A Critical Review on Plant Growth-Promoting Rhizobacteria (PGPR) as a Drought Stress Management Tool

Shamal S. Kumar[1*], Ananta G. Mahale[1], Md. Mifta Faizullah[1], J. Radha Krishna[1] and Tharun K. Channa[1]

[1]*Division of Soil Science and Agricultural Chemistry, Sher-e-Kashmir University of Agricultural Sciences and Technology of Kashmir, India.*

Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

Review Article

ABSTRACT

Water scarcity is known as a major stumbling block towards crop development and its output all over the world. Certain free-living bacterial strains have been found near the plant root zones which have shown to improve resistance of plants towards water stress. Despite availability of basic nutrients, drought an abiotic factor substantially inhibits growth, development and yield of crops by causing an increase in ethylene levels. It is a good idea to incorporate the use of a management tool which is the utilization of plant growth-promoting rhizobacteria to help several crops manage drought conditions. Drought stress in crops can be alleviated by reducing ethylene synthesis, exopolysaccharide, osmoregulation, Indole-3-acetic acid and aggregation with the ACC deaminase-containing plant growth-promoting rhizobacteria. Inoculating pathogens like root rot (*Macrophomina phaseolina*) affected plant with *Pseudomonas fluorescens* strain TDK1 with ACC deaminase function improves drought stress. Using plant growth-promoting rhizobacteria to mitigate the negative imbibes of drought in most crops is a good idea. Several studies have been carried out on plant growth-promoting rhizobacteria, as its inoculation not only manages drought related

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Corresponding author: E-mail: Shamalkumar1997@gmail.com;

conditions but increases root hair growth and lateral root, which assist in increased water and nutrient uptake. It limits ethylene supply, alternatively increases plant root growth by hydrolyzing 1-aminocyclopropane-1-carboxylic acid (ACC). This review will give us a perspective on the importance of plant growth-promoting rhizobacteria, as it is one of the efficient tools that helps manage drought stress on several crops.

ABBREVIATIONS

ACC	*: Aminocyclopropane-carboxylic acid*
PGPR	*: Plant growth-promoting rhizobacteria*
N	*: Nitrogen*
P	*: Phosphorus*
ePGPR	*: Extracellular plant growth-promoting rhizobacteria*
iPGPR	*: Intracellular plant growth-promoting rhizobacteria*
AMF	*: Arbuscular mycorrhizal fungi;*
ABA	*: Abscisic acid*
IAA	*: Indole-3-acetic acid*
PGP	*: Plant growth promotion/promoting*
VOCs	*: Volatile organic compounds*
EPSs	*: Exopolysaccharides*
Na^+	*: Sodium*
N_2O	*: Nitrous oxide*
CO_2	*: Carbon dioxide*
CH_4	*: Methane*
ROS	*: Reactive oxygen species*
ISR	*: Induced systemic resistance*
SAM	*: S-adenosyl-Methionine*

1. INTRODUCTION

Plant growth-promoting rhizobacteria (PGPR) alleviated as soil bacterium, is found in the soil as it is very well known for colonization on the root surfaces of plants. It has a tremendous beneficial effect on the growth and development of plants [1]. The rhizosphere which is a thin layer of soil covering the root has more nutrients as compared to other portion of the soil as plant release certain exudates such as sugars and amino acids. The so released exudates act as a source of nourishment and energy supplier for the growth and metabolic processes in many microorganisms [2]. As a result of this, the rhizosphere is the region in the soil which is more likely than other areas having a higher bacterial population [3]. In the rhizosphere most of the rhizobacteria are found to inhibit that may have symbiotic or non-symbiotic relationships with plants based on its dependent interactions [4]. Crop growth and its development are normally aided by PGPRs in both indirect and overt ways. These rhizobacteria indirectly promotes growth of plants by inhibiting harmful effects of phytopathogens by synthesizing antagonistic compounds and inducing pathogen resistance. Plant growth is enhanced more as a result of synthesis of growth-promoting compounds including phytohormones (IAA, cytokinin, ethylene, and others), antioxidants, enzymes, and nutrient acquisition from natural resources like fixed nitrogen (N), phosphorus (P), and phosphate in the case of direct promotion [5]. The degree between bacterial proximity towards roots and the intimacy of the PGPR relationship vary. The PGPR is classified as extracellular PGPR (ePGPR) which is found in the rhizosphere or spaces between cells of the root cortex and the second is the intracellular PGPR (iPGPR) which can be found within root cells, usually in forms of nodule like structures [6]. Water shortage is a serious threat towards world's long-term crop production [7, 8]. Owing to the continuing drought in Alabama, 32 counties were designated as initial natural disaster areas in 2016, and 15 more counties were designated as contiguous natural disaster areas. In 2011, drought in Texas decreased grain yields and harmed livestock that costed the farmers and ranchers more than $5 billion showing a 28 percent drop from the previous four years' average revenue [9]. Drought is expected to have a major impact accounting greater than half of the world's uncultivated land by 2050, having immense crop growth related problems [10]. Rainfall has started to decline in some areas, and extreme temperature fluctuations have become more common which is potentially due to the global warming crisis. Due to the consequence of severe drought problem in cotton (*Gossypium hirsutum* L.), corn (*Zea mays* L.), and soybean (*Glycine max* L.) have been observed in many areas around the world. As a consequence, developing management strategies that can solve drought problems is a major focus of the study. Assessing the effects of changing crop plans on drought-tolerant crops however, most of these approaches are cost-sensitive [11]. Microorganisms like arbuscular mycorrhizal fungi (AMF) have also taken into consideration as an additional method to eliminate the negative impact of drought stress

on crops [12, 13, 14]. Several studies have been done in investigating functions of PGPR on controlling biotic and abiotic stress [15, 16, 17]. For example: (1) Producing abscisic acid (ABA), gibberellic acid, cytokinins, and indole-3-acetic acid (IAA); (2) Using ACC deaminase to minimize ethylene proportion in roots; (3) Using bacterial compounds in inducing systemic tolerance and (4) Utilization of bacterial exopolysaccharides as a potential technique in drought tolerance caused by rhizobium. Also most studies has shown that specific PGPR strains improves plant growth in drought-stressed environments and shield crops in enduring the negative effects due to water scarcity [18,19,20]. The *Bacillus licheniformis* K11 strain is reported to alleviate drought stress in pepper (*Capsium annuum* L.) as described by Lim and Kim [21] due to the generation of auxin and 1- ACC deaminase. Kasim *et al.* [22] finding proclaim that PGPR also improves the lifespan of seedlings, fresh and dry biomass weight and plant tissue moisture content under drought by inoculation of *Bacillus* and *Azospirillum* strains on wheat. Similar findings have also been recorded under corn seedlings having distinct PGPR strains [23,24,25] where particular PGPR strains had boosted the physiological and biochemical parameters like the relative water quality, proline, free amino acids levels and it reduced the electrolyte leakage and antioxidant enzyme activity, as result enhanced the growth of plants and led to reduction in water stress. The aim of this review is to look at our current understanding of the role of plant growth-promoting rhizobacteria as a tool for drought stress management, as well as their potential benefits to overall plant/crop growth and development in agriculture.

1.1 Forms of Different PGPR

The extracellular plant growth-promoting rhizobacteria (ePGPR) and intracellular plant growth-promoting rhizobacteria (iPGPR) are known as two major types of PGPR. The ePGPR is known to inhibit the rhizosphere or the spaces between the cells of root cortex, while iPGPR is found primarily within the root cell's specialized nodular structures. The known genera of bacterium included in ePGPR are *Azotobacter*, *Serratia*, *Azospirillum*, *Bacillus*, *Caulobacter*, *Chromobacterium*, *Agrobacterium*, *Erwinia*, *Flavobacterium*, *Arthrobacter*, *Micrococcous*, *Pseudomonas*, and *Burkholderia*. When looking at iPGPR, endophytic microbes are *Allorhizobium*, *Bradyrhizobium*, *Mesorhizobium* and *Rhizobium* also including the *Frankia* species that has the potential to fix N from the atmospheric in the case for higher plant species [26].

1.2 Mechanisms Related to PGPR

To promote and protect plant growth, PGPR uses both direct and indirect mechanisms. Fig. 1 gives us an overview of the mechanisms that are related to PGPR.

2. DIRECT MECHANISM

PGPR can help plants to grow and develop by providing essential nutrients or increase nutrient supply through mechanisms like N fixation, organic compound mineralization, nutrient solubilization and phytohormone production [27]. Such mechanisms influence plant growth and its activities directly which depends on specific strains of microbes and host plant associated to it.
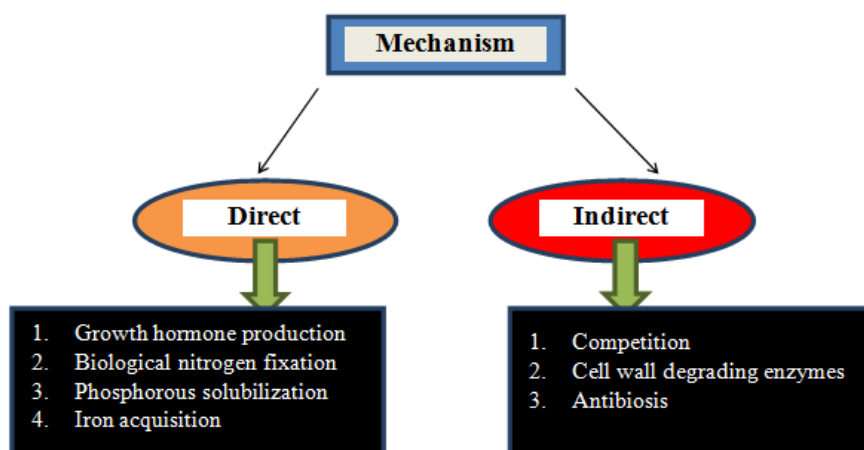

Fig. 1. Direct and indirect mechanisms in relation to PGPR

2.1 Phytohormone Production

Phytohormones, also known as plant growth regulators (organic compounds) that encourage, alter plant growth and development at small proportions (<1 mM) [28]. The regulars (gibberellins, cytokinins, abscisic acid, ethylene, brassino steroids, and auxins) can be induced by plant-associated bacteria such PGPR. Phytohormones alter the plant morphological and physiological functions even if they are in small ratios [29]. Such hormones alter plant growth patterns, resulting in branched, longer roots having large surface area that allows plant accessibility to water and several nutrients from the deeper soil profile layers. Plant growth regulators also are known as exogenous plant hormones because it is added exogenously to plants or plant tissues as derived hormones or synthetic analogues. Phytohormones are grouped based on its mode of site specific action which is:

a) **Root invigoration-** This involves many hormone-linked paths that intersect with the pathways which perceive and reacts to outside environment signals [30]. Hormone production on occasional basis by *Enterobacter asburiae*, *Pseudomonas aeruginosa* and many more by microbes all are considered as PGPRs. The hormones produced are especially important in root invigoration.

b) **Shoot invigoration-** Growth hormones (cytokinins, gibberellins, and auxins) are essential regulators of practically every aspect of growth and development in higher plants. Higher cytokinin concentrations serve as a significant regulator in shoot development rather than root development, according to Skoog and Miller, [31]. Microbes may be able to control the development of these plant hormones, which could revolutionize crop production and boost desired qualities. *Rhizobium leguminosarum* and other microbes that induce hormone production play an important role in shoot invigoration, which is common in PGPR [32].

2.2 Biological Nitrogen Fixation (BNF)

An essential element for plant growth is N which occurs readily in the air making up about 78 percent of the atmosphere. Most of the plants, on the other hand are unable to use this form of gaseous nitrogen. Most of the commercially produced synthetic fertilizers are currently being incorporated to fields for the improvement of agricultural productivity. As a result, biological alternatives are favored because they resolve concerns about economics, the atmosphere, and renewable energy. BNF can be non-symbiotic as well as a symbiotic relation in which rhizobia and leguminous plants (chickpea, pigeon pea, and groundnut) turn atmospheric nitrogen into plant-available nitrogen i.e. ammonia [33, 34]. *Rhizobium sp., Azoarcus sp., Beijerinckia sp., Pantoea agglomerans,* and *K. pneumoniae* are examples of symbiotic PGPR that have been identified to fix atmospheric N_2 in soil [35]. Legumes fix large proportions of nitrogen, which is harvested by crops. Free-living bacteria/diazotrophs like *Azoarcus*, *Cyanobacteria*, and *Azospirillum* can fix atmospheric N in sugarcane, wheat and rice crops. However, quantity of N that is fixed by the legume-rhizobia is quite higher than the amount fixed by free-living bacteria or diazotrophic non-symbiotic systems [36]. For improved N-fixation, *rhizobia* are often applied to leguminous seeds since in the absence of specific host plant they are able to survive in the natural soil system for several years [37]. N-fixation is mediated by a particular gene called "nif" which is involved in activation of iron protein, electron donation, biosynthesizing iron molybdenum cofactor, and several other regulatory genes needed for enzyme synthesizing and operation [38]. Inoculating biological N-fixing PGPR in field crops boosts productivity, assists in disease management and keeps agricultural soil N levels stable [39].

2.3 Phosphate Solubilization

P is one among essential nutrients required for plant cell metabolic processes, biosynthesis, and photosynthesis and signaling [40, 41]. Plants only utilize the monobasic ($H_2PO_4^-$) and dibasic (HPO_4^{2-}) forms of P because it is bound to inorganic or organic molecules [42]. As a result, P is widely used in synthetic fertilizers, but is widespread and uncontrolled usage has a negative effect on the climate [43]. Phosphorus solubilization and its mineralization can be achieved by phosphate-solubilizing bacteria which is an essential feature that is found in PGPR. Organic P is mineralized by acid phosphatases, C-P lyase, D-glycerophosphate, phosphor hydrolases, phosphonoacetate hydrolase, and phytase making it accessible to plants [44]. The phosphate solubilizing PGPR

belonging *Bacillus*, *Pseudomonas*, *Arthrobacter* and *Streptomyces* have gained much attention as it promotes plant growth and yield [45,46,47]. The two species form chickpea nodules; *Mesorhizobium ciceri* and *Mesorhizobium mediterraneum* potentially are considered among best P solubilizers [48].

2.4 Iron Acquisition

Iron is present in nature in the form of insoluble hydroxides and oxyhydroxides that are unavailable for plants. Plants and bacteria produce siderophores having high-affinity iron-chelating compounds which traps iron in the soil [49]. The strategy of microbial-origin siderophores in plant growth is unclear, but subjected to low iron supply, plant growth promotion (PGP) is thought to involve one of the following mechanisms:

a. Microbial-origin siderophores having a high redox potential migrate from ferrous form of iron to a plant's transport system by the apoplastic pathway.

b. Microbial-origin siderophores from soil chelate iron and exchange ligands with plant-origin siderophores based on concentration, pH, and redox potential. In this step, the iron-free plant-origin siderophores bind with receptor protein for the first time.

In addition to contributing to plant health, microbial-origin siderophores are included in biocontrol of plant pathogens. It competes with other pathogenic microbes in the area to acquire iron and supply it to the plant [50].

2.5 Indirect Mechanism

The process by which PGPR prevents/neutralizes the harmful effects of phytopathogens on plants by creating repressive substances that increase the host's natural resistance is known as indirect mechanisms [51]. It refers to the application of PGP agents to reduce the negative effects of biotic stresses on plant health [52]. The production of hydrolytic enzymes (chitinases, cellulases, proteases), antibiotics in response to plant pathogen or disease resistance, induction of systemic resistance against various pathogens and pests, and production of siderophores are all examples of PGPR's contribution to this process [53]. Some of the important mechanisms involved include:

2.6 Competition

Exudates from plant roots are important for identifying microorganisms in the region. Plant symbiosis with beneficial rhizobacteria has been shown to be influenced by flavonoids and phenolic compounds in the rhizosphere [54]. Important microbe nutrients have been defined as amino acids, organic acids, vitamins, and sugar [55]. Antagonism by competing for available nutrients is a form of biocontrol mechanism used by beneficial microbes to counteract pathogens and suppresses diseases [56]. Hydrolytic enzymes, siderophores, antibiotics, and volatile compounds are among the other pathways used by growth promoting microbes [57].

2.7 Cell Wall-Degrading Enzymes

The cell walls of insect pests and fungal pathogens of plants have polymers like lipids, glucan, chitin, cellulose, and proteins. The ability of PGP microbes to generate cell wall-degrading enzymes is well known. Insect pests and pathogens have their cell walls disrupted by these enzymes, which cause cell lysis. The microbes for growth promotion use these as a defense mechanism against plant pathogens and insect pests. Plant promoting microbes produce hydrolytic enzymes such as peroxidase, chitinase, glucanase and protease [58].

2.8 Antibiosis

For PGP microbes, antibiosis is one of nature's most essential biocontrol mechanisms. PGP bacteria produce diffusible compounds that are known to inhibit plant pathogens in the rhizosphere. Antibiotics like polygenes, macrolides, aminoglycosides, nucleosides, and benzoquinones have been discovered in PGP microbes. The antibiotics are primarily produced by *Actinobacteria* e.g. total number of microbial bioactive molecules since the year 2012 was near to 33,500; with *actinobacteria* producing 13,700 which is 41 percent of it ([59]. Also about 1800 metabolites were found having antibiosis against pathogenic fungus [60].

2.9 Benefits and Functions of PGPR

Microbial inoculants such as PGPs, beneficial biofertilizers and soil health managers are increasingly used to achieve sustainable crop production without sacrificing productivity, agroecosystems or environmental quality.

Modern agriculture is actively considering large numbers of bacterial strains from various groups and genera with multifaceted plant growth-promoting properties for their role in maximizing plant growth and yield. PGPRs' notes have been made by researchers, agriculturists, producers, and policymakers alike. Table 1 gives us an overview of plant growth enhancement by PGPR. PGPRs play an intrinsic role in nutrient absorption and conferring resistance to environmental stress, in addition to growing plant health and crop yield [61]. They aid in promotion of N transformation, phosphorus supply, iron acquisition, mineral solubilization, phytohormone synthesis (IAA, cytokinins, and gibberellin), synthesis of various volatile compounds and plant pathogen defense through the development of antibiotics [62]. PGPRs aid growing plants by performing several functions like N-fixation, organic compound solubilization and primary macronutrients, and lead in the formation of growth promoting hormones and siderophores [63]. Via systemic resistance and the development of volatile organic compounds (VOCs), exopolysaccharides (EPSs), defensive enzymes, hydrolytic enzymes, antibiotics, and other compounds, PGPRs promote growth of plants by providing resistance against biotic (phytopathogens) and abiotic (drought, salinity, heat, temperature) stresses. Some of the known functions of PGPRs that are considered good for plant growth and development are mentioned below:

2.10 Stress Relievers

Under unstressed natural conditions, the benefits of PGPR, such as increased development, are more or less comparable, but under stress, some strains become ineffective since their inability to thrive in unfavorable environment. Some PGPR strains, on the other hand, are able to cope with these stressors while also exhibiting improved plant growth. Since a wide range of biotic and abiotic stresses affect plant growth and development, PGPRs employ a number of mechanisms in mitigating stress-induced negative effects on plant physiological and biochemical processes [64]. The following are some of the roles of PGPRs in stress reduction:

2.11 Salinity

High salinity is caused by high sodium (Na^+) levels ion toxicity and dietary imbalance. Exopolysaccharides are produced by some PGPR strains which protect plants from negative effects of high Na^+ levels. Exopolysaccharides also bind onto Na^+ and preventing it from being absorbed by plants.

2.12 Drought Stress

Sandhya *et al.* [65] investigated the impact of exopolysaccharides on plant growth in water-stressed conditions. This results that, both plants and microbial flora suffer due to water scarcity. Exopolysaccharides provided by PGPR protect bacteria and plants from desiccation in such situations, allowing them to thrive even in drought. Owing to a rise in ethylene levels, plant growth has slowed in areas where there is a shortage of water. It's also been shown that when there's a severe drought, the amount of chlorophyll in the plants decreases. Inoculating *Achromobacter piechaudii* with ACC deaminase activity has been seen to increase the dry and fresh weight in pepper and tomato seedlings when exposed to relatively short-term water stress. Drought tolerance was improved by inoculating root rot pathogen (*Macrophomina phaseolina*) infected plants with *P. fluorescens* strain TDK1 with ACC deaminase activity.

2.13 Temperature

Frequent fluctuations in air temperature (both up and down) pose a major threat to people all over the world. If the current trend in temperature rises, the phenomenon of global warming could pose a significant threat to agriculture. Changes in temperature are thought to cause hormonal imbalances in plants which have a direct impact on plant growth and relative output. Plants when are subjected to high and chilling temperatures they create more ethylene [66].

2.14 Heavy metals

Some metals are considered as necessary for crop growth and development but yet they are a threat when it exceeds its required concentrations becoming toxic to the crop. According to several reports, PGPRs incorporation with ACC deaminase activity reduces the ethylene content in metal-stressed plants [67]. Canola seeds when inoculated with PGPR strain *Kluyvera ascorbata* SUD165 and ACC deaminase action show conferred plant tolerance towards higher nickel chloride concentrations [68].

Table 1. Rhizobacteria that promote plant growth and development

Host	Microbe specie	Function	Reference
Oryza sativa	*Herbaspirillum seropedicae*	Enhance gibberellin production	Araujo *et al.,* [69]
Vigna radiata	*Achromobacter xylosoxidans*	Regulates plant homeostasis	Ma *et al.,* [70]
Triticuma estivum	*Azotobacter chroococcum*	Phosphorous solubilization	Damir *et al.,* [71]
Dianthus caryophyllus	*Pseudomonas* sp.	Prevention of *Fusarium* wilt	Ahemad and Khan [72]
Piper nigrum	*Bacillus mucilaginosus*	Improve potassium intake	Liu *et al.,* [73]
Fagopyrum esculentum	*Azotobacter aceae*	N-fixation	Bhattacharyya and Jha [74]
Saccharum officinarum	*Azospirillum brasilence*	Alter plant root architecture	Orlandini *et al.,* [75]
Zea mays	*Azospirillum brasilence* and *Bradyrhizobium japonicum*	Synthesize indole acetic acid	Orlandini *et al.,* [76]
Brassica juncia	*Azotobacter chroococcum*	Stimulate plant growth	Narozna *et al.,* [77]
Piper nigrum	*Bacillus licheniformis*	Protection against *Myzus persicae*	Kumar *et al.,* [78]
Camellia sinensis	*Bacillus megaterium*	Phosphate solubilization	Stefanescu [79]
Brassica juncia	*Bacillus subtilis*	Facilitate Nickel accumulation	Prathap and Ranjitha [80]
Fruit plants	*Burkholderia* spp.	Induce ethylene production	Islam *et al.,* [81]
Sesamum indicum	*Paenibacillus polymyxa*	Protect against fungal disease	Ngumbi and Kloepper [82]
Triticum aestivum	*Pseudomonas fluorescens*	Prevention from *Fusarium culmorum*	Santoro *et al.,* [83]

2.14.1 Effect of drought stress on growth, development and crop production

The imbalance in turgor pressure and water potential under drought conditions affects many processes in plants including biochemical and physiological functions [84]. Drought stress has shown to have a negative impact on the production of a variety of crop plants, including rice, barley, wheat, and maize. It has resulted in a reduction in growth and productivity [85,86]. Drought has an effect on plant characteristics like water content, as well as fresh and dry matter content [87]. It hinders the transport system in plants and affected the absorption of water and nutrients in the soil by the roots. Under water-limiting conditions, nutrient diffusion and flow of soluble nutrients such as sulphates, nitrates, Ca, Si, Mg, and other basic trace elements are substantially reduced [88]. Free radicals are generated when water is scarce, and plant protection mechanisms, such as antioxidant levels, are gradually depleted, resulting in oxidative stress and cell death. When these are at higher concentrations, reactive oxygen species may have a negative impact on biochemical and physiological processes at various stages of molecular and cellular organization during plant development [89]. Under drought stress, photosynthesis is also reduced due to photosystem dysfunction [90]. Under water-stressed conditions, for example, productivity of *Paulownia imperialis*, bean, and *Carthamus tinctorius* has been reduced [91]. Plant biochemical activities such as nitrate reductase are also disrupted in drought-stricken areas due to reduced nitrate absorption from the soil [92]. Ethylene biosynthesis is also highlighted, which inhibits plant growth through a variety of mechanisms. Drought's multidimensional intrusion in the plant system causes harm and imbalance at various cellular

levels as well as in the plant's organs [90]. Drought stress has a negative impact on plant growth on both a qualitative and quantitative level. As a result, in order to ensure crop production, environmental stress, especially drought, must be alleviated as soon as possible. Abiotic stress like extreme temperatures, waterlogging, water deficit, salinity, and heavy metal and hydrocarbon toxicity, as well as heavy metal and hydrocarbon toxicity, can all negatively affect sessile plants' usual physiological functions and metabolism. When temperature decreases, the plant cells will freeze, resulting in dehydration. Extremely high temperatures, on the other hand, result in the creation of excessive heat that denatures proteins and disrupts cellular membranes due to reactive oxygen species (ROS). An important requirement for plant survival is the availability of a certain optimum amount of water. Insufficient water or over-flooding/waterlogging both have an effect on plant growth and metabolism. The microbial communities in the soil are influenced by the water content of the soil, as well as the form of soil, pH, and nutrients available in the soil. This has a positive or negative impact on the soil's ability to sustain plant development. Abiotic stresses, that restrict healthy plant growth due to changing climatic conditions, are currently putting a lot of pressure on global food production. Changes in the frequency and severity of severe conditions are indicative of climate change, which is characterized as various changes in climatic and weather conditions. In 2014, the Intergovernmental Panel on Climate Change issued a study indicating that increased greenhouse gas emissions are warming the Earth's atmosphere and oceans, with significant implications for Africa [93]. These greenhouse gases, especially nitrous oxide (N_2O), carbon dioxide (CO_2), and methane (CH_4), have risen in recent years, with net emissions nearing 300 parts per million [94]. This results in changes in weather conditions, such as higher air temperatures, a lack of water, and insufficient nutrients for crop production. Drought is a major abiotic factor limiting crop growth and productivity because it decreases crop yield globally due to changes in cell photosynthetic potential and other physiological functions caused by stomata closure, which reduces the amount of CO_2 available for photosynthesis while photorespiration increases. As a consequence, there is a discrepancy between carbon fixation and utilization, resulting in changes in cell osmotic potentials due to changes in sugar concentrations. Plant photosynthetic metabolism is disrupted as a result of the synthesis of reactive oxygen species (ROS) [95]. Under stressful conditions, overproduction of reactive oxygen species (ROS) occurs in the mitochondria, chloroplasts, and peroxisomes, resulting in a decrease in CO_2 takeup in green leaves that is harmful to green plants because they need CO_2 for food production. The effects of stomatal closure on photosynthetic machinery of plants were illustrated by Nocter *et al.* [96], with decrease in O_2 by photosystem I resulting in the development of superoxide (O_2) and H_2O_2, which speeds up the water-water cycle [97]. Photosystem II (PSII) produces single oxygen as a result of an excessive reduction in electron transport, which raises H_2O_2 production in the peroxisome while O_2 and H_2O_2 or single O_2 are formed in the chloroplast by photorespiration [98]. Excessive reduction in the photosynthetic electron transport chain is due to potential single O_2 output in PSII has an unintended effect on photosynthesis rate (Fig. 2).

Germination of seeds and its growth need sufficient moisture, but without it, seedling development is either slowed or fully stopped. The key abiotic stress limiting maize production, one of the main staple cereal crop found around the world, is drought. Maize is the most widely grown crop in Southern Africa, with maize accounting for up to 65 percent of the total area under cereal cultivation in Sub-Saharan Africa [100]. Southern Africa, on the other hand, is highly vulnerable to climate-related risk due to its low coping and adaptation capability [101]. The leaves of maize plants experience leaf rolling when they are subjected to prolonged water stress, resulting in a decrease in size in order to reduce water loss [102]. Drought during the reproductive stage of growth has the greatest impact on maize production. Premature flowering and a longer anthesis–silking period occur, reducing the plant's yield potentials in the long run. The number of grains per spike, dry matter accrual, and grain filling time has all decreased in barley kernels, resulting in lower grain weight [103]. To preserve homeostatic equilibrium, plants must acclimate to unfavorable environmental factors using physiological and molecular mechanisms. Due to cell dehydration, insufficient moisture for plant growth prevents cell division and elongation, resulting in osmotic stress. Drought-stressed plants have lower turgor pressure, which causes changes in chlorophyll (Chl) properties such as peroxidation of Chl and, as a result, decreased photosynthesis as a result of low Chl content in leaves [104]. Drought stress

affects plant water and nutrient relationships in crops, resulting in reduced water usage efficiency and low productivity [105]. In tillering and joint growth phases of wheat plants, turgor osmotic potential, leaf water potential, and RWC all decreased, while osmotic adjustment increased [106]. As seen in rice, chickpea, cowpea, and wheat, crops are intrinsically affected at the reproductive or flowering stages of growth as compared to the vegetative stage of growth, which inevitably influences the yield [107]. Table 2 presents the physiological parameters of different drought-stressed crops.

Drought sensitivity varies among legumes but the final yield is drastically reduced. Some of the results include low germination and photosynthetic activity [115], reduced assimilate translocation and carbon fixation [116], repressed flowering time and impact on reproductive organs [117], pollen grain sterility [118], less pods and less grain set [119]. Many

aspects of legume growth, production, including germination, shoot and root development, photosynthesis, and reproductive stage, are affected by drought. Drought has become a major uncontrollable and volatile factor limiting crop production and harming legume crops due to climate change. In the presence of drought-stress, soybean germination was significantly reduced [20]. Awari and Mate [121] discovered that when there is a water shortage, the germination rate of chickpeas decreases. Drought-stress is most commonly found in the seedling of Faba bean [122]. Drought during flower development resulted in a shorter flowering time, fewer buds, fewer pods, and, as a result, fewer seeds per plant, according to the report. Drought-stress, on the other hand, has been shown to reduce seed number during seed setting period [123], and thus final yield (Table 3). Drought stress is also linked to the soil and their associated bacterium diversity with profound influence on its functioning (Fig. 3).
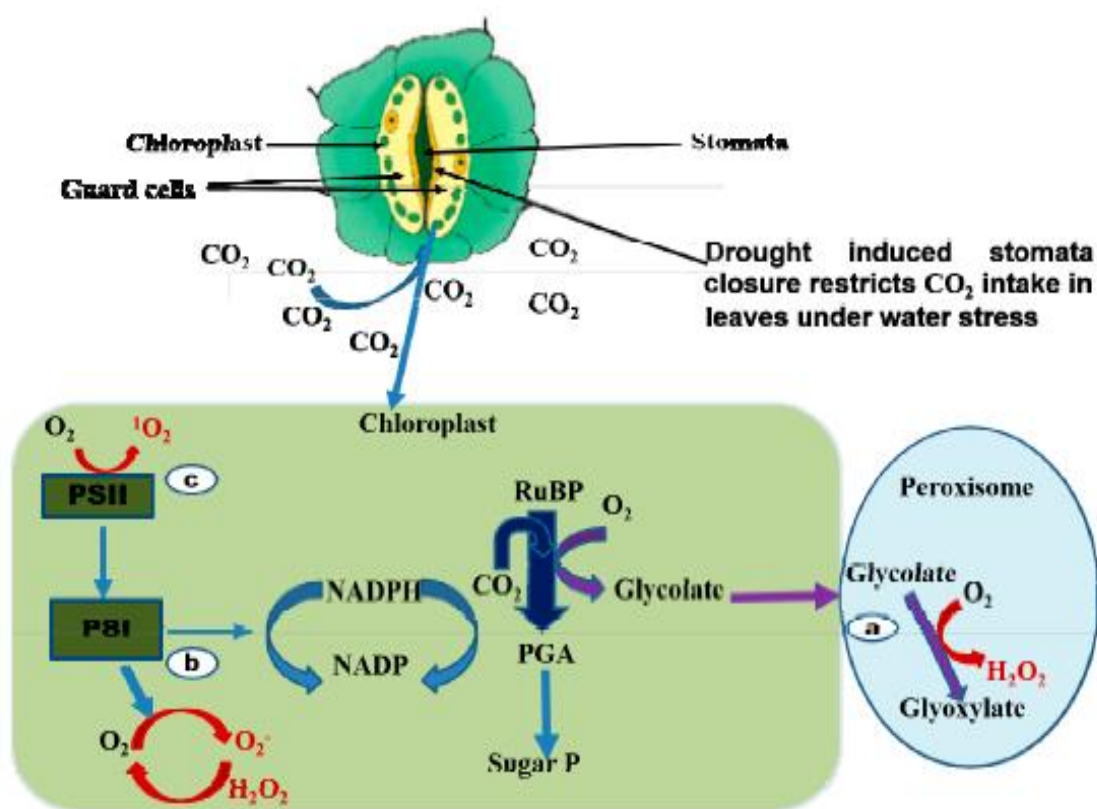

Fig. 2. Stomata closure reduces CO_2 uptake in drought-stressed plants' leaves, resulting in the development of (a) H_2O_2 in the peroxisome via photorespiration, which boosts (b) O_2 and H_2O_2 production, and (c) single O_2 production by the photosynthetic electron transport chain. RuBP, Ribulose 1-5 bisphosphate; PGA, 3-Phosphoglyceric acid; PSI and PSII (Photosystem 1 and Photosystem II); RuBP, Ribulose 1-5 bisphosphate; PGA, 3-Phosphoglyceric acid
Source: [99]

Table 2. Physiological parameters of drought-stressed crops

Crop	Effect of Drought Stress on Crop Growth and Yield	References
Barley	Reduction in grain and tiller number per plant having effect on the yield.	Samarah [108]
Chickpea	Reduction in chlorophyll a, chlorophyll b, and total chlorophyll content at vegetative and flowering stages.	Mafakheri *et al.,* [109]
Camptotheca acuminate	Reduction in water capacity, photosynthetic ability and chlorophyll a and b contents but increased content of antioxidant enzymes (Superoxide Dismutase and Peroxidase).	Ying *et al.,* [110]
Cowpea	Increased vegetative and flowering and caused reduced shoot dry weight.	Ndiso *et al.,* [111]
Faba bean	Elevated levels of proline, soluble sugars and protein content in the leaves of Faba bean. Reduction in grain yield, relative water content, plant height and leaf area.	Abid *et al.,* [112]
Wheat	Reduction in photosynthetic rate and stomatal conductance and increased total soluble sugars and proline levels. Also leaf water potential, osmotic potential, turgor osmotic potential, and relative water content reduced.	Abid *et al.,* [113]
Maize	Reduction in relative water content, smaller leaves, wilting and rolling of leaves due to a reduction in the photosynthetic rate.	Zhang *et al.,* [114]

Table 3. Yield loss in some important legumes under drought-stress condition

| Legume	Growth Stage	Loss (%)	Reference
Soybean	Pod set	73–82	Wei *et al.,* [124]
	Reproductive phase	46–71	Samarah *et al.,* [125]
	Pod set	45–50	Kobraee *et al.,* [126]
	Grain filling stage	42	Maleki *et al.,* [127]
Chickpea	Reproductive phase	45–69	Nayyar *et al.,* [128]
	Ripening stage	49–54	Samarah *et al.,* [129]
	Anthesis stage	27–40	Mafakheri *et al.*, [130]
	Ripening stage	50	Varshney *et al.*, [131]
Cowpea	Reproductive	60	Ogbonnaya *et al.,* [132]
	Reproductive phase	34–66	Ahmed *et al.,* [133]
	Pod filling stage	29	Kyei-boahen *et al.,* [134]
Common bean	Reproductive phase	58–87	Martinez *et al.,* [135]
	Pod filling stage	40	Ghanbari *et al.,* [136]
	Flowering stage	49	Rosales-Serna *et al.,* [137]
Pigeon pea	Reproductive phase	40–55	Nam *et al.,* [138]
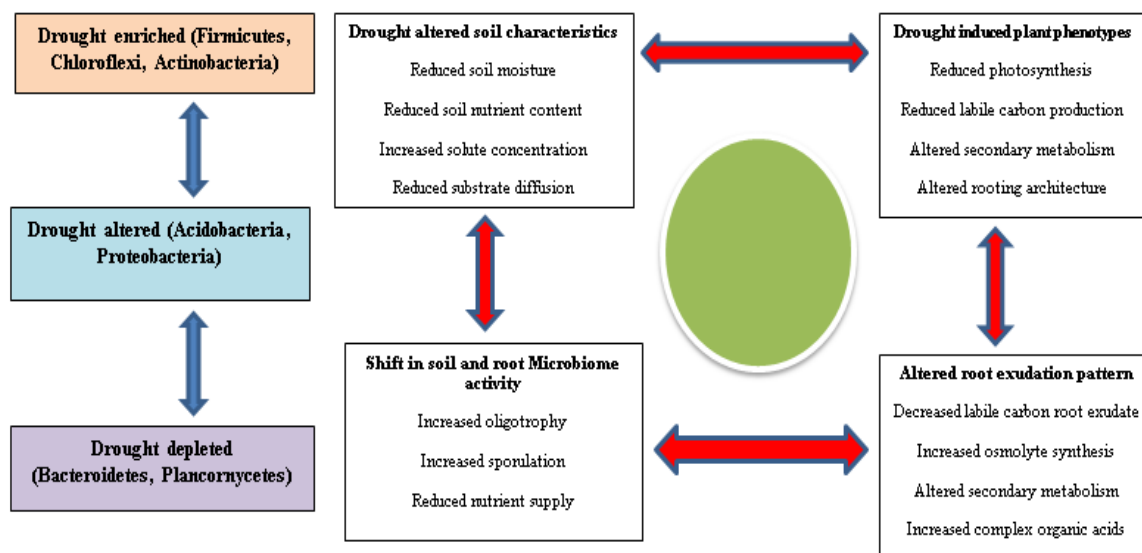
Fig. 3. Effect of drought on soil, plant and associated bacterial communities

3. MANAGEMENT STRATEGIC TOOL

3.1 Plant Growth-Promoting Rhizobacteria (PGPR)

Microorganisms are becoming widely recognized as a cost-effective useful tool which increases crop yield and plant stress tolerance. There are three types of beneficial microorganisms considered for bio-inoculation that improves plant growth: i. PGPR, ii. AMF and iii. N-fixing rhizobia [139]. These are bacterial microbes which are found residing in the rhizosphere, where they acquire nutrients, hormones, flavonoids and enzymes from plant root exudates or mucilage's [140], and vice-versa, they provide nutrients and promote healthy growth of plants. Adding onto soil type and physicochemical properties it has an effect on plant and ability of microbes to live whereby these exudates serve as sources of carbon and nutrients for the microbial metabolism [141]. The rhizosphere is a habitat where most microbial activities take place which ultimately enhances soil fertility by interactions with plant roots-soil and microbe [142]. Different PGPR genera employ various mechanisms to mitigate the effects of environmental stresses on plants. PGPR helps with iron storage, P mobilization and the synthesis of exopolysaccharides and beneficial enzymes like 1-aminocyclopropane, 1-carboxylate deaminase (ACC), and plant growth hormones like indole-3-acetic acid. These microbes indirectly promote plant growth by shielding plants from phytopathogens and generating compounds like hydrogen cyanide, antibiotics, ACC deaminase synthesis, lytic enzymes, and induced systemic resistance (ISR) [143]. The majority of PGPR have several PGP characteristics, allowing them to be used like bio-inoculants for crop production even in adverse circumstances. Utilization of soil microbes for improving soil health and agricultural sustainability has recently been extensively reviewed [144,145]. PGPR has been used in a variety of crops, including garden pea [146], maize [147], green gram [148], cucumber [149], potato [150], sorghum [151], wheat [152] and legumes [153]. Figure 4 summarizes the different pathways used by the PGPR to mitigate water stress in plants. PGPR's effects on plant growth are caused by a combination of PGP characters expressed by the PGPR that have beneficial effects on drought tolerance, such as ACC deaminase, exopolysaccharide production, and IAA synthesis.

3.2 Drought Stress Management in Plants by PGPR (ACC Deaminase)

The presence of plant hormones, nutrition and effects of other abiotic and biotic stresses all influence ethylene synthesis in a given plant [154]. In stressed plants, ACC synthase converts S-adenosyl-Methionine (SAM) to ACC, raising the concentration of ACC, which is the immediate precursor of ethylene, and thus the ethylene
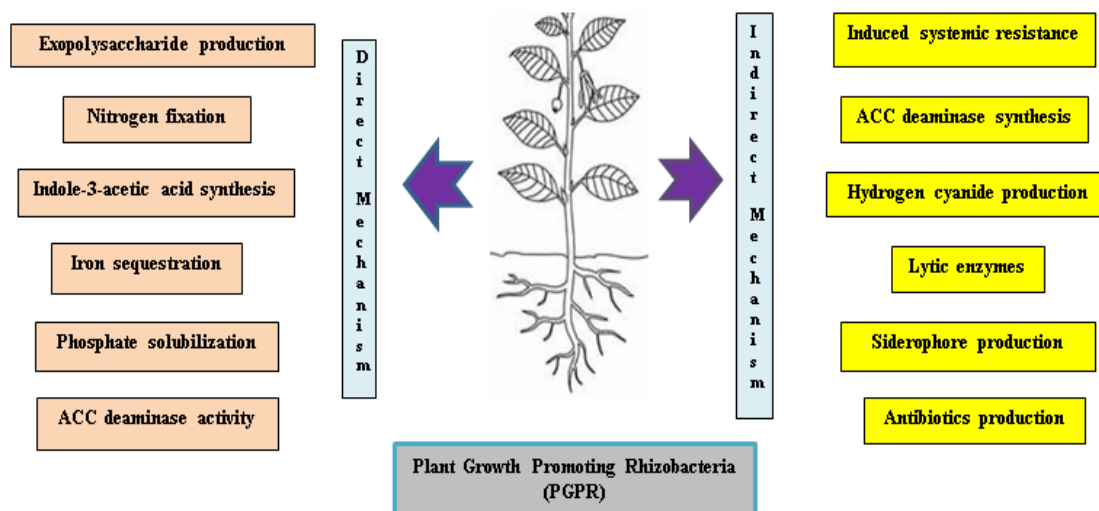
54

Fig. 4. PGPR's mechanisms for reducing drought stress and promoting plant growth

levels made. High levels of IAA released when conversion of tryptophan given out by plants and used by rhizospheric bacteria, that is then consumed by plants could probably cause ACC synthesis. When a plant is stressed by conditions like drought, waterlogging, or pathogenicity [155], it relies on an ACC deaminase-producing PGPR in its rhizosphere to assist in degrading ACC and, as a result, reduces ethylene production and restoring the plant to its normal growth. The ACC deaminase-producing PGPR achieves this by dissolving plant ACC, an ethylene precursor in plants, into ammonia and α-ketobutyrate, which reduces the amount of ethylene, produced by plants and improves their growth; thus, it represents an opportunity to boost crop yields [156]. Various works shows that inoculating plants with ACC deaminase-producing rhizobacteria reduces the negative effects of ROS caused by abiotic stress, like drought; thus, it is an important mechanism for plant survival in the mutualistic relationship with the bacteria. When compared to controls, ACC deaminase producing *Achromobacter piechaudii* ARV8 significantly increased the fresh weight and dry weight of tomato, as well as the fresh weight and dry weight of pepper, alleviating the impact of oxidative stress on tomato and pepper plants due to drought. In comparison to the control, biomass of the crops increased fourfold, and this led to lowering the ethylene levels in stressed plants. Other authors [157,158,159] have used ACC deaminase generating PGPR to encourage crop production and minimize yield loss in crops exposed to moisture stress since Mayak *et al.,* [160].

3.3 Osmoregulation Reduces Oxidative Stress in Drought-Stressed Plants

PGPR secrete osmolytes that function synergistically with osmolytes synthesized by stressed plants to promote growth. Many studies have been published on the ability of rhizobacteria to produce compatible solutes in response to drought stress, allowing plants to become drought tolerant. When *Azospirillum* sp. and *Herbaspirillum* sp. were inoculated on drought-stressed maize plants, they protected the plants from oxidative damage. The osmolyte proline concentration was seen to increase two-fold (*Azospirillum* sp.) and four-fold (*Herbaspirillum* sp.) in both species [161]. However, under water stress, the concentration of proline was eight times higher than the control plants under well-watered conditions. This means that the bacteria strains decreased stress levels, resulting in lower proline content in the plants than in the control plants. In chickpea plants when they were inoculated with *Pseudomonas putida*, a similar finding was made [162]. At the seventh day of water tension, treatments with *Pseudomonas putida* resulted in a substantial decrease in proline concentrations, with a decline of 114 percent and 214 percent proline in chickpea varieties cv. BG-362 and cv. BG-1003, respectively. In comparison to control plants, the concentration of proline was higher in pepper plants inoculated with *Burkholderia cepacia* [163]. As a result, the plants could withstand drought and salinity stress while producing more biomass.

3.4 Drought Stress Management in Plants by PGPR Exopolysaccharide (EPS)

Crop growth and productivity are reduced due to insufficient moisture due to drought since it influences the physicochemical and biological properties of soils that affect the support of soil microbial activity [164]. As a result, the roles of good soils are lost. Nonetheless, in such unfavorable environmental conditions, microbes, especially the PGPR, release high molecular weight compounds called exopolysaccharides, which are made up of primary complex organic macromolecules; polysaccharide with smaller percentages of protein and uronic acid [99], which account for 40 to 95 percent of bacterial weight. Slime EPS or Capsular EPS are two types of EPS produced by bacteria [165]. Microbial cells have exopolysaccharides on their surfaces, which defend them through stabilization of membrane structure against adverse environmental conditions [166]. EPS is produced intracellularly by bacterial cells primarily during late logarithmic or stationary growth phases, but the rate of development is affected by a variety of factors including imbalance in nutrients, drought, salinity, adverse temperatures and pH changes. Because of their EPS-producing abilities, *Rhizobacteria* of the genera *Bacillus*, *Pseudomonas*, and *Acinetobacter*, among others, are successful in conferring abiotic stress tolerance to plants and withstand harsh environmental conditions. Sandhya *et al.* [167] found that inoculating *Pseudomonas putida* on drought-stressed sunflower plants developed high levels of EPS and reduced the effects of drought stress by raising 64 percent of the total dry biomass of the plant and soil aggregation with an aggregate stability of 70.80 percent. The inoculated bacteria colonized the soil by adhering to the roots and rhizoplane, resulting in a higher proportion of stable soil aggregates [168]. Naseem and Bano [169] investigated the PGP abilities and EPS provided by a consortium of three bacteria strains, *Proteus penneri* (Pp1), *Pseudomonas aeruginosa* (Pa2), and A*lcaligens faecalis*, isolated from water deficit regions for their drought tolerance potentials when used as bio-inoculants alone or in combination with their EPS on drought-stressed maize plants. Isolate Pa2, in combination with its EPS, increased RWC and protein content in the leaves of inoculated maize plants by 45 percent compared to un-inoculated plants, which is significant in combating oxidative and osmotic stresses caused by drought on the plants.

3.5 Drought Tolerance in Plants by Indole-3-acetic Acid (IAA) PGPR

Bacterial-produced phytohormones could be a viable option for boosting plant growth in less-than-ideal conditions [170]. Such phytohormones help plants cope with abiotic stresses and increase their chances of survival [171]. Phytohormones like cytokinins, auxins, gibberellins, ethylene, abscisic acid, and jasmonates are known to promote shoot growth or regulate growth-inhibit in plants like dormancy, abscission, and senescence, thereby regulating plant growth activities [172]. The auxins are the most well-known phytohormones and acts as a controlling factor in plants, as it regulates many processes in plants and is thus can is considered crucial for plant development [173]. Due to the endogenic pool of plant IAA, which can be changed by the acquisition of IAA secreted by soil bacteria, indole-3-acetic acid controls plant developmental processes [174]. It is a plant hormone that helps rhizobacteria and plants communicate, boosting the plant's defense mechanism against phytopathogens and boosting its development [175]. Under drought stress, IAA development improves architecture of root systems and increases the amount of root tips and surface area of the plant, encouraging effective mineral and water takeup by the plants [176]. Genes needed for IAA synthesis pathways can be found in *Bacillus amyloliquefaciens* and *Paenibacillus polymyxa* BFKC01. The presence of these genes in bacteria allows the bacteria to generate adequate quantities of IAA that can be used for boosting plant growth. When applied to plants, *B. amyloliquefaciens* and *P. polymyxa* BFKC01 enabled iron acquisition mechanisms while also growing fresh plant weight, lateral roots, and biomass [177]. IAA promotes root elongation at low concentrations; but, when subjected to high concentrations, it stimulates lateral root formation as well as root hair formation while decreasing primary root lengths ([178]. Since excess IAA stimulates ACC synthase transcription, it may also alter more ethylene levels in plants. In consortium with *Pseudomonas* sp. strain RJ15 and *Bacillus subtilis* strain RJ46, *Ochrobactrum pseudogrignonense* strain RJ12, yielded high levels of IAA under osmotic stress, significantly increasing the length of the roots in black gram and garden pea under drought stress when compared to control [179].

4. CONCLUSION AND FUTURE RESEARCH PERSPECTIVE

As a result of the increased incidences of both biotic and abiotic pressures in farmer's fields as a result of global climate change, crop production survival is a significant challenge. Drought stress is gaining a lot of interest among the numerous abiotic stresses because it inhibits plant growth and production and induces major yield loss in most of the crops, resulting in global food insecurity. It has a detrimental effect on plant development at all stages, from seedling to reproductive and mature stages. Drought stress causes major disruptions in key physiological, biochemical, and metabolic processes, adversely affecting plant production. Several tactics may be used to combat the rising challenges of drought stress in various crops. Drought stress on crops may be controlled using PGPRs without any inherent effects on their growth and yield characteristics. Importantly, novel strategies such as genetically modified tools and PGPR 'speed breeding' can aid in a better understanding and efficiently speed up the production of drought stress-resistant crops, reducing the likelihood of global food insecurity.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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