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Review

Plant Growth Promoting Rhizobacterial Mitigation of Drought Stress in Crop Plants: Implications for Sustainable Agriculture

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Abstract: Abiotic stresses arising from climate change negates crop growth and yield, leading to food insecurity. Drought causes oxidative stress on plants, arising from excessive production of reactive oxygen species (ROS) due to inadequate CO_2, which disrupts the photosynthetic machinery of plants. The use of conventional methods for the development of drought-tolerant crops is time-consuming, and the full adoption of modern biotechnology for crop enhancement is still regarded with prudence. Plant growth-promoting rhizobacteria (PGPR) could be used as an inexpensive and environmentally friendly approach for enhancing crop growth under environmental stress. The various direct and indirect mechanisms used for plant growth enhancement by PGPR were discussed. Synthesis of 1-aminocyclopropane−1-carboxylate (ACC) deaminase enhances plant nutrient uptake by breaking down plant ACC, thereby preventing ethylene accumulation, and enable plants to tolerate water stress. The exopolysaccharides produced also improves the ability of the soil to withhold water. PGPR enhances osmolyte production, which is effective in reducing the detrimental effects of ROS. Multifaceted PGPRs are potential candidates for biofertilizer production to lessen the detrimental effects of drought stress on crops cultivated in arid regions. This review proffered ways of augmenting their efficacy as bio-inoculants under field conditions and highlighted future prospects for sustainable agricultural productivity.

Keywords: ACC deaminase; antioxidant systems; climate change; exopolysaccharide; IAA; oxidative stress; plant health; rhizobacteria; water deficit

1. Introduction

The global populace increases daily at a startling rate, which implies that food production would need to be increased through sustainable agriculture to meet food demands. It is projected that the global population, which is at present about 7 billion people, would likely increase to 10 billion or more in the next 50 years [1,2]. Feeding the ever-increasing population would require more land for the cultivation of crops, coupled with the numerous environmental challenges facing agriculture. Nonetheless, arable land for agriculture is scarce due to urban development and industrialization; hence, existing agricultural land will need to be utilized for greater crop productivity using appropriate strategies. The quality of the soil, which is essential for greater crop yield, needs to be sustained, but it is often affected by anthropogenic activities or by environmental factors, which depletes nutrients and degrades the soil. To obtain better yield and income, farmers are compelled to spend a lot of money on chemical fertilizer applications. It is recognized that this is not sustainable due to the inherent negative effects it has on the environment. The biological activity of soil is destroyed, and toxicities

build-up through improper fertilizer application. Moreover, runoff from the fields into water bodies leads to eutrophication with a resultant decrease in dissolved oxygen and the death of aquatic life due to disturbances in the hydro-biome from toxic chemicals.

In recent times, climate change has attracted much attention because of its link with global warming leading to severe drought and high temperatures in some parts of the world, which adversely affects farmer's income and agricultural productivity. Extreme temperatures are capable of inflicting permanent damage on plant growth. Furthermore, insufficient water in the soil reduces crop growth and yield since the physiological conditions of crops are distorted. Considering global food security, drought stress has been detrimental to its success; hence, innovative technologies and methods are indispensable for reducing food insecurity, especially in the developing world. It is, therefore, essential that more focus is given to research that will alleviate the effects of climate change on food security and agriculture by using cost-effective techniques. Over the years, conventional plant breeding approaches have been utilized to produce drought-tolerant cultivars of crops, but it is a time-consuming process, and the use of genetic engineering has not been fully adopted by all due to critics of possible environmental hazards, despite its potential for stress tolerance in plants. Hence, an alternative approach is required.

The highest microbial diversity on earth occurs in the soil, with numerous species of prokaryotes and fewer species of eukaryotes per gram of soil [3]. Many of these microbes aid in the recycling of mineral nutrients and carbon in the soil by their various activities, thus making nutrients available to plants and at the same time, safeguarding soil quality [3–5]. The vast majority of soil organisms are bacteria, which interact with the plant roots in relationships that could be neutral, harmful, or beneficial to plants [1,6]. Plant growth-promoting (PGP) factors are produced by beneficial bacteria within the rhizosphere of plants; the plant growth-promoting rhizobacteria (PGPR) that shield plants from biotic and abiotic stresses and promote their normal physiological functions. These beneficial soil bacteria, though abundant in the rhizosphere, are largely under-exploited as bio-inoculants for enhancing crop production, especially under abiotic stresses, due to the paucity of information on the manner in which they interact with other organisms and plants and their functions in the soil.

Utilization of PGPR as microbial inoculants is gaining more awareness as an environmentally friendly method of crop improvement compared to the constant application of chemical fertilizers, which harms the environment. Its application dates back more than 100 years, but in the last three decades, it has gained prominence, with several inoculants commercialized and available in the market [7]. The effectiveness of microbial inoculants, when applied on the field, depends on several environmental factors, which include salinity, soil pH, extreme temperatures, and inadequate water [8], which may hinder its function in plant growth promotion. A wide market for the biofertilizer industry exists, but it is yet to be fully harnessed. Based on the benefits derived from PGPR, this review discussed the mechanisms utilized by PGPR in enhancing plant growth, with particular focus on crops and their potential use as bio-inoculants for sustainable agricultural production in water deficit regions. We also highlighted prospects of exploitation of PGPR and ways of enhancing their efficacy using modern technologies.

2. The Effects of Drought Stress on Crop Production

Plants being sessile are easily confronted by abiotic stresses such as extreme temperatures (chilling/freezing or elevated temperatures, heat), waterlogging, water deficit/drought, salinity, as well as heavy metal and hydrocarbon toxicity, which negatively affect their normal physiological functions and metabolism. If the temperature becomes low, it could lead to freezing, which causes dehydration of plant cells. On the other hand, very high temperatures result in the generation of excessive heat, which denatures proteins and disrupts cellular membranes as a result of the production of reactive oxygen species (ROS). One major requirement of plants is the availability of a definite optimal quantity of water, which is central to its survival. In either way, inadequate water or over flooding/waterlogging affects the growth and metabolism of plants. The moisture content of the soil,

in addition to the type of soil, pH, and nutrients available in the soil, has much impact on the microbial communities found in the soil. This affects the function of the soil in supporting plant growth either positively or negatively. Global food production is currently under intense pressure from abiotic stresses, which limit healthy plant growth as a result of changes in climatic conditions. Climate change, defined as diverse changes in climatic and weather conditions, is discernible by variations in the frequency and severity of extreme conditions. The Intergovernmental Panel on Climate Change released a report in 2014 that indicated the Earth's atmosphere and oceans are warming due to increased greenhouse gas emissions, with much impact on Africa [9]. These greenhouse gases, notably nitrous oxide (N_2O), carbon dioxide (CO_2), and methane (CH_4), have increased over the years with net emissions close to 300 ppm in recent times [10]. This brings about changes in the weather conditions noticeable by elevated atmospheric temperatures, shortage of water, and inadequate nutrients for crop production. Drought is a prominent abiotic factor impeding crop growth and productivity as it causes a reduction in crop yield globally, as a result of an alteration in the photosynthetic capacity of cells and other physiological functions, due to stomata closure that reduces the amount of CO_2 available for photosynthesis while photorespiration increases. Therefore, an imbalance between the fixation and utilization of carbon is created, which results in changes in the osmotic potentials of cells by altering sugar concentrations. This disrupts the photosynthetic metabolism of plants with the production of ROS [11,12]. Overproduction of ROS occurs in the mitochondria, chloroplasts, and peroxisomes under stress conditions, and this leads to a reduction in CO_2 uptake in green leaves, which is detrimental to green plants as they require CO_2 for efficient photosynthesis. Nocter et al. [13] highlighted the effects of stomata closure on the photosynthetic machinery of plants with the reduction of oxygen by photosystem I resulting in the production of superoxide (O_2^-) and H_2O_2, which accelerates the water-water cycle [14]. Excessive reduction in the electron transport causes the production of singlet oxygen ($^1O_2$) in Photosystem II (PSII), which elevates H_2O_2 production in the peroxisome while O_2^- and H_2O_2 or $^1O_2$ are produced in the chloroplast due to photorespiration [13,15,16]. Excessive reduction in the photosynthetic electron transport chain as a result of the possible production of $^1O_2$ in PSII inadvertently affects the rate of photosynthesis (Figure 1).

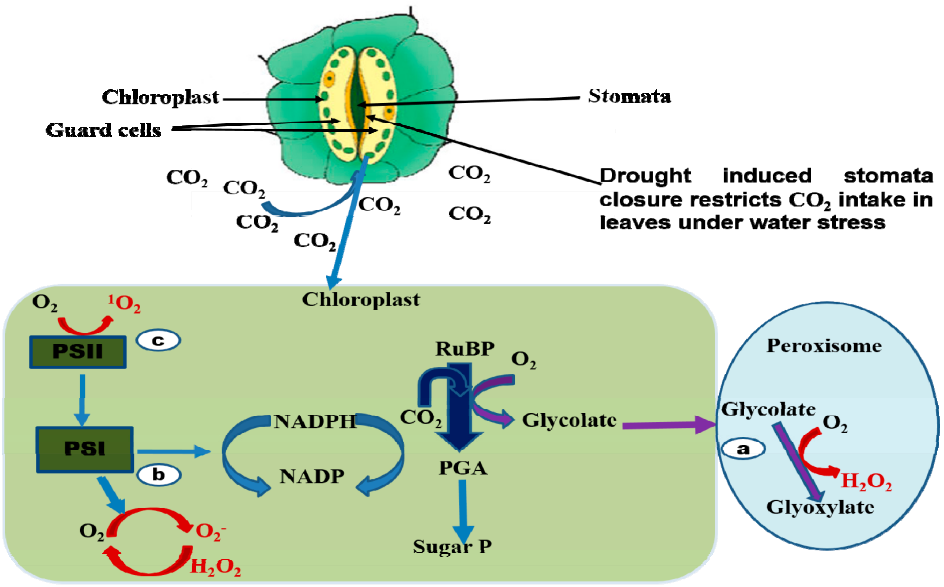

Figure 1. Stomata closure restricts the uptake of CO_2 in the leaves of a drought-stressed plant leading to the production of (**a**) H_2O_2 in the peroxisome by photorespiration, which enhances (**b**) O_2^- and H_2O_2 production, (**c**) $^1O_2$ production, by the photosynthetic electron transport chain. PSI and PSII (Photosystem 1 and Photosystem II); RuBP, Ribulose 1-5 bisphosphate; PGA, 3-Phosphoglyceric acid.

Seed germination and growth require adequate moisture, but in the absence of adequate water, the seedling development is either delayed or stops completely. Drought stress is the main abiotic stress limiting the production of maize, a major staple cereal crop globally. Maize is the number one crop grown in Southern Africa, which has up to 65% of the total area of land under cereal production in sub-Saharan Africa allocated to maize production [17]. However, due to the region's low coping and adaptation capacity, Southern Africa is highly susceptible to climate associated risk [18]. In 2016, the El-Nino induced drought was mostly felt in South Africa, which caused yield reductions in maize production and economic losses, especially in the North-West and Free State provinces. Under conditions of prolonged water stress, the leaves of the maize plants undergo leaf rolling, causing a reduction in size to minimize water loss. In essence, under these conditions, the survival rate of maize seedlings is very low, and embryo abortion rates may likely increase after pollination resulting in reduced crop yield [19–21]. Maize production is worst when hit by drought in the reproductive stage of growth. Premature flowering and a longer anthesis–silking interval are experienced, which in the long run reduces the yield potentials of the plant. Decreased grain weight has also been reported in barley kernels due to a decline in the number of grains per spike, dry matter accrual, and grain filling duration [22–24]. Evaluation of 38 maize cultivars at 10 different locations revealed an average yield reduction in grain yield of up to 52% due to water stress [25]. The effect of drought stress on maize and wheat production using a data synthesis approach was investigated by Daryanto et al. [26]. The authors observed, from meta-analysis results, a significant reduction in yield between both crops under comparable water reduction of about 40%. Furthermore, yield reduction was more pronounced in maize (39%) compared to wheat, which only had a 20% reduction in yield due to the development of male inflorescence over female inflorescence in maize under water stress, resulting in a failed reproductive process [26,27]. Highly positive correlations were also observed between yield and reproductive traits of maize under drought stress, indicating a high sensitivity to water stress compared to wheat [26,28,29]. Hence, farmers in arid regions use irrigation systems to optimize the yield of their crops.

Changes in Physiological Parameters of Drought-Stressed Plants

Plants have to acclimatize to unfavorable environmental factors by using physiological and molecular mechanisms to maintain homeostatic balance. Inadequate water for plant growth inhibits cell division and elongation due to cell dehydration, which results in osmotic stress. A major feature of drought-stressed plants is the reduction of turgor pressure, resulting in changes in chlorophyll (Chl) properties of the plant such as peroxidation of Chl and, consequently, photosynthesis due to reduced Chl content in leaves [30]. In addition to Chl content, other essential physiological factors, such as the relative water content (RWC), relative electrical conductivity in leaves, stomatal conductance (g_s), leaf water potential (ψ_w), transpiration rates, malondialdehyde (MDA) content, and Chl-fluorescence, need to be assessed in stressed plants as changes in these factors indicates the severity of drought [30–32]. Plant water and nutrient relations in crops are also affected under drought stress leading to reduced water use efficiency by the plant and low productivity [32–34]. Turgor osmotic potential, leaf water potential, and RWC were reduced at the tillering and jointing growth stages of wheat plants whereas osmotic adjustment increased [35]. In most cases, the crops are severely affected during the reproductive or flowering stages of growth compared to the vegetative stage of growth, which invariably affects the yield, as observed in rice, chickpea, cowpea, and wheat [36–38]. The physiological parameters of different crops affected by drought stress are shown in Table 1. The photosynthetic mechanisms of the water-stressed plants were altered due to reduced chlorophyll levels, and leaf areas and sizes, which affected pod setting and grain filling in the crops, ultimately leading to a reduction in yield.

Table 1. Physiological parameters of crops affected by drought stress.

Plant Species	Effect of Drought Stress on Crop Growth and Yield	References
Barley (*Hordeum vulgare* L.)	The number of grains per plant and tiller number and grain weight per plant was reduced, which consequently affected the yield. The grain filling period was most affected by drought stress.	[39]
Chickpea (*Cicer arietinum* L.)	The chlorophyll a, chlorophyll b, and total chlorophyll contents both at the vegetative and flowering stages were reduced under drought stress while proline accumulation increased in both stages but was more intense in the flowering stage and reduced crop yield due to the low number of pods produced under water stress.	[36]
Camptotheca acuminate (C. acuminata)	Relative water capacity, photosynthetic ability, and Chlorophyll a and b contents were reduced under drought stress. However, antioxidant enzymes Superoxide Dismutase and Peroxidase (POD) levels were increased.	[40]
Cowpea (*Vigna unguiculata* L.Walp.)	Drought stress at vegetative and flowering stages increased the number of days to anthesis by 4 and 7 days, respectively. A 100g weight of cowpea in both the vegetative and flowering stages were reduced but was more intense in the flowering stages. Drought stress at vegetative and flowering phases significantly reduced the shoot dry weight in cowpea varieties by 56.2% and 36.2%.	[37]
Faba bean (*Vicia faba* L.)	The concentrations of proline, soluble sugars, and protein contents in the leaves of the Faba bean were elevated. Relative water content was significantly ($p < 0.05$) reduced as well as the plant height and leaf area. Grain yield was reduced under water stress based on the cultivar.	[41]
Wheat (*Triticum aestivum* L.)	The net photosynthetic rate and stomatal conductance under severe and moderate water stress were reduced due to low CO_2 availability. Total soluble sugars and proline levels increased. Nonetheless, leaf water potential, osmotic potential, turgor osmotic potential, and relative water content declined.	[35]
Maize (*Zea mays* L.)	Drought decreased the RWC of leaves to 62.7% and 49.8% after 3- and 6-days treatment and significantly shortened the leaves. Wilting and rolling of drought-stressed leaves were observed with a reduction in the photosynthetic rate and efficiency of the PSII electron transport in the drought seedlings.	[42]

3. Mechanisms of Adaptation to Drought Stress by Plants

Plants acclimatize themselves to unfavourable conditions in order to survive because of abnormalities in their normal physiological functions, but this requires appropriate signaling, which makes it a priority for plant scientists to identify the relevant genes involved in stress tolerance [43]. Plants adapt to drought in several ways; a plant may complete its life cycle prior to the commencement of drought and undergo a period of inactivity prior to the commencement of the dry season [44], it may have the capacity to withstand high plant water status or cellular hydration under drought (drought avoidance) or sustain its metabolic activities at reduced water potential by different means such as producing compatible solutes and initiating antioxidant defense systems (dehydration tolerant plants) [32,45]. However, these mechanisms depend on the degree of drought stress experienced by the plant. Some of these adaptation mechanisms are regulated by stress tolerance genes, which enable plants to switch the balance between growth and initiation of defense mechanisms based on environmental factors, resist adverse environmental conditions, and hence, could be used as probable genomic candidates for extensive applications in crop improvement programs. The genotype and type of plant determine the genes elicited in response to environmental stress. According to Singhal et al. [46], genes responsible for adaptation and eventual tolerance to abiotic stresses are classified into four categories; (i) genes encoding enzymes involved in osmolyte biosynthesis; (ii) genes encoding antioxidants; (iii) genes encoding stress-induced proteins, which include late embryogenesis abundant (LEA) proteins, anti-freeze proteins, chaperones and heat shock proteins involved in maintaining cell integrity, and (iv) genes encoding for protein kinases and trans-acting factors such as DREB1/CBF, AP2/ERF, DREB2, NAC, MYB/MYC, basic leucine-Zipper proteins, and Zinc-finger [46–48]. Understanding the mechanisms by which these genes are switched on under abiotic stress, and the various responses elicited, would be crucial in the development of stress tolerance in plants.

One major response of plants is the adjustment of the osmotic potential of cells through the accrual of compatible solutes such as phenolics, proline (amino acids), trehalose (sugar), glycine betaine, amongst others [49,50], in response to drought stress [35,51]. These compatible solutes act as osmoprotectants, shielding cells from dehydration and also aiding the detoxification of stressed cells from detrimental levels of ROS. In the studies of Abid et al. [41] on water-stressed Faba bean at 90%, 50%, and 30% field capacity, protein content, proline, and total soluble sugar levels in all cultivars assessed were significantly ($p < 0.05$) increased, but the response of the plants was found

to be genotype-dependent. A similar observation was made on wheat (*Triticum aestivum* L.) under water stress with a reduction in soluble protein, but an increase in proline levels, total soluble sugars [52], and fructose accumulation under moderate and severe water stress at the tillering stage, compared to the well-watered plants [35]. Proline and glycine betaine (GB) increase osmotic potential or turgor within cells, which enable plants to adapt to drought stress by scavenging ROS, as well as maintaining the integrity of subcellular structures and enzymes, and protect the transcriptional and translational machinery of plants [53]. Additionally, proline elevates the thermo-tolerance of enzymes, inhibits denaturation of enzymes and proteins [44,54], and buffers cellular redox potential [44]. Exogenous applications of compatible solutes have also proved useful in enhancing plant growth under harsh environmental conditions. For example, the exogenous application of GB significantly improved the spike length, number of grain per spike, and grain yields of wheat plants under drought stress as well as water relations when applied alone at the rate of 100 mM and in combination with K (GB 100mM + K1.5%) in a pot and two years of field experiments [55]. These osmoprotectants are instrumental to the survival of plants under water stress conditions by scavenging ROS and maintaining cell membrane integrity.

Besides the production of osmolytes, plants have also developed advanced defense systems using both enzymatic and non-enzymatic forms, which mitigate oxidative damage due to water stress [56]. Detoxifying enzymes such as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutathione reductase (GR), glutathione peroxidase (GPX), monodehydroascorbate reductase (MDAR), and dehydroascorbate reductase (DHAR) defend plants by reducing oxidative stress [57,58]. In a recent study, the levels of SOD and CAT in sunflower genotypes were seen to be significantly increased when plants were exposed to salinity or drought stress singly or a combination of both stresses [59]. Hydrogen peroxide (H_2O_2), a stress indicator under abiotic stress, was also reported to have increased in all genotypes evaluated under both stresses with a higher increase observed under drought stress than salinity stress. The concentrations of SOD, CAT, and APX increased in wheat plants subjected to severe and moderate drought stress at the tillering stage in sensitive plants, while tolerant ones had higher antioxidant enzyme activity [35]. These antioxidant enzymes restore soluble antioxidants and aid in the maintenance of cell homeostasis as well as antioxidant response in plants and, hence, are essential for the sustenance of plants under stress.

4. Drought Stress Mitigation in Plants: Utilization of Plant Growth-Promoting Rhizobacteria (PGPR)

There is more awareness of the use of microorganisms as an inexpensive and valuable means of improving crop yield and providing stress tolerance to plants. These beneficial microorganisms used as bio-inoculants for plant growth enhancement can be classified into three key categories: (i) plant growth-promoting rhizobacteria (PGPR), (ii) *arbuscular mycorrhizal* fungi (AMF), and (iii) the nitrogen-fixing rhizobia [8,60]. These microbes are majorly bacteria that live in the rhizosphere of plants, where they derive nourishment, growth hormones, flavonoids, and enzymes from plant root exudates [61,62], and on the other hand, enhance nutrient availability, uptake, and support healthy plant growth promotion. These exudates serve as sources of carbon and nutrients for the microbial metabolism of the microbes [63], attract them to the rhizosphere, and determine the nature of organisms that colonize the rhizosphere, in addition to the soil type and physicochemical properties of the soil, which also have an impact on the plant and the ability of microbes to survive. The interactions of plant roots with the soil and microorganisms makes the rhizosphere a niche for abundant microbial activities while sustaining the fertility of the soil [63–67]. Different genera of PGPR make use of different mechanisms to lessen the damage caused by environmental stresses on plants (Figure 2).

The PGPR aid in sequestration of iron, mobilization of phosphorus in soils, and synthesis of exopolysaccharides and beneficial enzymes such as 1-aminocyclopropane−1-carboxylate deaminase (ACC), as well as plant growth hormones, especially indole-3-acetic acid. Indirectly, these microbes stimulate plant growth by protecting plants from phytopathogens and producing compounds such

as hydrogen cyanide, antibiotics, synthesis of ACC deaminase, lytic enzymes, and induced systemic resistance (ISR) [1,63]. Most PGPR have multiple plant growth-promoting (PGP) traits, which enable their utilization as bio-inoculants for crop production even in unfavorable environmental conditions.

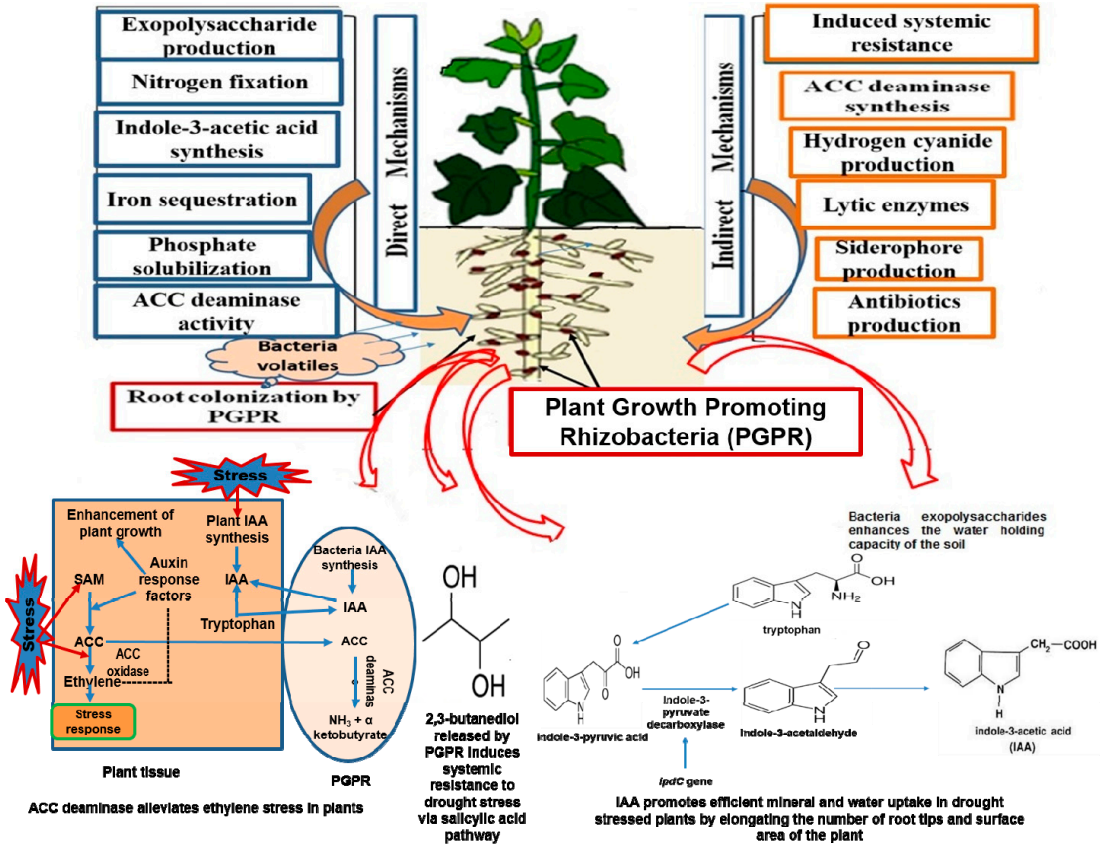

Figure 2. Mechanisms used by PGPR in alleviating drought stress and plant growth promotion.

Recent information on the utilization of rhizospheric microorganisms in enhancing soil health and agricultural sustainability has been extensively reviewed [63,68–72]. PGPR have been utilized in several crops such as garden pea (*Pisum sativum* L.) [73–75], maize (*Zea mays*) [21,76–79], green gram (*Vigna radiate* L.) [44,52,80–82], cucumber (*Cucumis sativus* L.) [83], potato (*Solanum tuberosum* L.) [44,84], sorghum (*Sorghum bicolar*) [85], wheat (*Triticum aestivum*) [86–88], foxtail millet (*Setaria italica* L.) [89] and lettuce (*Lactuca sativa*) [90]. The various mechanisms used by the PGPR for mitigation of water stress in plants are summarized in Table 2. In general, the effects of PGPR on plant growth result from a combination of PGP traits expressed by the PGPR with beneficial effects on drought tolerance such as ACC deaminase, exopolysaccharide production, and the synthesis of IAA. These bacteria may also be capable of solubilizing phosphate, fixing nitrogen in the soil, or sequestering iron from the soil. Most of these studies used field soils for controlled greenhouse studies due to the challenges involved in having adequate facilities to set up field trials for drought stress studies. However, Sahin et al. [90] showed that *Bacillus megaterium* TV 6D and *Bacillus subtilis* TV 12H increased nutrient uptake, leaf relative water content, stomatal conductance, and plant yield at 50% and 75% water regimes in a two-year field experiment.

Table 2. Rhizobacteria amelioration of drought stress in plants using different mechanisms.

Bacteria Strains	Test Crop	Mechanism of Action	Effects of Rhizobacteria Inoculation	References
Pseudomonas putida strain GAP-P45	Sunflower (Helianthus annuus L.)	Exopolysaccharide production.	Reduced drought stress and increased plant biomass.	[76]
Pseudomonas putida strain GAP-P45	Maize (Zea mays)	Exopolysaccharide production.	Enhanced plant biomass, relative water content, leaf water potential, and root length.	[76]
Bacillus sp.	Potato (Solanum tuberosum)	ACC deaminase activity, siderophore production, and phosphate solubilization.	Increased the photosynthetic efficiency of inoculated plants and expression levels of ROS-scavenging enzymes.	[84]
Bacillus spp strains KB122, KB129, KB133, and KB14	Sorghum (Sorghum bicolar)	Production of siderophore IAA and solubilization of phosphate.	Enhanced plant growth and biomass with dark greenish leaves due to high chlorophyll content as well as improved leaf relative water content and soil moisture content.	[85]
Burkholderia phytofirmans strain PsJN	Wheat (Triticum aestivum L.))	ACC deaminase activity, and siderophore production.	Reduced oxidative stress and increased mineral components of wheat.	[86]
Bacillus thuringiensis AZP2 and Paenibacillus polymyxa B	Wheat (Triticum aestivum)	EPS production, high Phosphate solubilizing efficiency, and ACC deaminase activity.	Improved crop growth and biomass.	[87]
Proteus penneri (Pp1), Pseudomonas aeruginosa (Pa2), and Alcaligenes faecalis (AF3)	Maize (Zea mays)	Exopolysaccharide production.	Improved plant biomass, leaf area, and growth parameters.	[78]
Azotobacter chroococcum strains 67B and 76°	Tomato (Solanum lycopersicum)	N_2-fixing activity, synthesis of siderophore, ACC deaminase activity, and indole-3-acetic acid production.	Increased nutrient availability to drought stressed tomato plants and enhanced water retention.	[88]
Bulkhorderia cepacia	Pepper (Capsicum annuum)	ACC deaminase activity.	Increased plant biomass and chlorophyll a content under drought stress.	[91]
Pseudomonas fluorescens DR7	Foxtail millet (Setaria italica L.)	Exopolysaccharide (EPS) production, and ACC deaminase activity.	Improved seed germination and seedling growth.	[89]
Bacillus megaterium TV 6D Bacillus subtilis TV 12H	Lettuce (Lactuca sativa)	ACC deaminase activity, phosphate solubilization, and indole-3-acetic acid production.	Increased plant growth, nutrient element content, leaf relative water content, stomatal conductance, and plant yield.	[90]
Bacillus spp. Enterobacter spp.	Velvet bean (Mucuna pruriens L.) DC.	ACC deaminase activity and indole-3-acetic acid production.	Enhanced plant biomass and reduced ACC concentration in leaves and roots of inoculated plants.	[92]
Ochrobactrum pseudogrignonense RJ12, Pseudomonas sp. RJ15 and Bacillus subtilis RJ46	Black gram ($_{Vigna\ mungo}$ L.) and Garden pea (Pisum sativum L.)	Synthesis of siderophore, ACC deaminase activity, indole-3-acetic acid production, and phosphate solubilization.	Increased seed germination percentage, root length, shoot length, dry weight of treated plants, and decreased ACC accumulation.	[75]
Variovorax paradoxus RAA3 (sole inoculation) Ochrobactrum anthropi DPC9 + Pseudomonas spp. DPB13 + Pseudomonas spp. DPB15 + Pseudomonas spp. DPB16 (consortium)	Wheat (Triticum aestivum L.)	Synthesis of siderophore, ACC deaminase activity, indole-3-acetic acid production, and phosphate solubilization.	Improved plant growth, and foliar nutrient concentrations, and significantly enhanced antioxidant properties of the plants.	[93]
Pseudomonas aeruginosa (JHA6) and Bacillus amyloliquefaciens (ROH14)	Pepper (Capsicum annum L.; Solanaceae)	Synthesis of siderophore, ACC deaminase activity and indole-3-acetic acid production.	Increased biomass production as well as chlorophyll content of inoculated plants and nutrient uptake.	[94].

4.1. ACC Deaminase Producing PGPR Ameliorates Water Stress in Plants

Synthesis of ethylene in a particular plant is affected by the presence and concentration of other plant hormones, temperature, light, nutrition, as well as the impact of other abiotic and biotic stresses [63,72,95]. Although ethylene is one of the plant hormones concerned in the control of several physiological responses in plants such as senescence, accelerated aging, fruit ripening, senescence, abscission, initiation of roots, regulation of root nodulation in legumes, inhibition of storage organs

formation [73,84,96], and supporting flowering in some species [97], it becomes deleterious to plant growth in high concentrations by affecting root and shoot development because it becomes "stress ethylene" due to the action of the enzyme ACC oxidase within plant tissues. S-adenosyl-Methionine (SAM) is converted by ACC synthase to ACC in stressed plants, thereby increasing ACC concentration, which is the immediate precursor of ethylene, and thus the ethylene levels produced. ACC synthesis could possibly be triggered by high levels of IAA secreted by the conversion of tryptophan exuded by plants and utilized by rhizospheric bacteria, which is subsequently absorbed by plants. In such cases that often arise when the plant is stressed as a result of conditions caused by salinity, drought, heavy metal contamination, waterlogging, and pathogenicity [98,99], the plants rely on the aid of ACC deaminase producing PGPR within its rhizosphere to assist in degrading ACC and consequently reducing ethylene production and restoring the plant to its normal development. The ACC deaminase producing PGPR does this by disintegrating plant ACC, an ethylene precursor in plants, into ammonia and α-ketobutyrate, which then reduces the ethylene synthesized by plants, and enhances their growth; therefore, it presents a promising opportunity to augment crop yields [98]. According to Glick et al. [100], stress ethylene is synthesized in two peaks. The first peak of smaller magnitude takes up much of the ACC present in stressed plants and initiates transcription of genes responsible for plant defense systems. The second larger peak of synthesized ethylene, due to increased production of ACC by ACC synthase genes activated by environmental stress, signals the initiation of processes detrimental to the well-being of plants such as leaf chlorosis, abscission, and senescence [63,95] and not the direct effect produced by the stress itself.

Studies have shown that the inoculation of ACC deaminase producing rhizobacteria on plants under abiotic stress, such as drought, ameliorates the negative effects of ROS; hence, it is an essential mechanism for plant survival in the mutualistic association with the bacteria. ACC deaminase producing *Achromobacter piechaudii* ARV8 alleviated the effect of oxidative stress on tomato and pepper plants due to drought by significantly increasing the fresh weight (574 ± 58.8 g) and dry weight (59.7 ± 5.43 g) of tomato (*Lycopersicum esculenta* Mill.), as well as the fresh weight (960 ± 60 g) and dry weight (120 ± 2.60 g) of pepper (*Capsicum annuum*), compared to the controls (155 ± 7.20 g and 15.6 ± 0.65 g, 560 ± 50 g, and 70 ± 0.16 g), respectively. The growth of the plants was enhanced by increasing the biomass of the crops four times when compared to the un-inoculated controls, as well as contributed significantly to reduced levels of ethylene in the stressed plants The growth of the plants was enhanced by increasing the biomass of the crops four times over compared to the un-inoculated controls, as well as contributed significantly to reduced levels of ethylene in the stressed plants [101,102]. Since the study of Mayak et al. [101], other authors have used ACC deaminase producing PGPR to promote crop production and reduce yield losses in crops exposed to water stress [75,86,89,91,92]. This was documented in a recent study in which *Pseudomonas fluorescens* DR7 and *Pseudomonas fluorescens* D11 with high ACC deaminase activities (24.56 ± 2.24 µmol α-KB mg protein^{-1} h^{-1} and 39.40 ± 0.68 µmol α-KB mg protein^{-1} h^{-1}) significantly ($p < 0.05$) enhanced the germination of foxtail millet (13.68%–141.82%) at water potentials of −0.49 MPa and −1.03 Mpa (enhancement of 13.68% and 141.28%), respectively [89].

The application of *Bulkhorderia cepacia* with ACC deaminase activity (12.8 ± 0.44, mM αKB mg^{-1} min^{-1}) and the ability to produce high levels of EPS (4.89 ± 0.06 mg/mg protein) resulted in increased chlorophyll a and b contents of inoculated *Capsicum annuum* plants (chlorophyll a 5.7 gmL^{-1} and chlorophyll b 3.4 gmL^{-1}, respectively) as well as plant biomass (fresh weight of 9g and dry weight of 3.6 g) compared to the control (chlorophyll a 3.2 gmL^{-1}, chlorophyll b 1.9 gmL^{-1}, fresh weight 6g, and dry weight 1.6 g) [91]. Inoculation of *Mucuna* plants with *Bacillus* spp. and *Enterobacter* spp. strains also ameliorated drought stress significantly by reducing the accumulation of ACC in the leaves of drought-stressed plants by 41% and 21%, respectively, and in the roots by 46% and 15%, respectively. With this development, the amount of excess ethylene produced by the plants was reduced under severe water stress by 45% (*Bacillus* spp.) and 65% (*Enterobacter* spp.), respectively, leading to survival of the plants [92].

Recently, the PGP and drought tolerance effect of ACC deaminase-producing rhizobacteria on wheat (*Triticum aestivum* L.) plants were investigated by Chandra, et al. [93] under simulated irrigated and drought stress conditions. The sole inoculation of wheat plants with *Variovorax paradoxus* RAA3 and co-inoculation of *Ochrobactrum anthropi* DPC9 + *Pseudomonas* spp. DPB13 + *Pseudomonas* spp. DPB15 + *Pseudomonas* spp. DPB16 significantly enhanced the growth of wheat plants and foliar nutrient concentrations, with significant modifications to the antioxidant properties of the plants, especially under drought stress. The above reports confirm the benefits derived from rhizobacteria with ACC deaminase producing abilities. Therefore, utilizing PGPR strains capable of producing sufficient amounts of ACC deaminase could lead to a significant reduction in the second peak of ethylene, which would subsequently lessen the detrimental effects of high ethylene levels on plants induced by biotic and abiotic stresses. This could be the reason behind the ability of *Pseudomonas fluorescens* DR7 and *Pseudomonas fluorescens* D11 to alleviate severe drought stress in foxtail millet. These strains can be used as inoculants for enhanced crop production, especially in arid environments. Some authors have also reported efficient utilization of ACC deaminase producing rhizobacteria in consortium with biochar [103,104], as well as in combination with plant growth regulators to enhance the yield of wheat plants under drought stress. Spraying of salicylic acid (SA) and putrescine (Put) at the rate of 150 mgL^{-1} on 25-day old chickpea seedlings in a consortium with PGPR resulted in significantly increased chlorophyll, protein, and sugar contents compared to the well-watered and drought conditions [105]. Similarly, the application of *Bacillus amyloliquefaciens* + 2BC (biochar) enhanced chlorophyll pigmentation up to 114% (chlorophyll a), 123% (chlorophyll b), 118% (photosynthetic rate), 73% (transpiration rate), 59% (100-grain weight), and grain composition, namely 58% (N), 18% (P), and 23% (K), under drought conditions [103]. In order to obtain success in the use of PGPR as biofertilizers for crop production, especially under stress conditions, it is crucial that isolates with high ACC deaminase-producing abilities be considered for possible exploitation for sustainable agricultural production of crops, especially in water deficit regions.

4.2. Reduction of Oxidative Stress in Drought-Stressed Plants via Osmoregulation

PGPR are known to secrete osmolytes, which synergistically act with osmolytes synthesized by stressed plants to boost their growth. Several reports have been made on the production of compatible solutes by rhizobacteria to withstand drought stress, which also enabled the plants to become tolerant to drought. *Azospirillum* sp. and *Herbaspirillum* sp., when inoculated on maize plants under drought stress, relieved the plants from oxidative damage. The concentration of the osmolyte proline was increased by two-fold (*Azospirillum* sp.) and four-fold (*Herbaspirillum* sp.), respectively [106]. However, proline concentration was highest in control plants (eight-fold) under water stress than control plants under well-watered conditions. This implies that the bacteria strains reduced the stress level, and hence, the plants had lower proline content than the control plants. A similar observation was made in the inoculation of chickpea plants with *Pseudomonas putida* [106,107]. The treatment with *Pseudomonas putida* had a significant reduction in proline concentration at all levels of stress, with a reduction of 114% and 214% proline in chickpea varieties cv. BG-362 and cv. BG−1003, respectively, on the seventh day of water stress [107]. Proline concentration was, however, increased in pepper plants inoculated with *Burkholderia cepacia* (0.143 mmoles gm^{-1}) relative to the control (0.065 mmoles gm^{-1}) plants [91]. Thus, the plants could tolerate drought and salinity stresses with increased biomass production.

Aside from proline, PGPR also synthesizes other osmolytes such as soluble sugars, proteins, and glycine betaine. The concentrations of these osmolytes are increased by beneficial PGPR, which helps to prevent cell destruction and, ultimately, death. Under harsh environmental conditions such as drought, the sugar content in the leaves of plants is drastically reduced, and this could be detrimental to macromolecules and cellular membranes. The accrual of soluble sugars in plants elicited by PGPR ameliorates the effect of drought on plants as they act as osmoprotectants. In a recent study, Khan et al. [105] reported that the application of a combination of PGPR + plant growth regulators aided the maintenance of the photosynthetic efficiency of Chickpea plants by inducing higher soluble sugar

accumulation, which subsequently made the plants tolerant to drought. Elevated levels of soluble sugar in plant leaves also leads to the activation and expression of relevant genes used in photosynthesis. In addition to acting as structural constituents of cells, high sugar levels in leaves also serve as signals that control several processes responsible for plant well-being under water deficit conditions.

4.3. Amelioration of Drought Stress in Plants by Exopolysaccharide (EPS) Producing PGPR

Rainfed or irrigated agriculture is required to meet food production, but when there is inadequate moisture as a result of drought, crop growth and production becomes limited as it alters the physicochemical and biological properties of soils, which affects the support of soil microbial activity [56,108]. Hence, healthy soils lose their functions. Nevertheless, microbes, mostly the PGPR in such unfavorable environmental conditions, secrete high molecular weight compounds into the environment called exopolysaccharides (EPSs), which are primarily composed of complex organic macromolecules; polysaccharide together with smaller percentages of protein and uronic acid [109], which represents 40%–95% of the bacterial weight. EPS production by bacteria could be Slime EPS or Capsular EPS [80]. Exopolysaccharides are found on the surfaces of microbial cells where they protect the cells by stabilizing membrane structure against unfavorable environmental stresses [109–111]. EPS are intracellularly synthesized by bacteria cells mostly during late logarithmic or stationary phases of growth, but the rate of production depends on several factors such as nutrient imbalance, drought, salinity, extreme temperatures, and changes in pH.

Rhizobacteria of the genera *Bacillus, Pseudomonas*, and *Acinetobacter*, amongst others, are effective in conferring abiotic stress tolerance to plants and withstand harsh environmental conditions due to their EPS producing abilities. In the study of Sandhya et al. [112], *Pseudomonas putida* (GAP-P45), when inoculated on sunflower plants under drought stress, produced high levels of EPS (63.30 ± 9.95 mg plant^{-1}) and alleviated the effects of drought stress by increasing 64% of the total dry biomass of the plant and soil aggregation with an aggregate stability of 70.80% ± 0.80%. The inoculated bacterium effectively colonized the soil adhering to the roots and rhizoplane, thereby increasing the proportion of stable soil aggregates [112,113]. The plant growth-promoting abilities and EPS produced by a consortium of three bacteria strains *Proteus penneri* (Pp1), *Pseudomonas aeruginosa* (Pa2), and *Alcaligens faecalis* isolated from water deficit regions for their drought tolerance potentials when used as bio-inoculants alone or in combination with their EPS on maize plants subjected to drought stress was investigated by Naseem and Bano [78]. Isolate Pa2, together with its EPS, increased RWC of the leaves of inoculated maize plants by 45% as opposed to the un-inoculated plants as well as protein content (1121.2 μg g^{-1}), which is important to combat the oxidative and osmotic stresses due to drought on the plants. Both strains, together with their EPS, also increased soil moisture by 68% and 67%, respectively [78]. The production of EPS by *Pseudomonas fluorescens* DR7 (11.63 ± 0.51 mg mg^{-1} protein), *Pseudomonas fluorescens* D11 (2.91 ± 0.19 mg mg^{-1} protein), and *Enterobacter hormaechei* DR16 (5.44 ± 0.24 mg mg^{-1} protein) also enhanced the growth of foxtail millet under drought stress and effectively colonized the root hairs, thereby increasing the soil/root tissue ratio adhering to the roots [89]. Exopolysaccharide-producing rhizobacteria are indispensable in promoting plant growth under abiotic stresses as they increase the water holding capacity of the soil, thereby relieving the plants from stress. Therefore, in selecting bacteria strains to use as bio-inoculants for plant tolerance to drought, strains producing high levels of exopolysaccharide should be chosen for effective results.

4.4. Indole-3-acetic Acid (IAA) Induced Drought Tolerance in Plants by PGPR

Phytohormones produced by bacteria are a possible means of augmenting plant growth in unfavorable environmental conditions [30]. These phytohormones relieve plants from abiotic stresses and improve their survival rates [56,114,115]. There is an array of phytohormones, such as the cytokinins, auxins, gibberellins, ethylene, abscisic acid, and jasmonates, which either promote shoot growth or regulates growth-inhibitory processes in plants such as dormancy, abscission, and senescence, thereby controlling growth activities in plants [116–118]. Abscisic acid is vital to the opening and

closing of the stomata, especially when plants are stressed. The concentrations of abscisic acid in plant cells is regulated in reaction to the availability of water to the plant; thus, it is important in the reaction of plants to water stress conditions by inducing several transcription factors [119]. The quantity of abscisic acid in maize plants inoculated with *Azospirillum Lipoferum* increased, resulting in stomata closure arising from a low transpirational loss of water [2,120]. Furthermore, the root architecture under salinity and drought stress conditions was changed due to increased water absorption, which enhanced root branching [2,121].

The most prominent phytohormone, which is a major control factor in plants, are the auxins, which regulate most of the processes in plants either directly or indirectly, and hence, can be considered key to the developmental patterns in plants [122]. Indole-3-acetic acid regulates the developmental processes of plants due to the endogenic pool of plant IAA, which may be modified by the acquisition of IAA secreted by soil bacteria [68,99]. It is the active plant hormone essential for rhizobacteria-plant interactions enhancing plant defense mechanisms against phytopathogens and improving its growth [99,123]. IAA production is a basic direct mechanism of PGPR on crops, which changes the root system architecture under drought stress and increases the number of root tips and surface area of the plant, thereby promoting efficient mineral and water uptake by the plants [124]. *Enterobacteria lignolyticus* strain TG1 produced a significant amount of IAA (92.5 ± 0.2 μg mL^{-1}) which increased root biomass production (4.3 fold) and root length (2.2 fold) when inoculated on economically essential tea clones TV1, TV19, and TV20 under greenhouse conditions in contrast to control plants [125]. Elevated levels of IAA are generally produced in the stationary phase of bacteria growth, and its synthesis follows the intermediate indolepyruvic acid pathway [118]. The *ipdC* gene, which codes for indolepyruvate decarboxylase, is used by beneficial IAA producing microorganisms to convert indole-3-pyruvic acid (IPyA) to indole-3-acetaldehyde in the indolepyruvic acid pathway [118,126,127].

In this pathway, indole-3-pyruvic acid is produced from tryptophan, which is converted to indole-3-acetaldehyde by the removal of a carboxyl group, catalyzed by indole-3-pyruvate decarboxylase, and subsequently leads to the formation of indole-3-acetic acid [128,129]. *Bacillus amyloliquefaciens* and *Paenibacillus polymyxa* BFKC01 possess genes required for IAA synthesis pathways. The presence of these genes in the bacteria gives the bacteria the ability to produce sufficient amounts of IAA, which could be used for plant growth enhancement. Both *B. amyloliquefaciens* and *P. polymyxa* BFKC01 activated iron acquisition mechanisms in addition to increasing fresh plant weight, lateral roots, and plant biomass [130,131] when applied on plants. At low concentrations, IAA stimulates primary root elongation; however, at elevated levels, it stimulates lateral root formation in addition to increasing root hair formation but decreases primary root lengths [124]. It could also trigger higher levels of ethylene in plants as the excess IAA activates ACC synthase transcription. *Ochrobactrum pseudogrignonense* strain RJ12, which produced high levels of IAA under the osmotic stress condition of −0.73 MPa (85.0 ± 1.0 μg mL^{-1}) when combined in a consortium with *Pseudomonas* sp. strain RJ15 (72.0 ± 1.1 μg mL^{-1}) and *Bacillus subtilis* strain RJ46 (68.0 ± 0.9 μg mL^{-1}), significantly increased the root length of black gram (12.1 ± 0.9 cm) and garden pea (10.2 ± 0.3 cm) under drought stress compared to the controls [75]. This enabled the plants to withstand water stress and survive. Screening of PGPR for IAA production is, therefore, crucial for its usefulness in bioformulation for enhanced crop growth under drought stress. Much emphasis has been placed on IAA as the major phytohormone, and hence, its utilization alone or in combination with IAA-producing PGPR strains could give a boost to plant growth and development. It will be meaningful for scientists also to have a mechanistic understanding of the roles of other plant hormones in alleviating abiotic stresses in crop plants.

4.5. The Beneficial Effects of PGPR in Mineral Nutrient Uptake in Plants under Abiotic Stress

The sessile nature of plants makes them acquire the majority of the mineral nutrients needed from the soil, which is then transported via protein transporters to cellular roots and shoots for growth and development. Having a mechanistic understanding of the beneficial traits of PGPR and interactions could promote the efficient utilization of these below-ground organisms in enhancing high plant

growth and yield under abiotic stresses. In addition to nitrogen and potassium, plants also require phosphorus and trace amounts of iron. Phosphorus is an indispensable mineral needed for the proper development of plants. However, it is scarce in most soils and only found in both organic and inorganic forms, hence, the use of rock phosphate to augment phosphorus deficiency in the soil and solubilize it through organic acid production [132].

Soil phosphorus deficiency is a global problem with about 5.7 billion ha of land deficient in soluble phosphate ($H_2PO_4^-$), which affects the efficiency of crop production [133–135]. A considerable amount of soil phosphorus occurs in the insoluble phosphate forms as apatite or as phosphomonoester and phosphotriester, making it unavailable for plant use [68]. Changes in climatic factors due to anthropogenic activities cause abiotic stresses, which impedes nutrient uptake in plants. Water stress results in decreased nutrient composition of agricultural soils, especially the concentration of nitrogen (%) and phosphorous (%) [136]. Recent studies by Bista et al. [136] revealed astonishing findings on nutrient acquisition and the levels of nutrient-uptake proteins in roots of drought-sensitive and drought-tolerant grasses (barley, corn, and bluestem). A correlation existed between the decrease in phosphorus uptake under drought stress with a fall in the amount and activities of phosphate uptake proteins. In other words, the concentration and activities of the phosphate uptake of proteins will result in a decrease in phosphorus uptake by plants. This was observed in drought-sensitive plants harvested at mid and late drought periods. The PHT I-type transport protein identified by homology with the yeast PHO84 Pi transporter is a given family of plant plasma membrane proteins, which aids the uptake of phosphorous by plant roots [137]. Drought reduced the shoot, root, and total percent phosphate in barley, corn, and bluestem by 41%, 48%, and 39%, respectively. The amount of PHT I per gram root mass declined with drought in barley, corn, and bluestem by 40%, 44%, and 59%, respectively, at the end of the water stress harvest period. In addition, the relative activity of PHT I was also reduced. Thus, under abiotic stress, there is always a decrease in plant mineral concentrations as a result of a decreased concentration of nutrient uptake proteins, which decreases proteins per gram of root. The lack of available phosphorus in soils has, over the years, made farmers depend more on chemical fertilizers to enrich the phosphorous content of agricultural soils, but this has negative implications since excessive fertilizer applications could affect soil quality. Therefore, an eco-friendly strategy is required to augment soluble phosphate levels in agricultural soils. Microbial P-solubilization and mineralization is the only probable eco-friendly way to increase phosphorus availability to plants. This is achieved by some microorganisms found in the soil and rhizosphere, referred to as Phosphorus Solubilizing Microorganisms (PSM).

Phosphate solubilizing rhizobacteria (PSRB) inhabiting the rhizosphere of plants could be used as effective bio-inoculants due to their ability to supply phosphate to plants using different mechanisms. The most significant PSRB has been reported to include *Azotobacter, Agrobacterium, Bacillus, Flavobacterium, Pseudomonas, Microbacterium, Enterobacter, Rhizobium, Serratia,* and *Burkholderia* [6,7,102,138–140]. *Bacillus* spp. strains KB122, KB129, KB133, and KB14 with IAA and phosphate solubilization ability increased chlorophyll content, root biomass, and relative water content of leaves of sorghum plants subjected to water stress [87]. Although PSRBs are abundant in the soil, their ability to solubilize phosphate could be hampered by environmental factors. For example, in the research of Zeng et al. [135], the ability of the *Pseudomonas frederiksbergensis* strain JW-SD2 to solubilize phosphorous declined significantly ($p < 0.01$) due to increased temperature and salinity. Nevertheless, the inoculation of the strain significantly promoted the growth of poplar (*Populus euramericana* cv NL-895) [135]. Furthermore, the authors reported that during the 150 days' trial of the experiment, fluctuations were observed in plant growth promotion as it initially increased then decreased over time; hence, periodic supplementation of the rhizobacteria strains into rhizosphere during field applications is proposed. Several PSRB have been obtained from rhizosphere soils and harnessed for plant growth promotion of a variety of field crops, such as garden pea [141] and maize [142,143]. However, isolating stress-tolerant PSRB from arid or semi-arid environments with multifunctional growth-promoting properties would be beneficial as such bacteria could enhance crop

growth under stress conditions such as drought and heat stress by enhancing nutrient uptake. In this perspective, rhizobacteria with phosphate solubilization potentials and other PGP traits are crucial in the enhancement of crop growth and yield, especially under environmental stress. It is also important to note that these beneficial bacteria will need to be protected from the harsh environmental factors that may hamper their performances under field conditions. In this context, better ways of delivery need to be investigated by researchers.

Multifaceted rhizobacteria strains are being used as bio-inoculants for crop improvement under unfavorable environmental conditions. Iron is also an essential micronutrient required by plants, and it is the fourth most abundant mineral element found in most soil types [144]. In recent times, more research is focused on the utilization of Fe as an important nutrient supplement and its key role in conferring abiotic stress tolerance to plants. Regardless of its abundance in the soil, its soluble ferric iron (Fe^{3+}) form is limited in the soil for plant utilization. Insufficient supply of Fe in plants results in reduced crop yields, interveinal chlorosis in plant leaves, etc. [145–147]. Several studies have shown that application of micronutrients, such as Fe and Zn, to various crops under water deficit conditions, can promote tolerance to plants as it aids assimilate production [147–152] Microorganisms adhering to the rhizosphere of plants have the ability to produce siderophores when growing in environments with inadequate accessibility to iron [144]. PGPR with siderophore producing ability indirectly enhances plant growth through sequestration of iron from the environment, thereby preventing potential pathogens of the plant from proliferating within the rhizosphere. The activities of microbial siderophores, therefore, aids in keeping the plants healthy and free from pathogenic diseases, in addition to providing iron for the plants.

Bacteria of the genus Rhizobium, e.g., *Rhizobium meliloti,* produces carboxylate type siderophore, but fluorescent pseudomonads are known to produce mixed siderophores containing both hydroxamate and catecholate types [153]. *Micrococcus yunnanensis* YIM 65004 (T) and *Stenotrophomonas chelatiphaga* LPM-5 (T) significantly improved grain weight and iron (Fe) content of roots and shoots of canola and maize plants under greenhouse conditions compared to the control [2,153]. *S. Chelatiphaga* significantly ($p < 0.05$) raised the root and shoot Fe contents by 64.99% and 10.55% in maize and by 8.97% and 462.18% in canola, respectively, while *M. Yunnanensis* elevated the root and shoot Fe contents by 43.12% and 14.81% in maize and by 38.26% and 212.72% in canola, respectively. Viscardi et al. [88] evaluated 106 bacterial strains and identified two strains of *Azotobacter chroococcum* strains 67B and 76A with the ability to synthesize ACC deaminase, IAA, and siderophore, in addition to being tolerant to salinity and drought stress. Both strains ameliorated the effects of drought on tomato seedlings and also possessed antimicrobial activity against *Sclerotinia minor* CBS 112.17 due to their siderophore producing ability. *Sclerotinia minor*, as well as *Botrytis cinerea,* and *Cochliobolus heterostrophus* are fungal phytopathogens that affect many essential food crops, siderophore producing PGPR will, therefore, be useful in the biocontrol of these pathogens.

The use of a consortium treatment of bacteria strains *Ochrobactrum pseudogrignonense* RJ12 + *Bacillus subtilis* RJ46 + *Pseudomonas* sp. RJ15 having high ACC, IAA, phosphate solubilization, and siderophore production abilities significantly increased the rate of survival of *Vigna mungo* and *Pisum sativum* after 45 days of water stress treatment [75]. In addition, the inoculated plants had increased seed germination rates, synthesis of total leaf chlorophyll, elongated root lengths, and increased antioxidant enzymes and osmolytes production compared to the controls [75].

There are several reports on the beneficial use of AMF in extenuating the effects of drought stress in plants [154–156]. AMF belongs to the phylum Glomeromycota, which consists of four orders (Archaeosporales, Diversisporales, Glomerales, and Paraglomerales), with 11 families, 25 genera, and approximately 250 species [154,157]. AMF colonizes the roots of 80% of terrestrial plants in a symbiotic relationship in which they augment nutrition, absorption of water, root architecture, flowering, and stress tolerance [156,158] and in return, obtain photosynthetic products from the host plant. Fungal hyphae of AM can get to soil pores not reachable by root hairs, accessing water and sources of nutrients that cannot be tapped by non-AM plants [155]. With this property, AMF effectively

augments the growth of plants by altering the plant-water relationship, leading to improved water-use efficiency and, consequently, improved crop yield. In a recent study by Li et al. [155] to investigate the ability of AMF to mitigate the effect of extreme water stress on *Leymus chinensis* (C3) and *Hemarthria altissima* (C4) grasses productivity, AMF significantly improved plant biomass (58%), photosynthetic rate (63%), stomatal conductance (38%), intrinsic water use efficiency (15%), and SOD activity (45%) with a reduction in the concentration of malondialdehyde by 32% of *Leymus chinensis* under mild (30%) and moderate (50%) drought stress, which was higher than the results of *Hemarthria altissima*. Beneficial strains of mycorrhizal are sometimes used in consortium with PGPR for enhanced efficiency in plant growth promotion. The benefits derived from mycorrhizal symbiosis makes their utilization more attractive for sustainable agricultural productivity. Most of the biofertilizers in the commercial market are composed of AMF.

The nitrogen-fixing bacteria, sometimes called intracellular PGPR, aid in providing nitrogen in legumes through symbiotic relationships. They can penetrate plant cells and produce nodules through which they fix atmospheric nitrogen symbiotically with higher plants. They include the *Allorhizobium, Azorhizobium, Bradyrhizobium, Mesorhizobium*, *Ensifer/Sinorhizobium,* and *Rhizobium* of the Rhizobiaceae family [159]. Like the PGPR, rhizobia also possess PGP traits such as the ability to synthesize EPS, IAA, ACC deaminase, siderophore, as well as to solubilize phosphate, in addition to fixing nitrogen in soils. Members of the Rhizobiaceae family are attracted to legumes through the release of flavonoids, which induces the transcription of *Nod factor* (lipochitin oligosaccharides (LCOs) and consequently, the formation of root nodules [160–163] within which they differentiate into bacteroids and fix atmospheric N in the root nodules of the crops [161,164] in exchange for photosynthetically obtained carbon. LCOs stimulate plant growth promotional activities through the initiation of mutualistic association to varying phytohormone levels, resulting in enhanced photosynthesis and improved resistance to biotic and environmental stresses [130,164,165]. Thus, LCOs are crucial signaling molecules within the rhizosphere, which stimulates plant growth enhancement and could have an impact on plant nutrition via modification of the root structure [165]. The effect of LCOs on nutrient uptake enhancement in plants was reported in *Medicago truncalata* by Oláh et al. [166], who observed an improvement in the number of lateral roots of the plant when LCOs were applied [167]. In the same way, a positive improvement in the root architecture of *Arabidopsis thaliana* was observed when plants were treated with LCOs from *Bradyrhizobium japonicum*. This resulted in an increase in the root surface area, the number of root tips, as well as the root lengths of *A. thaliana* treated plants [167,168].

4.6. Secretion of Volatile Organic Compounds (VOCs) by PGPR and Their Roles in Biocontrol and Plant Growth Promotion

In addition to the various mechanisms used for growth enhancement by PGPR just described, the production of gaseous organic molecules, commonly called volatile organic compounds (VOCs), is another probable mechanism utilized by soil microbes. Volatile organic compounds are carbon-containing compounds of low molecular weights (<300 Da) that easily evaporate at normal temperatures and pressures [169]. These VOCs, when released by microbes in the soil, act as elicitors of an induced systemic resistance/tolerance (ISR/IST) response, which stimulates plant defense systems without having any physical contact with plants [170]. In addition to the molecular mechanisms governing the interaction of rhizobacteria with plant roots, signaling also plays an essential role in maintaining plant health through the production of these VOCs. Microbial volatile organic compounds (mVOCs) form a plethora of chemical groups, including alkenes, alcohols, ketones, benzenoids, pyrazines, sulfides, and terpenes [171–174]. Having a better understanding of the mVOCs, and insights into the molecular underpinning linked to such mVOCs, could present ways for efficient control and utilization of microbes. Furthermore, VOCs are eco-friendly and could be used as an alternative technique for sustainable crop improvement. Organized exploration and classification of the biological functions and ecological roles of mVOCs could also bring about new mechanisms for regulating

various biological processes vital to the well-being of plants and will also give concrete benefits in proffering solutions confronting agricultural production and environmental management [174,175].

The vast majority of microbes in the soil are the bacteria, which are known to produce a wide array of VOCs, which play critical roles in promoting plant health and induced systemic resistance in plants (Figure 3). Bacterial VOCs include alcohols, ammonia, HCN, and phenazine−1-carboxylic acid, which possess antifungal properties that contribute to the biocontrol abilities of PGPR [176], as well as alkanes, alkenes, esters, ketones, sulfur compounds, and terpenoids [174].

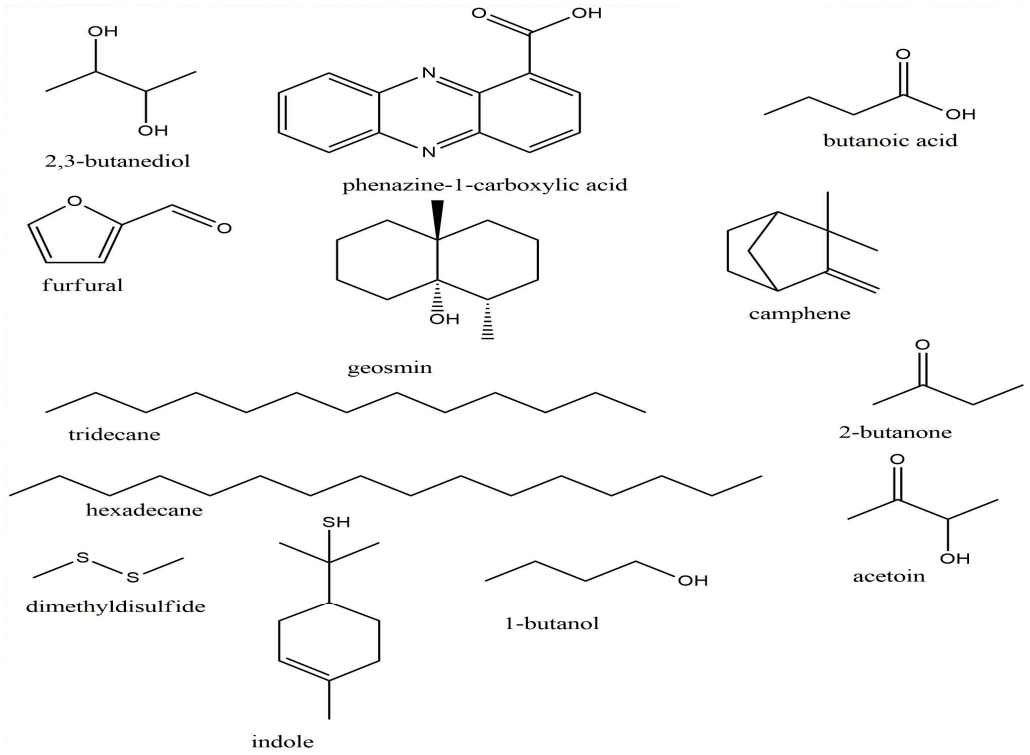

Figure 3. Structure of some bacterial volatile compounds with known functions in plant growth promotion and increased stress resistance.

Volatile indole released by indole-producing *Escherichia coli* and *Proteus vulgaris* has also been reported to enhance plant biomass as well as lateral root formation in *Arabidopsis thaliana* plants at 14-, 21- and 14-days exposure, respectively [177–179]. The plant root exudates composed of metabolites, such as sugars, amino acids, and organic acids, enrich the environment of the rhizosphere soil and are utilized by free-living rhizobacteria for their growth and metabolism. VOCs act as signaling molecules for facilitating both short and long-distance intercellular and organismal interactions owing to their ability to diffuse through air spaces as well as liquids [175,180]. Emission of VOCs by different rhizobacteria strains could change the root system architecture as well as control plant growth promotion. Recent analytical developments have given us insight into the nature of rhizobacterial VOCs, which are described as being lipophilic with very low boiling points, having molecular weights below 300Da, having a high vapor pressure (0.01 kPa at 20°C), and easily evaporating and diffusing through diverse mixtures of solids, liquids, and gasses [181–183]. The first study on mVOC was carried out on *Arabidopsis thaliana* by Ryu [184], who revealed that plants inoculated directly with *Bacillus amyloliquefaciens* (formerly *subtilis*) GB03 or with the GB03 volatiles showed elevated levels of tolerance to drought conditions, probably mediated by higher levels of choline and the osmo-protectant glycine betaine, which makes plants tolerant to dehydration [185]. The GB03 released volatiles, which contained 2, 3-butanediol, caused a 5-fold increase in the total leaf area of *A. thaliana* after 10 days of exposure of the plant to the volatile, promoting plant growth. Afterwards, other researchers reported plant growth promotion using the same bacteria species with a two-fold increment in shoot

biomass of sweet basil [186], 58% and 71% increases in fresh and dry weights of *A. thaliana* after two weeks of exposition [179,187], as well as an increase of root and shoot fresh weight of *A. thaliana* after six days of inoculation [180,188]. Also, 2, 3-butanediol is produced by *Pseudomonas chlororaphis* strain O6, which has the ability to elicit induced systemic resistance in plants. *Pseudomonas chlororaphis* O6 prevents water loss in plants when it colonizes the roots by closing the stomata due to the production of 2, 3-butanediol; however, bacteria lacking the metabolite showed no stimulation of drought tolerance [188]. Volatiles dimethylhexadecylamine (DMHDA) and indole produced by PGPR improved primary root length, lateral root length, and number, as well as root hair density, which altered the root architecture, with increased volume and root area when applied to *A. thaliana* plants [177,189]. These are essential features required by plants to withstand drought.

Researches on the effect of VOCs on the model plant *A. thaliana* paved the way for further research on mVOCs produced by other bacterial strains and fungi. An elaborate review of the plant growth enhancement of these volatiles, synthesis, and mechanism of action of the volatiles can be obtained from the recent publication of Fincheira and Quiroz [179]. The kind of volatiles produced by microbes is, however, dependent on the environmental conditions as well as the carbon source utilized for metabolism. Hence, the exudates released by plant roots, soil properties, and the soil microbial community, determine the composition of VOCs released by microbes and influences the metabolism of microbial strains [190]. VOCs activated the expression of FIT1, FRO2, and IRT1 genes, which improved uptake of iron and plant growth, and in conditions of sulfur deficiency, plants directly took up and assimilated the S-containing compounds (e.g., dimethyl disulfide) emitted from some PGPR [185]. Dimethyl disulfide (DMDS) is one of the most bioactive compounds produced by bacteria. *Bacillus ambifaria* cultured on LB agar enhanced lateral root formation and biomass significantly in *A. thaliana* plants after 21 days of exposure. DMDS acted as an induced systemic resistance elicitor from the bacterium. Isolates of *Bacillus* spp. were also reported to have affected the growth and root architecture of *Arabidopsis thaliana* by means of VOC production [175,191]. A vast majority of microbes producing volatiles are still yet to be fully explored for enhancement of plant growth, especially under environmental stresses. The biochemical pathways have to be studied, and the molecular mechanism elucidated. This is an area that requires more research focus to better harness PGPR for sustainable agricultural productivity since it helps in restoring the fertility of the soil.

5. Challenges in Exploitation of PGPR as Bio-Inoculants for Crop Improvement

The various benefits of using PGPR as bio-inoculants to either enhance plant growth through nutrient mobilization and synthesis of plant growth-promoting substances, as well as induced systemic resistance, have been highlighted in this review. This has been confirmed by the numerous articles on the beneficial effects of PGPR by several authors. In addition to improving plant nutrients, the use of beneficial PGPR restores the fertility of the soil without degrading the environment, unlike the chemical fertilizers used in agricultural farms; hence, it is environmentally friendly. Additionally, while carrying out these functions, some PGPR also mitigate the effects of environmental stresses, such as water stress on crops [63,78,86–88,91]. Despite these benefits, there are some drawbacks to the effective utilization and commercialization of beneficial microbes for sustainable agricultural productivity.

The success derived in the performances of PGPR *in vitro* and under greenhouse conditions is not often sustainable under field conditions where they are exposed to the natural environment, and there could be inconsistency in research results. Moreover, under field conditions, the efficacy of such microbes is often affected by changes in environmental conditions such as the soil texture and structure, as well as pH and mineral composition. This remains a drawback to the exploitation of these beneficial microbes on a large scale for crop production. Hence, PGPR strains need to be tested in pot experiments using both sterilized and unsterilized field soils to determine their actual efficacy, before final testing on the field under stressful conditions in the presence of the natural microflora, to determine if they will be able to effectively populate plant roots and compete with the indigenous microbes that are well-established in the environment. After the inoculum has been applied to the plant, there is a

need to conduct some assays to determine the localization of the bacteria. Are the PGPR likely to be systemic and spread to all tissues of the plant, or is it only localized within the vicinity of the roots of the host plant? These are pertinent questions that need to be addressed when bacteria strains are being selected for biofertilizer formulation. In the study of Gagné-Bourque et al. [192], *Bacillus subtilis* strain B26 was recovered from various parts of the *Brachypodium* plant; roots, stems, blades, as well as seeds, which is an indication of the ability of the bacterium to systemically spread inside the plant and establish itself in plant tissues and organs of the plant, and even to being transmitted to the next generation of plants [192].

Furthermore, in water-stressed environments, excessive heat may affect the effectiveness of selected PGPR strains, except those that are endospore formers with the ability to produce biofilms. Extreme temperatures could decrease the bacteria population in the soil since the bacteria inoculum used do not have any protective support. Therefore, in order to effectively formulate bio-inoculants from PGPR, a sufficient quantity of bacteria, together with physical protection to prevent a rapid decrease of the PGPR introduced, must be taken into consideration [193].

The choice of PGPR strains could also be problematic. PGPR strains need to be screened for at least two or three of the PGP factors to be useful in promoting plant growth under environmental stress. Some strains may be effective if used alone, but studies have shown that the use of a consortium of bacteria strains is often more effective than single strains. However, some strains that may have performed excellently when used alone may become the antagonist in a consortium due to incompatibility, hence the need to embark on greenhouse trials before being used for bacterization under field conditions. Lastly, a suitable carrier has to be used for the bioformulation of PGPR as biofertilizers for crop growth, which should be inexpensive, non-toxic, rich in organic matter content with at least 50% water holding capacity and should be readily available for the industry to strive [194]. Different carriers have been suggested and used for biofertilizer production. These include peat soil, lignite, vermiculite, charcoal, press mud, and farmyard manure, as well as soil mixture [194]. The processing of biofertilizer has to be carried out under strict quality control and assurance before it can be officially registered for commercial use. There is a lot of potential in the biofertilizer industry, but the local farmers who need this technology are often not aware of it, although its benefit is well known in the scientific community. In order for the benefits of PGPR to be fully harnessed, more awareness should be made to sensitize the farmers for sustainable crop production to be achieved.

6. Future Potentials for Harnessing PGPR in Crop Improvement

The exploitation of PGPR as bio-inoculants for healthy plant growth is indispensable in sustaining food security, especially under unfavorable environmental conditions. However, the beneficial activities of PGPR are often affected by extreme temperatures, drought, salinity, heavy metal pollution, and they may have a short shelf life when applied in field conditions, which reduces their efficacy. Nanotechnology, which deals with the study and application of tremendously small particles of about 1 to 100 nanometers, could enhance the efficacy of PGPR when employed under natural field conditions by acting as encapsulating agents. The effectiveness of beneficial rhizobacteria under field conditions varies among strains. It is, therefore, crucial to develop bacteria formulations that could protect plants from phytopathogens and also augment their growth and development under unfavorable environmental conditions for agricultural production to be sustained. Lately, the use of Titania (TiO_2) nanoparticles as plant growth enhancers in agricultural practices is gaining more attention due to their adhesive effect on bacteria cells, which binds them to the roots of plants. This was reported in oilseed rape in which beneficial PGP bacterium *Bacillus amyloliquefaciens* strain UCMB 5513 adhered to the roots of the plant and acted as a biocontrol agent by preventing fungal infections in *Brassica napus* [195] and mitigated the impact of drought on wheat (*Triticum aestivum*) [196]. Biofertilizer formulations from beneficial isolates could be coated with nanoparticles, which will enhance the root colonization ability of the bacteria strains. In this perspective, research efforts should focus on the development of nanoparticles, of which a wide array is produced by plants and microbes. These metal oxides

have much affinity to phosphate and phosphate ligands [197]. A clear and considerable increase in light absorbance of 600nm was obtained when *B. amyloliquefaciens* strain UCMB 5513 were grown on medium supplemented with titania nanoparticles, indicating an interaction between nanoparticles and the bacteria with the resultant increase in absorbance as opposed to absorbance with either the nanoparticles or the bacteria alone [197]. In actual fact, the nanoparticles aided clustering of the bacteria in addition to improved root colonization with extensively more bacteria when treated with titania nanoparticles. Two-dimensional (2D) gel electrophoresis also showed that the bacteria were not stressed, as the protein profiles remained unchanged. These findings by Palmqvist et al. [197] are crucial as it suggested that Sol-Gel synthesis of titania nanoparticles at particular amounts could be beneficial in improving bacteria formulations that could be explored for enhanced application of biofertilizers for sustainable agricultural production under field conditions. Apart from titania nanoparticles, research on other nanoparticles should also be considered and utilized.

The genes underlying drought tolerance are complex in plants, but with advances in omic technologies such as proteomics, transcriptomics, genomics and metabolomics, drought-tolerant genes as well as heat shock proteins, chaperones and other metabolic proteins that protects microbes and plants from dehydration can be identified and transferred to beneficial PGPR isolated from arid regions in order to enhance their performances and abilities to adapt to different soil types and physicochemical characteristics, as well as compete effectively with indigenous microflora for colonization of plant roots. Functional genomics of beneficial PGPR strains will give insights into the functions and interactions of the genes up-regulated under abiotic stresses aided by transcriptomic and RNA sequencing technologies. Knowing full well that PGPR produces osmolytes like proline, trehalose, and glycine betaine, which reduce the effect of ROS on drought-stressed plants, the overexpression of genes for production of these osmolytes could enhance the tolerance ability of these bacteria strains, which consequently confers stress tolerance ability to plants.

7. Conclusions

Drought is a major threat to food security and sustainable agriculture. It causes accumulation of ROS, which leads to oxidative damage in plants. Furthermore, it results in a reduction in crop yield and causes loss of income to farmers. If the increasing human population has to be fed, then a cost-effective means of promoting crop productivity under abiotic stresses is indispensable, and the use of beneficial PGPR represents an important strategy to achieve this aim. The abilities of PGPR to promote plant growth and provide protection from environmental stress is an inexpensive, eco-friendly, and promising means of mitigating the effects of drought on crops and the promotion of the well-being of plants. Plant growth-promoting traits highlighted in this review are key mechanisms utilized by PGPR for plant growth enhancement. In addition, these beneficial PGPR enhance the production of osmolytes and antioxidant defense systems, which reduces the detrimental effects of ROS on plants. Multifaceted PGPRs are, therefore, essential for sustainable crop productivity and food security, especially in unfavorable environmental conditions. The efficacy of these strains could be enhanced for better performance as bio-inoculants under field conditions using new technologies such as nano-encapsulation, which improves colonization of root hairs by beneficial bacteria. The studies highlighted give us a better understanding of the relationships between plants and beneficial soil microbes, which represent a step forward in taking the best out of this interaction; nonetheless, the current knowledge is still at the point of fully benefiting from these PGPR. There is, therefore, a need for more research focus on molecular plant-microbe interactions in order to have a mechanistic understanding of the pathways utilized by rhizospheric microbes in plant growth enhancement and disease suppression for sustainable agricultural productivity.

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