybean seed germination under 100 mM NaCl treatment [125]. Furthermore, the combined treatment of sodium nitroprusside (SNP) and *P. simiae* resulted in the higher biomass, the lower MDA content and electrolyte leakage in the treated soybean plants than other treatment plants [125]. Melatonin (Mel) (N-acetyl-5-methoxytryptamine) is a ubiquitous, highly conserved molecule among living organisms, and it exhibits pleiotropic biological activities such as growth regulation [126] and antioxidative property [127]. Abd El-Ghany and Attia (2020) [106] found that the combination of Mel and peat-based inoculants (*Rhizobium leguminosarum*, a N fixing bacterium, and *Azotobacter chroococcum*, an EPS-producing bacterium) synergistically enhanced salt stress tolerance in faba bean plants (*Vicia faba*) as compared to Mel- or inoculants-treated seeds alone. Specifically, in the combined treatment (100 µM Mel + inoculants), the content of Chl a, Chl b, Car, and Pro reached the highest, suggesting the synergistic effects of melatonin and beneficial PGPR in improving plant growth and other physiological aspects in salt stress conditions. The combination of Mel and bacterial inoculants, in contrast, helped to boost the faba bean plant growth, to increase photosynthetic pigments, proline, NPK uptake, and to reduce the Na^+/K^+ ratio.

Table 2. The use of PGPR in seed biopriming technique for improving salinity stress tolerance in plants.

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PGPR	Treatments	Growth parameters and yield	Photosynthetic pigments	Antioxidant enzymes	Lipid peroxidation (MDA)	Ion contents	Proline	Ethylene	Sources
P. putida (WT UW4 and Acd mutant strain). Seeds of *Brassica napus* var. Westar canola treated with bacterial suspension at room temperature, 1 h.	0 mM NaCl + Unprimed								Cheng et al. (2012)
	250 mM NaCl + Unprimed	↓ 54% SFW, ↓ 60% SDW	↓ 61% total Chl	N/A	N/A	In shoot: ↑ 178% Na^+ In root: ↑ 291% Na^+	N/A	↑ 1304%	
	250 mM NaCl + UW4	↓ 23% SFW, ↓ 22% SDW	↓ 44% total Chl			In shoot: ↑ 1246% Na^+ In root: ↑ 314% Na^+		↑ 400%	
	250 mM NaCl + Acd mutant	↓ 52% SFW, ↓ 65% SDW	↓ 60% total Chl			In shoot: ↑ 667% Na^+; In root: ↑ 287% Na^+		↑ 1296%	
S. maltophilia SBP-9. Bacterized wheat seeds with *S. maltophilia* SBP-9 for 1 h.	0 mM NaCl + Unprimed								Singh and Jha (2017)
	0 mM NaCl + SBP-9	↑ 15% SL, ↑ 10% RL, ↑ 12% SFW, ↑ 17% SDW, ↑ 33% RFW, ↑ 9% RDW	↑ 8% total Chl	↑ 33% SOD, ↑ 20% CAT, ↑ 33% POD	↓ 27%	In shoot: ↓ 4% Na^+, ↑ 12% K^+, Na^+/K^+ ratio ~ 0.54	↓ 10%	N/A	
	150 mM NaCl + Unprimed	↓ 11% SL, ↓ 5% RL, ↓ 8% SFW, ↓ 24% SDW, ↓ 11% RFW, ↓ 23% RDW	↓ 15% total Chl	↑ 58% SOD, ↑ 7% CAT, ↑ 67% POD	↑ 17%	In shoot: ↑ 48% Na^+, ↓ 17% K^+; Na^+/K^+ ratio ~ 1.12	↑ 74%		
	150 mM NaCl + SBP-9	↑ 4% SL, ↑ 15% RL, ↑ 4% SFW, ↑ 7% SDW, ↑ 22% RFW, ↓ 5% RDW	↑ 5% total Chl	↑ 133% SOD, ↑ 93% CAT, ↑ 133% POD	↓ 13%	In shoot: ↑ 20% Na^+, ↑ 3% K^+ Na^+/K^+ ratio ~ 0.73	↑ 23%		
	200 mM NaCl + Unprimed	↓ 37% SL, ↓ 20% RL, ↓ 32% SFW, ↓ 38% SDW, ↓ 33% RFW, ↓ 64% RDW	↓ 59% total Chl	↑ 217% SOD, ↑ 100% CAT, ↑ 192% POD	↑ 93%	In shoot: ↑ 107% Na^+, ↓ 25% K^+; Na^+/K^+ ratio ~ 1.73	↑ 165%		

	200 mM NaCl + SBP-9	↓ 11% SL, ↓ 5% RL, ↓ 16% SFW, ↓ 17% SDW, ↓ 6% RFW, ↓ 41% RDW	↓ 39% total Chl	↑ 350% SOD ↑ 180% CAT ↑ 283% POD	↑ 50%	In shoot: ↑ 54% Na^+, ↓ 3% K^+ Na^+/K^+ ratio ~ 1	↑ 110%		
Enterobacter P23. Seeds of *Oryza sativa* cv. Ratna were treated with bacterial suspension, 28 ± 2°C temperature, 70–80% humidity, 150 mM NaCl.	0 mM NaCl + Unprimed								Sarkar et al. (2018)
	150 mM NaCl + Unprimed	↓ 51% GP, ↓ 97% SVI, ↓ 45% SFW, ↓ 58% SDW, ↓ 33% SL, ↓ 39% RFW, ↓ 63% RDW, ↓ 44% RL	↓ 54% Chl a, ↓ 80% Chl b, ↓ 56% total Chl	↑ 120% SOD, ↑ 112% CAT, ↑ 174% POD, ↑ 700% PPO	↑ 300%	N/A	↑ 175%	N/A	
	150 mM NaCl + P23	↓ 22% GP, ↓ 58% SVI, ↓ 16% SFW, ↓ 11% SL, ↓ 23% SDW, ↓ 15% RFW, ↓ 30% RDW, ↓ 11% RL	↓ 13% Chl a, ↓ 10% Chl b, ↓ 8% total Chl	↑ 32% SOD, ↑ 46% CAT, ↑ 70% POD, ↑ 300% PPO	↑ 195%		↑ 75%		
B. pumilus FAB10. Wheat seeds cv. 343 inoculated with FAB10; 75, 125, 250 mM NaCl, 120 days	0 mM NaCl + Unprimed								Ansari et al. (2019)
	75 mM NaCl + Unprimed	↓ 17% SL, ↓ 35% RL, ↓ 49% SDW, ↓ 53% RDW, ↓ 35% SpDW, ↓ 21% GY, ↓ 17% GPr	N/A	↑ 20% SOD, ↑ 40% CAT, ↑ 50% GR	↑ 189%	N/A	↑ 105%		
	125 mM NaCl + Unprimed	↓ 24% SL, ↓ 49% RL, ↓ 42% SDW, ↓ 67% RDW, ↓ 48% SpDW, ↓ 31% GY, ↓ 22% GPr		↑ 23% SOD, ↑ 80% CAT, ↑ 75% GR	↑ 189%		↑ 146%		
	250 mM NaCl + Unprimed	↓ 35% SL, ↓ 52% RL, ↓ 40% SDW, ↓ 76% RDW, ↓ 61% SpDW, ↓ 41% GY, ↓ 29% GPr		↑ 25% SOD, ↑ 80% CAT, ↑ 75% GR	↑ 260%		↑ 171%		
	75 mM NaCl + FAB10	↓ 13% SL, ↓ 11% RL, ↓ 13% SDW, ↓ 20% RDW, ↓ 4% SpDW, ↓ 3% GY, ↓ 11% GPr		↑ 5% SOD, ↓ 20% CAT, ↓ 25% GR	↑ 103%		↑ 77%		

	125 mM NaCl + FAB10	↓ 17% SL, ↓ 22% RL, ↓ 18% SDW, ↓ 43% RDW, ↓ 9% SpDW, ↓ 13% GY, ↓ 16% GPr		↑ 10% SOD, ↑ 20% CAT, ↑ 0% GR	↑ 180%		↑ 123%		
	250 mM NaCl + FAB10	↓ 25% SL, ↓ 24% RL, ↓ 18% SDW, ↓ 51% RDW, ↓ 61% SpDW, ↓ 25% GY, ↓ 27% GPr		↑ 12% SOD, ↑ 20% CAT, ↑ 0% GR	↑ 237%		↑ 139%		
Consortium (*R. leguminosarum* + *A. chroococcum*) and/or Mel. Vicia faba seeds were treated with the consortium as peat-based inoculant and/or Mel solution	Saline soil (6.5 dS/m); 0 µM Mel + Unprimed								
	25 µM Mel + Unprimed	↑ 6% SL, ↑ 37% NL, ↑ 18% SFW, ↑ 24% SDW, ↑ 23% Y	↑ 6% Chl a, ↑ 11% Chl b, ↑ 9% Car	N/A	N/A	N/A	↑ 17%	N/A	Abd El-Ghany & Attia (2020)
	50 µM Mel + Unprimed	↑ 24% SL, ↑ 56% NL, ↑ 41% SFW, ↑ 36% SDW, ↑ 41% Y	↑ 30% Chl a, ↑ 26% Chl b, ↑ 18% Car				↑ 30%		
	100 µM Mel + Unprimed	↑ 41% SL, ↑ 93% NL, ↑ 72% SFW, ↑ 78% SDW, ↑ 58% Y	↑ 44% Chl a, ↑ 80% Chl b, ↑ 35% Car				↑ 39%		
	0 µM Mel + Primed	↑ 18% SL, ↑ 43% NL, ↑ 25% SFW, ↑ 36% SDW, ↑ 48% Y	↑ 31% Chl a, ↑ 35% Chl b, ↑ 28% Car				↑ 44%		
	25 µM Mel + Primed	↑ 30% SL, ↑ 79% NL, ↑ 49% SFW, ↑ 56% SDW, ↑ 71% Y	↑ 42% Chl a, ↑ 59% Chl b, ↑ 43% Car				↑ 57%		
	50 µM Mel + Primed	↑ 70% SL, ↑ 97% NL, ↑ 68% SFW, ↑ 68% SDW, ↑ 82% Y	↑ 56% Chl a,				↑ 89%		

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		↑ 107% Chl b, ↑ 66% Car						
100 µM Mel + Primed	↑ 74% SL, ↑ 118% NL, ↑ 98% SFW, ↑ 104% SDW, ↑ 96% Y	↑ 71% Chl a, ↑ 118% Chl b, ↑ 71% Car				↑ 110%		
Non-saline soil 0 µM Mel + Unprimed								
25 µM Mel + Unprimed	↑ 6% SL, ↑ 14% NL, ↑ 10% SFW, ↑ 21% SDW, ↑ 18% Y	↑ 9% Chl a, ↑ 10% Chl b, ↑ 4% Car				↑ 5%		
50 µM Mel + Unprimed	↑ 12% SL, ↑ 35% NL, ↑ 23% SFW, ↑ 31% SDW, ↑ 29% Y	↑ 11% Chl a, ↑ 24% Chl b, ↑ 21% Car				↑ 11%		
100 µM Mel + Unprimed	↑ 16% SL, ↑ 49% NL, ↑ 38% SFW, ↑ 69% SDW, ↑ 32% Y	↑ 16% Chl a, ↑ 34% Chl b, ↑ 24% Car				↑ 45%		
0 µM Mel + Primed	↑ 20% SL, ↑ 28% NL, ↑ 14% SFW, ↑ 27% SDW, ↑ 17% Y	↑ 17% Chl a, ↑ 24% Chl b, ↑ 21% Car				↑ 36%		
25 µM Mel + Primed	↑ 29% SL, ↑ 49% NL, ↑ 24% SFW, ↑ 46% SDW, ↑ 25% Y	↑ 23% Chl a, ↑ 30% Chl b, ↑ 30% Car				↑ 94%		
50 µM Mel + Primed	↑ 45% SL, ↑ 55% NL, ↑ 33% SFW, ↑ 57% SDW, ↑ 38% Y	↑ 26% Chl a, ↑ 42% Chl b, ↑ 33% Car				↑ 110%		

	100 µM Mel + Primed	↑ 49% SL, ↑ 76% NL, ↑ 52% SFW, ↑ 87% SDW, ↑ 45% Y	↑ 30% Chl a, ↑ 29% Chl b, ↑ 40% Car				↑ 139%		
A. aneurinilyticus ACC02, *Paenibacillus* ACC06 and Consortium (ACC02+ ACC06). French bean seeds inoculated with ACC02, ACC06 and consortium (ACC02 + ACC06) in normal and 25 mM NaCl	Normal (0 mM NaCl) + Unprimed								
	0 mM NaCl + ACC02	↑ 10% SL, ↑ 50% RL, ↑ 158% SFW, ↑ 10% SDW, ↑ 50% RFW, ↑ 21% RDW	↑ 36% total Chl	N/A	N/A	N/A	N/A	↑ 9%	Gupta and Pandey (2019)
	0 mM NaCl + ACC06	↑ 30% SL, ↑ 30% RL, ↑ 216% SFW, ↑ 10% SDW, ↑ 60% RFW, ↑ 14% RDW	↑ 29% total Chl					↓ 9%	
	0 mM NaCl + Consortium (ACC02+ ACC06)	↑ 50% SL, ↑ 70% RL, ↑ 233% SFW, ↑ 80% SDW, ↑ 90% RFW, ↑ 85% RDW	↑ 57% total Chl					↑ 27%	
	Salinity (25 mM NaCl) + Unprimed								
	25 mM NaCl + ACC02	↑ 33% SL, ↑ 79% RL, ↑ 120% SFW, ↑ 300% SDW, ↑ 46% RFW, ↑ 182 % RDW	↑ 28% total Chl	N/A	N/A	N/A	N/A	↓ 38%	
	25 mM NaCl + ACC06	↑ 47% SL, ↑ 58% RL, ↑ 120% SFW, ↑ 350% SDW, ↑ 36% RFW, ↑ 142% RDW	↑ 35% total Chl					↓ 42%	

	25 mM NaCl + Consortium (ACC02 + ACC06)	↑ 60% SL, ↑ 110% RL, ↑ 255% SFW, ↑ 425% SDW, ↑ 81% RFW, ↑ 220% RDW	↑ 57% total Chl					↓ 61%	
P. fluorescence, B. pumilus, E. aurantiacum and consortium. Wheat seeds soaked in bacterial inoculant containing single PGPR strains, and the consortium of three bacterial cultures for 2 h. Saline soil EC_e 13.41	Unprimed seeds								Nawaz et al. (2020)
	Seeds primed with *P.fluorescence*	**Galaxy-13:** ↑ 5% SL, ↑ 7% RL, ↑ 3% SFW, ↑ 2% SDW, ↑ 33% 100 GW, ↓ 13% RFW, ↓ 29% RDW **Aas-11:** ↑ 11% SL, ↑ 24% RL, ↑ 48% SFW, ↑ 144% RFW, ↑ 57% SDW, ↑ 75% RDW, ↑ 23% 100 GW	N/A	**Galaxy-13:** ↓ 30% SOD, ↓ 0% POD, ↑ 27% CAT **Aas-11:** ↓ 57% SOD, ↓ 14% POD, ↑ 25% CAT	Not mentioned	**Galaxy-13:** In root: ↑ 50% Na^+, ↑ 40% K^+, Na^+/K^+ ratio ~ 0.19 In shoot: ↑ 28% Na^+, ↑ 23% K^+, Na^+/K^+ ratio ~ 3.9 **Aas-11:** In root: ↓ 13% Na^+, ↑ 99% K^+, Na^+/K^+ ratio ~ 0.16. In shoot: ↑ 92% Na^+, ↑ 16% K^+, Na^+/K^+ ratio ~ 3.4	**Galaxy-13**: ↓ 20% **Aas-11**: ↑ 33%	N/A	
	Seeds primed with *B. pumilus*	**Galaxy-13:** ↓ 7% SL, ↓ 18% SFW, ↓ 26% SDW, ↓ 8% RFW, ↓ 57% RDW, ↑ 67% RL, 31% 100 GW **Aas-11:** ↑ 13% SL, ↑ 21% RL, ↑ 61% SFW, ↑ 678% RFW, ↑ 66% SDW, ↑ 838% RDW, ↑ 53% 100 GW		**Galaxy-13:** ↓ 35% SOD, ↓ 5% POD, ↑ 4% CAT **Aas-11:** ↓ 65% SOD, ↓ 38% POD, ↑ 35% CAT		**Galaxy-13:** In root: ↑ 0% Na^+, ↑ 34% K^+, Na^+/K^+ ratio ~ 0.13 In shoot: ↓ 8% Na^+, ↓ 19% K^+, Na^+/K^+ ratio ~ 4.3 **Aas-11:** In root: ↓ 13% Na^+, ↑ 195% K^+, Na^+/K^+ ratio ~ 0.11. In shoot: ↑ 59% Na^+, ↓ 12% K^+, Na^+/K^+ ratio ~ 3.7	**Galaxy-13:** ↑ 287% **Aas-11:** ↑ 150%		
	Seeds primed with *E.aurantiacum*	**Galaxy-13:** ↑ 6% SL, ↑ 47% RL, ↑ 3% SFW, ↑ 49% 100 GW, ↓ 17% RFW, ↓ 2% SDW, ↓ 28% RDW **Aas-11:** ↑ 10% SL, ↑ 7% RL, ↑ 52% SFW, ↑ 511% RFW, ↑ 71% SDW,		**Galaxy-13:** ↑ 2% SOD, ↑ 48% CAT, ↓ 43% POD. **Aas-11:** ↓ 65% SOD, ↓ 57% POD, ↓ 5% CAT		**Galaxy-13:** In root: ↑ 33% Na^+, ↑ 34% K^+, Na^+/K^+ ratio ~ 0.18 In shoot: ↑ 27% Na^+, ↑ 0% K^+, Na^+/K^+ ratio ~ 4.77. **Aas-11:** In root: ↓ 13% Na^+, ↑ 286% K^+, Na^+/K^+ ratio ~ 0.08	**Galaxy-13:** ↑ 227% **Aas-11:** ↑ 110%		

		↑ 713% RDW, ↑ 47% 100 GW				In shoot: ↑ 40% Na^+, ↑ 22% K^+, Na^+/K^+ ratio ~ 2.36			
	Seeds primed with consortium (*P.fluorescence* + *B. pumilus* + *E.auranti-acum*)	**Galaxy-13:** ↓ 1% SL, ↑ 73% RL, ↑ 6% SFW, ↑ 30% RFW, ↑ 7% SDW, ↑ 43% RDW, ↑ 53% 100 GW **Aas-11:** ↑ 13% SL, ↑ 3% RL, ↑ 65% SFW, ↑ 556% RFW, ↑ 77% SDW, ↑ 725% RDW, ↑ 48% 100 GW		**Galaxy-13:** ↑ 37% SOD, ↓ 32% POD, ↓ 6% CAT **Aas-11:** ↓ 57% SOD, ↑ 24% POD, ↑ 28% CAT		**Galaxy-13:** In root: ↑ 0% Na^+, ↑ 114% K^+, Na^+/K^+ ratio ~ 0.08 In shoot: ↑ 17% Na^+, ↑ 15% K^+, Na^+/K^+ ratio ~ 3.8 **Aas-11:** In root: ↑ 0% Na^+, ↑ 173% K^+, Na^+/K^+ ratio ~ 0.13 In shoot: ↑ 68% Na^+, ↑ 30% K^+, Na^+/K^+ ratio ~ 2.67	**Galaxy-13:** ↑ 327% **Aas-11:** ↑ 17%		
Sphingobacterium BHU-AV3. Bacterized tomato seeds with BHU-AV3 for 24h	0 mM NaCl + Unprimed								
	200 mM NaCl + Unprimed	↓ 52% SL, ↓ 49% RL, ↓ 54% TPDW	↓ 44% total Chl	In shoot: ↑ 90% SOD, ↑ 260% POD, ↑ 100% PPO In root: ↑ 83% SOD, ↑ 100% POD, ↑ 53% PPO	Not mentioned	In shoot: ↑ 258% Na^+, ↓ 63% K^+, Na^+/K^+ ratio ~ 3.6 In root: ↑ 190% Na^+, ↓ 53% K^+; Na^+/K^+ ratio ~ 3.5	In shoot: ↑ 153 % In root: ↑ 56%	N/A	Vaishnav et al. (2020)
	0 mM NaCl + BHU-AV3	↓ 11.3% SL, ↑ 16% RL, ↑ 11% TPDW	↑ 5% total Chl	In shoot: ↓ 20% SOD; 0% POD, 25% PPO In root: ↑ 16% SOD, ↑ 6% POD, ↓ 12% PPO		In shoot: ↑ 9% Na^+, ↑ 9% K^+, Na^+/K^+ ratio ~ 0.3 In root: ↓ 5% Na^+, ↑ 8% K^+, Na^+/K^+ ratio ~ 0.5	In shoot: ↓ 7 % In root: ↓ 5%		
	200 mM NaCl + BHU-AV3	↓ 30% SL, ↓ 22% RL, ↓ 29% TPDW	↓ 14% totoal Chl	In shoot: ↑ 10% SOD, ↑ 1000% POD, ↑ 50% PPO		In shoot: ↑ 130% Na^+, ↓ 20% K^+, Na^+/K^+ ratio ~ 1	In shoot: ↑ 84 % In root:		

				In root: ↑ 117% SOD, ↑ 200% POD, ↑ 71% PPO		In root: ↑ 115% Na^+, ↓ 24% K^+, Na^+/K^+ ratio ~ 1.6	↑ 111%		
K. sacchari MSK1. Mung bean seeds primed with MSK1, 40 or 80 days after sowing	0 mM NaCl + Unprimed								
	50mM NaCl + Unprimed	↓ 8% SL, ↓ 8% RL, ↓ 5% SDW, ↓ 5% RDW, ↓ 15% SY, ↓ 3% GP	↓ 15% total Chl, ↓ 4% Car	↑ 5% GR, ↑ 33% CAT, ↑ 13% SOD, ↑ 23% APX	↑ 32%	In shoor: ↑ 100% Na^+, ↑ 44% K^+, Na^+/K^+ ratio ~ 0.46, ↓ 4% N, ↓ 19% P	↑ 63%	N/A	Shahid et al. (2021)
	100mM NaCl + Unprimed	↓ 16% SL, ↓ 20% RL, ↓ 10% SDW, ↓ 15% RDW, ↓ 21% SY, ↓ 6% GP	↓ 35% total Chl, ↓ 9% Car	↑ 15% GR, ↑ 58% CAT, ↑ 39% SOD, ↑ 45% APX	↑ 47%	In shoot: ↑ 200% Na^+, ↑ 100% K^+, Na^+/K^+ ratio ~ 0.5, ↓ 4% N, ↓ 28% P	↑ 88%		
	200 mM NaCl + Unprimed	↓ 24% SL, ↓ 28% RL, ↓ 21% SDW, ↓ 35% RDW, ↓ 26% SY, ↓ 8% GP	↓ 42% total Chl, ↓ 19% Car	↑ 35% GR, ↑ 108% CAT, ↑ 52% SOD, ↑ 73% APX	↑ 84%	In shoot: ↑ 450% Na^+, ↑ 222% K^+, Na^+/K^+ ratio ~ 0.57, ↓ 12% N, ↓ 44% P	↑ 213%		
	400 mM NaCl + Unprimed	↓ 41% SL, ↓ 52% RL, ↓ 34%, ↓ 55% RDW, ↓ 34% SY, ↓ 26% GP	↓ 62% total Chl, ↓ 33% Car	↑ 64% GR, ↑ 208% CAT, ↑ 96% SOD, ↑ 102% APX	↑ 153%	In shoot: ↑ 800% Na^+, ↑ 378% K^+, Na^+/K^+ ratio ~ 0.63, ↓ 21% N, ↓ 59% P	↑ 350%		
	0 mM NaCl + MSK1	↑ 5% SL, ↑ 12% RL, ↑ 7% SDW, ↑ 15% RDW, ↑ 9% SY, ↑ 7% GP	↑ 29% total Chl, ↑ 7% Car	↓ 9% GR, ↓ 33% CAT, ↓ 22% SOD, ↓ 9% APX	↓ 37%	In shoot: ↓ 67% Na^+, ↓ 22% K^+, Na^+/K^+ ratio ~ 0.14, ↑ 9% N, ↑ 15% P	↓ 25%		
	50 mM NaCl + MSK1	↓ 3% SL, ↓ 2% SDW, ↑ 4% RL, ↑ 3% RDW, ↑ 10% SY, ↑ 2% GP	↓ 3% total Chl, ↓ 0% Car	↑ 2% GR, ↑ 8% CAT, ↑ 9% SOD, ↑ 9% APX	↑ 11%	In shoot: ↑ 33% Na^+, ↑ 22% K^+, Na^+/K^+ ratio ~ 0.36, ↓ 1% N, ↓ 41% P	↑ 30%		
	100 mM NaCl + MSK1	↓ 8% SL, ↓ 12% RL, ↓ 7% SDW, ↓ 10% RDW, ↓ 19% SY, ↓ 5% GP	↓ 31% total Chl, ↓ 8% Car	↑ 11% GR, ↑ 50% CAT, ↑ 22% SOD, ↑ 32% APX	↑ 37%	In shoot: ↑ 183% Na^+, ↑ 89% K^+, Na^+/K^+ ratio ~ 0.5, ↓ 4% N, ↓ 22% P	↑ 75%		

	200 mM NaCl + MSK1	↓ 22% SL, ↓ 16% RL, ↓ 17% SDW, ↓ 25% RDW, ↓ 24% SY, ↓ 7% GP	↓ 35% total Chl, ↓ 13% Car	↑ 33% GR, ↑ 100% CAT, ↑ 48% SOD, ↑ 64% APX	↑ 79%	In shoot: ↑ 433% Na^+, ↑ 211% K^+, Na^+/K^+ ratio ~ 0.57, ↓ 9% N, ↓ 37% P	↑ 200%		
	400 mM NaCl + MSK1	↓ 35% SL, ↓ 24% RL, ↓ 32% SDW, ↓ 48% RDW, ↓ 32% SY, ↓ 25% GP	↓ 54% total Chl, ↓ 27% Car	↑ 60% GR, ↑ 192% CAT, ↑ 91% SOD, ↑ 91% APX	↑ 137%	In shoot: ↑ 783% Na^+, ↑ 367% K^+, Na^+/K^+ ratio ~ 0.63, ↓ 19% N, ↓ 57% P	↑ 325%		

Abbreviation in the Table 2: *A. calcoaceticus, Acinetobacter calcoaceticus; A. aneurinilyticus, Aneurinibacillus aneurinilyticus; A. chroococcum, Azotobacter chroococcum*; APX, Ascorbate peroxidase; *B. pumilus, Bacillus pumilus;* Car, Carotenoids; CAT, Catalase; Chl, Chlorophyll; *E. aurantiacum, Exiguobacterium aurantiacum;* GP, Germination percentage; GPr, Grain protein; GR, Glutathione reductase; GW, Grain weight; GY, Grain yield; *K. sacchari, Kosakonia sacchari*; MDA, Malondialdehyde; Mel, Melatonin; N/A, Not available; NL, Number of leaves per plant; *P. fluorescence, Pseudomonas fluorescence;*; POD, Peroxidase; *P. putida, Pseudomonas putida;* PPO, Polyphenol oxidase; RDW, Root dry weight; RFW, Root fresh weight; *R. leguminosarum* , *Rhizobium leguminosarum* ;RL, Root length; SDW, Shoot dry weight; SFW, Shoot fresh weight; SL, Shoot length; *S. maltophilia, Stenotrophomonas maltophilia;* SOD, Superoxide dismutase; SpDW, Spike dry weight; SVI, Seedling vigor index; SY, Seed yield; TPDW, Total plant dry weight; Y, Yield.

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3.2. The reduction in antioxidant enzymes and osmolytes in PGPR-inoculated plants and PGPR-primed seedlings under salt stress

The changes in antioxidant enzymes and osmo-regulators have been noticed in both un-inoculated- and inoculated plants under normal and salinity conditions. However, the reduction or increase of these enzymes in PGPB-inoculated plants in response to salt conditions remains controversial. In the study of Kang et al. (2014a) [35], the activities of CAT, PPO, and POD enzymes and the PP contents in the inoculated plants (e.g., *B. cepacia* SE4, *Promicromonospora* sp. SE188 or *A. calcoaceticus* SE370) were lower than those in the uninoculated plants under salt stress (120 mM of NaCl). The reduced profiles of antioxidant enzymes in Kang and his colleagues' findings were in agreement with their another study on soybean using the bacterium *P. putida* H-2-3 [33] and also in line with the study of Sapre et al. [36]. According to Sapre and colleagues' findings, the *Klebsiella* sp.-treated wheat plants increased by 96% SOD and 286% POD, while the SOD and POD in untreated plants were increased by 353% and 540%, respectively. These data were in agreement with those found by Shahid et al. [25], and Sarkar et al. [41] as these investigators found that the highest antioxidant enzyme activities were recorded in the non-inoculated mung bean and rice plants, respectively. In parallel with the report of Sarkar et al. [41], Rojas-Tapias et al. [110] also recorded the highest Pro content was found in the non-inoculated maize seedling leaves under salt stress. The increase of PP contents in bacterized plants was also recorded in [33,35], however, to a lesser extent than those in the untreated plants. Similarly, Pro accumulations in the tissues of the control oat plants and the control rice plants were much higher than those in the *Klebsiella*-inoculated oat plants and *Entorobacter*-inoculated rice plants (230% and 175%, respectively vs. 155% and 75%, respectively) [36,41]. These studies showed similar findings with Manaf and Zayed [128] as the SOD activity and proline content in the cowpea plants treated with mycorrhizae or *P. fluorescence* alone were lower than those in the untreated plants under 3000 ppm NaCl irrigation regime. Manaf and Zayed assumed that the harmful effects of high salinity made the plants lose the ability to control their metabolites [128], whereas Sapre et al. [36] speculated that the treated plants did not sense much stress as the untreated plants did, leading the lower levels of antioxidant enzymes, non-enzymatic antioxidants and osmoregulators in their tissues. Misra and Chauhan [98] proposed that the reduced Pro and antioxidant enzymes in *Bacillus* sp.-treated maize plants may be due to the formation of EPS and biofilm on plant root surfaces that prevented plants from over-uptake Na^+, thereby attenuating the detrimental effects of toxic ions on plants. This assumption was corroborated by a study of Mukherjee et al. [102], who found that the amount of EPS-bound Na^+ increased with the increase in NaCl concentration in the solution, thus confirming an efficient role of EPS in NaCl sequestration. In addition, Sarkar et al. [41] explained that the increased antioxidant enzyme activities of *Enterobacter* sp. P23 under saline stress could indirectly quench a significant amount of ROS in rice seedlings, thus delaying the urge to synthesize ROS scavengers by stressed plants.

3.3. The increase in antioxidant enzymes and/or osmoregulators in PGPR-inoculated plants and PGPR-primed seedlings under salt stress

As compared with the decreased profiles of osmolytes and/or ROS-scavenging enzymes that were remarked by Kang et al. (2014 a) [35], Kang et al. (2014 b) [33], Barnawal et al. (2014) [87], Khan et al. (2016) [32], Bhise et al. (2017) [91], Abd_Allah et al. (2018) [24], Sapre et al. (2018) [36], Ansari et al. (2019) [43], Alexander et al. (2020) [40], Misra and Chauhan (2020) [98], and Shahid et al. (2021) [25], the increased activities of antioxidant enzymes and/or the elevated accumulations of osmoregulators were widely observed in PGPB-inoculated plants in the studies of Li and Jiang [34], Akram et al. [37], Vaishnav et al. [39], Khalid et al. [49], Kim et al. [88], Habib et al. [89], Kang et al. [96], Zhu et al. [99], Halo et al. [129], Bharti et al. [130], El-Esawi et al. [131], Vimal et al. [132], El-Nahrawy and Yassin [133], Sun et al. [134]. For instance, the activity of ROS-scavenging enzymes SOD, CAT of *Enterobacter*-treated okra plants was the highest amongst all treatments, in parallel with their highest vegetative parameters SFW, SDW, RFW, and RDW [89]. Likewise, APX

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activity in *Enterobacter*-inoculated tomato plants was 20% higher and DPPH assay showed 24% increase in scavenging capacity in the inoculated plants relative to the control plants [88]. In the study of Abd_Allah et al. [24], the activities of POD, CAT, GR, and SOD, and the contents of AsA, GSH and proline were always the highest in the inoculated chickpea plants. The Arabidopsis plants inoculated with *Burkholderia phytofirmans* PsJN revealed an elevated Pro accumulation in comparison with the control plants [135]. In the *Leclercia adcarboxylata*-treated tomato plants, Pro, serine (Ser), glycine (Gly), methionine (Met), and threonine (Thr), as well as citric acid (CA) and malic acid (MA) were significantly accumulated [96].

In summary, the findings in these previous studies, taken together, suggest that an increase or a reduction in the activities of antioxidant enzymes and/or osmolytes in PGPB-inoculated plants during salt stress adaptation depends mainly on the specificities of plant species, on PGPB species and on plant-microbe interactions. These controversial data indicate not only that the fine-tuning of the ROS quenchers might be critical for plants to tolerate better to salt stress, but also pose questions concerning the exact mechanisms of salt stress tolerance imposed by PGPB.

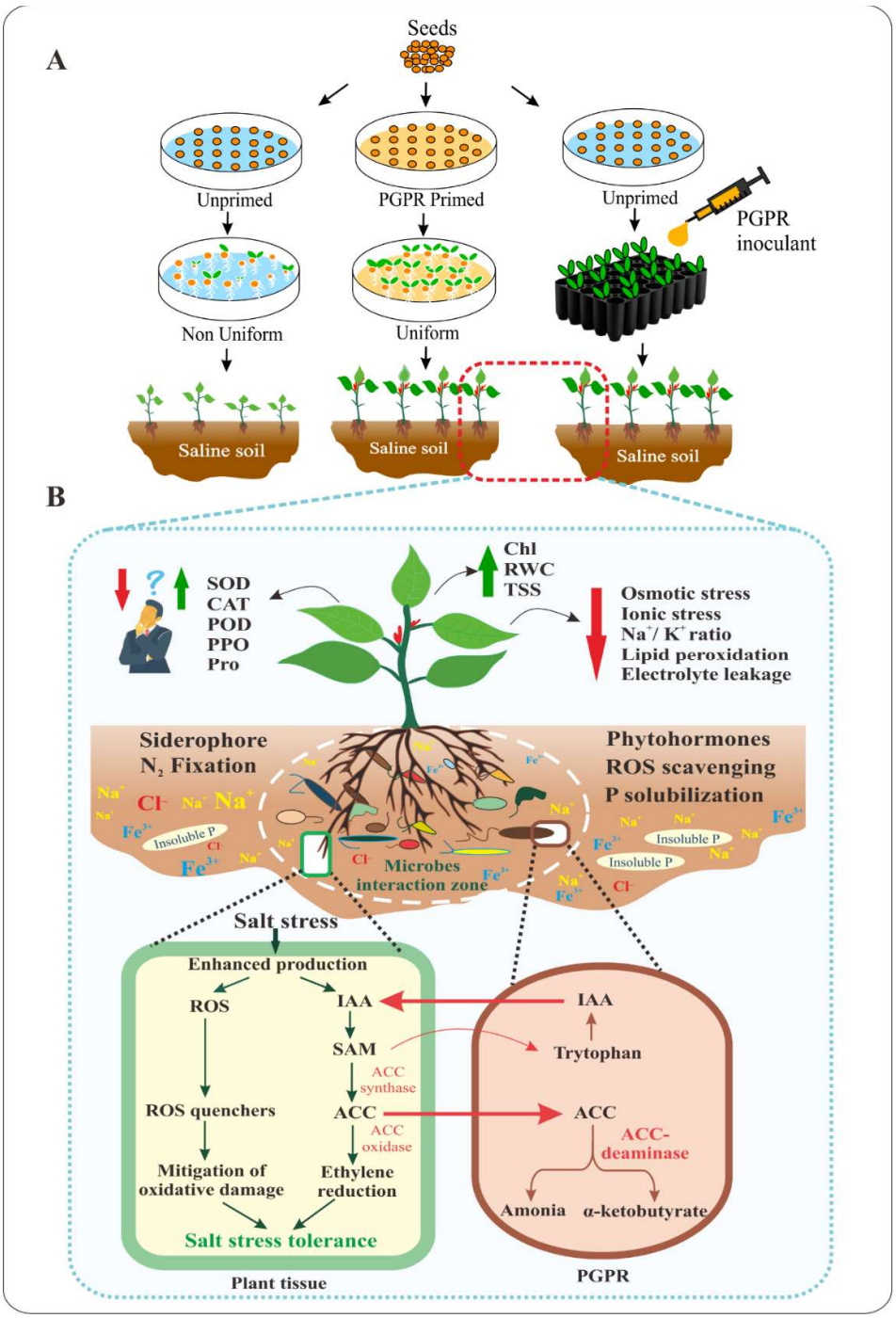

Figure 1: Roles of PGPR in alleviating salinity stress in plants. (A) represents the application of PGPR as microbial beneficial tools in seed biopriming technique and as green bio-inoculants in seedlings treatment. The primed seeds demonstrate rapid germination and robust, uniform seedlings. (B) shows positive effects of PGPR on vegetative parameters and physiological index of PGPR-inoculated plants via various mechanisms e.g., production of osmolytes, antioxidant enzymes to reduce osmotic and ionic stress, EPS suppress toxic ions uptake and ion exposure, etc. The fluctuation of antioxidant enzymes and osmolytes profiles in PGPR-treated plants is also displayed in the left panel. The middle panel demonstrates key characteristics of PGPR including the production of siderophore, phytohormones, EPS and PGP attributes like N fixation and P solubilization. The lower

panel emphasizes the importance of ACC deaminase-producing PGPR in ameliorating the inhibitory effects of excess ethylene on plant growth.

5. Conclusion

Considerable PGPB-related studies that have been carried out in the last decades help to improve our knowledge concerning advantageous characteristics of PGPB, in both basic and applied aspects. Most studies, however, focused on estimating the parameters (e.g., shoot and root length, shoot and root fresh and dry weight, etc.) in vegetative growth stage, but rarely on evaluating the parameters that are related to reproductive stage such as grain and fruit weight, numbers of flower, numbers of seed and fruit per plant, and plant yield, etc. We found a scarcity of studies that evaluated beneficial effects of PGPB on attenuating the yield loss and on improving nutrient values [43] under saline conditions [43,104,128,136–138]. In our opinion, this could be one of the main drawbacks of PGPB-related studies thus far if we consider that the improvement of crop yields, productivity, and the quality of fruit/grain under high saline conditions to be our main goal in plant agriculture studies. In addition, in some studies, the lack of important measurements regarding ion contents, ROS levels, phytohormone concentrations, and electrolyte leakage between non-saline and saline conditions in many studies make them difficult to evaluate the overall effects of PGPB on plants. Furthermore, the short exposure of plants to salinity in various studies unlikely reflects the real situation in fields where a variety of biotic and abiotic stresses endures simultaneously and lasts permanently.

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Abbreviation: *A. aneurinilyticus, Aneurinibacillus aneurinilyticus;* ABA, Abscisic acid; *A. brasilense, Azospirillum brasilense; A. calcoaceticus, Acinetobacter calcoaceticus;* ACC, 1-aminocyclopropane-1-carboxylate; Alg, Alginate; *A. macrostachyum, Arthrocnemum macrostachyum; A. protophormiae, Arthrobacter protophormiae;* APX Ascorbate peroxidase; AsA, Ascorbic acid; ASC, Ascorbate; *B. aquimaris, Bacillus aquimaris; B. gibsonii, Bacillus gibsonii; B. iodinum, Brevibacterium iodinum B. megaterium, Bacillus megaterium; B. pumilus, Bacillus pumilus;* BR, Brassinosteroids; *B. safensis, Bacillus safensis; B.subtilis, Bacillus subtilis*; CA, Citric acid; Car, Carotenoids; CAT, Catalase; *C. gleum, Chryseobacterium gleum*; Chl, Chlorophyll; Ci, Intercellular CO_2 concentration; CK, Cytokinins; DHAR, dehydroascorbate reductase; *E. aurantiacum, Exiguobacterium aurantiacum*; EL, Electrolyte leakage; EPS, Exopolysaccharide; FLA, Flavonoids; FLI, Feather lysate inoculum; FW, Fruit weight; FY, Fruit yield, GA, Gibberellins; GP, G-POD, Guaiacol peroxidase; GP, Germination percentage; GPr, Grain protein; GR, Glutathione reductase; gs, Stomatal conductance; Glutathione reductase; GSH, Glutathione; GST, Glutathione-S-transferase; GW, Grain weight; GY, Grain yield; IAA, Indole-3-acetic acid; JA, Jasmonates; K, Potassium; *K. sacchari, Kosakonia sacchari; L. adecarboxylata, Leclercia adecarboxylata;* MA, Malic acid; MDA, Malondialdehyde; MDHAR, monodehydroascorbate reductase; Mel, Melatonin; MeSA, Methyl salicylate; *M. oleivorans, Microbacterium oleivorans;* N, Nitrogen; N/A, Not available; NF, Number of fruits per plant; NL, Number of leaves per plant; NT, Number of tillers per plant; P, Phosphate; *P. agglomerans, Pantoea agglomerans; P. argentinensis, Pseudomonas argentinensis; P. azotoformans, Pseudomonas azotoformans; P. fluorescence, Pseudomonas fluorescence;* PGPR, Plant growth- promoting rhizobacteria; PH, Plant height; PHE, Phenols; POD, Peroxidase; PP, Polyphenol; PPO, Polyphenol oxidase; *P. putida, Pseudomonas putida;* Pro, Proline; P. yonginensis, Paenibacillus yonginensis RDW, Root dry weight; RFW, Root fresh weight; RL, Root length; *R. massiliae, Rhizobium massiliae;* ROS, Reactive oxygen species; RWC, Relative water content; SA, Salicylic acid;

SAM, S-adenosyl-L-methionine; SDM, Water-soluble dry matter; SDW, Shoot dry weight; SFW, Shoot fresh weight; Sid, Siderophore; SL, Shoot length; *S. maltophilia, Stenotrophomonas maltophilia;* SOD, Superoxide dismutase; SpDW, Spike dry weight; StDW, Stem dry weight; StFW, Stem fresh weight; SVI, Seedling vigor index; SW, Seed weight; SY, Seed yield; TLA, Total leaves area per plant, TPDW, Total plant dry weight; TPFW, Total plant fresh weight; Tr, Transpiration rate; Tre, Trehalose; TSS, Total soluble sugar; *X. autotrophicus, Xanthobacter autotrophicus*; Y , Yield; *Z. halotolerans, Zhihengliuella halotolerans*. p

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