



REVIEW ARTICLE

# Plant Growth Promoting Microbes as Biofertilizers: Promising solutions for sustainable agriculture under climate change associated abiotic stresses

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## Abstract

Abiotic stresses are major constraints for plant growth, crop yield and global food security. Plant physiological, biochemical and molecular processes are highly affected under unfavorable environmental conditions, resulting in substantial losses to crop productivity and requiring an immediate response. Abiotic stress resistant plant growth-promoting rhizobacteria (PGPR) are a profitable and sustainable solution because of their efficiency in plant growth regulation, crop yield improvement and abiotic stress alleviation. They help plants to cope with growth inhibitory effects of abiotic stresses through several mechanisms, mainly phytohormones and osmolyte production, improvement of nutrient acquisition, enhancement of antioxidant system. Plant-PGPR interactions are vital for sustainable agriculture and industrial purposes, because they are based on biological processes and replace conventional agricultural practices. PGPR may play a key role as an ecological engineer to solve environmental stress problems. The use of microbes is a feasible and potential technology to help meeting the future global food needs with reduced impact on soil and environmental quality. Present review deals about the abiotic stresses (drought and salinity) affecting plant growth and highlights the impact of PGPR on restoration of plant growth under the stressful conditions with the goal of developing an eco-friendly and cost-effective strategy for agricultural sustainability.

## Keywords

Agricultural sustainability, Abiotic stresses, Climate Change, Plant-microbe interactions, Stress alleviation

## Introduction

The 21<sup>st</sup> century has been marked by global climate change. Many research studies have reported that environmental stresses induced by climate change are a major global threat to agricultural production and future food security. According to a recent estimate by the United Nations (UN), the world's population is currently about 7.3 billion people and is projected to reach 9.7 billion by 2050. This growing population requires increasing quality and quantity of food, which may soon become insufficient to feed the world's population, especially in countries where resources have been damaged by uncontrolled human activities and environmental degradation. Increasing climate variations, human population and reduction in available land for cultivation are major threats to crop production and agricultural

sustainability (1, 2). Agriculture is the main food source for humankind and animals and in order to satisfy the increasing global food demand, agricultural production has to increase by 70-100% over the next few years (3). However, agricultural production and sustainability are continuously affected by various biotic and abiotic constraints, which cause large crop losses and change soil health and fertility (4).

Abiotic stresses are stress conditions to plants arising from the environment. They are among the main limiting factors for agricultural productivity because they affect almost all plant functions, in different ways and at different developmental stages (5). According to FAO (2007), only 3.5% of the global land area has not been affected by any environmental stress. Abiotic stresses hamper microbial functions and diversity, soil physicochemical properties and plant growth by affecting plant morphology, physiology and biochemistry through its gene regulation, thus, preventing plants from achieving their full genetic potential (6). The main abiotic stresses affecting plants are drought, salinity, extreme temperatures (high/low), acidic conditions, mineral deficiencies or toxicities, heavy metals, nutrient depletion and soil erosion (7). The FAO (2015) has predicted that, due to global changes, abiotic stresses such as drought, salinity and extreme temperature will cause crop yield reductions of up to 50% of average productivity by 2050. Among these constraints, drought is one of the main limiting factors for crop productivity especially in arid and semi-arid regions. Drought stress is considered to arise when the critical precipitation level is not reached (8). Prolonged water deficit conditions lower the soil water potential and cause detriment to plant growth and productivity (9). In order to combat drought-induced stresses and boost crop productivity and yield, farmers resort to the use of irrigation, which indirectly induces soil salinity stress.

Soil salinity is the second most devastating stress for agriculture, following drought. It severely restricts crop growth and production, mainly in arid and semi-arid regions (10). It has been estimated that 20% of total cultivated and 33% of irrigated agricultural land worldwide is afflicted by high salinity and 30% of arable land is expected to be affected by salinity by 2025 and 50% by 2050 (11, 12). Abiotic factors affect 10 ha of land per min. worldwide, 3 of which are lost due to soil salinization (13). Salinity costs the world US\$ 27.3 billion a year in reduced income in irrigated areas. Saline soil is defined as soil in which the electrical conductivity (EC) (decisiemens/meter or millisiemens/centimeter) of the saturation extract (EC<sub>e</sub>) in the root zone exceeds 4 dS m<sup>-1</sup> (approximately 40 mM NaCl) at 25 °C and an exchangeable sodium percentage (ESP) of 15% or more. Detrimental effects on plant health and productivity and crop yield losses due to soil salinity have been extensively reported. Many strategies have been used to mitigate the detrimental effects caused by abiotic stresses on plant and to increase crop productivity especially those resulting from drought and salinity stress. These include i) breeding methods and genetic modification to develop new abiotic stress tolerant crop varieties;

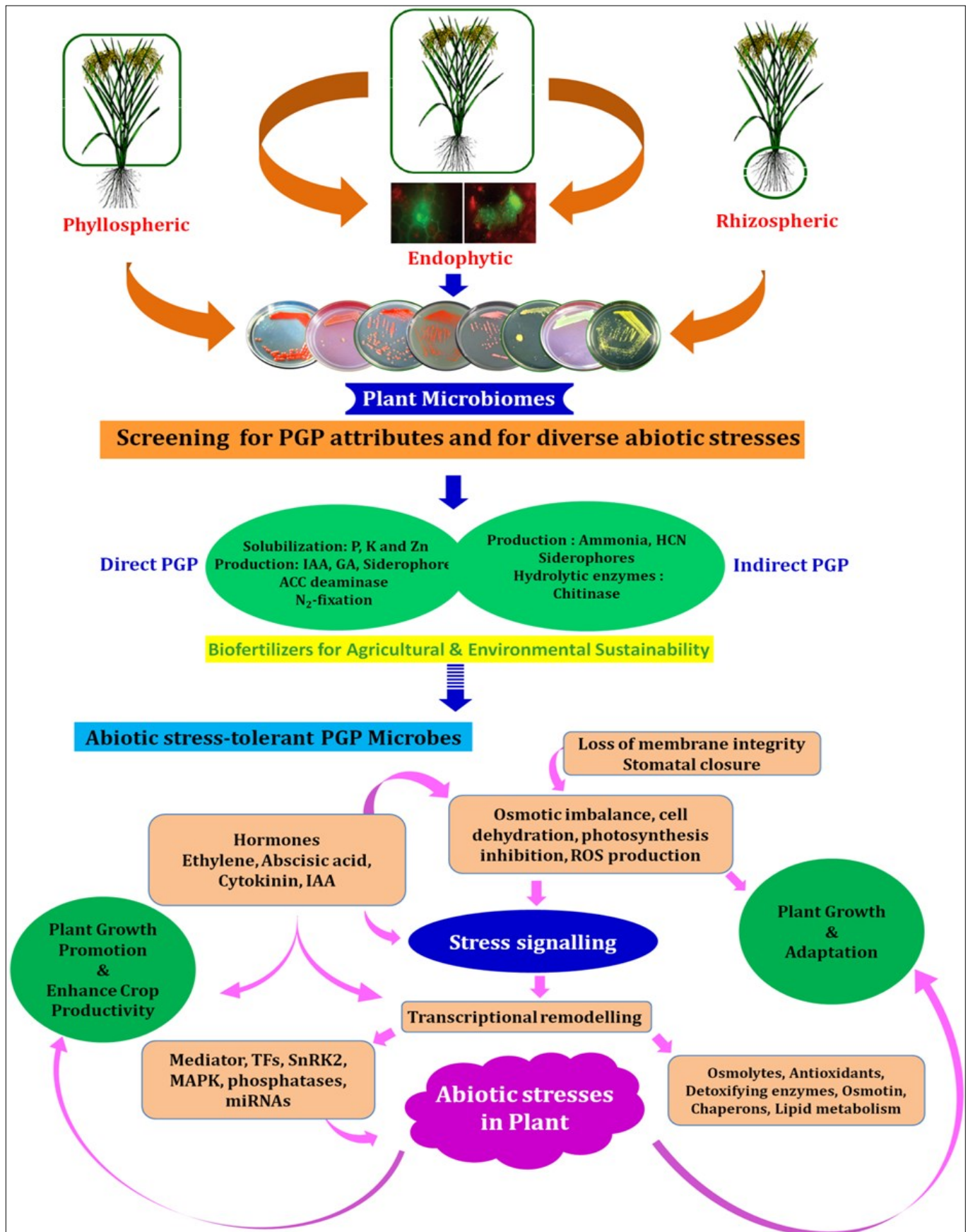
ii) management of the planting time to avoid stress periods; iii) adjustment and optimization of irrigation; and iv) implementation of beneficial microorganisms known for their ability of improving plant health, productivity, and resistance to abiotic stresses through various mechanisms as biological fertilizers (Fig. 1).

The use of microorganisms as biofertilizers is considered the most important of these solutions, being a suitable and eco-friendly solution to alleviate the climate changes that threaten the global food production and food security. Much interest has been directed toward sustainable agriculture over the last few years, with an emphasis on soil inoculation with beneficial rhizospheric microorganisms known for their stress resistance and plant growth promotion under various abiotic stresses (14, 15). Depending on their effects on plant growth, soil bacteria are classified into three groups: beneficial, deleterious and neutral. However, the same bacterial species can change between groups depending on the local ecology. PGPRs are believed to promote plant growth and development and maintain soil health under both normal and stress condition (16). Stress-tolerant PGPRs alleviate harsh environmental conditions and promote plant growth via several mechanisms. Plant growth promoting microbiomes have positive effects on plant health and growth under both normal and stress conditions. The rhizosphere is the soil zone influenced by plant roots. It is the most dynamic and nutrient-rich soil ecological niche resulting from the accumulation of root exudates, including amino acids, sugars and organic acids, which are used by rhizospheric bacteria to support their growth and metabolism. These beneficial bacteria colonize the rhizosphere and/or the endorhizosphere and promote plant growth and development via both direct and indirect mechanisms, therefore constituting a potential and promising strategy for sustainable agriculture. Indirect mechanisms are involved in decreasing or preventing detrimental effects caused by plant pathogens (usually fungal species) through one or several mechanisms, including induction of systemic resistance (ISR), generation of extracellular enzymes (chitinases, glucanases, cellulases and proteases) that hydrolyze the fungal cell wall, production of siderophores that can restrict pathogen growth by reducing iron accessibility, production of antibiotics and/or antifungal substances, and competition for nutrients and/or space (niche) within the rhizosphere (17, 18).

PGP microbes directly enhance plant growth by facilitating nutrient uptake, fixing atmospheric nitrogen, solubilizing and mineralizing nutrients (particularly phosphate and potassium), expressing plant growth regulators and signal molecules and producing phytohormones (e.g., abscisic acid-ABA, gibberellic acid-GA, indole-3-acetic acid-IAA and cytokinins-CK) (13, 20). Amongst the phytohormones, IAA is the most ubiquitous signal molecule in plant-microbe interactions, being involved namely in phyto-stimulation and phytopathogenesis (21, 22). PGPR also synthesize ACC (1-aminocyclopropane-1-carboxylate) deaminase, an enzyme involved in decreasing the level of stress-induced ethylene in roots of developing plants.

Through many of these mechanisms, PGPRs help plants to maintain their natural growth under stress conditions by mitigating the negative effects of stress on plant growth and development. The importance of their use in sustainable agriculture has been therefore increasing in recent

years. The present review attempts to explore the success of stress tolerant PGPRs in abiotic stress alleviation and emphasize the PGPR associated mechanisms involved in increasing agricultural sustainability and productivity under stress conditions of drought and salinity.



**Fig. 1.** Plant growth promoting microbes as biofertilizers for PGP and soil fertility under the natural and stressed conditions. Adapted with permission from Kour, Rana (19).

### **Abiotic stresses and their impact on plant growth and productivity**

Drought and soil salinity negatively affect plant growth, development and productivity, directly or indirectly, therefore decreasing crop production. They affect almost all plant functions and aspects ranging from germination to maturity.

#### **Drought stress**

Drought is the most common and devastating abiotic stress to plant growth and productivity. It results from periods of unusual decrease in soil moisture content following a prolonged period of low rainfall, which is the major water source in subsistence agriculture in many parts of the world. In some regions, decreases in rainfall event and increases in extreme temperatures (leading to higher evapotranspiration rates) are becoming more prevalent, potentially due to global warming (23, 24). Increasing drought severity therefore leads to large economic losses and may pose a serious threat to food security. Drought stress may decrease the average crop yield worldwide in more than 50%, and further limit agricultural productivity (25, 26). In recent years, losses related to drought have been the main challenge for grain production. In the last 40 years, drought stress has reduced cereal yields by approximately 10% (27). In Southern Brazil, for example, which is responsible for more than 40% of the national soy production, over 25% of soy harvests were lost due to drought stress (28). Global climate models have predicted increases in drought frequency and severity in the near future due to global climate change, indicating the threat of water scarcity (27). In order to satisfy global food demands, there is therefore a need to find eco-friendly solutions that help plants to cope with drought stress while maintaining their growth and productivity under limited water conditions.

#### **Impact of drought stress on plant growth and productivity**

Drought is a multidimensional stress that affects plant growth and productivity and induces huge crop yield reductions, which may exceed 40%. It has detrimental effects on plant growth and metabolic processes in major field grown crops, especially during grain filling and the reproductive phase (29, 30). Drought stress which is mainly caused by water deficiency due to decreases in rainfall levels, high temperatures and low moisture contents, affects various plant growth parameters and stress responsive genes and induces several changes in morphological and physiological plants traits (31, 32). Drought stress affects several morphological traits in plants, such as stem height, root length, leaf morphology and number, leaflet length, leaflet width, fruit number and size, primary and secondary branches and fresh and dry weight. It decreases germination rates, seedling vigor, cell size and division, membrane integrity, seed size and number, seed viability and other biomass parameters, induces senescence in matured leaves, and delays flowering and fruiting (2, 33). Water deficit affects nutrients availability to plant roots, because it decreases nutrient diffusion and the mass flow

of water-soluble nutrients (e.g., nitrate, sulfate, calcium, magnesium and silicon). It also affects plant biochemical activities such as nitrate reductase (NR) activity due to lower uptake of nitrate from the soil. Drought as a multidimensional stress affects plants at the sub cellular compartment and whole plant level. It weakens the photosynthesis process by affecting photosynthetic enzymes namely enzymes involved in chlorophyll biosynthesis and inducing stomatal closure. During drought stress stomata close in response to decreased leaf turgor, increased atmospheric vapor pressure deficit or root-generated chemical signals. In addition, drought stress triggers the production and results in accumulation, of free radicals and reactive oxygen species (ROS) such as superoxide radicals, hydrogen peroxide and hydroxyl radicals which induce oxidative stress and affect antioxidant defenses. When the ROS level is high, it can damage certain systems, namely through lipid peroxidation, membrane deterioration and protein, lipid and nucleic acid degradation, leading to cell death (33). Drought, like other abiotic stresses increases ethylene biosynthesis, which inhibits plant growth through several mechanisms. Drought stress also weakens the plant immune system and enhances their susceptibility to microbial infections (34). Plant sensitivity to drought depends on plant developmental stage, genetic potential, genotypic variability and duration and severity of the drought stress (35, 36).

Plants have developed diverse mechanisms to deal with drought stress, namely: i) drought escape, when there is rapid plant growth and development, allowing completion of the plant life cycle before the beginning of the dry season; ii) drought avoidance when there is increased water uptake from the soil or decreased water loss via transpiration; and iii) drought tolerance when normal plant growth and metabolic activities are maintained even under water stress, e.g., via osmolyte synthesis. Plant adaptations to drought stress can be physiological, morphological, biochemical, or molecular and the type of plant response depends on the plant species (37). However, the development of new approaches to improve plant drought tolerance is critical for reducing yield losses in water-deficient environments.

#### **Role of PGPR in drought stress alleviation**

Plant growth promotion rhizobacteria are well known to stimulate plant growth and increase crop yield under both normal and stress conditions. Their role in abiotic stress management has been acquiring increasing importance in recent years (38). Under water deficient conditions, drought stress tolerant plant growth promotion rhizobacteria may enhance plant growth and development. They help plants cope with negative drought impacts through various mechanisms including production of phytohormones, ACC deaminase, osmolytes, antioxidants and exopolysaccharides (EPS), and by inducing systemic tolerance (IST) (39) (Table 1). Phytohormones help plants to withstand abiotic stresses by mediating a wide range of adaptive responses. However, one of the ways in which abiotic stresses decrease plant growth is by decreasing endogenous plant hormone levels. PGPR enhance plant

**Table 1.** Role of plant growth promoting rhizobacteria in drought stress alleviation

Organism	Mechanisms	Crop	Reference
<i>Achromobacter xylosoxidans</i>	ACC deaminase producing	Maize	Danish, Zafar-ul-Hye (45)
<i>Acinetobacter calcoaceticus</i>	Phosphate solubilization, product of siderophore	Foxtail millet	Kour, Rana (46)
<i>Arthrobacter protophormiae</i>	ACC deaminase producing	Wheat	Barnawal, Bharti (47)
<i>Azospirillum brasilense</i>	Higher carbon, nitrogen, and chlorophyll levels; and lower levels of abscisic acid and ethylene	Maize	Curá, Franz (48)
<i>Azospirillum lipoferum</i>	Increased accumulation of soluble sugars, free amino acids and proline.	Maize	Bano, Ilyas (49)
<i>Bacillus amyloliquefaciens</i>	Production of indole-3-acetic acid (IAA), indole-3-carboxylic acid (ICA) and indole-3-lactic acid (ILA)	Wheat	Raheem, Shaposhnikov (50)
<i>Bacillus haynesii</i>	ACC deaminase activity and siderophores production	Rice	Joshi, Chaudhary (51)
<i>Bacillus licheniformis</i>	ACC deaminase activity and siderophores production	Rice	Joshi, Chaudhary (51)
<i>Bacillus paralicheniformis</i>	ACC deaminase activity	Rice	Joshi, Chaudhary (51)
<i>Bacillus thuringiensis</i>	Decreased GR and APX activity, increased K <sup>+</sup> content and micro-nutrient uptake	<i>Lavandula dentate</i>	Blanco-Montenegro, De Ritis (52)
<i>Bradyrhizobium japonicum</i>	Improved soil water content, cell membrane stability and root nodulation and plant growth	Soybean	Silva, Zoz (53)
<i>Burkholderia seminalis</i>	Chlorophyll content, root length, catalase activity, and guaiacol peroxidase	Tomato & Bell pepper	Tallapragada, Dikshit (54)
<i>Curtobacterium herbarum</i>	Reducing oxidative stress, lipid peroxidation and Al accumulation in plant parts	Lettuce	Silambarasan, Logeswari (55)
<i>Enterobacter cloacae</i>	ACC deaminase producing	Maize	Danish, Zafar-ul-Hye (45)
<i>Ochrobactrum anthropic</i>	Synthesis of Siderophore, ACC deaminase activity, indole-3-acetic acid production, and phosphate solubilization.	Soybean	Susilowati, Puspita (56)
<i>Pseudomonas fluorescens</i>	increasing relative water content (RWC), accumulated metabolites such as sugar, free amino acids and enhanced the activity of non-enzymatic antioxidants; phenolics, ascorbate (AsA) and glutathione (GSH) and reactive oxygen species scavenging enzyme like superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX) and guaiacol peroxidase (GPX)	Okra	Pravisya, Jayaram (57)
<i>Pseudomonas jessenii</i>	High SOD, CAT and POD expression	Rice	Gusain, Singh (58)
<i>Pseudomonas libanensis</i>	Solubilization of potassium and zinc, production of siderophores, hydrogen cyanide, ammonia and 1-aminocyclopropane-1-carboxylate deaminase	Wheat	Kour, Rana (59)
<i>Pseudomonas moraviensis</i>	ACC-deaminase activity	Wheat	Yaseen, Zafar-ul-Hye (60)
<i>Pseudomonas putida</i>	Downregulation of ethylene biosynthesis (ET), abscisic acid (ABA) and auxin signaling, superoxide dismutase, catalase, and peroxidase; genes involved in $\beta$ -alanine and choline biosynthesis, heat shock proteins, and late embryogenesis abundant (LEA) proteins	Maize	SkZ, Vardharajula (61)
<i>Pseudomonas simiae</i>	Production of abscisic acid (ABA) and salicylic acid (SA) hormones and reduction of ethylene emission	Soybean	Vaishnav and Choudhary (62)
<i>Pseudomonas stutzeri</i>	Increased plant biomass, leaf water potential, relative water content, root adhering soil/root tissue ratio, aggregate stability, mean weight diameter, and proline, sugar, and free amino acid contents and decreased transpiration rates	Maize	(63)
<i>Pseudomonas synxantha</i>	High SOD, CAT and POD expression	Rice	Gusain, Singh (58)
<i>Pseudomonas syringae</i>	Increased plant biomass, leaf water potential, relative water content, root adhering soil/root tissue ratio, aggregate stability, mean weight diameter, and proline, sugar, and free amino acid contents and decreased transpiration rates	Maize	Sandhya, Ali (63)
<i>Rhizobium tropici</i>	Increased nodulation and nitrogen content	Common bean	Figueiredo, Burity (64)
<i>Streptomyces laurentii</i>	Solubilization of zinc and potassium; production of Fe - chelating compounds, in dole acetic acid, hydrogen cyanide and ammonia	Great millet	Kour, Rana (59)

tolerance to drought by synthesizing and secreting plant hormones. Among plant hormones, IAA is a signal molecule of great importance being the main regulator of many

aspects of plant growth and development, e.g., seed germination, cell division, tissues differentiation, leaf expansion, lateral and adventitious root initiation, root hair

development, root and stem elongation and resistance to stressful conditions. As already mentioned drought stress negatively affects roots and reduces their growth. Under such condition, IAA-producing PGPR stimulate root growth (increase the number of root tips and root surface area) leading to increased nutrient, mineral and water uptake, which is expected to alleviate the drought stress effects on plants (40).

ABA is an important plant growth regulator with crucial role in drought stress alleviation. It is involved in modulation of various key physiological processes during drought stress. Namely, it is involved in regulation of leaf transpiration by inducing stomatal closure to reduce water losses, stimulation of root hydraulic conductivity, up-regulation of aquaporins and alleviation of ROS production. ABA is also involved in increasing water absorption by enhancing root growth and branching and regulating osmolytes to maintain osmotic adjustments. Increased ABA contents were associated with enhanced osmotic stress tolerance and decreased leaf transpiration in *Arabidopsis thaliana* inoculated with *Phyllobacterium brassicacearum* strain STM196 (41) and with increased stomatal conductance in *Platycladus orientalis* seedlings inoculated with *Bacillus subtilis* (42).

Cytokinins (CK) stimulate cell division and enlargement and shoot growth, and induce stomatal opening. Under drought conditions, it plays a vital role in delaying premature leaf senescence and death and has been considered to enhance plant drought tolerance by several researchers. Inoculation with CK-producing *Bacillus* sp. Increased shoot biomass of 12-days-old lettuce seedlings growing in drying soil. Inoculation with CK-producing *Bacillus subtilis* alleviated water deficit stress in *Platycladus orientalis* seedlings, but increased CK levels led to stomatal opening, which was reversed by increased ABA levels (42). Recently, (43) reported a drought tolerance enhancement effect of a drought-tolerant CK-producing *Methylobacterium oryzae* isolate in lentil plants. Likewise, JA behaves as an antioxidant, protecting plants from oxidative stress damages. Similarly, GA is involved in several developmental and physiological processes, such as seed germination, stem elongation, flowering and senescence (44).

Ethylene is an important modulator of normal plant growth and development. It is involved in the regulation of several plant metabolic activities, and its biosynthesis increases under environmental stresses such as drought. High ethylene accumulation adversely impacts plant physiology and growth. It regulates plant homeostasis resulting in restricted root and shoot growth. Rhizospheric bacteria prevent ethylene damage by sequestering and hydrolyzing 1-aminocyclopropane-1-carboxylate (ACC), the immediate precursor of ethylene, therefore interfering with its synthesis and decreasing ethylene accumulation (65, 66). The sequestered ACC is hydrolyzed into ammonia and  $\alpha$ -ketobutyrate by bacterial ACC deaminase to supply nitrogen and energy. Plant inoculation with ACC deaminase-producing PGPR increases seed yield, number and nitrogen content, and restore root nodulation inhibited by

drought (13). Ethylene reduction induces root system development, leading to increased plant access to water and nutrients, therefore increasing plant drought resistance. Alleviation of drought stress by ACC deaminase-producing PGPR has been reported in tomato (*Lycopersicon esculentum* cv. F144) and pepper (*Capsicum annum* L. cv. Maor) seedlings inoculated with *Achromobacter piechaudii* ARV8 (67) and wheat inoculated with *Pseudomonas palleroniana* DPB16, *Pseudomonas* sp. UW4 and *Variovorax paradoxus* RAA3 (68).

Plant adaptation to drought stress is associated with metabolic adjustments leading to accumulation of several compatible solutes or osmolytes, such as proline, soluble sugars, polyamines, betaines, quaternary ammonium compounds, polyhydric alcohols and other amino acids and water stress proteins like dehydrins. Some PGPR also produce osmolytes to combat severe stress conditions. These osmolytes act synergistically with those produced by plants and promote plant growth. Proline is a major osmolyte, produced in plants via protein hydrolysis to counter osmotic stress. It is a multifunctional molecule which helps increase plant tolerance to stress by adjusting cytosolic acidity, stabilizing proteins and membranes, maintaining cell water status, reducing lipid peroxidation by scavenging ROS and acting as an antioxidant defense molecule. High proline accumulation in plants therefore indicates high drought tolerance. Inoculation of tomato plants with *Bacillus polymyxa* (69), maize plants with *Pseudomonas putida* GAP-P45 (63) or with *Pseudomonas fluorescens* (70) resulted in increased plant biomass, relative water content and leaf water potential due to proline accumulation under drought conditions. Observations are on the increased proline contents in basil plants (*Ocimum basilicum* L.) inoculated with *Azotobacter chroococcum*, leading to improved water uptake and water use efficiency and photosynthetic efficiency (71). Trehalose is another osmolyte that confers osmoprotection to plants through membrane and protein stabilization (72). Trehalose metabolism in PGPR is important for signaling plant growth, yield, and adaptation to abiotic stresses and its manipulation has a major agronomical impact on plants (73). It was reported that priming maize plants with *Azospirillum brasilense* over-expressing genes involved in trehalose biosynthetic enhanced trehalose accumulation, conferring drought tolerance (73). Polyamines such as cadaverine, spermidine, spermine and putrescine are low molecular weight compounds involved in increasing osmotic tolerance in drought-affected plants and are implicated in cell division, root elongation, floral development, fruit ripening, DNA synthesis, transcription and translation and in programmed cell death (74, 75). Likewise, Glycine betaine is involved in inhibition of ROS accumulation, protein and cell membrane stabilization, photosynthesis enhancement, induction of stress-responsive genes and prevention of water loss during osmotic stress (76, 77).

Drought stress induces ROS production including superoxide anion radicals ( $O_2^-$ ), hydrogen peroxide ( $H_2O_2$ ), hydroxyl radicals (OH), singlet oxygen ( $O_{12}$ ) and alkoxy radicals (RO) (78). Increased ROS levels in plants, above

threshold have results in oxidative stress. It causes inhibition of protein synthesis, protein disruption, lipid peroxidation, decreased membrane fluidity, DNA damage and impairs the normal functioning of plant cells leading to cell death. To protect themselves against the harmful effects of ROS, plants are equipped with antioxidant defense systems by both non-enzymatic (e.g., ascorbate, cysteine, tocopherols and glutathione) and enzymatic components, such as monodehydroascorbate reductase (MDHAR), superoxide dismutase (SOD), peroxidase (POD), glutathione reductase (GR), catalase (CAT) and ascorbate peroxidase (APX) (79). These enzymes play a crucial role in drought stress alleviation. *Bacillus thuringiensis* has been reported to increase GR, CAT and SOD activity in wheat under drought stress (39) and *Pseudomonas aeruginosa* GGRJ21 to increase SOD, POD and CAT activity in mung bean (80). Similarly, *Pseudomonas mendocina* increased CAT activity in lettuce (*Lactuca sativa*) plants, protecting them from oxidative damage caused by drought stress (81). Some studies reported lower levels of antioxidant enzymes, namely APX, CAT, GR and glutathione peroxidase (GPX) in plants inoculated with PGPR, suggesting that they experienced lower oxidative stress than uninoculated plants (82).

Exopolysaccharides (EPS) are bacterial compounds with an important role in protecting bacteria from inhospitable conditions and enable their survival. Under water deficit stress, EPS-producing PGPR not only protect them but also have a crucial role in enhancing plant tolerance (83). EPS can protect plants against desiccation due to the formation of hydrophilic biofilms on the root surface (84). The EPS-producing PGPR ability for water retention varies depending on the polysaccharide constituents of EPS and it may exceed 70 g water per 1 g polysaccharide (85). EPS provides a microenvironment that holds water and dries up less quickly than the surrounding environment, thus protecting bacteria and plant roots against desiccation. EPS also improve soil structure and aggregation (increase the number of soil micro-aggregates in the rhizosphere and their stability), leading to higher root adhering soil per root tissue (RAS/RT) ratio increasing water and nutrient uptake and ensuring higher plant growth and survival under drought stress (86). Several researchers have reported the efficiency of EPS-producing PGPR in drought stress alleviation for plant growth improvement.

Induced systemic tolerance is an important mechanism in growth promotion by PGPR. It consists of induced physical and chemical changes in plants that result in increased tolerance to abiotic stresses, namely through up regulation of genes involved in stress tolerance (79). Induced expression of the drought responsive genes Early Response to Dehydration 15 (*ERD 15*) and ABA-responsive gene (*RAB18*) was observed in *Arabidopsis thaliana* inoculated with *Paenibacillus polymyxa* (87), and priming with *Bacillus licheniformis* K11 induced the expression of six different stress proteins in pepper plants, resulting in increased plant growth under drought stress (88). Similarly, co-inoculation of wheat (*Triticum aestivum*) with of *Bacillus amyloliquefaciens* 5113 and *Azospirillum brasilense*

NO40 alleviated the effects of drought stress through up-regulation of the stress related genes *APX1*, *SAMS1* and *HSP17.8* in leaves, and increased activity of enzymes involved in the plant ascorbate-glutathione redox cycle (89). Drought stress alleviation was also observed in mung bean plants inoculated with *Pseudomonas aeruginosa* GGRJ21 due to up regulation of three drought stress-responsive genes, dehydration responsive element binding protein (*DREB2A*), catalase (*CAT1*) and dehydrin (*DHN*) (80). Likewise, priming of sugar cane cv. SP70-1143 with *Gluconacetobacter diazotrophicus* PAL5 resulted in activation of ABA-dependent signaling genes conferring drought resistance (90). Further studies are however needed in order to clarify the main molecular mechanisms behind induced systemic tolerance by PGPR in plants.

### Salinity Stress

Salinity is one of the major land degradation problems. It consists on the accumulation of soluble salts (including cations such as  $\text{Na}^+$ ,  $\text{K}^+$ ,  $\text{Ca}^{2+}$  and  $\text{mg}^{2+}$  and anions such as  $\text{Cl}^-$ ,  $\text{SO}_4^{2-}$ ,  $\text{NO}_3^-$ ,  $\text{HCO}_3^-$  and  $\text{CO}_3^{2-}$ ) in soils at levels that negatively affect agricultural productivity, environmental health and economic welfare (91). Salinization changes soil physicochemical properties causing permanent land degradation. It imposes enormous challenges for agricultural production and sustainability because most of crop plants are sensitive to high salts concentrations in soil. In 2005, the FAO estimated that over 6% of the world's total continental area is affected by salinity. Salinity is predicted to become a larger problem in the coming decades because the level of salt-affected land areas is increasing daily in several parts of the world, including the Mediterranean Basin, Australia, Central and Southern Asia, the Middle East, Europe and Northern Africa (92, 93). According to FAO (2002), the total land area that can be used for agriculture is decreasing by 1-2% every year, hitting hardest in arid and semi-arid regions. This alarming increase in salt-affected soils is mainly caused by low rainfall, high temperatures leading to high surface evaporation, weathering of native rocks, irrigation with saline water, exaggerated use of fertilizers and desertification processes (94).

### Impact of salinity on plant growth and productivity

Salinity negatively affects plant growth and development and plant metabolism, inducing physiological, morphological, biochemical and molecular changes leading to decreases in plant yield. It affects almost every aspect of plant growth, from seed germination to maturity. Seed germination and early seedling growth are the most salt-sensitive plant growth stages. Seed germination inhibition has been observed in various crops, namely soybean, faba bean, wheat, rice and maize. High salt concentrations in the rhizosphere severely affect plant growth through complex interactions (95). It induces osmotic and nutrient imbalances, ionic toxicity, reduces photosynthetic capability, increases ethylene production, lowers moisture retention, affects protein synthesis and lipid metabolism, generates ROS, impairs nitrogen fixation, induces stomatal closure and early desiccation of flowers and fruits (96).

Many water-soluble salts in soil are plant nutrients,

but their excessive accumulation in the root zone induces nutritional imbalance due to competition between  $\text{Na}^+$  and  $\text{Cl}^-$  and other nutrient ions, such as:  $\text{K}^+$ ,  $\text{NO}_3^-$  and  $\text{H}_2\text{PO}_4^-$  for binding sites and transport proteins in root cells, and thereafter for translocation, deposition and partitioning within the plant (3, 97). Under salinity conditions, an increase in  $\text{Na}^+$  uptake causes metabolic disturbances in some processes where low  $\text{Na}^+$  and high  $\text{K}^+$  or  $\text{Ca}^{+2}$  are required for optimal functioning and growth. The replacement of  $\text{K}^+$  by  $\text{Na}^+$  induces protein conformational changes leading to ionic toxicity.  $\text{K}^+$  is a co-factor of several enzymes and cannot be replaced by  $\text{Na}^+$ . In addition, excessive  $\text{Na}^+$  accumulation in cell walls can rapidly lead to osmotic stress and cell death and  $\text{Cl}^-$  accumulation may disrupt photosynthetic function through inhibition of NR.  $\text{Na}^+$  and  $\text{Cl}^-$  are mostly up taken by the cell vacuoles and organic solutes (that are compatible with metabolic activity even at high concentrations) then accumulated and stored in the cytosol. Once the plant cell capacity for storing salts is exhausted, salts build up in the intercellular spaces, inducing cell and organ death. Perturbation of plant nutrient relations by salinity results in higher susceptibility to invasion by pathogenic microorganisms (98).

Under saline conditions, osmotic pressure is higher in the rhizosphere soil solution than in root cell making water uptake by plants harder resulting in cells dehydration, loss of turgidity and plant wilting and death. Salinity also creates water deficit by changing the soil texture and decreasing soil porosity (79). Leaf area, size and production decrease whereas plant defoliation and senescence accelerate at high salt availability. During salt stress, photosynthesis is mainly affected by decrease in water potential, leaf area, chlorophyll and carotenoid contents, photosystem II (PSII) activity, electron transport, photosynthetic enzymes and partial stomata closure. In addition, salt stress disturbs photorespiration, affecting normal cell homeostasis and physiological and metabolic processes in plants. It also reduces cell division and expansion, triggers membrane disorganization and genotoxicity, resulting in decreased growth and premature activation of programmed cell death (99).

Salinity is also known to affect phytohormones synthesis and other plant growth-stimulating factors e.g., it significantly increases the rate of ethylene biosynthesis by increasing the level of ACC, leading to negative physiological changes in plant tissues. Soil salinity negatively affects nodulation and nitrogen fixation through inhibition of nitrogenase enzyme activity, therefore reducing nitrogen contents in legumes. It also decreases plant phosphorus uptake because phosphate ions precipitate with Ca ions. Like other abiotic stresses, salinity leads to oxidative stress due to increased production and accumulation of ROS which are potentially harmful to biomembranes, proteins, nucleic acids and enzymes (100). Moreover, salinity adversely affects plant reproductive development by inhibiting microsporogenesis and stamen filament elongation, enhancing programmed cell death in some tissues, ovule abortion and senescence of fertilized embryos (94). The

edible parts of salt-affected plants have markedly less economic and nutritional value due to reduced fruit size and shelf life, non-uniform fruit shape and decreased vitamin (98). Plant salt tolerance is not easy to quantify because it varies considerably with several environmental factors (soil fertility, soil physical conditions, salt distribution in the soil, irrigation regime and climate) and plant factors (growth stage, root stock and plant species and cultivar) (101).

Several strategies for salt stress alleviation have been developed, such as: development of salt-resistant cultivars, leaching of excess soluble salts from upper to lower soil depths, flushing soils that have soil crusts at the surface, reducing soil salt contents through the use of salt-accumulating plant and harvesting of their aerial parts in areas with irrigation or rainfall insufficient for leaching, etc. But all these methods showed many disadvantages and limits. Crop seed and seedling priming with halotolerant PGPR is a promising alternative for salt stress alleviation. Considering the prospects of crop production losses due to salinity stress, tolerance provided by bacterial inoculants becomes more important. Beneficial effects of PGPR under salinity have been associated with phytohormone production, osmolyte accumulation, toxic ion sequestration  $\text{Na}^+$ , maintenance of higher stomatal conductance etc.

#### **Role of PGPR in salinity stress alleviation**

Salinity effects on plant physiology, health and growth can be alleviated with the use of halotolerant microbial inoculants (102). PGPR exhibit various mechanisms which alleviates the salinity stress in plants (Table 2). Phytohormone production by PGPR is believed to increase root length and surface area and the number of root tips, leading to higher water and nutrient uptake under salinity stress (103). IAA production is relatively common in PGPR, and many reports have showed its role in salt stress alleviation. PGPR produce IAA and transfer it into the rhizosphere of salt stressed plants, where it acts in combination with the endogenous IAA plant pool to stimulate plant growth. IAA-producing *Azospirillum brasilense* NH has been reported to promote wheat (*Triticum durum* var. *waha*) growth under salinity (150 mmol/l and 200 mmol/l NaCl) (104). Priming with IAA-producing *Pseudomonas* strains (*P. extremorientalis* TSAU20, *P. aurantiaca* TSAU22 and *P. extremorientalis* TSAU6) increased root and shoot growth of wheat seedlings by 40% and 52% respectively at 100 mmol/l NaCl, when compared to the control plants (103). Inoculation of cotton (*Gossypium hirsutum*) seeds with *P. putida* Rs-198 resulted in increased seed germination and seedling growth and inoculation with *P. putida* R4 and *P. chlororaphis* R5 increased seed germination up to 64 and 73% respectively and root and shoot length (105).

In addition to its role as plant growth stimulator and salt stress alleviator, IAA can stimulate ACC synthase activity (106). ACC synthase converts S-adenosyl methionine to ACC, which is the ethylene precursor (107). High IAA concentrations therefore lead to higher ethylene synthesis, which negatively affects many aspects of plant



**Table 2.** Effects plant growth promoting rhizobacteria in salinity stress alleviation

PGP Rhizobacteria	Mechanisms of actions	Crop	Reference
<i>Achromobacter piechaudii</i>	Reduced ethylene level and improved plant growth	Tomato	Mayak, Tirosh (118)
<i>Acinetobacter bereziniae</i>	Activities of antioxidant enzymes (SOD and POD)	Pea	Sapre, Gontia-Mishra (119)
<i>Arthrobacter woluwensis</i>	Production of IAA, siderophores, extracellular polymeric	Soybean	Khan, Sahile (120)
<i>Azospirillum brasilense</i>	Restricted Na <sup>+</sup> uptake and increased K <sup>+</sup> and Ca <sup>2+</sup> uptake; increased NR and nitrogenase activity	Maize	Hamdia, Shaddad (121)
<i>Azotobacter chroococcum</i>	Increased chlorophyll, polyphenol and K <sup>+</sup> /Na <sup>+</sup> ratio	Maize	Rojas-Tapias, Moreno-Galván (122)
<i>Bacillus amyloliquefaciens</i>	Modulation of differential transcription of a set of at least 14 genes	Rice	Nautiyal, Srivastava (123)
<i>Bacillus aryabhatai</i>	Decreased ethylene levels of and increased plant growth	Canola	Siddikee, Chauhan (124)
<i>Bacillus cereus</i>	Proline and soluble sugars contents, Na <sup>+</sup> and oxidative stress biomarkers (e.g., O <sub>2</sub> <sup>-</sup> and H <sub>2</sub> O <sub>2</sub> ), and antioxidant activities were increased	Wheat	Desoky, Saad (125)
<i>Bacillus firmus</i>	Activities of antioxidant enzymes (APX, CAT, SOD and POD)	Soybean	El-Esawi, Alaraidh (126)
<i>Bacillus megaterium</i>	ACC deaminase and exopolysaccharides EPS secreting	Wheat	Haroon, Khizar (127)
<i>Bacillus methylotrophicus</i>	EPS production, Sequestration of Na <sup>+</sup> ion	Wheat	Din, Sarfraz (128)
<i>Bacillus pumilus</i>	Increased glycine betaine concentrations and NR activity, decreased APX activity	Rice	Jha, Subramanian (129)
<i>Bacillus sonorensis</i>	Production of NH <sub>3</sub> , IAA and siderophores	Tomato	Kapadia, Sayyed (130)
<i>Bacillus subtilis</i>	Increased chlorophyll content and K <sup>+</sup> /Na <sup>+</sup> ratio	White clover	Han, Lü (131)
<i>Bacillus tequilensis</i>	ACC deaminase and exopolysaccharides EPS secreting	Wheat	Haroon, Khizar (127)
<i>Enterobacter aerogenes</i>	ACC deaminase activity	Maize	Nadeem, Zahir (132)
<i>Enterobacter ludwigii</i>	Activities of antioxidant enzymes (SOD and POD)	Pea	Sapre, Gontia-Mishra (119)
<i>Marinobacter lipolyticus</i>	Production of EPS	Wheat	Atouei, Pourbabaee (133)
<i>Micrococcus yunnanensis</i>	Decreased ethylene levels of and increased plant growth	Canola	Siddikee, Chauhan (124)
<i>Providencia stuartii</i>	EPS production, floc yield production, biofilm formation	Rice	Shultana, Tan Kee Zuan (134)
<i>Pseudomonas aeruginosa</i>	Proline and soluble sugars contents, Na <sup>+</sup> and oxidative stress biomarkers (e.g., O <sub>2</sub> <sup>-</sup> and H <sub>2</sub> O <sub>2</sub> ), and antioxidant activities were increased	Wheat	Desoky, Saad (125)
<i>Pseudomonas anguilliseptica</i>	Biofilm formation and exopolysaccharides production	Faba bean	Mohammed (135)
<i>Pseudomonas fluorescens</i>	ACC deaminase activity	Maize	Nadeem, Zahir (132)
<i>Pseudomonas mendocina</i>	Increased ACC deaminase activity and plant nutrient uptake	Lettuce	Kohler, Hernández (136)
<i>Pseudomonas pseudoalcaligenes</i>	Increased glycine betaine concentrations and NR activity, decreased APX activity	Rice	Jha, Subramanian (129)
<i>Pseudomonas psychrotolerans</i>	Production of IAA and gibberellic acid	Maize	Kubi, Khan (137)
<i>Pseudomonas putida</i>	Decreased transpiration rates, stomatal conductance, and ABA and SA levels, and increased plant growth	Citrus	Vives-Peris, Gómez-Cadenas (138)
<i>Pseudomonas syringae</i>	ACC deaminase activity	Maize	Nadeem, Zahir (132)
<i>Pseudomonas fluorescens</i>	Antioxidant enzymes	Soybean	Abulfaraj and Jalal (139)
<i>Rhizobium massiliae</i>	Activity of antioxidant enzymes (ascorbate peroxidase, guaiacol peroxidase, and catalase)	Pepper	Hahm, Son (140)
<i>Serratia marcescens</i>	Proline and soluble sugars contents, Na <sup>+</sup> and oxidative stress biomarkers (e.g., O <sub>2</sub> <sup>-</sup> and H <sub>2</sub> O <sub>2</sub> ), and antioxidant activities were increased	Wheat	Desoky, Saad (125)

growth (108). An important amount of plant produced ACC is exuded from seeds and roots. Production of ACC deaminase is an important PGP trait, especially under salinity stress, because PGPR take up the exuded ACC and convert it to ammonia and  $\alpha$ -ketobutyrate (106). ACC reduction therefore leads to lower ethylene contents in plants, alleviating the inhibitory effect of high ethylene concentrations and promoting plant growth under salinity stress. ACC-deaminase producing rhizobacteria have been reported to improve plant mineral nutrition, resulting in mitigation

salt stress (109). Many reports have shown the efficiency of ACC-deaminase producing PGPR in alleviating salinity effects in different plants. Salt stress alleviation has been observed in canola inoculated with *Pseudomonas putida* UW4 strain (110), groundnut seedlings with *Pseudomonas fluorescens* TDK1 (111), bean with *P. fluorescens* and *Rhizobium phaseoli* (112) and rice seedling with *Enterobacter* sp. (113).

ABA is another plant hormone, known as stress hor-

more, responsible for increasing plant resistance to salinity. It is involved in many physiological changes in stressed plants. It decreases plant transpiration by inducing stomatal closure and mediates root branching to increase water uptake (114). Inoculation with ABA-producing PGPR resulted in increased growth and nutritional status of soybean seedlings affected by salinity (115). Gibberellins (GA) are other important plant growth regulating hormones that are produced by numerous PGPR. GA-treated plants have been observed to have increased water uptake, showing the role of GA under salt stress (116). Exogenous application of GA has also been shown to increase germination and growth of wheat plants (117).

Osmotic adjustment is a major mechanism involved in salt stress alleviation by PGPR. It consists in accumulation of compatible solutes (e.g., proline, trehalose and Glycine betaine) and helps plants maintaining their cellular swelling for normal cellular functioning. Proline, for example, can alleviate salinity stress in salt-affected plants by maintaining leaf water potential, eliminating free radicals and buffering the cellular redox potential and stabilizing sub-cellular structures such as proteins and membranes (141). Numerous studies on halophilic and halotolerant PGPR showed their ability to increase compatible solute contents in plants under salt stress, thus improving plant growth. It was observed high proline contents in shoots and roots of soybean plants inoculated with PGPR isolates Rkh-1, Rkh-4 and Rkh-3 conferring salt tolerance to the inoculated plants (115). Similarly, inoculation with *Pseudomonas pseudoalcaligenes* and *Bacillus pumilus* resulted in enhanced salinity tolerance in rice plants, mediated by high glycine betaine concentrations in the plant cells (142). Likewise, studies are on the efficiency of co-inoculation by *Bacillus subtilis* and *Arthrobacter* sp. in improving salt stress tolerance in wheat and reported that increased proline and total soluble sugar contents are an important defense strategy to cope with salinity stress, since they significantly contributed to the plant osmotolerance (143). Priming with *Azospirillum lipoferum* FK1 resulted in higher accumulation of soluble sugars, proteins, GB and proline in salt-treated chickpea plants, leading to salt tolerance via osmotic regulation and higher plant biomass (144). Positive effects of proline accumulation in chickpea inoculated with *Bacillus subtilis* under salinity has also been reported by Abd\_Allah, Alqarawi (145).

Salinity induces oxidative stress via overproduction of ROS, causing changes to redox homeostasis of plant cells. The role of antioxidants in salt stress alleviation is therefore noteworthy. Several studies have reported alleviation of oxidative stress in salt-stressed plants by inoculation with PGPR. PGPR inoculation decreased the activity of GR and APX in lettuce plants (146). Inoculation with *Pseudomonas pseudoalcaligenes* and *Bacillus pumilus* reduced lipid peroxidation and SOD activity in salt sensitive rice GJ-17 during salt stress (147). Inoculated with PGPR has been shown to reduce the levels of enzymatic components (e.g., APX, CAT, GR and glutathione peroxidase (GPX)) (148). This reduction indicates that PGPR-treated plants experienced less stress than non-inoculated plants.

However, some authors have reported increased antioxidant enzyme activities in PGPR-inoculated plants. Tomato seedlings inoculated with *Enterobacter* spp. EJ01 showed higher APX activities than uninoculated plants under salinity stress (149), and inoculation of *Gladiolus* with *Bacillus* spp. resulted in higher SOD and CAT activities under saline stress, physiologically protecting plants against oxidative damage and promoting plant growth (150). These increases may be explained by the fact that PGPR induce high expression of genes encoding antioxidant enzymes in inoculated plants (151). Gururani, Upadhyaya (152) monitored the changes in expression of the genes encoding ROS-scavenging enzymes in potato plants under salinity stress and observed considerably increased mRNA expression of the genes encoding for SOD, APX, CAT and GR in PGPR-inoculated than in non-inoculated plants. PGPR inoculation can therefore be concluded to confer the ability to cope with oxidative damages to plants. Further studies are needed in order to establish which synthetic and molecular mechanisms are involved in the production of antioxidant enzymes and how antioxidant activity varies in PGPR-treated plants under saline and non-saline conditions.

Exopolysaccharides (EPS) are responsible for bacterial attachment, often together with other bacteria, to soil particles and plant root surfaces (153). They play a significant role in drought and salinity stress alleviation because they are involved in hydrophilic biofilm formation on plant roots, thus conferring protection against desiccation (84). It is well known that salt stress causes imbalances in ion fluxes in plants. However, application of EPS-producing PGPR results in decreased Na<sup>+</sup> and increased K<sup>+</sup> uptake by plants. This is due to an acyl group that confers anionic properties to EPS, facilitating their binding to free Na<sup>+</sup> cations. This decreases Na<sup>+</sup> availability in the rhizosphere, resulting in improved plant nutrition and growth (154). Inoculation with the halotolerant PGPR *Bacillus amyloliquefaciens*, *Bacillus insolitus*, *Microbacterium* spp. and *Pseudomonas syringae* led to improved growth in wheat plants grown under salinity and the authors attributed this to the formation of EPS-derived rhizosheaths, which restricted Na<sup>+</sup> influx into the stele. Priming with salt-tolerant *Halomonas variabilis* HT1 and *Planococcus rifietoensis* RT4 increased the growth of chickpea plants (*Cicer arietinum* var. CM-98) and soil aggregation with plant roots under high salt concentrations (up to 200 mM NaCl) (155). Improved growth of sunflower plants inoculated with *Pseudomonas aeruginosa* and grown under salinity stress has been attributed to EPS production by the PGPR (156). Further studies and deeper analysis are needed in order to understand the role of EPS in salt and other abiotic stress alleviation by EPS-producing PGPR and explore the variations in EPS composition under different stresses, since the water retaining capacity and structure of all polysaccharides are known to vary substantially (16, 79).

PGPR induce systemic tolerance in inoculated plants by triggering physicochemical changes that increase plant abiotic stress resistance. Numerous studies have reported the role of PGPR in the regulation of stress responsive genes, either through up or down-regulation

during severe environmental stresses. For example, inoculation with *Burkholderia phytofirmans* PsJN induced high salt tolerance in *A. thaliana* by inducing changes in the expression of genes involved in ion homeostasis (*KT1*, *HKT1*, *NHX2*, and *SOS1*) (157). Similarly, priming of maize plants with *Bacillus amyloliquefaciens* SQR9 resulted in increased salinity tolerance through down-regulation of 9-*cis*-epoxycarotenoid dioxygenase (*NCED*) gene expression which is the key enzyme in ABA synthesis (158).

#### Limitations of PGPR in the natural conditions

The benefits of PGPR in agricultural fields are restricted by numerous factors, such as: i) Suboptimal rhizosphere colonization and persistence in foreign soils: despite their initial proximity to the developing root, after inoculation, PGPR must compete for colonization of the rhizosphere with resilient resident microbiota that may have become well-adapted to the soil conditions over years of evolutionary selection. Competitive PGPR may adapt structurally and/or metabolically to survive and provide tolerance to abiotic stresses; ii) Promiscuous host-specificity: Epiphytic and endophytic rhizobacteria lack active mechanisms for stringent partner-specificity which could be problematic in the field due to promiscuous colonisation and growth promotion of wild or invasive plant species which compete with target crops, negatively impacting yield (36). The root exudates are known to influence the plant-PGPR interaction. It is difficult to predict root exudates in the field because they are dynamically influenced by the plant developmental stage, rhizo-microbiome and abiotic stresses; iii) Undesirable regulation of PGP traits: many beneficial processes to the plant are energetically costly to PGPR. As such, PGPR have evolved tight regulatory systems to control expression of PGP genes and activity of PGP traits in response to environmental or internal conditions, enabling conservation of energy and resources. The existence of this undesirable regulation in agriculture can lead some PGPR to lose their performance and therefore perform sub-optimally in the field.

#### Conclusion

Plant growth promoting bacteria play a crucial role in enhancing plant tolerance to different abiotic stresses. These bacteria live in association with plant-roots and induce several changes in plants via several mechanisms, leading to restoration of plant health, growth and productivity under harsh environmental conditions. Bio-inoculants can therefore be developed using these microorganisms to effectively improve soils affected by abiotic stresses, making them productive again. Under field conditions, survival and growth promotion activities of PGPR strains are affected by many constraints such soil conditions (i.e., pH, soil nutrient status, water retention capacity etc.), autochthonous microorganisms and environmental stresses (abiotic stresses). Climatic changes are the main cause for appearance and progression of several abiotic stresses such as drought and salinity. In most agricultural fields, most of these stresses are occurring simultaneously. Therefore, in order to select the most efficient PGPR strains that could

improve plant growth under field conditions, it is highly recommended to investigate the efficacy of those strains in presence of the aforementioned stresses concurrently. So, for plant growth restoration in drought-affected fields and/or salt-affected ones the use of drought-salinity tolerant PGPR is highly recommended. PGPR-mediated abiotic stress tolerance in plants has been the focus of many recent studies, but the pronounced changes in phytohormone pools, antioxidant enzyme expression, and other changes in PGPR-inoculated plants growing under stress conditions has not been explored in detail. In-depth studies of PGPR-associated mechanisms and plant-PGPR interactions under stress conditions are needed so that PGPR-mediated ameliorative strategies of abiotic stresses can be successfully developed.

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#### Authors contributions

ABS wrote the manuscript. AC, CC, ANY and EN read and review the manuscript. All authors read and approved the final manuscript.

#### Compliance with ethical standards

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