Phyton-
International Journal of
Experimental Botany

Tech Science Press

http://doi.org/10.32604/phyton.2026.075288

REVIEW

Emerging Roles of Plant Growth-Promoting Rhizobacteria in Drought Management: Mechanisms and Advanced Strategies for Enhanced Efficiency

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Received: 29 October 2025; Accepted: 18 March 2026; Published: 29 June 2026

ABSTRACT: Drought represents a major environmental challenge, limiting water availability to plants and disrupting their physiological functions and growth, particularly in dryland regions. Traditional strategies, including water conservation practices, plant breeding, and advanced tools such as genetic engineering, have been employed to enhance drought tolerance. However, these methods are often time-consuming and expensive. Plant growth-promoting bacteria (PGPR) present a promising alternative by forming symbiotic relationships with plant roots and boosting drought resilience. PGPR enhances plant tolerance to drought-induced water stress through complex biochemical and physiological mechanisms, including phytohormone modulation, exopolysaccharides production, nutrient uptake, and gene regulation. Despite these advantages, their performance is often restricted by reduced microbial viability under drought conditions. Recently, nanoencapsulation has emerged as an effective technique in improving PGPR survivability, controlled release, targeted delivery, and root colonization efficiency in semi-arid and arid soils. This review emphasizes the role of PGPR in enhancing drought tolerance by summarizing recent insights on PGPR-mediated drought stress tolerance mechanisms, including phytohormone regulation, antioxidant activity, and osmotic balance. It also explores nanoencapsulation strategies to improve their survival and efficacy under water-limited conditions. Finally, the review highlights the knowledge gaps and future research directions to advance the practical application of PGPR for climate-resilient and sustainable agriculture in dryland regions.

KEYWORDS: Drought; water stress; plant growth-promoting bacteria; nanoencapsulation; phytohormone regulation

1 Introduction

Agricultural productivity is greatly affected by global climate change, which has intensified the impacts of various abiotic stresses in crops [1]. Among these stresses, drought is widely recognized as the most damaging constraint to plant growth, development, and crop yield [2,3]. Rising temperatures, unpredictable precipitation patterns, and frequent extreme weather conditions further aggravate the frequency, severity, and duration of drought [4]. Moreover, human activities, including deforestation and intensive farming, further degrade soil structure and reduce its water-holding capacity, thereby exacerbating drought impacts [5,6]. This issue is particularly more pronounced in dryland areas, including arid, semi-arid, and dry sub-humid regions, which account for approximately 44% of the global agricultural system [7]. With the average global temperature projected to rise by 1.5°C, drought intensity and water deficit conditions are expected to worsen, especially in Asia, Africa, and the Near East, where agriculture consumes 80–90% of available freshwater [8]. Furthermore, over 75% of global agricultural land relies on rainfall, making crop production highly susceptible to declining and uneven precipitation, particularly in many developing countries [9]. Consequently, drought stress has become one of the most serious threats to sustainable agriculture, causing annual yield reductions of 20–50% in several affected regions [10]. Future projections suggest that between 2010 and 2050, cereal production may decline by approximately 0.9–1.9% due to decreasing irrigation water availability, and without effective adaptive measures, global crop productivity is expected to decrease even further, posing a serious threat to global food security [11]. Fig. 1 illustrates the long-term impact of global climate change on agricultural sustainability.

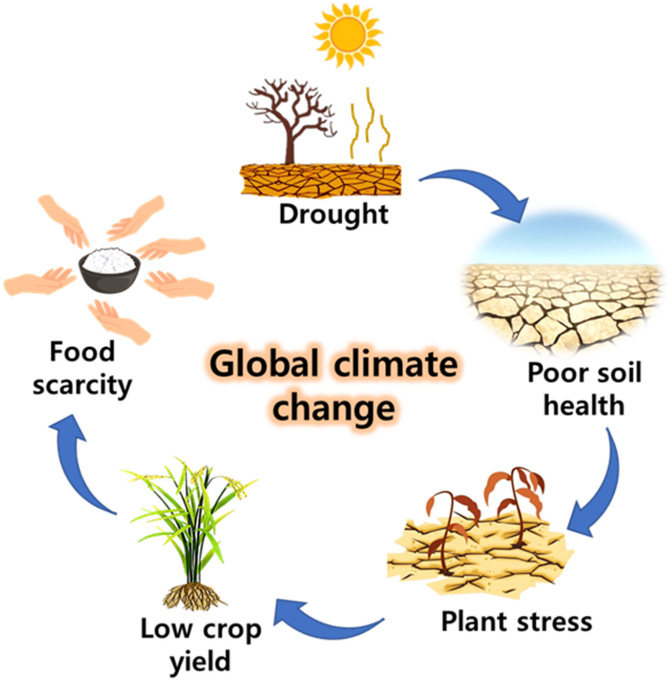

Figure 1: Effects of global climate change on agriculture and food security.

Drought is a major cause of water stress in plants, which severely affects plant growth by reducing soil moisture and availability and limiting the transport of essential nutrients, inducing physiological, photosynthetic, and morphological impairments, particularly during reproductive stages, leading to significant yield losses [12–14]. To combat drought stress, a range of agronomic and technological strategies have been adopted, including sustainable farming practices, compost and fertilizer application, modified planting schedules, water harvesting, and improved irrigation management [15]. Water harvesting and conservation techniques can increase agricultural water availability by two to threefold, leading to substantial improvements in crop yields [16,17]. In addition to these measures, proactive methods such as soil management, breeding drought-resistant cultivars, fostering plant-microbe symbiosis, and genetic engineering of drought-tolerant genes are increasingly recognized as essential for enhancing crop resilience under drought [18–20]. However, despite their potential, many of these strategies remain costly, difficult to implement, and pose economic and environmental constraints, particularly in developing countries.

In recent years, there has been increasing interest in eco-friendly and sustainable alternatives to enhance plant adaptation to drought. Among these, plant growth-promoting rhizobacteria (PGPR) are particularly promising, as they enhance soil quality, improve plant water-use efficiency, and boost crop yields under both stressed and non-stressed conditions, especially in dryland regions [21–24]. PGPR are beneficial non-pathogenic soil bacteria that boost plant tolerance to drought by minimizing water loss, enhancing nutrient uptake, and improving water absorption, offering a scalable and viable alternative to conventional water-management techniques [25–27]. They confer drought resistance through multiple mechanisms, including phytohormone regulation, exopolysaccharides (EPS) production, volatile organic compounds (VOCs), osmolyte accumulation, nitrogen fixation, enhancement of root structure, and induction of systemic tolerance, thereby strengthening plant adaptation to water-deficit conditions [28–30].

PGPR application offers an environmentally friendly approach for sustainable agriculture. However, their effectiveness depends on various factors such as specific microbial strains, soil conditions, plant genotype, and environmental interaction [31–33]. A major challenge is maintaining the viability of PGPR inocula under field conditions, as bacterial populations often decline over time. Therefore, effective delivery requires suitable carriers that provide protection, sustained nutrient availability, and extended shelf life [34]. In this context, emerging nanoencapsulation strategies show great promise in enhancing PGPR survival under stress. Nevertheless, their effective implementation requires a comprehensive understanding and systematic evaluation. This review aims to evaluate the critical gap by combining recent experimental data to provide a comprehensive and current overview of PGPR-mediated drought tolerance, while also emphasizing encapsulation as a promising and scalable strategy to improve their practical use in sustainable agriculture. In particular, the review explores the recent advances in understanding the molecular mechanisms through which PGPR improve drought tolerance, including phytohormone regulation, antioxidant enzyme activities, and maintenance of osmotic balance. Additionally, it provides a comprehensive evaluation of PGPR encapsulation and delivery technologies to improve microbial stability, survivability, and efficacy under water-limited environments. Lastly, future research directions required to advance PGPR applications in sustainable agriculture are discussed, offering valuable guidance for researchers to identify knowledge gaps, optimize experimental approaches, and develop more effective, field-relevant PGPR-based solutions.

2 PGPR and Rhizosphere Microorganisms in Enhancing Drought Tolerance and Soil Fertility

Drought stress is one of the most critical abiotic factors affecting agricultural productivity, as it disrupts soil processes and imposes severe pressure on microbial communities, thereby altering soil microbial activity through changes in nutrient dynamics and chemical availability [30,35]. Under such conditions, plants face significant challenges in growth and productivity. However, studies have shown that rhizosphere microorganisms significantly enhance plant growth even under limited water conditions [36]. Plants are involved in complex and dynamic interactions with both mutualistic and pathogenic rhizosphere microorganisms [37]. Among them, PGPR represent an important group of microorganisms that colonize plant roots and contribute to drought stress tolerance and improved soil quality [38].

PGPR exhibit various kinds of association with crops, which include free-living non-symbiotic (*Azotobacter*, *Alcaligenes*, *Burkholderia*, *Bacillus*, *Enterobacter*, and *Pseudomonas*), endophytic (*Azospirillum*), and symbiotic (*Mesorhizobium*, *Rhizobium*, and *Bradyrhizobium*) relationships [39,40]. Based on their location, PGPR can be categorized into intracellular and extracellular [41]. Intracellular PGPR are commonly localized within the nodular root cells of plants, whereas extracellular PGPR are typically located within the intercellular spaces of root cells and the rhizoplane [42]. Intracellular species such as *Frankia*, *Bradyrhizobium*, *Rhizobium*, *Allorhizobium*, and *Mesorhizobium* contribute significantly to nitrogen fixation by utilizing plant-derived carbon sources, thereby enhancing soil fertility and plant growth [39]. For instance, *Rhizobium* species take part in biological nitrogen fixation, particularly in leguminous crops.

This symbiotic process improves soil fertility and enhances crop yields by providing plants with essential nitrogen [27]. Similarly, *Frankia* spp. fix atmospheric nitrogen in non-leguminous plants, supporting growth under nitrogen-deficient conditions [43]. Extracellular PGPR, including *Burkholderia*, *Erwinia*, *Serratia*, *Bacillus*, *Micrococcus*, *Agrobacterium*, *Azotobacter*, *Chromobacterium*, *Arthrobacter*, *Azospirillum*, *Pseudomonas*, *Flavobacterium*, and *Caulobacter*, also play essential roles in nutrient mobilization, plant growth promotion, and stress adaptation [44,45].

Rhizosphere bacteria, including PGPR, have been widely integrated into agronomic production systems due to their ability to control plant diseases and promote crop growth [46,47]. Numerous studies demonstrate that PGPR alleviate drought stress through multiple physiological and biochemical mechanisms, including delaying leaf senescence, altering phenological development, and accelerating flowering, thereby enhancing drought escape and tolerance strategies in crops [48,49]. For instance, *Pseudomonas fluorescens* DR7 has been shown to enhance foxtail millet growth under limited water availability by increasing soil moisture retention [50], while PGPR treatments in tomato and wheat significantly alleviate the adverse impacts associated with water stress [36,48]. Likewise, in peppermint, PGPR mitigated drought stress by boosting antioxidant activity, reducing reactive oxygen species (ROS) accumulation [51]. *Bacillus licheniformis* has been reported to enhance drought stress tolerance by improving plant water-use efficiency [52]. In arid and semi-arid regions, *Phyllobacterium brassicacearum* STM196 has demonstrated the ability to improve agricultural productivity by various mechanisms, which include optimizing water-use efficiency, modulating abscisic acid (ABA) signaling and transpiration rates, enhancing photosynthetic efficiency, and postponing flowering under prolonged drought stress [53,54].

Besides, PGPR promotes plant development by facilitating the uptake of essential nutrients, particularly potassium and nitrogen, which are crucial for root growth. This increased nutrient availability expands root surface area and subsequently improves water uptake [45]. Collectively, these findings highlight that PGPR not only enhances plant tolerance to drought stress but also strengthens soil fertility and overall agricultural sustainability. Nevertheless, their responses to drought are not uniform and may vary depending on bacterial developmental stages, host plant species, and the duration and severity of the stress [55].

3 Mechanisms of PGPR in Drought Stress Tolerance

PGPR enhances drought tolerance in plants through various mechanisms, which are described in detail in the following sections.

3.1 PGPR-Mediated Phytohormonal Regulation

Certain PGPR can produce phytohormones like cytokinins (CK), ABA, gibberellins (GA), auxins, and ethylene, which are essential for regulating plant cell division, growth, and development [56,57]. During drought conditions, osmotic stress triggers hormonal signaling and metabolic responses involving CK, auxins, ethylene, and ABA, leading to developmental adjustments in plants [58]. Drought stress induces higher production of ABA, which subsequently regulates CK biosynthesis by controlling the expression of important enzymes implicated in the pathway. In contrast, CK can reduce auxin concentration and stimulate biosynthesis of ethylene [58,59]. Thus, CK production, in connection with ethylene and auxin signaling, impacts drought stress response of plants under water-limited conditions [60]. Collectively, these PGPR-derived phytohormones help plants withstand drought stress and contribute significantly to enhancing agricultural productivity [61]. The roles of PGPR-regulated hormones under drought stress are summarized in Fig. 2 and discussed in the following sections.

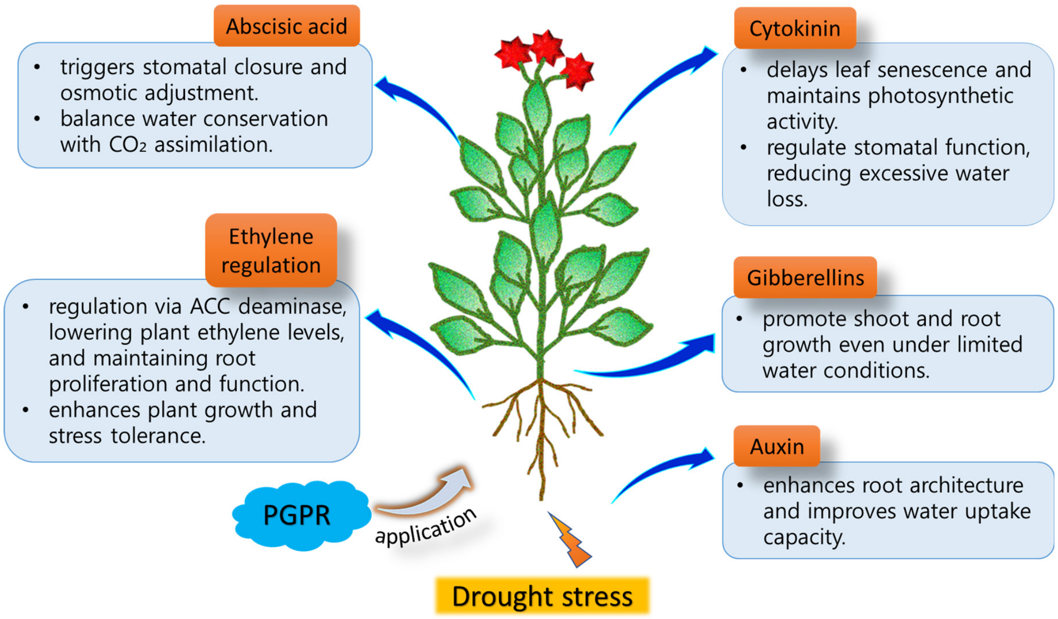

Figure 2: PGPR-mediated phytohormonal regulation under drought stress.

3.1.1 Auxin Production

Indole-3-acetic acid (IAA), one of the most active forms of phytohormone auxin, regulates plant development, cell growth, and defense response against pathogens [62]. IAA enhances bud development and growth while improving the expansion of juvenile stem cell walls. Besides its growing functions, it also serves as a key auxin regulating the abscission of flowers and buds [63,64]. Moreover, IAA influences gene expression in particular species and is a reciprocal hormone in the interaction between crops and microbes [65].

In dryland regions, IAA-synthesizing PGPR can enhance stress resistance, where water scarcity primarily limits agricultural productivity. For instance, under water scarcity conditions, *Azospirillum brasilense* treated maize seedlings substantially increased their absolute and relative water levels [66]. Moreover, treatment of *Azospirillum brasilense* Sp245 in wheat enhanced phytohormone levels under water scarcity conditions, leading to enhanced grain yield, water potential, higher minerals (Ca, Mg, and K) quality, and absolute and relative water content [67]. Many PGPR isolates, including *Pseudomonas*, *Bacillus*, and *Arthrobacter* species, are capable of producing IAA [68]. Studies revealed that IAA-producing PGPR treatment in plants significantly enhances root growth by promoting the development of root filaments and lateral roots, and expanding root surface area [69,70]. This enhanced root development improves nutrients and water uptake, allowing crops to thrive in dry and semi-dry conditions. In cereals, the microbial-induced root development is particularly important, as many modern cultivars possess relatively weak root systems [71]. When auxin-producing PGPR are applied in combination with compost and biochar, they can alleviate drought stress by improving soil porosity and moisture-holding ability [72]. PGPR have been shown to increase endogenous IAA levels, thereby improving plants' resilience to water scarcity by boosting root length, xylem tissue flow, root nodule formation, and root surface area [73]. Similarly, soil bacterial IAA facilitates the softening of crop cell walls, thereby enhancing root exudation and promoting rhizobacterial proliferation via improved nutrient availability [74].

IAA-producing PGPR have been shown to improve chlorophyll levels, delay leaf senescence, improve nutrient absorption, and alleviate drought stress conditions by reducing ROS levels [38,75]. Under drought conditions, the growth of lavender plants was promoted by *Bacillus thuringiensis* via IAA synthesis, which subsequently enhances the plant's metabolic activities, nutritional uptake, and physiological processes [69,76]. Another PGPR, *Azospirillum brasilense*, generates a diffusible gas, like nitric oxide, in tomatoes and takes part in the IAA biosynthesis pathway. Such gases stimulate the advancement of adventitious roots, consequently enhancing plant growth [69,76]. Furthermore, during drought, PGPR influence the gene expression involved in auxin synthesis, signaling, and transport mechanisms [77]. PGPR strains like *Bacillus* sp. LZR216 and *Phyllobacterium brassicacearum* STM196 stimulate endogenous IAA production by promoting the genes associated with IAA biosynthesis [78]. In *Arabidopsis thaliana*, *Burkholderia phytofirmans* PsJN boosts auxin synthesis and induces tryptophan gene expression in the IAA precursor [79]. Another PGPR *Bacillus* sp. LZR216 inhibits the production of auxin transporters AUX1 and PIN1–3, whereas *Burkholderia phytofirmans* PsJN improves the expression of PIN2 and PIN3 [79]. Through such interactions, PGPR alter the efflux and inflow of auxin carriers, thereby affecting auxin transportation. Therefore, the dry and semi-arid farming regions have the potential to utilize IAA-producing PGPR as promising bioinoculants to improve stress resilience and enhance plant production [80].

3.1.2 CK Production

CK is an essential phytohormone synthesized by both microorganisms and plants and plays a vital role in intercellular phytohormone signaling networks [81]. It directly regulates cell division and, in association with auxin, serves as a key regulator of root development and organogenesis [82]. Consequently, CK promotes plant growth and enhances adaptability to water stress.

CK can be produced through several PGPR, including *Arthrobacter*, *Azospirillum*, *Rhizobium*, *Bacillus*, *Azotobacter*, and *Pseudomonas* [83,84]. *Bacillus subtilis* was found to enhance drought tolerance and growth of *Platycladus orientalis* seedlings by maintaining higher CK and ABA levels, improving plant water status, increasing shoot biomass, and mitigating drought-induced growth suppression [83]. Moreover, CK produced by PGPR can enhance cell division; however, its accumulation in roots inhibits root development [85]. CK has shown the potential to delay leaf senescence under water stress by enhancing the expression of antioxidant genes, which in turn moderate ROS synthesis [86]. A study in alfalfa crops demonstrated that inoculation with CK-producing PGPR *Sinorhizobium* enhances water resistance, primarily by increasing antioxidant activity and decreasing ROS accumulation [87]. Similarly, root inoculation with *Pseudomonas fluorescens* G20-18 greatly enhanced tomato growth and drought resistance by improving hormonal balance, photosynthesis efficiency, antioxidant activities, and gene expression related to drought stress, highlighting the key role of PGPR-derived CK in preparing systemic plant resilience to water stress [88].

3.1.3 ABA Production

ABA is a vital phytohormone synthesized in various plant tissues, including chloroplast-containing cells and roots. It plays a pivotal role in controlling moisture loss by inducing stomatal closure and activating stress signaling networks, thereby promoting crop resilience to abiotic stresses like drought [89]. ABA hormones are synthesized in response to water loss, leading to the production of dehydrins that protect plants from dehydration [90]. Under water-deficient conditions, ABA is rapidly produced and transported to the stomata, where it reduces the water transpiration rate. Additionally, it promotes root branching to improve water absorption and accelerates leaf growth, collectively contributing to improved plant adaptation to drought [91,92].

Various plant species inoculated with PGPR demonstrated enhanced drought tolerance through ABA hormone regulation [93]. When exposed to drought stress, *Arabidopsis* plants treated with *Azospirillum* *brasilense* demonstrated an increase in ABA levels that triggered adaptive responses, including enhanced growth and lateral root development, increased photosynthetic pigment production, and reduced water loss via closure of stomatal pores [94]. Similarly, the *Phyllobacterium brassicacearum* SMT196 strains, isolated from *Brassica napus*, modulated ABA levels, reduced leaf transpiration, and improved water-use efficiency in *Arabidopsis*, thereby enhancing drought tolerance [53]. Plants inoculated with *Bacillus licheniformis* Rt4M10 and *Pseudomonas fluorescens* Rt6M10 exhibited 5% and 10% lower transpiration, respectively, compared to non-inoculated control plants, which is associated with increased ABA levels in leaf tissues. These findings indicate that PGPR either produce ABA or induce its biosynthesis, leading to improved plant tolerance to drought stress [95].

3.1.4 GA Production

Another crucial phytohormone, GA, is actively involved in various physiological processes, including germination, shoot elongation, and stress responses [96]. PGPR can alter endogenous GA levels in plants. For example, under drought stress, GA secreted by the rhizobacterium *Pseudomonas putida* H-2-3 improves soybean plants' growth and enhances stress-tolerant capability [97]. Another PGPR, *Burkholderia phytofirmans* PsJN, however, does not synthesize GA directly but enhances the *AtGA3ox1* gene expression, which encodes an enzyme in *Arabidopsis thaliana* during the last steps of GA biosynthesis [98]. In maize, *Azospirillum lipoferum* alleviated drought- and fluridone-induced growth inhibition and water loss through increased ABA levels. Despite increased ABA levels, growth was still constrained when GA synthesis was inhibited, indicating that both ABA and GA contribute to *Azospirillum*-mediated drought tolerance [99].

3.1.5 Ethylene and 1-Aminocyclopropane-1-Carboxylate (ACC) Deaminase Production

Ethylene is another vital phytohormone that regulates important processes in the growth and development of plants, including fruit ripening and abscission [100,101]. However, an increased concentration of ethylene results in defoliation and a reduction in crop yields [102]. Ethylene is synthesized under abiotic stress conditions, and increased ethylene production is one of the physiological responses of plants against water stress [103].

Many PGPR possess ACC deaminase enzyme, which inhibits ethylene production by utilizing ACC from root exudates and converting it into a-ketobutyrate and ammonia. By reducing plant ACC availability, PGPR lowers stress-induced ethylene levels, thereby promoting the growth and enhancing stress tolerance [104]. In addition, PGPR can influence ethylene-induced gene expression. For instance, *Pseudomonas putida* MTCC5279 suppresses the ethylene signaling-related transcription factor ERF13 in *Arabidopsis thaliana* [105]. Similarly, under water stress in soybeans, *Pseudomonas simiae* AU enhances auxin-related gene expression while reducing ethylene-responsive gene expression, thereby promoting drought stress adaptation [106].

The integration of ACC deaminase-synthesizing PGPR with the crop has shown remarkable agronomic benefits, including enhanced rhizobial nodulation, increased phosphorus, potassium, and nitrogen availability, and improved shoot growth and root elongation [107–110]. For instance, *Achromobacter piechaudii* ARV8 inoculation in pepper and tomato plants showed decreased ethylene content, which led to a significant enhancement in dry and fresh weights, and improved drought tolerance [111]. Similarly, *Variovorax paradoxus* 5C2 enhanced tolerance to water stress and improved growth and development in pea plants via ACC deaminase enzyme activity [112]. In pepper plants, *Bacillus licheniformis* K11 conferred water stress tolerance by producing ACC deaminase and regulating stress-related proteins and genes, including *VA*, *Cadhn*, *CaPR-10*, and *sHSP* [113]. Moreover, under drought stress, ACC deaminase-producing bacterial species, including *Serratia and Pseudomonas*, increased relative water content, improved growth, and decreased ABA and malondialdehyde (MDA) levels, accompanied by enhanced antioxidant activity, collectively contributing to improved tolerance to water scarcity [114,115].

The role of PGPR in regulating and synthesizing phytohormones in plants under drought conditions is summarized in Table 1.

Table 1: Phytohormonal and physiological modulation by PGPR under drought conditions.

Plants	***PGPR* spp.**	***PGPR*'s Effects on Drought-Stressed Plant Growth**	**Reference**
French lavender	*Bacillus thuringiensis*	Enhancement of the plant's metabolic activities, nutritional status, and physiological functions	[116]
Soybean	*Pseudomonas putida*	Improvement in drought resilience and growth of soybean plants	[97]
Alfalfa	*Sinorhizobium*	Enhancement of drought tolerance, primarily through increased CK production	[117]
Wheat	*Azospirillum brasilense*	Enhancement of phytohormone, leading to enhanced grain yield, water potential, higher minerals (Calcium, Magnesium, and Potassium) quality, and an increase in absolute and relative water content	[67]
Thale cress		Enhancement in plant growth by initiating the photosynthetic process, lateral root growth, and reducing water loss via stomatal closure when exposed to water-limited stress conditions	[94]
Tomatoes		Development of adventitious roots, consequently improving the growth of the plants	[118]
Maize	*Azospirillum lipoferum*	Enhanced ABA levels	[119]
Thale cress	*Phyllobacterium brassicacearum*	Prolonged vegetative growth and delayed flowering	[53]
Platycladeus orientalis	*Bacillus subtilis*	Alleviated drought stress effects by improving CK levels, which enhanced stomatal opening	[120]
Soybeans	Pseudomonas simiae	Enhancement of auxin gene expression while reducing ethylene-responsive gene expression	[106]
Pepper and tomato plants	Achromobacter piechaudii	Enhancement of dry and fresh weights, and reduction of drought stress conditions	[111]
Warminster broom	Variovorax paradoxus	Lowered ethylene production	[121]

Footnote: CK—cytokinins, ABA—Abscisic acid.

3.2 PGPR-Mediated Osmotic Adjustment and Antioxidant Defense System Activation

In dry climates, plant growth and development rely on the continuous functioning of their physiological system. PGPR enhances plant growth by producing diverse enzymes that control physiological functions [122]. During moderate to severe water scarcity conditions, ion and salt concentrations in the uppermost soil layers can increase ion toxicity and cause osmotic stress in plants. In plant cells, a decrease in osmotic pressure leads to reduced turgor pressure, causing the cell to wrinkle and the cell walls to become more flexible [123]. Consequently, it leads to reduced plant growth and weak resistance to pests and diseases associated with pathogens [124].

To counteract these effects during drought stress, plants activate their antioxidant defense system, which is composed of both enzymatic and non-enzymatic components. This system helps mitigate oxidative damage and prevents the accumulation of ROS [125]. The non-enzymatic factors include cysteine, ascorbic acid, and glutathione, whereas the enzymatic factors comprise glutathione reductase (GR), superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX). Peroxidase (POD) carries out both reduction and oxidation functions to minimize ROS.

In plant cells, SOD serves as the key defense mechanism against oxidative stress caused by superoxide radicals. The manganese isoforms of SOD are primarily found in the peroxisomes and mitochondria, while zinc and copper isoforms are mainly located in the cytosol and chloroplasts [126]. CAT, which is present in peroxisomes and mitochondria, acts as a primary enzyme responsible for scavenging hydrogen peroxide. It functions as a key enzyme along with GR within the ascorbate-glutathione cycle located in the chloroplast [126]. However, the decreased activity of CAT is often balanced through an increase in PODs, which serve as alternative hydrogen peroxide scavenging enzymes and are mainly found in the cytosol, chloroplast, and cell wall [127]. Glutathione interacts with singlet oxygen, hydroxyl radicals, and water to mitigate oxidative damage. It also prevents the oxidation of thiols in enzymes and regenerates ascorbate. Alterations in glutathione and ascorbate levels, including the balance between reduced and oxidized glutathione, as well as the ratio of ascorbate to dehydroascorbate, are closely linked to plant stress responses [128,129].

Under water scarcity conditions, the ability of plants to regulate ROS decreases, leading to drought-induced alterations in stress indicators such as CAT, APX, and SOD. Inoculating PGPR in plants can enhance antioxidant defense by increasing the activity of all these enzymes, while reducing lipid peroxidation, as indicated by lower MDA concentrations [49,130]. For instance, *Ocimum basilicum* inoculated with microbial consortium including *Bacillus lentus*, *Pseudomonas* sp., and *Azospirillum brasilense*, showed a significant increase in glutathione peroxidase and APX activities under water stress [56]. A similar antioxidant response, including increased APX and CAT activity and reduced lipid peroxidation, was reported in *Bacillus thuringiensis*-treated *Lavandula* plants and *Funneliformis mosseae* administered strawberries [131,132]. Similarly, cucumber plants inoculated with *Serratia* spp, *Bacillus subtilis*, and *Bacillus cereus*, and *Arabidopsis thaliana* treated with *Azospirillum brasilense* showed a reduction in MDA levels compared to the controls under drought stress conditions [78,94]. In groundnut, inoculation with *Acinetobacter* sp. *AC06* and *Bacillus* sp. *BA01* further reduced MDA and electrolyte leakage while also causing osmotic adjustment capabilities [133]. These PGPR-induced enhancements in antioxidant enzyme activity contribute to membrane stability, improved drought tolerance, and overall plant performance under drought stress [134].

3.3 PGPR-Mediated EPS Production

EPS are made up of structurally complex polysaccharides, organic molecules, uronic acid, and proteins, produced by PGPR under water stress conditions [135]. During the late growth phase of microbial development, EPS is synthesized within the cells [136]. Under water stress, EPSs are located on the surface of bacterial cells, where they stabilize and protect the membrane structure, while their production rate depends on various stresses, including water conditions.

Rhizobacteria secrete capsular EPS and slime materials into the soil, which adhere to the clay surface through bridges, hydrogen bonding, anion absorption, and Van der Waals forces, to make a protective capsule-like structure. These capsular EPS retain water and reduce its movement relative to the surrounding environment, thereby safeguarding bacteria as well as plant roots from water stress [137,138]. Certain PGPR synthesize EPS that supports the survival of bacterial cells by forming a protective layer around them [139]. PGPR-synthesized EPS can promote soil aggregation and help maintain higher moisture levels in the root zone of plants, hence facilitating nutrient absorption, enhancing permeability, promoting crop growth, and offering protection against drought conditions [140]. Crops treated with EPS-producing PGPR demonstrated improved water resistance (Fig. 3) [69].

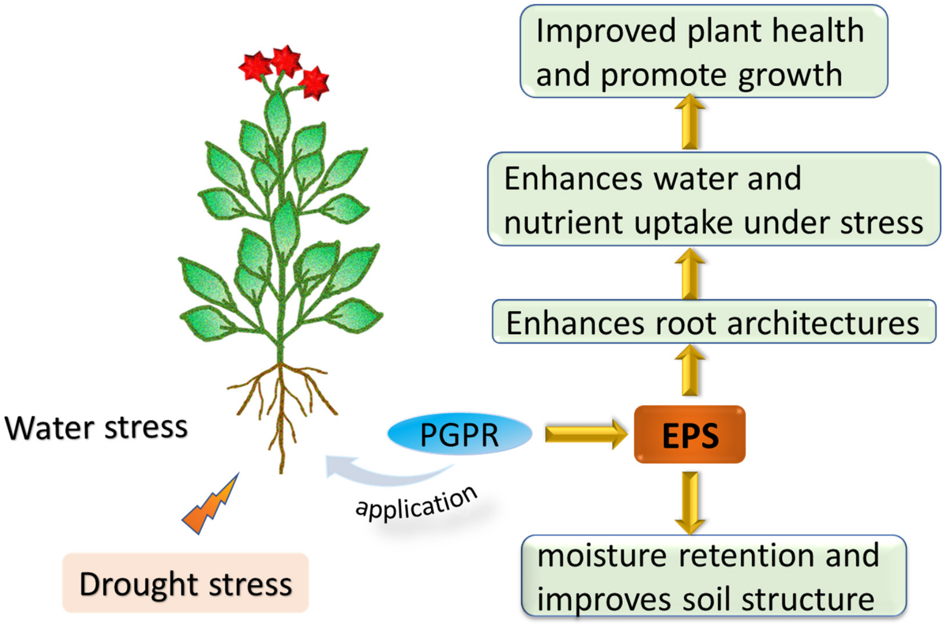

Figure 3: PGPR-mediated EPS production enhances water absorption under drought stress.

Azospirillum brasilense SP24 capsular material comprises carbohydrate complexes, including lipopolysaccharide-protein and polysaccharide-lipid complexes, to protect the bacteria under desiccating conditions and enhance their survival rates [141]. Wheat treated with EPS-synthesizing rhizobacterial strains, including *Klebsiella* sp. (LEW16), *Chryseobacterium* sp. (LEW3), and *Acinetobacter* sp. (LEW9), showed significant improvement under water stress. These strains markedly enhanced germination rates, root surface area, and root diameter, establishing them as effective bioinoculants [142]. Likewise, EPS-producing bacterial strains, including *Proteus penneri* (Pp1), *Alcaligenes faecalis* (AF3), and *Pseudomonas aeruginosa* (PA2), when treated in the maize rhizosphere, enhanced leaf area, shoot and root growth, plant biomass, and improved soil moisture content. The isolated PA2 strain, along with EPS, was treated in maize plants, increasing the leaves' relative water content ratio by 45% in comparison to untreated plants, which is crucial for mitigating osmotic and oxidative stresses [143]. Moreover, EPS-producing strains, including *Pseudomonas fluorescens* (DR7), *Enterobacter hormaechei* (DR16), and *Pseudomonas fluorescens* (D11), facilitated the growth and development of *Setaria italica* under conditions of water scarcity [50].

In conclusion, incorporating EPS-producing PGPR in agriculture represents a promising strategy to mitigate water scarcity issues, offering biogeological, ecological, and economic benefits, while enhancing agricultural sustainability and resilience to climate variability, thereby supporting global food security [144,145].

3.4 PGPR-Mediated VOCs Production

In plants, VOCs serve as signals for systemic responses and play a role in developing priming mechanisms against stresses [146,147]. Open-field studies have demonstrated that VOCs can contribute to sustainable crop cultivation and protection, with about 350 bacterial species identified as potential VOC producers, releasing up to 846 different compounds [148].

Moreover, research studies on the function of VOCs released through PGPR highlight their potential to promote crop growth under water stress conditions [56,149]. PGPR synthesizes a diverse range of VOCs, including hydrocarbons, ketones, ethers, sulfur compounds, short-chain aliphatic aldehydes, alcohols, and esters. These include camphene, methanol, acetaldehyde, 2-pentanone, 2-heptanol, 1-octen-3-ol, camphor, butanoic acid, 4-heptanone, propanoic acid, 2-methyl isoborneol, and a-pinene [149,150]. However, the composition and quantity of these compounds vary across different PGPR species.

PGPR releases VOCs that indirectly enhance crop resistance. For example, *Bacillus subtilis* 3610 synthesizes acetic acid, which regulates bacterial biofilm formation surrounding the roots [151]. Additionally, PGPR-derived VOCs function as biocontrol agents against various plant pathogens and trigger crop-induced system tolerance to promote the crop's defense mechanisms [152]. VOCs, such as 2-butanone, 2-methyl-n-tridecene, and 13-tetradecadien-1-ol, released by *Pseudomonas fluorescens* SS101, have been shown to enhance the growth of tobacco plants and improve plant resilience by inducing systemic resistance against abiotic and biotic stresses [153]. PGPR *Bacillus* species IN937 and GB03 release acetoin and 2R, 3R-butanediol in *Arabidopsis thaliana*, which significantly reduced the severity of infections caused by phytopathogens and promotes plant development [152,154]. Additional research on *Arabidopsis thaliana* revealed that VOCs released by *Bacillus megaterium* XTBG34 led to a twofold increase in biomass [155]. VOCs produced by *Bacillus subtilis* species GB03 enhanced choline production in *Arabidopsis thaliana*, which functions as a building block for glycine betaine during water-deficient conditions, playing a key role in regulating cell turgor pressure [156].

Maize treated with *Pseudomonas pseudoalcaligenes*, which synthesizes 2-pentyl furan, dimethyl disulfide, and 2,3-butanediol under water stress, promotes the protection of phytohormones, photosynthetic pigments, and proline, while reducing MDA levels and electrolyte leakage [157]. In conclusion, PGPR that synthesize VOCs show potential as a stress-alleviating factor in dryland cultivation and hold significant agronomic value [158,159].

3.5 PGPR-Mediated Nutrient Uptake Enhancement

Drought-induced water stress significantly affects the intake and mobilization of macronutrients (nitrogen, phosphorus, potassium) and micronutrients (manganese, iron, molybdenum) in the roots, causing stunted plant growth and development [160,161]. Water deficit and impaired nutrient uptake hinder plant growth, accelerate premature senescence, and decrease crop yields [162]. Additionally, water stress also reduces membrane permeability for essential cations such as Mg^+, K^+, and Ca^+, thereby reducing their uptake by the roots [163]. This impaired nutrient acquisition is further intensified in dry soils, where the reduced radius of water-filled pores limits phosphorus mobility, leading to lower phosphorus uptake and diminished foliar phosphorus content [164,165]. PGPR are pivotal in ameliorating the drought stress effects by promoting nutrient uptake and availability. Some of the PGPR reported for nutrient mobilization are as follows (Table 2).

Table 2: PGPR in nutrient mobilization.

Essential Nutrient	Reported PGPR Strains	References
Nitrogen	*Azospirillum* spp., *P. fluorescens* S3X, *Cupriavidus necator* 1C2, *Bacillus polymyxa*, *Mycobacterium phlei*, *Pseudomonas*, *Alcaligenes*, *Rhizobium*, *Azorhizobium*, *Bradyrhizobium*, *Mesorhizobium*, *Allorhizobium*, *Sinorhizobium*/*Ensifer*	[166–168]
Iron	*Pseudomonas putida* and *Pseudomonas aeruginosa*, *Rhizobium meliloti*, *Micrococcus yummanensis* YIM 65004 (T), and *Stenotrophomonas cheletiphaga* LPM-5 (T)	[169,170]
Phosphate	*Bacillus* spp. strains KB14, KB122, KB129, and KB133, *Pseudomonas frederiksbergensis* strain JW-SD2,	[170,171]
Phosphorous	*Serratia*, *Pseudomonas*, *Bacillus*, and *Rhizobium*, *Kocuria turfanensis* 2M4, *Azospirillum* sp.	[114,172–174]

PGPR improve nutrient uptake under drought stress through several mechanisms, including biological nitrogen fixation, phosphate solubilization, phosphorus solubilization, siderophore production, improving root architecture, and facilitation of active transport processes (Fig. 4) [175]. PGPR increases nitrogen availability during water stress by preventing nitrogen loss from the soil and facilitating atmospheric nitrogen fixation [176]. Moreover, PGPR inoculation can alleviate drought stress by increasing shoot and root biomass, enhancing soil nitrate and phosphate levels, stimulating key soil enzymes, and restoring microbial functional activity [177]. PGPR act as biofertilizers and bio-enhancers and improve plant tolerance to drought stress or water scarcity by enhancing both micro- and macronutrients accessibility, thereby stimulating growth and productivity [178,179]. These benefits result in higher protein content in grain and increased crop yields while reducing dependency on costly chemical fertilizers, making PGPR a cost-effective alternative [180]. In addition, the sustainable use of PGPR-based biofertilizers minimizes nutrient loss and limits nitrate and phosphate leaching, thereby improving the quality of groundwater in farming areas [181].

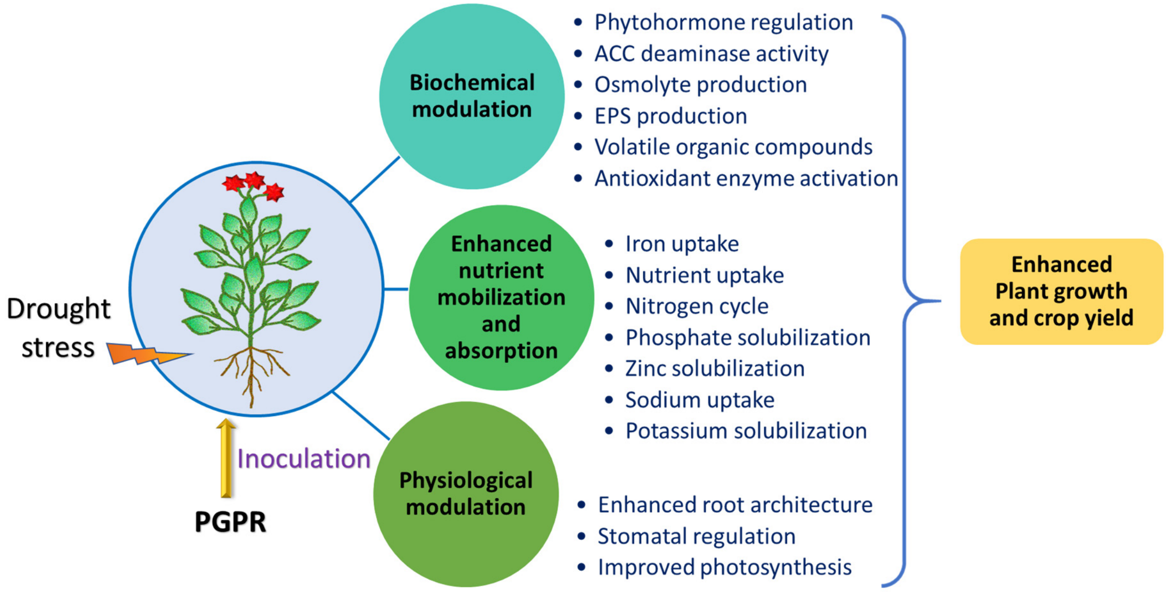

Figure 4: PGPR-plant symbiosis for drought stress mitigation.

3.6 PGPR-Mediated Modulation of Secondary Metabolites

Secondary metabolites are linked to various ecological functions, playing a crucial role in protecting plants from biotic and abiotic stressors [182,183]. During drought, plants synthesize a diverse range of metabolites that maintain cell integrity, facilitate signaling, store energy, stabilize membranes, support growth, and enhance drought stress responses [184,185]. Under drought stress, drought-intolerant wheat cultivars showed an increase in branched amino acids such as leucine, valine, and isoleucine levels [186]. Similarly, in cool-season grasses and maize, the expression of metabolites has been associated with resilience to high–temperature drought [187]. Under high-temperature stress, maize plants accumulated higher concentrations of urea, proline, beta-alanine, glutamine, and serine. Furthermore, some metabolites showed correlation with grain production either negatively (trehalose, glycerol, threonine, and valine) or positively (succinate, fumarate, and raffinose), and metabolite profiles differed significantly between crops grown in greenhouse and open field setups [188].

PGPR-derived secondary metabolites have been shown to improve crop yield, with combined applications of PGPR consortia proving more effective than single strains in mitigating water stress. PGPR species like *Bacillus megaterium* and *Bacillus thuringiensis* has shown to improve hydrogen cyanide and proline content in chickpeas under water stress [189]. Similarly, in maize, *Pseudomonas fluorescens* and *P. putida* GAP-P45 enhanced proline and water content, and promoted plant biomass under drought conditions [190]. *Bacillus polymyxa*-treated *Lycopersicon esculentum* enhanced plant physiological and biochemical parameters by increasing proline accumulation [191].

PGPR enhances soluble sugar accumulation in plants under water stress, where soluble sugars act as osmoprotectants and aid in stress endurance [192]. For instance, maize seedlings treated with *Pseudomonas* sp. exhibited increased soluble sugar content compared to non-treated plants, suggesting enhanced starch hydrolysis and improved osmotic adjustment through sugars to counteract the effects of water stress [193]. Similarly, PGPR enhanced leaf sugar content in chickpeas, acting as signaling molecules to regulate growth and developmental processes [77]. In plants, allantoin, a nitrogen-containing heterocyclic molecule, serves as an intermediate metabolite in purine catabolism. In tropical legumes, allantoin and its cyclic metabolite allantotate, often called ureides, play a vital role in the assimilation and mobilization of biologically fixed nitrogen [194]. In non-legume plants, purine catabolism is considered a key pathway for nitrogen remobilization and recycling. This process begins with the oxidation of xanthine, followed by ureide hydrolysis, ultimately releasing four molar equivalents of ammonia [195]. In *Arabidopsis thaliana*, a purine catabolism mutant revealed that allantoin, acting as an intermediate, induces ABA synthesis and thereby enhances drought [196].

Previous research works have explored the effects of allantoin on jasmonic acid signaling and responses, highlighting the interaction between ABA and jasmonic acid as a key regulatory mechanism in plant defense reactions [197,198]. Another amino acid, arginine, also plays a crucial role in nitrogen storage and transport in crops. Beyond its function in protein synthesis, arginine serves as a precursor for polyamines and nitric oxide. Nitric oxide and polyamines are both essential in regulating developmental processes and in responding to abiotic and biotic stress [199,200]. Consequently, arginine catabolism may facilitate nitrogen storage mobilization and enhance defense mechanisms against stress.

3.7 PGPR Induces Drought-Responsive Genes

PGPR enhances the expression of various stress-responsive genes, playing a crucial role in plant adaptation to drought-stressed conditions [201]. For instance, *Paenibacillus polymyxa* has been reported to upregulate *Early Responsive to Dehydration 15* (*ERD15*) genes in *Arabidopsis thaliana*, enhancing the plant's ability to mitigate water stress [202]. Similarly, inoculation with *Bacillus licheniformis* K11 enhanced drought tolerance in pepper by upregulating stress-related proteins and genes such as *sHSP*, *VA*, *Cadhn*, and *CaPR-10* by 1.5 times, offering a sustainable approach to improve crop survival without relying on heavy agrochemical use [113].

PGPR primarily reduces water severity by regulating ABA-responsive signaling pathways through transcription factors. For example, under drought stress conditions, the treatment of sugarcane cv. SP70-1143 with *Gluconacetobacter diazotrophicus* stimulated ABA-regulated signaling genes, allowing inoculated plants to survive prolonged water deficit conditions [203]. In rice, *Pseudomonas fluorescens* inoculation upregulates genes such as *Hsp20*, *AP2-EREBP*, and *bZIP1*, enhancing ABA-dependent responses and improving drought tolerance [204]. In another study, inoculating sugarcane with *Bacillus megaterium* increased auxin transporter expression, which in turn enhanced the expression of photosynthesis-related genes (*PEPC*, *RBC-L*, *SPS*) under drought stress [205]. Application of *Bacillus megaterium* in rice upregulated drought-related genes (*OsDREB2*, *OsWRKY47*, *OsAREB1*, *OsZIP23*), enhancing its tolerance to drought, as shown by reduced water loss, increased chlorophyll content, and higher survival compared to untreated plants [206].

In *Arabidopsis thaliana*, *Pseudomonas chlororaphis* 06 significantly induced more than 100-fold upregulation of stress-related genes, including *LEA* and dehydrins [207]. Similarly, priming wheat plants with two different strains of PGPR, *Azospirillum brasilense* N040 and *Bacillus amyloliquefaciens* 5113, demonstrated upregulation of stress-related genes such as *SAMS1*, *APX1*, and *HSP17.8*, alleviating the negative impacts of drought stress on wheat plants [208].

Overall, PGPR boosts drought tolerance by employing an integrated network of mechanisms that enhance plant resilience during drought conditions. In addition to regulating hormones, adjusting osmotic balance, and facilitating nutrient uptake, PGPR influence gene expression, plant metabolism, strengthen antioxidant defenses, and modify root system structure [209]. These coordinated responses collectively lead to better water-use efficiency, cellular protection, and sustained growth under drought stress, as illustrated in Fig. 4.

4 Advanced Techniques for Enhancing PGPR Efficiency

4.1 Genetic Engineering Technology

Genetic engineering offers opportunities to enhance PGPR efficiency by improving their capacity to colonize roots, produce phytohormones, solubilize nutrients, and tolerate various biotic and abiotic stresses [210]. Through genetic engineering, the genetic makeup of the microbes is modified to control the biosynthetic processes, including various biochemical compounds and metabolites. Modifying genes related to traits like ACC deaminase activity, EPS production, and nitrogen fixation can strengthen their plant growth-promoting abilities. These engineered strains hold potential for improving crop yields and resilience, particularly under environmental stress such as drought [211,212].

Various molecular methods have been developed to manage environmental stresses, including genetic modifications such as the addition or deletion of stress-tolerant genes, which present new opportunities for stress alleviation [213,214]. Gene regulation research serves as a powerful method to explore the transcriptome of a biological system, enabling a better understanding of its response to environmental changes at different developmental stages. Advanced technologies, including microarray and RNA sequencing, have been widely utilized for transcriptome analysis [215,216]. Liu et al. found that downregulating microRNA-156 and overexpressing its target genes *IPA1* and *OsSPL7* increased rice resistance to bacterial blight but reduced yield, partly due to gibberellin signalling. To overcome this trade-off, they engineered rice with *IPA1* under a pathogen-inducible promoter (*OsHEN1*), which improved both disease resistance and yield [217]. Similarly, the CRISPR-Cas9 system, a highly efficient genome editing technique, was utilized in *B. substilis* HS3 and *B. mycoides* EC18 to create gene knockouts for investigating plant-microbe interactions. In HS3, surfactin and fengycin mediated antifungal activity and selective root-hair colonization, while in EC18, petrobactin is key for promoting growth and root colonization, highlighting the system's potential for functional analyses in rhizosphere *Bacilli* [218].

Advanced systems like CRISPR-Cas9 can be utilized to precisely modify PGPR strains with desirable traits tailored to specific soil types and plant species, thereby enhancing their effectiveness under drought conditions [219]. Modern genetic engineering tools enable the study of transcriptomics, which is important for understanding how plants respond to drought stress. For instance, transcriptome studies demonstrated that plants exhibit higher expression of genes for dehydration-responsive proteins, ABA-regulated factors, and aquaporins, which help maintain water conservation, stomatal regulation, and osmotic balance during drought [220]. Chen et al. engineered plants to express D1 protein from the nuclear genome using a heat-responsive promoter, which safeguarded photosystem II, minimized protein degradation, and improved survival rates in *Arabidopsis*, tobacco, and rice when exposed to heat stress. This nuclear supplementation of D1 boosted photosystem II repair, enhanced photosynthetic efficiency, and promoted growth and yield under both normal and heat-stress conditions, offering a new bioengineering strategy for crop productivity [221]. These findings enable the development of efficient strategies to produce more resilient cultivars suited for challenging agricultural environments such as drylands.

4.2 Co-Inoculation of Various PGPR Strains

Natural ecosystems consist of diverse microbial consortia, including multiple genera of PGPR, which help plants alleviate environmental stressors, such as drought stress [140,222]. Although much research focuses on the contribution and utilization of specific PGPR strains to promote crop vitality, utilizing multiple PGPR species associated with various growth-promoting mechanisms has been shown to be more effective than relying on a single strain [223]. For instance, co-inoculation of PGPR and phosphate-solubilizing bacteria in plants boosts their growth by improving hormone production, phosphorus availability, and pathogen protection [224]. Similarly, dual inoculation of *Pseudomonas fluorescens* and *Burkholderia cepacia* showed better plant growth in the mung bean compared to the single inoculant [225].

Studies showed that plants showed better stress responses when PGPR were co-inoculated. A PGPR consortium, including *Arthrobacter chlorophenolicus*, *Enterobacter*, and *B. megaterium*, was utilized in an agricultural field experiment targeting straw enhancement, crop production, and height [226]. Co-inoculating drought-stressed soybean plants with *Pseudomonas putida* NUU8 and *Bradyrhizobium japonicum* USDA110 boosted growth, nodulation, nutrient uptake, and soil enzyme activity, suggesting their use as a biofertilizer to improve drought tolerance [227]. When wheat plants were primed with a combination of *Azospirillum brasilense* Sp245, *Bacillus subtilis* OSU142, and *Bacillus megaterium* M3, they exhibited higher nutrient levels in contrast to plants inoculated with a single species or treated with mineral fertilizers alone [228]. Co-innoculation of three different PGPR strains, *Azospirillum*, *Herbaspirillum*, and *Pseudomonas* in drought-stressed perennial ryegrass increased dry biomass by approximately 30% [229].

The combined application of PGPR improved their ability to enhance drought tolerance. Two varieties of rice subjected to severe water conditions and inoculated with proline in combination with PGPR, such as *Pseudomonas* and *Bacillus*, exhibited elevated proline levels, demonstrating enhanced water tolerance [230]. Similarly, a PGPR consortium containing *Pseudomonas fluorescens* Biotype G and *Mesorhizobium ciceri* CP41 was also found to promote growth and mitigate drought stress in chickpea [231]. Thus, the combined use of PGPR further increases their effectiveness, highlighting the necessity to expand their availability for global agricultural systems [226].

4.3 Encapsulation of PGPR for Drought Stress Management in Drylands

In addition to the detrimental effects of drought stress on plants, it also affects the survival of beneficial PGPR microbes. Therefore, encapsulation of PGPR offers an effective strategy to relieve or minimize the adverse effects of drought on plants while promoting their growth [232]. Encapsulation of PGPR refers to the technique that involves entrapping PGPR within a protective matrix or carrier materials such as biopolymers [233]. The purpose of encapsulation is to enhance microbial cell stability, regulate the release of microbes, and protect against both abiotic and biotic stressors [234]. For effective encapsulation of PGPR, it is essential to employ biocompatible and non-toxic encapsulation materials and a method that preserves microbial cell viability during handling and storage [235]. Numerous studies have explored diverse techniques for encapsulating PGPR using different carrier materials to enhance their stability, viability, and functions under various stressful conditions [236,237].

4.3.1 Encapsulation Matrix or Materials

Alginate-Based Encapsulation

Alginates are natural anionic polysaccharides mostly isolated from brown algae and are widely used for encapsulating PGPR due to their non-toxicity, biocompatibility, cost-effectiveness, and hydrogel-forming properties [238]. In the alginate-based encapsulation method, PGPR cells are enclosed within calcium alginate beads, forming a moisture-retaining microenvironment that protects the bacteria from desiccation and severe soil conditions associated with drought [239]. The permeable nature of the alginate matrix aids the gradual release of PGPR into the rhizosphere, thereby ensuring continuous microbial activity and root colonization during water-scarce conditions [240]. This encapsulation enhances PGPR functions, including phytohormone production, nutrient solubilization, and activation of plant stress resistance mechanisms, enhancing plant growth under drought stress [241].

An alginate microbead inoculant containing *Bacillus* sp. strains XT13 and XT14 was utilized to enhance drought tolerance in guinea grass. The findings showed that co-inoculation effectively modulated the plant's response to drought, as evidenced by improved growth, increased plant total biomass production, enhanced proline accumulation, and reduced oxidative stress [242]. Similarly, *Acinetobacter calcoaceticus* encapsulated with alginate matrix showed enhanced growth of groundnut plant compared to non-encapsulated *A. calcoaceticus* [243]. Alonso et al. found that the alginate beads encapsulated *Pseudomonas libanensis* TR1 were still viable over a period of 90 days, highlighting the role of alginate encapsulation in bacterial viability. In addition, *Vigna unguiculate* plants inoculated with encapsulated bacteria retained high relative water content with turgidity above 80% under water-restricted conditions [244]. Another PGPR species, *Paenibacillus lentimorbus* B-30488, treated with sodium alginate and calcium chloride, enhanced seed germination and increased colony-forming units in the rhizosphere of chickpea. This encapsulation helped ameliorate drought stress by positively influencing the physiological responses triggered by dehydration [245]. Encapsulation of PGPR with alginate offers an eco-friendly alternative to traditional agrochemicals, strengthening the sustainability and efficiency of agricultural systems in arid and semi-arid regions.

Chitosan-Based Encapsulation

Chitosan is a natural cationic polysaccharide mainly derived from chitin and offers various benefits for microbial encapsulation, including controlled-release potential, antimicrobial properties, and biofilm-forming abilities [246]. Chitosan as a carrier matrix can protect PGPR cells from environmental stresses such as pH variations, UV radiation, and desiccation, thereby enhancing their shelf-life and viability during storage and after application in the agricultural field [247–249]. In addition, chitosan can stimulate plant defense responses and improve nutrient uptake, exerting a synergistic effect with the encapsulated PGPR [250]. Research studies have indicated that chitosan-based encapsulation can boost bacterial colonization in the rhizosphere, promote seed germination, and enhance plant adaptability under abiotic stresses, including drought [251,252].

In Zea mays, nanochitosan applied along with *Pseudomonas taiwanensis* and *Pantoea agglomerans* significantly enhanced physiological parameters under stress. The treated maize plants exhibited increased plant height, elevated levels of sugar, protein, photosynthetic pigments, and improved antioxidant activity compared to the control [253]. Similarly, the combined inoculation of *Enterobacter* sp. NRRU-N13 and oligochitosan effectively mitigated drought stress in rice plants. Their synergistic interaction enhanced drought tolerance by decreasing proline accumulation and increasing relative water content, chlorophyll content, and antioxidant enzyme activity [254]. Thus, chitosan encapsulation represents a promising approach for improving crop productivity under stress-prone agricultural systems.

Miscellaneous Materials Encapsulation

Besides alginate and chitosan, several other natural and synthetic materials, such as biochar, polyvinyl alcohol, sugars, etc., are being explored for the effective encapsulation of PGPR, each offering distinct advantages in terms of microbial viability, environmental compatibility, and controlled release [255]. For instance, biochar, a byproduct of biomass pyrolysis, provides a highly porous structure that facilitates microbial colonization and provides protection against environmental stressors [256,257]. Its inherent nutrient and moisture-retaining abilities also enhance soil fertility and microbial viability in the rhizosphere. Biochar encapsulated *Pseudomonas putida* significantly improved soil nutrient retention, and demonstrated synergistic effects on the accumulation of plant osmoregulants in soybean seeds exposed to drought stress [258]. Similarly, the use of biochar derived from waste wood of *Morus alba* in combination with *Pseudomonas* sp. on drought-stressed canola significantly enhanced nutrient uptake, reduced osmolyte accumulation, and increased antioxidant enzyme activities, underscoring the potential of biochar in drought stress mitigation [23].

Likewise, to improve the encapsulation matrix's mechanical strength and stability, natural polymers like starch and alginate are often combined with a synthetic polymer called polyvinyl alcohol (PVA). A study on the microencapsulation of *Bacillus megateriuma* using a formulation of PVA, cationic starch, and zinc oxide demonstrated excellent cell protection under various stress conditions, including UV exposure and heat. Moreover, during storage, the encapsulated bacteria's estimated shelf life was twice that of free bacteria, demonstrating their effectiveness in maintaining bacterial viability. Additionally, this approach significantly boosted the growth of soybean plants by enhancing both aerial and root biomass and promoting enhanced uptake of phosphorus and zinc nutrients by the soybean biomass [259]. Chain et al. assessed the enhancement of drought tolerance in *Eucalyptus grandis* seedlings after inoculating them with *Pseudomonas* strains M25 and N33 via an acrylic-cellulosic polymer SAPH. During a gradual water deficit, M25 improved plant water content and cell wall elasticity, and both strains exhibited tendencies to promote growth [260].

Another study on maize treated with PGPR encapsulated in a sodium alginate and starch mixture demonstrated enhanced bacterial survival and soil compatibility, along with an increase in shoot growth, root biomass, photosynthetic pigments level, and osmolyte accumulation. These results indicate that the encapsulation can boost maize resilience, reduce irrigation needs, and support yields in water-limited conditions [240]. In encapsulation systems, sugar such as trehalose is commonly used as a cryo- and osmoprotectant, aiding to stabilize cell membranes, particularly during desiccation, freeze-drying, or heat exposure [261,262]. These sugars enhance bacterial viability over extended storage periods. Furthermore, the encapsulation of *Bacillus pumilus* with alginate, kaolin, and trehalose significantly increased the soil microbial population, activities of invertase, urease, and catalase, contents of available nitrogen and phosphorus in the soil, and finally improved growth and increased biomass of *Pharbitis nil* seedlings under drought stress [263].

These alternative encapsulation materials, either used alone or in combination, contribute to the development of robust bioformulations that ensure effective delivery, persistence, and functionality of PGPR under diverse agroecological conditions. Although encapsulation improves the survival and delivery of PGPR, its effectiveness is hindered by several challenges, such as reduced microbial viability in field conditions, limited nutrient and oxygen diffusion, inconsistent release rate, high production costs, mechanical instability, shortened shelf life, and variable compatibility with different soils [264,265]. Ongoing research aims to optimize such carriers to address specific crop needs, stress environments, and field application strategies, thereby reinforcing their potential in sustainable agriculture.

4.3.2 Encapsulation Strategies for PGPR Delivery

Spray Drying Method

Spray drying is one of the most commonly employed techniques for encapsulating microbial cells, offering protection to viable cells against adverse environmental conditions [266]. This method involves the integration of microbes with polysaccharide-based matrices. These matrices typically include substances like pectin, starch, cellulose, and Arabic gum derived from plants and microbial sources [267]. When passed through the drying chamber, these polysaccharides are capable of transforming into spherical particles.

Spray drying offers significant advantages such as rapid processing and time efficiency, making it a viable option for large-scale microbial cell encapsulation with minimal resource use [268]. For instance, the spray drying method demonstrated a 330-fold increase in the viability at 4°C for the living conidia compared to non-encapsulated conidia following 8 weeks of storage [269]. Similarly, encapsulation of *Bacillus cereus* strain C1L isolated from the rhizosphere using 12% gum Arabic and 18.3% maltodextrin achieved a viability rate of 42% when spray–dried at 73.5°C, and it was further used for bio-pesticide production [270]. Despite its notable advantages, exposure to high temperature and dehydration stress during spray drying can negatively impact cell viability and restrict its applicability to small-scale operations [271]. Nevertheless, numerous researchers have successfully used this technique for encapsulating bacterial and fungal strains that promote plant growth [272].

Extrusion Method

Extrusion is a method rooted in physical principles that is used to encapsulate live microbial cells by modifying wall materials and applying intense pressure [233]. This method provides a simple and cost-effective approach for immobilizing microbial agents, which helps in extending the viability of microbes while preserving their viability [273]. This technique involves passing the microbe in the medium through a calcium chloride mixture under a high-pressure nozzle [274]. This technique is suitable for enclosing both anaerobic and aerobic microbes without affecting their viability [273]. Extrusion has been successfully used to encapsulate useful microorganisms, comprising fungal and bacterial species, for improved performance and stability. For instance, *Pseudomonas putida* Rs-198 (FJ788425.1) was encapsulated using alginate and starch through this method, which improved its survival under salt stress compared to the non-encapsulated form. When applied to cotton crops under saline conditions, the encapsulated *P. putida* s-198 [275] enhanced plant biomass more effectively than its non-encapsulated counterpart. This method shows promise in developing bio-pesticides by encapsulating beneficial fungal and bacterial strains. However, its application in enhancing microbial performance and plant responses under drought-induced water stress remains largely unexplored, indicating a significant research gap in the development of drought-oriented PGPR delivery systems.

Emulsion Method

The emulsion method is commonly recognized as a chemical technique used to encapsulate viable microorganisms [276]. The method ensures increased viability of microorganisms and is easy to scale up. Emulsification is performed using suitable materials to create a stable formulation that improves the viability of biological control agents used for crop protection, as well as promoting growth [255,277]. Many investigations have reported the application of this technique in entrapping useful microorganisms to support crop defense, along with biofertilizer use. For example, nanocapsules of *Bacillus subtilis* CRU1 and *Pseudomonas fluorescens* VUPF5 were prepared using the emulsification method by incorporating 10 CFU/mL of the bacterial strains into a sterilized solution containing 1% gelatin and 2% sodium alginate, with soybean oil serving as the continuous phase [278]. This encapsulation technique effectively extended the viability of microbial strains and enhanced plant growth parameters, including improved stem and root growth relative to the control. However, limited studies have evaluated emulsion-encapsulated PGPR for drought tolerance in crops, highlighting the need for further research to optimize formulations for drought stress conditions.

5 Challenges, Future Perspective, and Strategic Utilization of PGPR in Dryland Agriculture

As the demand for sustainable agriculture grows, research on the application of PGPR has gained increasing importance, necessitating a better understanding of PGPR diversity and its mechanisms of action. However, the effective utilization of PGPR in dryland agriculture is constrained by several environmental, biological, and technical challenges. PGPR performance can vary considerably under the influence of diverse field circumstances. For instance, they can promote growth in one crop while negatively affecting another, limiting productivity under optimal conditions but offering benefits under stressful situations [279]. Thus, evaluating PGPR in real field conditions is essential to establish their efficacy, as their responses often differ from those observed in laboratory settings [280]. Additionally, some PGPR can hinder plant growth even under favorable conditions, and they may turn into pests under adverse conditions. This issue arises from the cultured strain's inability to compete with the indigenous bacterial community and from insufficient inoculation rates [49]. Therefore, understanding and identifying the problems is important for identifying significant gaps, uncertainties, and discrepancies related to the utilization of PGPR in real-field situations [281,282].

Although PGPR have shown promising outcomes under controlled conditions, their application in real agricultural field settings remains limited. To fully explore the potential of PGPR in dryland agriculture, it is essential to address the existing challenges while identifying future research directions that enhance their effectiveness, consistency, and field-level applicability. Therefore, future research should prioritize field-based studies conducted under natural environments to assess the real-world effectiveness of PGPR in dryland agriculture systems. Some of the key approaches are outlined below:

i. Compared to laboratory experiments, field applications often exhibit inconsistent PGPR performance due to variability in soil type, climate, microbial competition, and plant species. Therefore, exploration of diverse PGPR species and their synergistic effects on plant growth and stress tolerance is essential. Particular emphasis should be placed on developing efficient, drought-tolerant, soil and crop-specific multi-strain PGPR consortia, along with a deeper understanding of their interaction with native soil microorganisms to ensure ecological harmony and long-term effectiveness. Moreover, long-term field-based trials, coupled with sustainable agronomic practices, are crucial to validate PGPR performance across diverse dryland environments. Such research efforts will contribute to the development of climate-resilient and sustainable agricultural practices.
ii. The utilization and integration of omics approaches, including transcriptomics, genomics, and metabolomics, are essential for identifying key drought-responsive genes, deciphering the underlying mechanisms by which PGPR enhance plant stress responses, and optimizing strain selection. Priority should be given to developing PGPR strains capable of conferring tolerance to abiotic stresses, like drought and high temperature, which are commonly prevalent in dryland areas. In this context, genetic engineering and CRISPR-based technologies can be applied to further enhance stress tolerance, colonization ability, and the functional efficiency of PGPR, thereby improving their effectiveness under challenging environmental conditions.
iii. The development and refinement of nanoencapsulation technologies should be prioritized to enhance PGPR stability, controlled release, and boost colonization efficiency under drought. These advancements should be integrated with suitable carrier materials and effective delivery systems to maximize the microbial performance in field conditions.
iv. Scalability and cost related to the production, formulation, and inoculation methods of PGPR-based bioformulations can be overcome by optimizing industrial-scale processes and developing sustainable and cost-effective bioformulations. Specifically, designing inoculation methods suited for dryland areas should be prioritized to improve shelf-life and ensure effective field application under environmental stress.
v. Biosafety considerations, long-term ecological studies, and clear regulatory frameworks, especially regarding genetically engineered PGPR, are necessary to ensure their safe and responsible adoption in the field.
vi. Moreover, awareness should be created among farmers regarding the use of climate and crop-specific PGPR to maximize their adaptability and efficacy, thereby improving agricultural productivity in dryland regions.

6 Conclusion

Drought poses a serious threat to crop production, particularly in dry and semi-arid regions. Compared to conventional agronomic practices, PGPR offers a promising and sustainable strategy to enhance drought resistance and improve crop productivity in these challenging environments. By employing multiple mechanisms, including phytohormonal regulation, osmolyte and exopolysaccharide production, ACC-deaminase activity, and antioxidant enhancement, PGPR can improve root colonization, water-use efficiency, plant growth, and soil health. Their efficiency can be further improved through nanoencapsulation, which increases microbial survival and enables controlled release. However, numerous challenges remain, including nanobioformulation optimization, interactions among various PGPR species and with soil microbiota, and practical field application under variable dryland environments. Despite the existing challenges, current research focused on identifying diverse PGPR strains, understanding their mechanisms under the influence of various biotic and abiotic stresses, and developing novel encapsulation materials with multifunctional properties is paving the way for cost-effective and efficient PGPR bioinoculants. Future efforts should be placed on optimizing formulation methods, including nanoencapsulation and the use of multi-strain consortia, alongside long-term field-based trials across various environments to validate effectiveness and adaptability. These improvements aim to support the development of climate-resilient, eco-friendly, and sustainable agricultural systems that reduce reliance on chemical fertilizers and pesticides.

Acknowledgement: Not applicable.

Funding Statement: This research was carried out with the support of the funding (RS-2025-02223124) of the Cooperative Research Program for Agriculture Science and Technology Development, RDA, Republic of Korea.

Author Contributions: Conceptualization, Sajida, Hamdy Kashtoh and Kwang-Hyun Baek. Writing—original draft preparation, Sajida, Tensangmu Lama Tamang and Hamdy Kashtoh. Writing—review and editing, Hamdy Kashtoh, Tensangmu Lama Tamang and Kwang-Hyun Baek. Funding acquisition, Kwang-Hyun Baek. All authors reviewed and approved the final version of the manuscript.

Availability of Data and Materials: Not applicable.

Ethics Approval: Not applicable.

Conflicts of Interest: The authors declare no conflicts of interest.

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