Water Conservation and Plant Survival Strategies of Rhizobacteria under Drought Stress

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Abstract: Drylands are stressful environment for plants growth and production. Plant growth-promoting rhizobacteria (PGPR) acts as a rampart against the adverse impacts of drought stress in drylands and enhances plant growth and is helpful in agricultural sustainability. PGPR improves drought tolerance by implicating physio-chemical modifications called rhizobacterial-induced drought endurance and resilience (RIDER). The RIDER response includes; alterations of phytohormonal levels, metabolic adjustments, production of bacterial exopolysaccharides (EPS), biofilm formation, and antioxidant resistance, including the accumulation of many suitable organic solutes such as carbohydrates, amino acids, and polyamines. Modulation of moisture status by these PGPRs is one of the primary mechanisms regulating plant growth, but studies on their effect on plant survival are scarce in sandy/desert soil. It was found that inoculated plants showed high tolerance to water-deficient conditions by delaying dehydration and maintaining the plant’s water status at an optimal level. PGPR inoculated plants had a high recovery rate after rewatering interms of similar biomass at flowering compared to non-stressed plants. These rhizobacteria enhance plant tolerance and also elicit induced systemic resistance of plants to water scarcity. PGPR also improves the root growth and root architecture, thereby improving nutrient and water uptake. PGPR promoted accumulation of stress-responsive plant metabolites such as amino acids, sugars, and sugar alcohols. These metabolites play a substantial role in regulating plant growth and development and strengthen the plant’s defensive system against various biotic and abiotic stresses, in particular drought stress.

Keywords: PGPR; RIDER; drylands; water conservation

1. Introduction

Desertification, drought, and land degradation are major challenges to sustainable crop production throughout the world especially in developed countries. Water scarcity mainly due to low annual precipitation is very damaging for plant growth, and ultimately sustainable crop production. However,
there is an inordinate need to use these areas even with marginal productivity due to damage to basic farmlands. Therefore, there is more interest in producing crops using low or marginal yields of soil (e.g., sandy soil) [1]. However, sandy soil has high temperatures and suffers severe drought. Stress losses can range from 50% to 80%, depending on the stress period and type of plant species [2]. Drought stress in desert areas affects plant water potential, restricts the normal plant performance, [3], and alters the plant physiological and morphological characteristics [4,5]. Drought stress-induced plant growth was studied in wheat [6], barley [7], rice, and corn [8]. Moisture content and plant biomass are common growth factors impacted by drought stress in these plants [9]. Besides, drought stress stimulus negatively impacts the nutrient uptake and translocation as the soil nutrients are transferred to the roots via water.

Consequently, drought stress reduces the absorption of nutrient and mass-flux of water-soluble nutrients, for example, calcium, nitrate, sulfate, silicon, and magnesium [10]. Drought stress enhances formation of free radicals that damage plant defence system resulting in an increase in reactive oxygen species (ROS), such as superoxide radicals, hydroxyl radicals, and hydrogen peroxide induces oxidative stress. ROS can cause tissue damage, to membrane corrosion, proteins and nucleic acids by causing their lipid peroxidation [11–13].

Water stress is responsible for high economic losses in arid and semi-arid regions. It disturbs plant–water relations at cellular and whole plant levels, resulting in specific and non-specific responses [14]. Plant reaction to water stress is a complex process that tends to include polyamine formation and a collection of novel proteins with relatively unknown functions. Drought decreases the photosynthesis supply of carbon dioxide, which may contribute to ROS production from misguided electrons in the camera system [15,16]. It also creates free radicals during abiotic tension. ROS, such as radical superoxide (O2−), radical hydroxyl (OH), and hydrogen peroxide, enhance the damaging effect of lipid peroxidation throughout the membrane [17]. Plants have an antioxidant defensive system which prevents cellular membranes and DNA from ROS-induced oxidative damage by converting ROS into non-toxic forms such as water and oxygen [18,19].

Inoculation of plants with growth-promoting microorganisms can improve water retention strategies and drought tolerance of plants grown in arid or semi-arid regions [20]. These useful microbes inhabit the rhizosphere/endogenous rhizosphere of the plant through various direct-indirect mechanisms and promote plant growth (Figure 1). The rhizosphere is a thin layer of soil surrounding the roots of the plant and is a very critical and active area of root activity and metabolism [21–23]. A significant number of microorganisms coexist in the rhizosphere, such as bacteria, fungi, protozoa, and algae, but mostly different types of bacteria. Plants release organic compounds through exudate to select the bacteria that contribute most to the plant’s health under stressful conditions [24]. The beneficial relationships of plant-microbes in the rhizosphere are the key determinants in water conservation, soil productivity, and plant health. Plant growth-promoting rhizobacteria (PGPR) affect growth, yield, and nutrient uptake through a series of mechanisms. Some strains (e.g., Azospirillum brasilense, Aeromonas punctata, Bacillus megaterium, Pseudomonas fluorescens, Serratia marcescens) directly modulate plant physiology by stimulating the production of plant hormones, while others upturn minerals and nitrogen in the soil as a means of increasing growth under water-deficient conditions [25–28].

The current review comprehensively covers major research to evaluate the effectiveness of PGPR in alleviating crop water stress and to find effective PGPR to help crops in maintaining water status under drought conditions. The aim of the present review is to provide insights into the role of phytohormones, plant metabolites, exopolysaccharides (EPS), and 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase activity in stress tolerance of plants in response to PGPR inoculation. This review identifies the challenges of drought stress and involvement of PGPR in the mitigation of drought stress in plants for sustainable production.
2. Plant Survival Strategies under Drought Stress

A species may have a complementary set of survival strategies enabling it to survive under small and unpredictable distribution of rain [29]. Desert plants may have no water for many years. Plants exhibit different responses when sensing abiotic stimuli, which are related to specific stress-tolerance mechanisms [30–32]. A series of epidermis waxes protect plants from excessive moisture loss and provide protection against various pathogenic antagonistic activities [33]. In addition, osmoprotectants like proline accumulation aid in sustaining the plant’s water potential, and promotes the plant’s extraction of water from the soil [34]. Changes in primary metabolism are considered to be the most obvious of all metabolic reactions and comprise changes in the level of sugar/sugar alcohol, amino acid, and tricarboxylic acid cycle intermediates, exhibiting a common tendency for ecological stress reactions. However, changes in secondary metabolism are exact to particular stress and are precise to the type of plant species [35,36].

Some of the metabolic compounds that are associated with abiotic stresses and act as protectants include the sorbitol, polyols, mannotol, sucrose, fructan, proline, and ectoine [37]. Other small molecules such as carotenoids, ascorbic acid, tocopherols and anthocyanins also protect plants from being subjected to oxidative injury and protect plants by eliminating stress-induced ROS in plants. The production of phytoalexins and initiation of phenylpropanoid pathways and lignin biosynthesis are related to plant defence mechanisms [38–40]. Plant molecules such as salicylic acid, jasmonic acid, methyl salicylate, and methyl jasmonate are formed under stress. They can also act as signalling molecules that trigger defences against various biotic and abiotic stresses in crop plants [41]. In recent years, metabolomics has been used for various purposes, such as (1) assessing the effect of various stresses in plants; (2) pursuing the contribution of specific compounds in a specific biosynthetic or secondary deprivation pathway and (3) organizing various plant samples [42]. Stability, defence, and signalling of metabolites can be used to measure the degree of plant lenience to diverse abiotic stresses [43,44]. Extensive research is carried out to develop policies against drought stress by growing drought-tolerant crops, improving crop calendars and resource management practices [45].
3. Water Conservation Strategies of Plant Growth-Promoting Rhizobacteria (PGPR)

Using PGPR and commensal microorganisms, in particular arbuscular mycorrhiza (AM) fungi, may help to develop strategies to improve water retention potential in plants. More specifically, *Pseudomonas* sp. in the soil is of specific importance due to its versatility in catabolism, exceptional root colonization capacity, and the capability to produce a variety of enzymes and metabolites that contribute to abiotic stress tolerance in plants [46]. Relatively few pathways have been found to clarify the improved tolerance of *Pseudomonas*-treated plants to environmental stresses. Tolerance mechanisms such as increased osmotic adjustment and hydration of the leaves decreased oxidative damage, enhanced nutritional status, or increased the efficiency of intrinsic water usage have been suggested to elaborate the contribution of PGPR in improving stress tolerance [47].

Soil microbes have developed complex survival methods in desiccated soil. For example, bacteria have been documented to alter their membrane structure to improve their survival during the phases of low external water potential [48]. Increased water content in bacterial colonies can increase nutrient utilization [49]. In particular, the release of soluble carbohydrates in rhizosphere in PGPR-treated plants are higher, which can improving the survival rate of microorganisms under water deficit conditions. Some PGPR, such as *Azospirillum*, have the capacity to preserve water by developing cyst formation around the roots and by synthesizing polyhydroxybutyrate and melanin [50]. Likewise, extracellular bacterial polysaccharides will form organic mineral sheaths around cells along with surrounding mineral particles, which contributes to an improvement in development of macro-aggregates as an additional indirect consequence [51]. On the other hand, excessive drought stress decreases the amounts of water-soluble carbon and carbohydrates in rhizosphere of plants inoculated with *Glomus intraradices*, suggesting that mycorrhizal fungi serve as an effective sink for photosynthates and that these carbon fractions contribute to the stabilization of soil aggregates to a lesser extent. As a result, increased soil accumulation can be expected to increase water absorption by plants, thereby improving plant growth [52].

The free-moving soil bacteria sustain associations with the plant roots, thereby helping plant defence against various stresses, including drought, heavy metals toxicity, pathogens, and salinity [53–55]. Some PGPR such as *Azospirillum* sp., *Pseudomonas fluorescens* and *Azotobacter* sp. are widely used for increased crop yield [56,57]. The increased hydration caused by the PGPR strain could be due to improved water efficiency and/or enzymatic reduction of the concentration of plant ethylene, thus diminishing the inhibitory effect of ethylene on seedling root biomass [58]. The co-inoculation of arbuscular mycorrhizal fungi (*Glomus intraradices* or *Glomus mosseae*) and PGPR *Pseudomonas mendocina* with *Lactuca sativa* L. improved antioxidant catalase under extreme drought conditions, indicating that inoculants can be used to mitigate oxidative damage induced by drought [59,60]. Kohler et al. [61] demonstrated that when PGPR, *P. mendocina*, and arbuscular mycorrhizal fungi were inoculated, antioxidant catalase activity was higher in lettuce plants under severe drought conditions. The aforementioned PGPR species were also found to be useful in reducing drought-induced oxidative damage in plants (Figure 2). Interestingly, the plant growth promoting bacteria (PGPB) strain *Pseudomonas fluorescens* Pf1 augmented enzymatic activities of catalase and peroxidase in green grams under water stress. Similarly, it can also serve as a storing compound for protein synthesis. Starch biosynthesis is reduced under stressed conditions, and proline accumulation is used as a carbon and nitrogen source for plant survival [62–65]. Other common mechanisms of maintaining water status by plants in response to PGPR under water stress are as follows:
3.1. Modifications in Phytohormones Content

Plant growth-promoting rhizobacteria have developed various phytohormones, such as abscisic acid (ABA), ethylene, gibberellins, auxins, cytokinins and salicylic acid. Such hormones stimulate plant growth either directly or through certain secondary bacterial metabolites [66]. These plant hormones maintain plant water status under deficient conditions and are important for plant growth and disease prevention. **Acetobacter**, **Bacillus**, **Herbaspirillum** and **Rhizobium** species render gibberellins (Figure 2) [67]. Indole-3-acetic acid (IAA) is generated by some species of **Micrococcus**, **Pseudomonas** and **Staphylococcus**. Furthermore, cytokinins are produced by **Azotobacter chroococcum** that helps plants in sustaining proper moisture under extreme drought conditions [68]. The plant stress hormone abscisic acid (ABA), mediates plant stress tolerance by regulating several stress response genes and is responsible for maintaining proper moisture level in cells under drought conditions [69,70]. It has been previously reported that about 80% of the microorganisms extracted from the rhizosphere of different crops are recorded to be able to synthesize and release auxin as a secondary metabolite [71]. The rhizosphere bacteria-secreted IAA can interfere with plant growth and development, since receiving IAA from the soil bacteria may change the endogenous level of Plant IAA [72]. The IAA also serves as a signalling molecule that influences gene expression in a variety of microorganisms. The previous studies confirmed that phytohormones work as bi-directional communication between microbes and plant. For example, under nitrogen or phosphate starvation, the strigolactones exuded from the root, which attracts AM fungi, and downregulated their biosynthesis upon colonization [73]. Auxin and ABA have concentration-dependent positive effects on AM development while salicylic acid (SA), ethylene (ET), and gibbrillic acid (GA) inhibit the root nodule and AM symbiosis. To understand the underlying complexity, it is essential to complement the genetics with system biology approaches, including hormone profiling, metabolomics, global network analysis, and computational molecular modeling of various processes in plants and soil. IAA is produced by many plant-associated microbes, including PGPR, nitrogen-fixing symbionts, and pathogens, which assist in interactions between plant-microbes [74,75]. The pathogenic bacteria that produce IAA, when grown in culture including...
Erwinia herbicola, Xanthomonas campestris, Erwinia Chrysanthemi, and several Pseudomonas syringae pathovars [76–79].

In plant-associated microbes, the IAA regulates the expression of genes that promote the interaction with plants. IAA induced large-scale changes in the transcriptome of PGPR, A. brasilense, which upregulate the gene expression involved in IAA biosynthesis and genes involved in the metabolism, respiration, and transportation [80]. These findings suggest that IAA promotes physiological and metabolic adjustment for growth in the rhizosphere [81]. Furthermore, IAA induces the expression of genes predicted to be involved in the Type VI secretion system (T6SS). In PGPR and other plant-associated bacteria, the role of the Type VI secretion is not well understood but may help the bacteria by injecting toxins into other microbes in the vicinity. Also, the exogenous IAA enhanced the expression of genes involved in stress responses. In Escherichia coli and Bradyrhizobium japonicum the IAA treatments enhanced the cell viability when the bacteria was grown in stressful conditions, including oxidative stress, heat shock, and osmotic shock, and furthermore promoted biofilm production [82]. Consequently, IAA plays a very significant function in the relationship between rhizobacteria and plants [83]. Bacterial IAA can have enhanced the root length and surface area, making soil nutrients and water easier for plants to obtain. In addition, rhizobacteria IAA can relax plant cell walls, thereby increasing the root secretions and thus providing more nutrients to promote the growth of rhizosphere bacteria [84–87].

Agrobacterium tumefaciens strains STM196 isolated from the rhizosphere of rapeseed rape [88] have been shown to improve resistance to moderate water deficit, and alter plant physiology and delay developmental transition in Arabidopsis thaliana [89]. In addition, previous in vitro experiments have shown that STM196 modifies root architecture and hormonal signalling [90]. Importantly, STM196 not only improved plant longevity but also improved recovery of growth in living plants in post-stress and increased biomass production during flowering [91]. In A. thaliana, it was interpreted that the inoculation of Bacillus subtilis augmented the photosynthetic rate by reducing the concentration of ABA [92]. In the common bean, co-inoculation of Rhizobium tropici and Paenibacillus polymyxa has been shown to reduce the ABA content in water-deficient conditions [93]. The caronatine is exuded from Pseudomonas syringe, which inhibits the signalling pathways of ABA and prevents stomatal closure [94]. Arabidopsis thaliana inoculated with A. brasilense showed contrast results by increasing ABA content two-fold [95], and this increase in the content of ABA plays an important role in water conservation and alleviation of drought effects [96].

In addition to this, B. subtilis produces numerous polyamines which promote plant growth and development under water stress. The different types of polyamines, including spermine, spermidine, cadaverine and putrescine, are natural small-molecular-weight compound that modify physiological and biochemical attributes in plants and improve plant growth and development under drought environments [97]. Polyamine functions in the regulation of plant growth and water conservation. It has been reported to play a significant role both in promoting active growth and the division of cells into young tissues of the plants [98]. Polyamines promote the growth and cell differentiation in plant roots and provide insight into morphological variations [21,99]. Furthermore, they also play a major role in sustaining optimal ionic and pH environments, cell differentiation, organ development and secondary metabolite production under stress [100]. Polyamine has previously been documented to assist in stress tolerance either by regulating ROS homeostasis or by regulating antioxidant processes or by suppressing ROS production [101,102].

3.2. PGPR Mediated Metabolites Involved in Drought Stress Tolerance

Genetically engineered rhizobacteria, which overproduce trehalose in their cells, thereby allow plants to retain their water status and may increase survival of plants under extreme water-deficient conditions, in particular by increasing leaf water contents or by causing an accumulation of trehalose in the soil [103]. Some sugars including galactinol and raffinose act as osmoprotectants, which are synthesized in response to water-deficient conditions, mannitol scraps ROS, hydroxyl radicals and
stabilize the structure of the enzyme [104,105]. The osmolytes prevent the creation of intramolecular hydrogen bonds in macromolecules by forming hydrogen bonds with them. Trehalose stabilizes the formation of membranes and macromolecules during water stress conditions and allows plants to retain water under harsh conditions. During different environmental pressures, the aggregation of different osmolytes such as glycinebetaines, proline, ectoine, etc. has been reported [106]. Similarly, Khan et al. [107] reported a different accumulation of metabolites such as L-proline, L-arginine, L-histidine, L-isoleucine, and tryptophan in chickpea cultivars grown under drought conditions (Figure 3). Furthermore, other metabolites like alanine, choline, phenylalanine, tyrosine, glucosamine, guanine gamma-aminobutyric acid, and aspartic acid had reduced accumulation under drought conditions. Amino acids, such as branch chain alanine, valine, leucine also increased in samples of Triticeae species (IG132864, TR39477 and Bolal) under water-deficient conditions [108,109]. Urano et al. [110] also described the increased accretion of these branch chain amino acids in A. thaliana. Less and Galili [111] have suggested that activities of enzymes of amino acid catabolism were rapidly increased under drought stress.

Figure 3. A principal component analysis (PCA) based biplot showing association among different metabolites induced by PGPR in chickpea leaves grown under consortium (Cons) and water deficit (WD) conditions. Samples with consortium and water deficit treatments did not overlap with each other showing that both the treatments have different levels of metabolites. G1-Drought Sensitive genotype; G2-Drought Tolerant genotype.
On the other hand, sugar and its compounds such as fructose, mannitol, galactose, mannose and other non-reducing sugars and oligosaccharides provide a hydration shield around drought-sensitive proteins which can provide an initial defensive condition against further water depletion [112]. It has been reported previously that trehalose, glycinebetaine, carnitine, glutamate, proline, mannitol, polyols, fructans, sorbitol, oligosaccharides, and inorganic ions such as K+, sucrose, etc. are used as osmolytes to suppress cellular osmotic shock under water stress. The osmolyte accumulation prevents macromolecules by stabilizing the tertiary structure of proteins and by scavenging ROS [113,114].

3.3. Biofilm and Exopolysaccharides (EPS) Production by PGPR under Water Deficiency

Biofilms are microbial communities in which differentiated cell populations are encapsulated by bacterial made extracellular matrices [115]. Most microorganisms are capable of forming biofilms in natural, clinical and industrial environments (Figure 4). Rhizobacteria are often found to form micro-colony or biofilm-like structures at the roots of plants [116,117]. Biofilms enhance soil accumulation, improve water status and enhance microbial biomass, thereby stimulating root exudates under pressure. Therefore, the production of a viscous extracellular matrix layer at the rhizosphere has a strong selectivity advantage, especially under stress conditions [118]. The matrix may also contribute to the mechanical stability of the biofilm and interact with other macromolecules and solutes of low molecular weight to provide several microenvironments within the biofilm [119–121].

![Figure 4](image)

Figure 4. Microbial aggregates result in the formation of exopolysaccharides (EPS) and biofilm that provide protection to roots under abiotic stresses and improve the soil moisture content and soil porosity.

Studies have shown that the formation of PGPR biofilms has a pivotal role in defending plants under water deficient conditions. For example, *P. polymyx*a has been shown to colonize plant root tips, form biofilm-like structures and protect plants from water stress and pathogen infection [122]. As another example, a high mucus mutant of *P. fluorescens* CHAO strain indicating enhanced biofilm formation is believed to be beneficial for water budget and exhibits significantly enhanced carrot root colonization compared to its wild-type parent [123]. Khan et al. [124] reported that PGPR *Planomicrobium chinense*, *Bacillus cereus* and *P. fluorescens* alone or in combination resulted in biofilm formation in inoculated chick pea plants and protecting the roots of plants from the adverse effects of unfavourable conditions. Besides this, *B. subtilis* strain ATCC 6051 is capable of forming biofilm-like structures on the roots of *Arabidopsis* plants and protecting *Arabidopsis* from high temperatures and infection with *P. syringae* [125–127].

Microbial EPS is essential for the production of biofilms and cell aggregates that help to protect cells from harsh conditions and may protect the substantial amount of heavy metals (Figure 4) [128]. Many studies demonstrated the importance of microbial EPS in water conservation under water-deficient conditions [129]. Furthermore, the bacterial EPS has also been found to
be important in the bioremediation of wastes from water [130]. Exopolysaccharides produced by PGPR improved soil moisture content, plant biomass and leaf area of maize plant grown under stress condition [131]. Alami et al. [132] reported that the EPS-producing rhizobacteria control the aggregation of root-adhering soils. EPS-producing rhizobacteria will dramatically increase the number of soil macropores and soil aggregation in the rhizosphere, contributing to increased supply of water and fertilizer to inoculated plants [133–135]. EPS-producing rhizobacteria also bind cations such as Na\(^{+}\), with a rise in the population density of EPS-producing bacteria in the root zone expected to reduce the Na\(^{+}\) amount available for plant absorption, thereby alleviating salt stress in plants grown in saline environments [136]. The EPS-producing bacterial population responded to adverse environmental conditions by contributing to soil aggregation and increased the retention of water in the root rhizosphere under water stress conditions [137]. The efficacy of inoculation with rhizobacteria, *P. mendocina*, has been documented for both soil stabilization and soil fertility enhancement under non-saline conditions [138]. The function of alginates in bacterial adhesion and biofilm formation for *Pseudomonas aeruginosa* has been examined in depth. It has been shown that alginate increases the binding and anchoring of *P. aeruginosa* strains on many surfaces and is the key constituent in the biofilm matrix [139,140].

### 3.4. 1-Aminocyclopropane-1-Carboxylic Acid (ACC) Deaminase Activity of PGPR to Combat Water Deficit Stress

One of the key pathways used by PGPR to promote water conservation by plant growth and development during a water shortage is the reduction of ethylene levels by 1-aminocyclopropane-1-carboxylic acid (ACC), the immediate precursor of ethylene in plants (Figure 2) [141]. The enzyme hydrolyzes ACC to α-ketobutyrate and ammonia [142]. Plants that are inoculated with PGPR containing ACC deaminase have been found to be substantially more resistant to the deleterious effects of stress ethylene that is synthesized as a result of adverse environments such as heavy metals toxicity [143], presence of phytopathogens [144], hypoxia [145], high salinity and drought stress [146]. It has been stated in most of these cases that the PGPR containing ACC deaminase significantly decreases the ACC activity in the stressed plants, thus reducing the level of ethylene biosynthesis and consequently protecting the plants from their deleterious effects. The usage of plant growth-promoting bacteria containing ACC deaminase is helpful to facilitate plant growth and water conservation in water-deficient conditions [147].

The impact of inoculation with ACC deaminase-containing rhizobacteria on water use efficiency was clearly evident in crop plants. *Pseudomonas fluorescens* biotype G (ACC-5) was found to be more promising at low humidity (25% field capacity), because of its maximum water use efficiency compared to the respective uninoculated controls. Similarly, inoculation was shown to be efficient in increasing the productivity of water usage when measured on a dry weight basis [148]. The inoculation of ACC deaminase PGPR *Achromobacter piechaudii* ARV8 with pepper and tomato seedling exposed to transient water stress significantly increased the fresh and dry weights of the plants [149]. Recently, beneficial effects of ACC deaminase-producing bacterium *Variovorax* sp. in improving the nodulation and growth of spiny brooms grown in arid regions of Tunisia have been observed [150]. Likewise, ACC deaminase-containing *Variovorax paradoxus* has also caused physiological modifications in *Pisum sativum* L. grown under moisture deficient condition [151]. Positive effects of ACC deaminase bacteria on shoots and roots biomass, transpiration rate and leaf area of plants were also observed in short-term experiments (Table 1). In long-term studies, plants inoculated with ACC deaminase bacteria provided more seed yield (25–41%), number of seeds, and accumulation of seed nitrogen than uninoculated plants, and helped preserve water status [152].
**Table 1.** Impacts of 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase-producing bacteria on plant growth and drought stress tolerance.

| ACC Producing PGPR | Host Plants | Results | References |
|---------------------|-------------|---------|------------|
| *A. piechaudii* ARV8 | *Solanum lycopersicum* L. | Enhanced plant biomass and decrease in ethylene levels. | [153] |
| *A. piechaudii* ARV8 | *Pisum sativum* L. | Improve root-shoot ratio under low soil moisture content. | [154] |
| *Pseudomonas* sp. | *Pisum sativum* L. | Improve the plant growth and yield and reduce the triple response of ethylene. | [155] |
| *P. fluorescens* | *Pisum sativum* L. | Positive impacts on plant growth under severe drought stress. | [156] |
| *V. paradoxus* 5C-2 | *Pisum sativum* L. | Induce the abscisic acid (ABA) signalling in plants and improve the soil nutrient content. | [157] |
| Rhizosphere bacteria containing ACC-deaminase | *Triticum aestivum* | Enhance root-shoot length and improve the water and nutrient uptakes. | [158] |
| *Bacillus* 23-B + *Pseudomonas* sp. 6-P + *Mesorhizobium ciceri* | *Pisum sativum* L. | Improve seed germination and root length in chickpea under moisture stress. | [159] |
| *Bacillus licheniformis* K11 | *Pepper nigrum* | Enhance the expression of stress related genes e.g., Cadh, VA, shSP, and CaPR-10. | [160] |
| *Citricoccus zhacoinesis* B-4 | *Allium cepa* | Promote plant growth and germination index. | [161] |
| *Ochrobactrum pseudogrignonense* RJ12, *Pseudomonas* sp. RJ15 and *B. subtilis* RJ46 | *Vigna mungo* L. | Show positive impacts on seed germination, improve root and shoot length and regulate ethylene level. | [162] |

### 4. Development of Root System by PGPR

Rhizobium helps plants in maintaining a favourable water status in their tissues under water-deficient conditions by enhancing root development (Figure 1). Rhizosphere bacteria that promote plant growth colonize roots and maintain symbiotic interactions to promote plant growth and provide protections against stresses [163]. Different strains of PGPRs are well known for their positive impact on plant growth and also helping in water stress such as *Azospirillum* sp., *Azotobacter* sp., and *P. fluorescens* [164]. Root biomass was large in plants inoculated with *Phyllobacterium brassicacearum* STM196, and also increased the water absorption by changing root architecture. Studies conducted under reproductive conditions have shown that STM196 increases lateral root length [165], as well as the density and length of root hairs [166]. STM196 resulted in a greater contact surface with the soil causing higher water flow from roots to the shoot. Some rhizosphere bacteria help plants in maintaining a desirable moisture level in their tissues under water-deficient conditions by improving the root development [167]. Inoculation with PGPR strains improved plant growth by strengthening the root architecture, consequently increasing nutrient uptake [168,169].

Some PGPRs like *A. brasilense*, *B. japonicum*, *B. cereus*, *Paenibacillus illinoisensis*, *P. fluorescens* promote root development and alter root structure by producing plant hormones such as IAA, resulting in increased root surface area and increased number of root tips [170]. This root stimulation can help plants fight pathogens. It has also been suggested that PGPR increases plant uptake of water and mineral ions by proton pump ATPase stimulation, despite the lack of experimental evidence [171].
5. Improving Nutrient Availability and Maintenance of Soil Quality

Drought stress affects soil biological, physical and chemical activities. It not only decreases plant nutrient supply but also has harmful impacts on plant and soil health due to a rise in soil temperature [172]. Under drought conditions, the nutrient availability to the plant is seriously impaired; however, the usage of appropriate microorganisms restores nutrient bioavailability in drought-stressed conditions. Several PGPR have been isolated in recent decades and have been suggested for use in sustainable agriculture under water deficit conditions [173]. Plant growth-promoting bacteria found to be very effective in substantially increasing soil nutrients content thus improving crop yields [174]. PGPRs of the genera *Arthrobacter*, *Azotobacter*, *Azospirillum*, *Bacillus*, *Enterobacter*, *Pseudomonas*, *Serratia* and *Streptomyces* were largely documented for this purpose [175]. PGPR may have a beneficial impact on plant growth and development, possibly because of a nutrient mobilization in the soil, nitrogen fixation and excretion of different plant hormones (Figure 2). Using PGPR may help in reducing the use of chemical fertilizers or increase the nutrient-use efficiencies, particularly for low-mobility nutrients such as iron and phosphorus [176,177]. In particular, iron forms insoluble hydroxides in high pH soils, and supply of bioavailable Fe to plants is reduced. It was previously reported that the production of siderophores by genus *Pseudomonas* enhanced the solubility of Fe and contributed to the overall iron requirements of plants, especially in calcareous soils [178].

Soil quality is critical for the improvement of sustainable farming under extreme drought conditions. It encourages penetration of water, provides optimal habitat for soil organisms and an optimal aeration to roots and soil organisms, and helps in preventing soil erosion [179]. Microorganisms have been observed to have a direct impact on soil properties and quality, since they may associate with other microorganisms in the rhizosphere (Figure 4) [180–182]. Soil microorganisms play an important role in controlling the processes of decomposition of organic matter, and the supply of plant nutrients, such as N, P and K. Microbial inoculants are well known as an essential component of advanced nutrient management contributing to sustainable agriculture [183]. In addition, microbial inoculants can be used to improve crop production as an economic input; fertilizer doses can be reduced, and nutrient use efficiencies can be increased [184].

6. Changes in Plant Functional Traits

It is well established that extreme deficient water stress affects plant growth, water status, and is responsible for a decrease in photosynthetic ability, especially through stomatal closure and leaf senescence. Non-destructive experiments based on chlorophyll fluorescence imaging were commonly used to decipher the effect of different water potentials on plant physiology, but only rarely used at high performance [185]. Measurements of chlorophyll fluorescence were performed at high throughput to unravel the influence of rhizobacteria on the responses of plants to drought (Figure 5). There are numerous photosynthetic parameters that exist; dark-adapted $F_{v}/F_{m}$ represents the optimal efficiency of photosystem II (PSII) and is thus one of the most commonly used parameters for analyzing the physiological modulations in leaf. Most commonly, the mean $F_{v}/F_{m}$ of the photosynthetic organ or the whole plant is used to describe the stressor response [186]. The major decrease in mean $F_{v}/F_{m}$ during a prolonged water deficit is commonly correlated with high leaf senescence. With a higher proportion of leaf senescence, STM196-inoculated plants may persist and thus provide higher resistance to photosynthetic damage from the leaves [187–189].

Inoculated plants thus demonstrated reduced mortality rate after the establishment of water tension. Leaf senescence reflects a common way to conserve resources. It allows translocation to reproductive organs and decreases water intake of older and less-productive leaves [190]. Therefore, leaf senescence is an adaptive trait which will help plant survival under stressful conditions. The increase in chlorophyll content may contribute to the improvement in plant photosynthetic efficiency triggered by PGPR. Rice plants inoculated with arbuscular mycorrhizal fungus under water tension showed a positive association between water budget and PSII efficiency [191]. In *A. thaliana*, the inoculation of the *Burkholderia phytofirmans* PsJn strain enhances the senescent leave at flowering under well-watered
environments. It is widely confirmed that rhizobacteria increase the content of leaf water which results in increased plant resistance under drought stress [192–194].

![Figure 5. Effects of PGPR on leaf chlorophyll content and photochemical efficiency of chickpea plants grown under moisture stress conditions.](image)

7. Molecular Mechanisms to Mitigate Drought Stress Induced by PGPR

Plant responses to environmental stresses are complex mechanisms which involve modulation in the expression of stress-related genes [195,196]. These genes support stress management by inducing two different types of protein, either functional proteins that act directly, such as mRNA binding proteins, chaperones, LEA proteins, and osmotic regulators, or regulatory proteins that regulate transcription and signalling pathways [197]. Plants recognise abiotic stresses by specific receptors in the cell walls or intracellularly, which involve various sensing system. ABA plays a significant role in abiotic stress responses by influences in the expression of various genes to mediate systemic stress tolerance [198–200]. Additionally, a variety of compounds serve as systemic signals to alleviate stress within the plants, for example, small RNAs (sRNA), peptides and metabolites [198].

Stress tolerance can be enhanced by treating plants with several PGPR stains which up-regulate stress tolerance inducing genes. The rice plants treated with *P. fluorescens* induced multiples differential gene expression, for example, ERD15 (Early response to dehydration15), COC1, Hsp20 and bZIP1 (chaperones in ABA signalling pathway), PKDP (protein kinase), and COX1 (regulate energy and carbohydrate metabolism). *Arabidopsis thaliana* treated with *Pseudomonas* strains promote the expression of ACO, ACS (ethylene biosynthesis), ADC, CPA, AIH, SPMS, SPDS and SAMDC (polyamine biosynthesis), VSP1 (ethylene-responsive gene), Pdf1.2 (JA marker genes) and PR1 (SA regulated gene). Similarly in *Lycium barium* it increased the expression of LbKT1, LbSKOR (encoding potassium channels) and RAB18 (ABA-responsive gene) in drought conditions [201–203]. Pepper plant inoculated with *Bacillus* sp. enhanced 1.5 fold increased the expression of sHSP (small heat-shock proteins), VA, and Cadhn. Under drought conditions, the inoculation of *A. brasilense* NO40 and *Bacillus amyloliquefaciens* 5113 alleviates the deleterious effects in the leaves of wheat plants by upregulation of APX1, HSP17.8 and SAMS1 stress-responsive genes [204]. This overexpression of genes increased the ascorbate-glutathione redox cycle, which helps to overcome the adverse effect of water stress.

Recent approaches to system biology and omics analysis of transcripts, proteins and metabolites have improved our knowledge of molecular responses in stressed plants and plant–microbe
interactions [205,206]. PGPR-induced physiological and metabolic alternation is anticipated to be driven by molecular alteration that has culminated in protein and post-translation modifications. The combination of proteomics and metabolomics profiling for stressed, non-stressed and PGPR-treated plants will also help to classify metabolic and molecular modulations involved under stress conditions in beneficial plant–microbe interactions and help to elucidate the essence of the defence. Under drought stress, the proteomic and metabolic studies and PGPR responses have been reported in many plants [207,208]. However, the impact of beneficial microbes on gene expression and metabolite aggregation in PGPR-treated crop plants remains poorly investigated.

8. Conclusions and Future Perspectives

Many plant-associated bacteria are well known for their ability to promote plant growth and improve water-use efficiency and tolerance to various abiotic stresses. These PGPR species improve the water conservation status in many plants and are capable of overproducing biofilms, exopolysaccharides and trehalose, in their cells and improve the root system and soil fertility status. They help plants to improve their root system and maintain its proper cellular moisture status, resolutely improving plant survival under severe water-deficient conditions. Phytohormones are an important component of plant growth and development under drought stress. The PGPR inoculation changes the levels of plant hormones and other metabolites which help in plant adaptations through their response to the plant water balance, nutrient uptake and translocation, gas exchange, and the movement of photosynthates between tissues. In addition, polyamines are also found to be highly associated in enhancing the water balances and promote the growth of the plants.

In future research, studies can be focused on how PGPR can alter metabolic profiling in plants under water deficiency and on examining further the gene expression or protein changes that are directly involved in the production of these metabolites. It is also important to unravel the complex genetic network and metabolic-interacting events which mediate the host–microbe interactions.

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