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Application of Plant Growth-Promoting Bacteria as an Eco-Friendly Strategy for Mitigating the Harmful Effects of Abiotic Stress on Plants

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ABSTRACT

Plant growth-promoting bacteria (PGPB) play an important role in improving agricultural production under several abiotic stress factors. PGPB can be used to increase crop growth and development through hormonal balance and increase nutrient uptake. The positive effect of PGPB may be due to its pivotal role in morphophysiological and biochemical characteristics like leaf number, leaf area, and stem length. Furthermore, relative water content, chlorophyll content, carotenoids, antioxidant enzymes, and plant hormones were improved with PGPB treatment. Crop yield and yield components were also increased with PGPB treatment in numerous crops. The anatomical structure of plant organs was increased such as lamina thickness, stem diameter, xylem vessel diameter, and number of xylem vessels as well as phloem thickness under treatment with PGPB. Additionally, PGPB can alleviate the negative effects of several abiotic stresses by regulating the antioxidant defense system to scavenge the reactive oxygen species resulting in an improvement of yield production in the stressed plants. Additionally, gene expressions were controlled by calcium ion modulation during secondary messengers that act upon calcium-dependent protein kinase and protein phosphatases. This includes many transcription factors such as MYB, AP2/ERF, bZIP, and NAC which regulate genes related to salinity stress signals. PGPB can demonstrate induction genes of signaling under abiotic stress conditions. This review gives an outline of the PGPB role in alleviating the harmful effects of abiotic factors such as salinity, drought, and heat associated with the improvement of the morpho-physiological and biochemical features especially, leaves and branches number, leaf area, antioxidant compounds, plant hormones, and relative water content.



KEYWORDS

PGPB; salinity; drought; heat; reactive oxygen species; antioxidants; gene expressions

1 Introduction

Under field or greenhouse conditions, plants are exposed to biotic and abiotic stress factors. Biotic stress factors are caused by living organisms such as fungi [1–3], bacteria [4,5], viruses [6], insects [7–10] and weeds [11–13]. Abiotic stress factors include many stress factors, among them; drought [14–16], heat [17], and salinity [18–20] are the main abiotic stress factors. Drought stress is one of the most harmful abiotic stresses that hinders the growth of stressed plants, especially in arid regions. Under drought conditions, plant height, leaf number, and leaf area were significantly decreased in wheat [16]. Also, physiological characteristics such as chlorophyll a and b concentrations, carotenoids, and relative water content were decreased under drought conditions in several economic plants such as pea plants [21], barley [22], and sugar beet [23]. Under heat stress, the reduction in chlorophyll concentrations, decrease in fatty acids, and increase in cell membrane permeability were recorded [24]. The plants have different mechanisms to cope with these conditions such as the reduction in photosystem II efficiency. Farooq et al. [25] found that the growth and physiological characteristics of chickpea plants such as relative water content, photosynthesis, and activity of antioxidant enzymes were negatively affected under chilling stress. Additionally, salinity is one of the main abiotic stress factors, it is a detrimental stress for many plants all over the world. Salinity stress led to a decrease in the morphological characters in the stressed plants like, faba bean [26] and sweet pepper plants [27]. Under salinity conditions, reactive oxygen species are important signs, superoxide and hydrogen peroxide were significantly augmented in the salt-stressed plants [28,29], furthermore, lipid peroxidation significantly increased in pea plants under salinity conditions. These characteristics were related to oxidative stress in the stressed plants under various stresses.

The use of plant growth-promoting bacteria has become one of the most important strategies to overcome oxidative stress. PGPB naturally exists in various media, the most known genera in the agricultural improvement are *Pseudomonas*, *Paenibacillus*, *Rhizobium*, *Azospirillum*, *Bacillus*, and *Azotobacter*, they can enhance plant growth and yield via amino acids production, nitrogen fixation, and plant hormones production [25]. The positive effects of PGPB may be due to its role in the production of phytohormones, siderophores, phosphate solubilization, and antibiotics [30]. PGPB acts as biofertilizers by increasing the accessibility of water and nutrients [31] under stressful conditions [27]. Inoculation of PGPB led to an increase in the root yield of sugar beet plants [32] and the growth characteristics as well as the yield of sorghum [33]. Abdelaal [32] reported that the inoculation with plant growth-promoting bacteria led to an increase in the growth characteristics of sugar beet consequently improving the anatomical structure such as the thickness of lamina and mesophyll tissue. PGPB may take up the tryptophan exuded by roots and convert it to IAA, which may be taken up by the plant, consequently, facilitate plant growth. Application of *Azospirillum brasilense* and *Pseudomonas fluorescens* led to increased shoot biomass of *Urochloa* spp. [34]. The active role of *A. brasilense* was also recorded on shoot dry mass production of rangeland plants, dry biomass was increased in both years [35]. Several studies were carried out regarding the effect of PGPB, but the information about this effect on drought, heat, and salinity is still insufficient, therefore, this review aimed to study the pivotal role of PGPB as a promising strategy to alleviate the negative impacts of abiotic stresses in several crops and increase the yield production.

2 Alleviating Drought Stress Effects on Growth and Yield Characters Using PGPB

Drought has become a major problem threatening agricultural production and sustainability, the harmful effects on the growth and yield of drought or water deficit stress were recorded in various plants. Oxidative stress components such as superoxide ($O_2^{\bullet-}$), peroxy radical (ROO^{\bullet}), singlet oxygen (1O_2), and hydrogen peroxide (H_2O_2) were produced in mitochondria, chloroplasts, and peroxisomes as a result to stress conditions such as drought. Furthermore, plants have another defense system to deal with oxidative stress, this defense system is antioxidant components which include enzymatic antioxidants and non-enzymatic antioxidants. The main enzymatic antioxidants are glutathione reductase, peroxidase, catalase, superoxide dismutase, ascorbate peroxidase, and dehydroascorbate reductase [36,37]. However, non-enzymatic antioxidants include α -Tocopherols (Vitamin E), ascorbic acid, proline, carotenoids, and glutathione [38,39]. Additionally, under stress conditions, plants have important adaptive mechanisms like reducing the growth of the shoot system, improving solute content, and osmotic adjustment also, stomatal closing is a very significant response to reduce water loss under drought stress [40]. There are some signaling pathways regulated by phytohormones such as JA, auxins, ABA, and cytokinin that control in closure mechanism's response [41]. Another adaptive mechanism depends on the drought periods; under a short drought period, plants regulate water loss to avoid significant damage to their water-transport system. Nevertheless, under a long drought period, the evaporation was significantly increased, however, soil water decreased, resulting in a significant reduction in soil water content, consequently, decreasing cell differentiation and seedling growth [21].

Under drought conditions, plant growth-promoting bacteria can be used to improve plant growth by different mechanisms, these mechanisms include phosphorus solubilization, nitrogen uptake, and availability of essential nutrients as well as regulation of phytohormones that, maintain root structure to increase water and nutrient uptake [42,43]. Many studies showed the promotional effects of PGPB via improving water uptake and nutrient availability in soil, resulting in improving soil characters, consequently, increasing crop yield (Table 1). Application of PGPB led to improved morpho-physiological characters and yield production of various plants, through nitrogen fixation, and phosphate solubilization such as *Azoarcus* sp. [44], *Serratia* spp. [45] and *Rhizobium* spp. [46]. Additionally, the phosphorus availability was increased in the soil after treatment with phosphorus-solubilizing bacteria such as *Rhizobium* spp, *Bacillus* spp., and *Pseudomonas* spp, however, some genera of PGPB like *Bacillus mucilaginosus*, *Ferrooxidans* spp, *Paenibacillus* spp. and *Pseudomonas* sp. can solubilize potassium for plant uptake. Under drought conditions, the application of some genera of rhizobacteria led to an increase the growth characteristics and grain yield of wheat plants, this positive effect of rhizobacteria may be due to its role in increasing the production of phytohormones [47]. Moreover, García et al. [47] found that the application of *Azospirillum* led to an increase in the tolerance of maize plants to drought stress and enhanced its growth. In the experiment of Shirmohammadi et al. [48], they reported that the application of *Pseudomonas* (phosphate-solubilizing bacteria) led to increased phosphorus uptake and improved the yield of wheat plants. Previous studies showed that phosphate and phosphorus-solubilizing bacteria such as *Bacillus edaphicus*, *Bacillus mucilaginosus*, *Acidithiobacillus* sp, *Ferrooxidans* sp, *Paenibacillus* spp, and *Pseudomonas* sp. play a significant role as biofertilizer especially, under stress conditions to improve the growth and yield in the stressed plants via increasing the accessibility of free phosphorus, phosphate, increasing the efficiency of nitrogen fixation and improve the availability of essential nutrients for plant absorption [49,50].

The positive role of PGPB in enhancing plant growth under drought conditions was recorded with *Azospirillum brasilense* and *Herbaspirillum seropedicae* in maize plants [51] and *Bacillus* in pea plants [26]. This positive role could be due to the improvement of water availability and antioxidant components as well as accumulation of ABA and osmoprotectants which, improve the plant growth under drought conditions. Inoculation with *Azospirillum* led to improved growth of wheat roots and an

increase in the formation of lateral roots due to indole acetic acid production under drought conditions [52,53]. Similarly, the application of *Pseudomonas* caused an increase in fresh weight and stem height as well as chlorophyll content and salicylic acid under drought conditions [54]. Inoculation with *Azospirillum brasilense* and *Bacillus thuringiensis* led to increased nutrient concentrations, enhanced metabolic activity, relative water contents, and improved membrane stability, consequently increasing the tolerance of wheat plants and *Platycladus orientalis* plants to drought stress conditions [55]. Meenakshi et al. [56] reported that the application of *Bacillus subtilis*, *Bacillus thuringiensis*, and *Bacillus megaterium* led to a significant increase in metabolic activities and chlorophyll concentration in the drought-stressed *Cicer arietinum*. The beneficial effects of PGPB under stress conditions are mediated by the formation of proline and osmolytes as well as improving the activity of the antioxidant system.

Table 1: Effect of PGPB in improving the growth and yield of plants under drought conditions

PGPB	Effect of PGPB on growth and yield	Plant species	References
<i>Bacillus thuringiensis</i>	Enhance physiological characters and increase seed yield	Pea	[23]
<i>Bacillus amyloliquefaciens</i>	Improve growth characters via IAA production	wheat	[54]
<i>Azospirillum</i>	Improve growth characters with osmoprotectant formation	Maize	[55]
<i>Bacillus</i> spp.	Increase metabolic activities and chlorophyll concentration	<i>Cicer arietinum</i> t	[56]
<i>Azospirillum brasilense</i>	Improve growth characters and increase grain yield	wheat	[57]
<i>Arthrobacter protophormiae</i>	Increase IAA and 1-aminocyclopropane-1-carboxylate (ACC)	wheat	[58]
<i>Pseudomonas and Bacillus</i>	Improve physiological characters and increase marketable yield	Tomato	[59]
<i>Pseudomonas</i> spp.	Increase compatible solutes, and improve antioxidant status	Maize	[60]
<i>Pseudomonas helmanticensis</i>	P solubilization, indole-3-acetic acid production, and growth improvement	wheat	[61]
<i>Bacillus</i> spp.	Exopolysaccharide production, phosphate (P)-solubilizing activity and production of organic acids	wheat	[62]
<i>Bacillus cereus</i>	induced a significant increase in IAA, gibberellins, and zeatin	walnut	[63]
<i>Pseudomonas</i> spp.	Decreased osmotic stress, enhanced dry weight, and plant water content	<i>Arabidopsis</i>	[64]
<i>Pseudomonas</i> spp.	Improving root elongation and NPK		[65]
<i>Rhizobium</i> spp	Improving growth and yielding characters	soybean	[66]
<i>Bacillus</i> spp and <i>Pseudomonas</i> spp	Increased fruit yield	pepper	[67]
<i>Azotobacter</i> and <i>Pseudomonas</i>	Improve seed germination and seedlings' radical	<i>Spinacia oleracea</i>	[68]

3 Mitigating the Effects of Salinity Stress on Growth and Yield Characters Using PGPB

Salinity is a main abiotic factor that detrimentally affects the growth and yield of many plants like strawberry [17], cucumber [19], faba bean [26], pea plants [28], and mung bean [69]. The negative effects of salt stress were observed on vegetative and reproductive stages particularly, physiological characteristics such as relative water content, chlorophyll content, the activity of antioxidant enzymes, and yield of several plants [16,34]. The reduction in chlorophyll content under salt stress might be due to the photooxidation process for chlorophyll [69,70]. Also, salinity stress is usually accompanied by oxidative stress due to the excessive production of ROS such as hydrogen peroxide and superoxide, which, cause lipid peroxidation in plant cells such as pepper plants [27] and pea plants [28]. The oxidative stress markers such as ROS, MDA, and EL% are the main indicators in the stressed plants and were significantly increased due to the oxidative damage to mitochondria and chloroplasts as well as other organelles under salt stress [71]. Under salinity conditions the plants can produce antioxidant components to scavenge the excessive formation of ROS, these components include enzymatic and nonenzymatic antioxidants. The production of enzymatic antioxidants for example SOD, CAT, and POX were recorded in stressed plants under salt stress to scavenge the ROS [16,34]. Also, nonenzymatic antioxidants like proline, carotenoids, and total phenolic compounds were observed under salinity stress. These antioxidants play a key role as osmo-regulators to protect the plant cells against oxidative damage. The adverse effects of salinity may be due to the inhibition of carbon fixation and the accumulation of hydrogen peroxide and superoxide, consequently reducing chlorophyll concentration [72].

Plant growth-promoting bacteria (PGPB) can improve physiological processes such as water uptake, nutrient absorption, and photosynthesis processes that enhance plant growth and development [73]. Application of plant growth-promoting bacteria was used to improve plant growth and increase yield production under salt stress (Table 2). Inoculation with PGPB led to an increase in relative water content and improved the structure of the root system and growth characters under salinity conditions, this increased because of the phytohormones production like IAA which increases the length and weight of roots [74]. The beneficial impact of PGPB might be attributed to the production of exopolysaccharides (EPSs) and an increase in the concentration of ABA, which decreases the negative effects on stomatal conductance and photosynthesis [75]. *Azotobacter vinelandii*, *Enterobacter cloacae*, and *Rhizobium* sp. were recorded to produce exopolysaccharides and enhance soil structure and fertility, improve water potential, and increase the plant tolerance to abiotic stress factors such as drought, and salinity to improve crop production [76]. Moreover, PGPB can produce important organic compounds such as ACC-deaminase and siderophores which enhance Fe concentrations and increase its availability in the soil. The activity ACC deaminase was reported for *Enterobacter* might alleviate salinity stress by reducing ethylene concentration [77]. The application of *Bradyrhizobium japonicum* + *Enterobacter Delta* PSK significantly improved the growth characteristics of soybean, while malondialdehyde, electrolyte leakage, and hydrogen peroxide were significantly decreased under salt stress conditions. Also, chlorophyll concentrations were increased with the application of *Bradyrhizobium japonicum* + *Enterobacter Delta* PSK and *Pseudomonas* 42P4 under salinity stress, this effect may be due to alleviating the oxidative damages of salinity in soybean [78] and in tomato plants [79]. Ali et al. [80] reported that inoculation with *Enterobacter cloacae* PM23 led to improved growth characteristics and increase relative water content, proteins, and flavonoid content in maize plants under salinity conditions. Under salt stress, Mahmood et al. [81] found that *Enterobacter cloacae* and *Bacillus drentensis* treatment caused an improvement in the growth of mung beans by increasing the water uptake and nutrient accessibility in the stressed plants. Mukherjee et al. [82] studied the role of *Halomonas* sp. in promoting the growth characteristics and productivity of rice plants growing under salt conditions via siderophores production. Also, Sen et al. [83] found that the application of *Pseudomonas* species under salinity conditions increased root colonization of rice plants by secreting exopolysaccharides. Secretion of phytohormones,

increased nutrient uptake, and nitrogen fixation are some of the various mechanisms that plant growth-promoting microbes use to promote plant growth and reduce the adverse effects of salt stress [83]. Several studies indicated that PGPB was effective in alleviating the harmful effects of stress factors improving the growth characteristics of many plant species that belong to cereals legumes, and vegetables, and enhancing stress tolerance [84]. Application with PGPB led to an increase in nutrient uptake such as N, K, and P due to the solubilizing power of P-solubilizing PGPB and K-solubilizing PGPB [85,86]. Under salt stress, *Streptomyces* sp. and *Achromobacter* sp. displayed the highest activity of ACC deaminase, however, *Bacillus* sp. gave the highest activity of siderophore compounds. These isolates also produced antioxidant enzyme activities such as superoxide dismutase, glutathione oxidase, and catalase in rice plants [87]. Also, *Klebsiella variicola* SURYA6 produced many compounds under salt stress conditions such as organic acid, high phosphorous solubilization index and siderophore, indole acetic acid, 1 aminocyclopropane-1-carboxylate deaminase, and exopolysaccharides as well higher activities of antioxidant enzymes like catalase, superoxide dismutase and glutathione oxidase [88]. Moreover, Bisht et al. [89] and AlKahtani et al. [90] reported that the application of plant growth-promoting bacteria markedly improved photosynthetic rate, stomatal conductance, carotenoids and chlorophylls concentration in *Trigonella foenumgraecum* and lettuce under salinity conditions.

Salinity stress is associated with oxidative damage to cell structures in the plant cells. Under salt stress conditions, the presence of PGPB can activate the antioxidant defense system to scavenge the reactive oxygen species that are produced under salt stress. Antioxidant enzymes such as CAT, SOD, and GSH were recorded to protect plants from oxidative stress. In this regard *Klebsiella* sp. IG 3 produced IAA, antioxidant enzymes, and proline, under salinity conditions, and increased growth characters in *A. sativa* [91]. Previous studies on wheat plants showed that the application of PGPB such as *Pseudomonas* sp. and *Serratia* sp. led to improved growth characteristics in the salt-stressed wheat plants (Table 2) via increasing ACC-deaminase production [92]. Also, Abdelaal [32] reported that the anatomical characteristics of sugar beet stems and leaves were improved with biofertilizer treatment which are clean and inexpensive sources of fertilizers, and act as alternative sources for chemical fertilizers.

Table 2: Mitigation of salinity effects on the plant growth and yield with PGPB application

PGPB	Effect of PGPB on growth and yield	Plant species	References
<i>Rhizobium</i> spp.	Improve physiological and yield characters	Faba bean	[26]
<i>Paenibacillus yonginensis</i>	Activating the defense system and increasing salinity tolerance	<i>Panax ginseng</i>	[78]
<i>Enterobacter cloacae</i>	Production of ACC deaminase	Wheat	[85]
<i>Bradyrhizobium japonicum</i> + <i>Enterobacter Delta</i> PSK	Reducing malondialdehyde, electrolyte leakage, and hydrogen peroxide	Soybean	[86]
<i>Pseudomonas</i> 42P4	Alleviate the oxidative damages	Tomato	[87]
<i>Enterobacter cloacae</i> PM23	Regulating antioxidant defense, and solute accumulation	Maize	[88]
<i>Azotobacter chroococcum</i> and <i>Enterobacter asburiae</i>	Improved photosynthesis process	<i>Trigonella foenumgraecum</i>	[89]
<i>Klebsiella</i> sp.	Production of IAA, antioxidant enzymes, and proline	<i>Avena sativa</i>	[91]

(Continued)

Table 2 (continued)			
PGPB	Effect of PGPB on growth and yield	Plant species	References
<i>Pseudomonas</i> sp. and <i>Serratia</i> sp	ACC-deaminase production	Wheat	[92]
<i>Acinetobacter bereziniae</i>	Enhanced osmolytes such as proline and soluble sugar	Pea	[93]
<i>Pseudomonas azotoformans</i> FAP5	Improved morphological and physiological attributes	Wheat	[94]
<i>Gluconacetobacter diazotrophicus</i>	Improved chlorophyll content	Maize	[95]
<i>Bacillus</i> sp.	Improved antioxidant enzymes and AAC	Pea	[96]
<i>Azospirillum</i> sp.	Improved phosphate solubilization	Chickpea	[97]
<i>Pseudomonas pseudoalcaligenes</i>	Improved antioxidant enzyme activity	Soybean	[98]

4 Justifying the Effects of Heat Stress Using PGPB

Heat stress is one of the most common abiotic stresses that negatively affects morphophysiological and biochemical functions in many plants, like stem height, branch number, membrane permeability, relative water content, and photosynthetic rate. Photosynthesis is an important physiological process and is highly sensitive to temperature changes, so, the photosynthetic rate in leaves was decreased under high temperatures. Chlorophyll fluorescence parameters were decreased under heat stress conditions, this negative effect of heat stress may be due to heat-induced inhibition of light energy absorption and energy distribution. Ahammed et al. [99] reported that heat stress negatively affected the electron transport efficiency in tomato plants, also, enzyme activity, cell division, reactive oxygen species, and other oxidative stress markers have been linked to heat-stressed plants [100]. Exposure to heat stress negatively affects growth characteristics, metabolic processes, chlorophyll concentrations, and the efficiency of photosynthetic apparatus [101].

The effect of plant growth-promoting bacteria was studied to protect the plants from heat stress, in this concern, Mukhtar et al. [102] reported that the application of *Bacillus safensis* (SCAL1) caused an increase in growth characteristics of tomato plants under various heat stress regimes via increasing ACC deaminase and exopolysaccharide. Shaffique et al. [103] stated the increase of various heat stress regulators such as IAA, gibberellin, cytokinin, and organic acids in stressed plants under heat stress conditions. Previous studies have proved that PGPB plays a significant role in the justification of heat stress. Inoculated wheat plants with *Bacillus amyloliquefaciens* UCMB5113 reduced heat stress parameters such as ascorbate peroxidase, glutathione reductase, and heat-shock protein (HSP17) expression [104]. In another study, inoculated soybean plants with *Bacillus cereus* improved chlorophyll a, b concentrations, carotenoids, and proteins [104]. Application of *Pseudomonas aeruginosa* strain 2CpS1 led to ameliorating heat stress effects in wheat plants [105]. Another report stated that Rhizobia increases thermotolerance by activating the heat shock proteins [106]. Application of *Bacillus licheniformis* strain BE-L60 can ameliorate the harmful effects of heat stress via secreting IAA and dissolving phosphorus, increasing proline content, and soluble protein, and improving the activity of antioxidant enzymes such as superoxide dismutase, peroxidase, and catalase in heat-stressed spinach plants [107]. Duarte et al. [108] studied the role of plant growth-promoting bacteria on *Salicornia ramosissima* plants under heat stress, they found that physiological

stress levels were decreased such as excessive fluidity and several antioxidant enzymes as well as lipid peroxidation products, however, membrane stability was improved in the stressed plants.

5 Gene Expression and Signaling Mechanisms under Salinity Stress and PGPB Application

Plants have genetic traits and developed mechanisms to cope with abiotic stress factors such as salinity stress. Plant growth-promoting bacteria become one of the most important methods to improve the salt tolerance mechanism in stressed plants [108]. The signaling mechanisms start with surface receptors that perceive the signals, then, secondary messengers are produced such as ROS that start the plant signal transduction. During the stress period, gene expressions are managed by calcium ion regulation brought about by the secondary messengers that act upon calcium-dependent protein kinase and protein phosphatases [109,110]. Cotton plants treated with *Bacillus pumilus* markedly expressed ascorbate metabolism and glyoxylate pathways as well as dicarboxylate metabolism pathways. However, cotton plants treated with *Bacillus subtilis* caused expressed pentose and glucuronate pathway genes [111].

Under environmental stresses, plants have two important pathways (MAPK and CDPK) to overcome the adverse effects of various stresses. Under stress conditions, MAPK is activated by many signals and the response to environmental stress occurs quickly by the presence of proteins sensing calcium (CDPK and calmodulins) and via modifying cytoplasmic calcium ions. CDPK plays a significant role in ROS production and ABA in plants under abiotic stresses. Additionally, plant-promoting growth-promoting bacteria can produce various phytohormones such as gibberellin, cytokinin, IAA, ABA, and ethylene which act as important signals in the plant tolerance to cope with stress factors [112]. Also, the application of PGPB led to an increase in the production of organic compounds that help in plant-bacteria communication [113]. Under salt stress, PGPB plays an important role in salinity tolerance by regulating ion homeostasis and uptake. The results of Ilangumaran et al. [114] proved that numerous genes such as MAPK, DREB, and CIPK12 of PGPB are involved in modulating phytohormones which play a significant role in the plant defense and adaptation against salinity stress (Table 3).

Table 3: Effect of plant growth-promoting bacteria on the regulation of gene expressions under salinity stress conditions

PGPB	Expressed gene	Role of gene expression under abiotic stresses	Plant species	Reference
<i>Arthrobacter protophormiae</i> and <i>B. subtilis</i>	<i>TaDREB2</i>	Enhanced salt stress tolerance	Wheat	[63]
<i>Bacillus amyloliquefaciens</i>	<i>RBCS, RBCL, HKT1, NHX2, and NHX3</i>	Improved enzyme activity and decreased salinity toxicity	Maize	[115]
<i>Bacillus megaterium</i> <i>ZmPIP</i>	<i>ZmPIP</i>	Increased root hydraulic conductivity	Maize	[116]
<i>Enterobacter</i> sp.	<i>RD29B, RAB18, P5CS2, and MPK</i>	Increased proline biosynthesis	Tomato	[117]
<i>Enterobacter</i> sp.	<i>APX and CAT</i>	Increased antioxidant enzyme	Okra	[118]
<i>Dietzia natronolimnaea</i>	<i>APX, MnSOD, CAT, POD, GR, and TaWRKY</i>	Increased antioxidant enzymes and proline content	Wheat	[119]
<i>Bacillus amyloliquefaciens</i>	<i>EREBP, SOS1, BADH, and SERK1</i>	Increased growth characters	Rice	[120]

6 Conclusions and Future Perspectives

This review displays the significant role of plant growth-promoting bacteria in improving growth and yield under various environmental conditions such as salinity, drought, and heat. Generally, the application of plant growth-promoting bacteria in alleviating the adverse effects of abiotic stress factors such as salinity, drought, and heat in the agricultural system is a promising, safe, and effective strategy, they can improve growth characteristics of plants under abnormal conditions such as drought, salinity, and heat via production of growth hormone, fixation of atmospheric nitrogen, solubilizing of inorganic phosphate and exopolysaccharides production. Furthermore, PGPB helps in the accumulation of osmoprotectants, activating the antioxidant enzymes, organic compounds production, and the production of the ACC deaminase enzyme as well as scavenging the reactive oxygen species. It can be concluded that PGPB is an important alternative method to control abiotic stress in plants, improve plant growth characteristics, and increase yield production under stress conditions. Additional studies are still required to find the best strain of plant growth-promoting bacteria for plant species to improve the growth and yield under several stress factors as well as improve agricultural sustainability.

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