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Review Article

Microbial interventions for abiotic and biotic stress management in plants - A brief review

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ABSTRACT: Crop plants are perpetually subjected to several abiotic and biotic stresses which serve as limiting factors that impede plant growth and reduce agriculture productivity. Among the abiotic stresses, drought significantly limits global agricultural productivity, with its impact expected to intensify. Adaptation and mitigation strategies are essential to combat drought stress, and Plant Growth-Promoting Rhizobacteria (PGPR) offer a promising and eco-friendly solution. The microbial population adjacent to plant roots colonise the plant rhizosphere/endo-rhizosphere and enhance drought tolerance through mechanisms such as the production of plant hormones (IAA, and GA), HCN and siderophores production, solubilisation of phosphorus (P), potassium (K), zinc (Zn), and by oxidising sulphur and silica, as well as reducing nitrate and citrate to improve plant resilience to drought. This review provides an in-depth understanding of interactions between PGPR and plants in mitigating the adverse effects of abiotic and biotic stress in various crops.

KEYWORDS: Microbial ecosystem, plant microbiome, plant growth regulators, root zone

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INTRODUCTION

Climate change is one of the most significant factors currently affecting crop production worldwide. It encompasses various biotic stressors, such as pathogens and pests, and abiotic stressors like drought, waterlogging, salinity, temperature fluctuations, and changing weather patterns. Among these, drought is the most detrimental, reducing global crop productivity by 50%-80% causing greater annual yield losses than plant diseases or pathogens (Naylor & Coleman-Derr, 2018). In Asian countries like China, Bangladesh, Bhutan, and Nepal, altered rainfall patterns exacerbate drought-related issues (Miyan, 2015). Drought-affected croplands are predicted to double, while water resources could decline by 30% globally by 2050 (Falkenmark, 2013). In India, 42% of total agricultural land is affected by drought (Gogoi & Tripathi, 2019).

Drought stress reduces fresh weight and water content in plants, which are critical for growth and development. To enhance crop yields, mitigating the adverse effects of drought stress is essential. Various strategies are being developed globally to address drought stress, including the development of drought-tolerant crop varieties, adjusting cropping schedules, and implementing resource management practices. Advances in agricultural biotechnology have led to the creation of transgenic drought-tolerant varieties with modified gene expression, offering a promising and effective approach to improving agricultural productivity and water use efficiency (Lu *et al.*, 2013). However, the development of such transgenic varieties is a lengthy process, and their acceptance in certain regions remains limited.

Microbial interactions with plants serve diverse and critical roles. These microbes not only support plant growth and development by facilitating nutrient fixation, mobilization, and the production of hormones and organic phyto-stimulants, but they also activate local and systemic stress-relief mechanisms. This dual function enables plants to better withstand and adapt to abiotic stress conditions (Singh *et al.*, 2023). These beneficial microbiomes associated with plant roots and tissues called as Plant Growth-Promoting Rhizobacteria (PGPR) help mitigate plant stress through various mechanisms. The interaction between plants and

PGPRs is crucial for enabling plants to swiftly adapt to environmental stresses, especially by optimizing root water absorption under drought conditions.

Yasmin *et al.,* 2021 observed that PGPRs significantly enhance plant resilience to drought stress. Though the physiological and morphological responses of plants to drought are well-documented, the impact of rhizospheric microbial communities on drought stress remains insufficiently understood (Zhao *et al.,* 2016). Since water facilitates the transport of nutrients from the soil to the entire plant through the roots, drought stress directly impacts the availability and movement of soil nutrients, affecting processes such as nutrient diffusion and the mass flow of water-soluble nutrients like nitrate, sulphate, calcium, magnesium, and silicon (Selvakumar *et al.,* 2012). Drought stress primarily alters the morphology, physiology, and biochemistry of crop plants, disrupting key functions such as photosynthesis, respiration, translocation, ion uptake, carbohydrate metabolism, nutrient assimilation, and growth regulation (Farooq *et al.,* 2008). These disruptions negatively affect plant growth and yield both qualitatively and quantitatively, as observed in several crops, including barley (Samarah, 2005), maize (Kamara *et al.,* 2003), rice (Lafitte *et al.,* 2007), and wheat (Rampino *et al.,* 2006).

PGPRs AND RHIZOSPHERE

Rhizosphere enriched with a variety of microorganisms is called rhizobacteria and classified into different groups, *i.e.*, beneficial, deleterious and neutral, according to their effects on plants. Beneficial bacteria living in the rhizosphere are known as plant growth-promoting rhizobacteria (PGPR). The high levels of nutrients including amino acids, sugars and organic acids released from the roots, are used by the bacterial community residing in the rhizospheric region which supports plant growth, metabolism and yield (Raza *et al.,* 2016a, b). The PGPRs have the ability to maintain the sustainability of plants under stress conditions by enhancing metabolic activities **(**Kavamura *et al.,* 2013). There are diverse bacterial genera such as *Acinetobacter, Arthrobacter, Bacillus, Corynebacterium, Delftia, Duganella, Exiguobacterium, Kocuria, Lysinibacillus, Methylobacterium, Micrococcus, Micrococcus, Paenibacillus, Paenibacillus, Pantoea, Pseudomonas, Psychrobacter, Serratia* and *Stenotrophomonas* has been reported to produced diverse group of phytohormones (Glick, 1995; Jones *et al.,* 2007; Verma *et al.,* 2015; Verma *et al.,* 2015; Rana *et al.* 2016; Verma *et al.,* 2017; Kour *et al.,* 2017; Yadav *et al.,* 2017; Ahmad *et al.,* 2022). Tiwari *et al.,* 2021, 2022 also recorded *Trichoderma harzianum* as a potential plant growth-promoting micro-organism *in vitro* as well as in protected areas for sugarcane crops.

The role of rhizobacteria in enhancing plant growth, nutrient availability, and biological control is well-established, involving both direct and indirect mechanisms. These mechanisms include the use of PGPMs to mitigate the harmful effects of plant pathogens, typically fungi, and the solubilization of essential soil elements such as phosphate, potassium, sulfur, and zinc to increase their availability to plants. Additionally, PGPMs contribute to nitrogen fixation (Glick, 2012), siderophore production for iron acquisition (Jahanian *et al.,* 2012), and the biosynthesis of key phytohormones like Abscisic Acid (ABA), Gibberellic Acid (GA), cytokinin, and Indole-3-Acetic Acid (IAA) (Glick, 2012; Srivastava *et al.,* 2012; Nautiyal *et al.,* 2013). The production of ACC deaminase by these bacteria further alleviates ethylene-induced stress in plant roots (Liu *et al.,* 2016). Moreover, rhizobacteria play a role in degrading environmental pollutants and producing antibiotics, lytic enzymes, and additional growth hormones. Notably, drought conditions can reduce phytohormone levels, exacerbating stress and negatively impacting plant health (Farooq *et al.,* 2012).

The application of beneficial bacteria has been globally recognized for enhancing soil characteristics and fertility, contributing to increased crop productivity by driving various biotic activities within the soil ecosystem that promote dynamic nutrient turnover and sustainability (Gabriela *et al.,* 2015; Gupta *et al.,* 2015). Figure 1 shows the morphological and physiological effects of drought on plants as well as tolerance mechanisms used by various micro-organisms.

The use of PGPRs, such as *Azospirillum*, has been widely adopted to enhance crop yields by up to 30% in crops like wheat, corn, rice, and sugarcane (Vogel *et al.,* 2013) while also conferring specific traits such as heavy metal detoxification (Singh *et al.,* 2023), salinity tolerance, and biological control of phytopathogens and insects (Egamberdieva & Lugtenberg, 2014). Environmentally sustainable practices have driven the use of diverse agriculturally important bacteria, resulting in improved nutrient uptake, soil fertility, plant health, and pollutant remediation (Zhang *et al.,* 2019; Kumar *et al.,* 2020). In the context of climate change and excessive fertilizer use, the role of rhizobacteria in mitigating abiotic stresses has gained significant attention (Nautiyal *et al.,* 2013). Researchers are focusing on these beneficial microbes to not only boost crop productivity but also enhance resistance to stress conditions.

Potential of PGPRs

In recent years, numerous studies have highlighted the potential of PGPRs to enhance abiotic stress tolerance, particularly in response to drought (Khan *et al.,* 2019a;

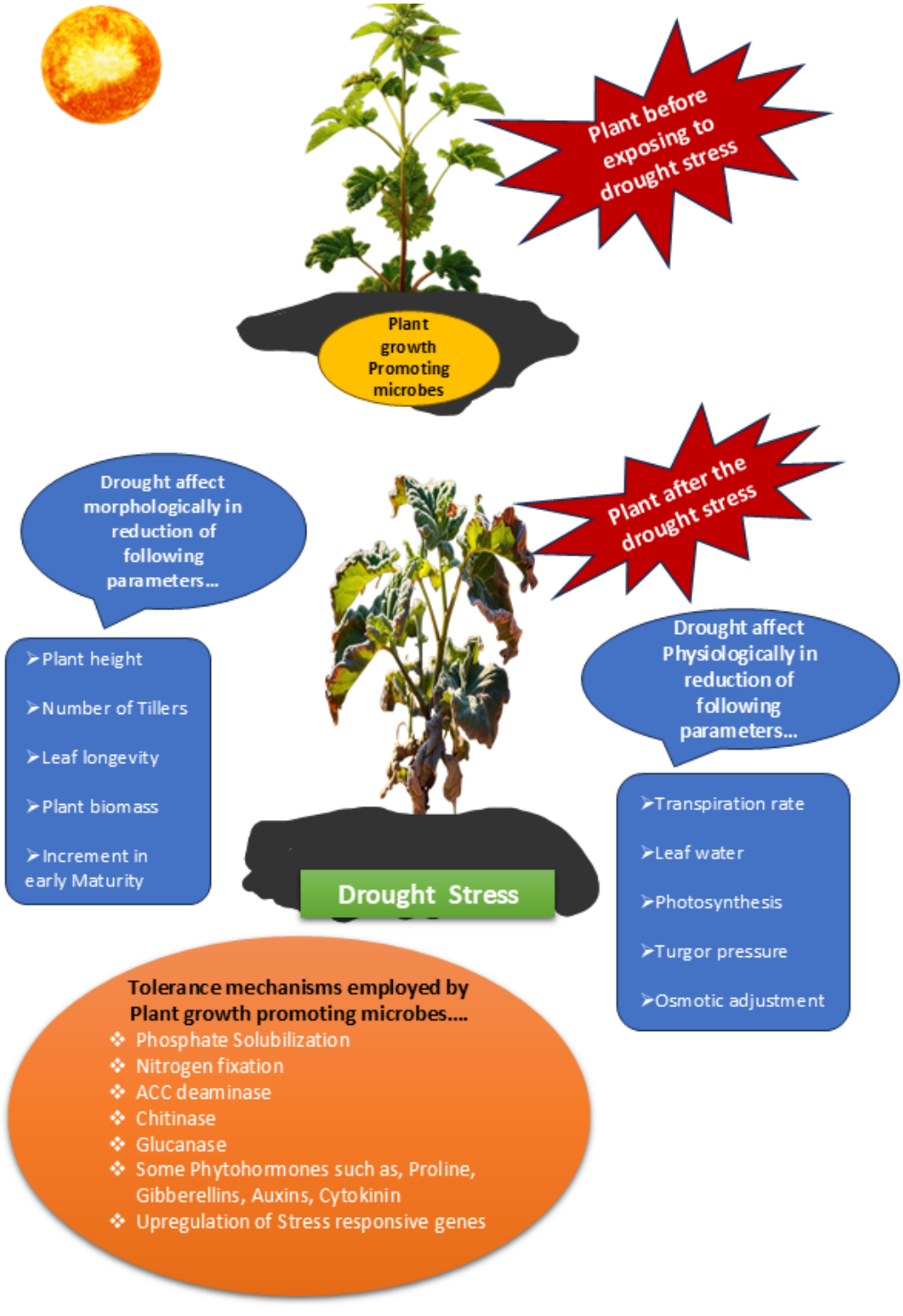


Figure 1. Healthy and drought affected plants, its morphological and physiological disorders as well tolerance mechanism employed by various beneficial micro-organisms

Nautiyal *et al.,* 2013). PGPR demonstrate the ability to mitigate the detrimental effects of drought stress, leading to improved crop productivity in arid, semi-arid, and dryland regions. This is achieved through various biochemical and physiological mechanisms, including the production of auxin or indole-3-acetic acid (IAA) (Cassan *et al.,* 2013), cytokinin (Zaheer *et al.,* 2022), gibberellins (Kang *et al.,* 2010), exopolysaccharides (EPS) (Sandhya *et al.,* 2009), and microbial biofilm formation (Asari *et al.,* 2015). Additionally, PGPR has been shown to alleviate the adverse effects of other stress factors such as flooding, pathogenicity, and salinity (Ahmad *et al.,* 2022).

Several PGPRs have been reported to induce drought stress tolerance in crops such as wheat, maize,

sunflower, sugarcane, and green gram (Moutia *et al.,* 2010; Saravanakumar *et al.,* 2011; Kasim *et al.,* 2013; Qudsaia *et al.,* 2013). Among them, *Pseudomonas* species represent one of the largest groups of PGPR, naturally occurring in agricultural soils, and are known for possessing multiple plant-beneficial traits (Srivastava *et al.,* 2012). The molecular mechanism involved in conferring drought stress to Pseudomonas spp. has shown expression or overexpression genes of several stress-tolerant genes (Rangeshwaran *et al.*, 2012; Karkera *et al.*, 2018). Microbes employ diverse biochemical and molecular pathways through plant-microbe interactions to alleviate the adverse effects of drought stress on plant growth and development presented in Table 1.

A comprehensive understanding of the defense mechanisms utilized by PGPR is crucial in improving plant productivity and advancing their application to a commercial scale. PGPR employ both direct and indirect mechanisms to enhance plant resilience. Direct mechanisms include mineral solubilization and the production of growth-regulating hormones, such as Indole-3-Acetic Acid (IAA) and Gibberellic Acid (GA3). Indirect mechanisms involve the suppression of pathogens through the release of antibiotics, secondary metabolites, and siderophores (Aeron *et al.,* 2011; Govindasamy *et al.,* 2011).

DIRECT METHODS

The direct mechanisms involve the synthesis of beneficial substances by the bacteria or the facilitation of nutrient uptake from the environment (Glick *et al.,* 1999). Many PGPR produce phytohormones, such as Indole Acetic Acid (IAA), gibberellic acid, cytokinin, and Abscisic Acid (ABA), which closely resemble those synthesized by plants (Ullah *et al.,* 2021; Shah *et al.,* 2021). These phytohormones enhance plant growth by increasing the availability of essential nutrients in the rhizosphere, such as the solubilization of phosphorus, potassium, zinc, and sulfur, as well as the absorption of iron through the production of siderophores (Gonzalez *et al.,* 2019).

Table 1. Beneficial effect of Microbes on drought stress resilience

Plants	Microbes	Tolerance mechanisms	References
Cicer Arietinum L.	*Bacillus subtilis, Bacillus thuringiensis* and *Bacillus megaterium*	Increased leaf proline content, activities of antioxidant enzymes (CAT, APOX, POD, and SOD), significant accumulation of riboflavin, L-asparagine, aspartate, glycerol, nicotinamide, and 3-hydroxy-3-methyglutarate	Khan *et al.*, 2019
Hordeum vulgare	*Pseudomonas* spp. and *Pantoea* spp.	By improving growth, metal acquisition, photosynthesis and oxidative stress tolerance	Abideen *et al.*, 2022
Potato	*Bacillus pumilus* strain DH11	Enchanced photosynthesis via increment in ROS production	Gururani *et al.*, 2013
Peach	*Bacillus cereus* AR156 *Bacillus subtilis* SM21	Production of reactive oxygen species scavenging enzymes often results in decreased lipid peroxidation and enhances the protection of plant membranes.	Wang *et al.*, 2013
Pea	*Pseudomonas* spp.	Modifications to the root system's architecture and the synthesis of acc deaminase	Arshad *et al.*, 2008
Sunflower	*Bacillus pumilus* SF3 *A. xylosoxidans* SF2	Improvement in phytohormone production.	Castillo *et al.*, 2013
Sugarcane	*Rhizobiales* and *Streptomycetales*	Regulating the response of the bacterial community in the sugarcane rhizosphere to drought stress	Liu *et al.*, 2021
Triticum aestivum and *Zea mays*	*Bacillus* sp. and *Enterobacter* sp.	Production of indole-3-acetic acid (IAA) and salicylic acid (SA)	Jochum *et al.*, 2020
Triticum aestivum	*Rhizophagus intraradices, Funneliformis mosseae, Funneliformis geosporum*	Increased RWC, Maximum photochemistry, higher Chl content, restoration of electron transport in PSII, Higher PI(abs), PSI photochemistry	Mathur *et al.*, 2018
Zea mays L.	*Glomus versiforme*	Improved chlorophyll content, mineral uptake and assimilation, increased content of compatible solutes, such as proline, sugars, and free amino acids, up-regulation of the antioxidant system	Begum *et al.*, 2019

Production of IAA

Indole-3-Acetic Acid (IAA) is a critical phytohormone that plays a fundamental role in regulating plant growth and development. Additionally, it contributes significantly to enhancing plant resilience under drought stress conditions (Zhang *et al.,* 2020). The production of IAA by rhizobacteria, particularly under abiotic stresses such as drought, is a rapidly growing area of research in plant-microbe interactions. Approximately 80% of rhizobacteria possess the ability to regulate IAA production in plants under stress (Khan *et al.,* 2020b). Various bacterial strains, including strains of *Pseudomonas*, *Rhizobium*, *Bacillus, Bulkoderia, Azotobacter*, *Arthrobacter*, *Azospirillum*, *Stenotrophomonas*, *Microbacterium*, *Sphingomonas*, and *Mycobacterium* strains etc. have been reported to produce IAA under drought conditions when inoculated with crops like wheat and tomato (Bharucha *et al.,* 2013; Vishwakarma *et al.,* 2018). Numerous studies showed that IAA-producing bacteria enhance drought tolerance by improving root development, increasing water and nutrient uptake, and modulating stress responses, which helps crops penetrate deeper into the soil and absorb more water (Cardoso *et al.,* 2018). These PGPRs manage drought stress effectively by promoting root and lateral root growth (Ahmad *et al.,* 2022).

Studies by Khan *et al.,* 2020a demonstrated that IAA production is upregulated in response to drought stress in various plant species. Similarly, Nita *et al.,* 2011 and Sevilla *et al.,* 2001 indicates that *Acetobacter diazotrophicus* exhibits an enhanced capacity to produce IAA, which may have significant physiological implications for root development in plants during drought stress. Recent research has demonstrated several species of rhizobacteria capable of producing IAA under drought conditions. *Bacillus subtilis* shown to enhance root elongation and drought tolerance by producing IAA and modulating the plant's antioxidant system (Akinrinlola *et al.,* 2021). *Pseudomonas putida* effectively increases drought tolerance in maize by improving root growth and water retention (Arora *et al.,* 2022). *Azospirillum brasiliense* known for its significant IAA production, which helps in maintaining plant growth under water deficit conditions (Rodriguez-Salazar *et al.,* 2020).

Production of gibberellic acid

Gibberellic Acid (GA) is a key plant hormone involved in various growth processes, including seed germination, stem elongation, and flowering. PGPRs that produce GA have emerged as an important tool in alleviating drought stress in crops (Urbanova & Leubner-Metzger, 2016). The application of GA-producing PGPR can significantly improve plant resilience to drought by enhancing root growth, nutrient uptake, and overall plant vigor (Javid *et al.,* 2011). Several researches have shown that rhizospheric bacteria produce gibberellins exhibit better plant growth (Poupin *et al.,* 2013). Some of the bacteria such as *Acetobacter diazotrophicus, Acinetobacter calcoaceticus, Azospirillum brasilense, Herbaspirillum seropedicae, Bacillus* spp., *Burkholderia* spp. and *Rhizobium phaseoli* have identified as GAs producing bacteria (Joo *et al.,* 2005, 2009; Kang *et al.,* 2009; Kang *et al.,* 2014) promotes plant growth during water stress condition in various crops. *P. putida* and *Azospirillum lipoferum* reported to improve plant growth under drought conditions in Soybean and maize respectively (Cohen *et al.,* 2009; Sang-Mo *et al.,* 2014).

Ahmed *et al.,* 2022; Sharma *et al.,* 2023; Rodriguez *et al.,* 2023 recorded *Bacillus amyloliquefaciens* in wheat, *Pseudomonas fluorescens* in rice, and *Azospirillum lipoferum* in maize respectively, enhance growth under drought stress by increasing the production of gibberellic acid, leading to greater biomass accumulation and improved water use efficiency. The ability of GA to promote plant growth, even under adverse conditions, highlights the importance of integrating GA-producing rhizobacteria into sustainable agricultural practices, particularly in regions prone to drought.

Production of cytokinin

Cytokinin, a key phytohormone regulating stomatal behaviour by promoting stomatal opening and shoot development while reducing root growth (Honig *et al.,* 2018), declines significantly during drought stress, contributing to stomatal closure (Farber *et al.,* 2016); however, cytokinin-producing PGPR enhance drought tolerance by improving root and shoot development, maintaining water retention, and delaying leaf senescence, thereby improving crop resilience in drought-prone regions (Arkhipova *et al.,* 2007; Liu *et al.,* 2019).

Several PGPR strains, including *Pseudomonas*, *Bacillus*, *Bradyrhizobium*, *Azospirillum*, and *Arthrobacter* species, are known to produce cytokinin. Drought tolerance by cytokinin production revealed by *Bacillus subtilis* in wheat, *Paenibacillus polymyxa* inoculated in maize and *Pseudomonas fluorescens* in rice (Ali *et al.,* 2022; Singh *et al.,* 2023; Kumar *et al.,* 2021).

Chieb and Gachomo (2023) highlights the role of *Bacillus subtilis* in enhancing drought tolerance and promoting plant growth through various mechanisms. By reducing drought-induced impacts on cytokinin production by up to 30%. *B. subtilis* helped maintain improved relative water content, better leaf water potential, and increased root and shoot dry weights. This cytokinin-driven mechanism supports plant growth even under water-limited conditions, suggesting that the ability of rhizobacteria to produce cytokinin is a critical factor in enhancing plant drought tolerance (Gowtham *et al.,*

2022). According to Zaheer *et al.,* 2022 cytokinin producing *Azospirillum brasilense* proved to be more beneficial for the growth, yield, antioxidant activity, and physiological systems of wheat compared to its non- cytokine producing counterpart. The presence of cytokinin production in *A. brasilense* is associated with enhanced plant vigour, improved stress tolerance, and greater overall productivity, underscoring the importance of cytokinin in promoting wheat growth and resilience under various conditions.

Production of abscisic acid

Abscisic acid (ABA) is a key plant hormone synthesized in response to various abiotic stresses, such as drought, cold, salt stress, and soil contamination, triggering the activation of stress-responsive genes (Saha *et al.,* 2016). It plays multiple roles in plant development, including inhibiting seed germination, inducing leaf and fruit abscission, promoting stomatal closure to minimize water loss, and modulating root architecture to enhance water and nutrient uptake (Saha *et al.,* 2016).

Several strains of PGPRs are known to produce abscisic acid (Salomon *et al.,* 2014; Cohen *et al.,* 2015). When plants are inoculated with ABA-producing strains, such as *Bacillus licheniformis*, *Pseudomonas fluorescens*, and *Azospirillum Brasiliense,* the internal levels of ABA increase, enhancing the plant's resistance to drought (Salomon *et al.,* 2014; Cohen *et al.,* 2015). Recent research highlights the crucial role of PGPRs in producing abscisic acid under drought stress, which enhances plant drought tolerance. PGPR strains, such as *Bacillus* and *Pseudomonas*, are known to stimulate ABA synthesis in plants. This phytohormone regulates stomatal closure, reducing water loss and improving water use efficiency under drought conditions (Al-Turki, 2023).

Chieb and Gachomo (2023) explained that under drought conditions, roots transmit stress signals to the shoots by modulating levels of abscisic acid, cytokinin, and other signaling molecules within the root-shoot communication pathway. These signals trigger physiological adaptations in the plant to cope with the stress. As a result of disrupted cell membranes or reduced cell turgor due to drought, plants increase ABA accumulation in their tissues to promote stomatal closure. For example, *Vitis vinifera* responds to water deficits by regulating stomatal closure through the accumulation of ABA, maintaining this state to conserve water (Tombesi *et al.,* 2015).

Phosphorus solubilization

Phosphorus (P) is the second most critical nutrient for plant growth, following nitrogen, and is required in sufficient quantities for optimal development. However, over 90% of the phosphorus in soils exists in insoluble forms, making it inaccessible to plants. Certain rhizobacteria possess the capability to solubilize these inorganic phosphates into soluble forms, make phosphorus accessible to plants, enhancing nutrient uptake and overall plant development. Such, Phosphorus-Solubilizing Bacteria (PSB) play a vital role not only in boosting crop yields but also in alleviating the impacts of drought stress. Plants treated with 0.5% PSB exhibited significant improvements in both physiological and biochemical parameters, demonstrating their effectiveness in promoting growth under stress conditions (Shintu *et al.,* 2015).

Oteino *et al.,* 2015, and Yadav, 2017 reported *Arthrobacter, Bacillus, Beijerinckia, Burkholderia, Enterobacter, Microbacterium Pseudomonas, Erwinia, Rhizobium, Mesorhizobium, Flavobacterium, Rhodococcus*, and *Serratia* are some Phosphate solubilizing PGPRs, help plants to combat water scarcity and overcome the problem of phosphorus unavailability to plant systems and improve plant growth and yield. Several researchers reported that PGPRs have also the ability to make P available to plant by ameliorating the adverse effects of drought stress as well make phosphorus available to the crops including pepper and tomato seedlings (Mayak *et al.,* 2004), pea (Arshad *et al.,* 2008), lettuce (Arkhipova *et al.,* 2007), maize (Viruel *et al.,* 2014), chickpea and barley (Peix *et al.,* 2001), Indian mustard (Kumar *et al.,* 2013), and sunflower (Ekin, 2010).

Potassium solubilization

Potassium, following nitrogen and phosphorus, plays a critical role in promoting plant growth (Meena *et al.,* 2014). However, over 90% of the potassium in soil exists as insoluble rock and silicate minerals, making it inaccessible to plants. Rhizospheric bacteria have been shown to solubilize potassium from these K-bearing minerals (Meena *et al.,* 2014). Potassium-Solubilizing Bacteria (KSB) are regarded as key agents in facilitating K dissolution in the soil, with several studies employing strains of these bacteria to enhance nutrient availability and boost crop yields.

Acidothiobacillus sp., *Bacillus edaphicus, Ferrooxidans* sp., *Bacillus mucilaginosus, Pseudomonas* sp., *Burkholderia* sp. and *Paenibacillus* sp. are few rhizospheric strains, having ability to solubilize K-bearing minerals and convert the insoluble K to soluble forms (Liu *et al.,* 2012). There beneficial effects have been reported in several crops. Inoculation with KSB has been shown to positive impact on the growth of various crops, including cotton and rape (Sheng *et al.,* 2005), pepper and cucumber (Han *et al.,* 2006), sorghum (Badr *et al.,* 2016), wheat (Sheng *et al.,* 2006), and Sudan grass (Basak & Biswas, 2010). Similarly, treating maize and wheat plants with *Bacillus mucilaginosus*, *Azotobacter chroococcum*, and *Rhizobium* spp. significantly

enhanced potassium mobilization from waste mica, serving as an additional potassium source for plant growth (Singh *et al.,* 2010).

Zinc solubilization

Zinc (Zn) is an essential micronutrient critical for optimal plant development. Zinc deficiency, which arises from its limited availability in soils, is one of the most prevalent micronutrient deficiencies, leading to several growth impairments like stunted shoot growth, chlorosis, reduced leaf size (Singh *et al.,* 2024) including photosynthesis, sugar and protein synthesis, fertilization and seed formation, and disease resistance, *etc*. Under drought conditions, zinc application, either as zinc sulfate ($ZnSO_4$) or zinc oxide (ZnO), enhances seed germination, plant water relations, cell membrane integrity, osmolyte accumulation, stomatal regulation, water use efficiency, and photosynthetic activity, resulting in improved plant performance (Umair *et al.,* 2020).

Certain bacteria, particularly zinc-solubilizing and zinc-accumulating strains, play a pivotal role in enhancing zinc availability and uptake by plants (Yadav *et al.,* 2022). These Zn-Solubilizing Bacteria (ZSB) offer a promising alternative to conventional zinc supplementation, a low-cost alternative technique for Zn biofortification as they transform applied inorganic zinc into bioavailable forms. *In vitro* studies have shown that several bacterial strains have been identified for their zinc-solubilizing capabilities, including *Pseudomonas aeruginosa* (Fasim *et al.,* 2002), *Gluconacetobacter diazotrophicus* (Saravanan *et al.*, 2007), *Bacillus* sp., *Pseudomonas striata*, *P. fluorescens*, *Burkholderia cenocepacia* (Pawar *et al.,* 2015).

Khan *et al.,* 2019a observed that Zn-mobilizing PGPRs notably enhanced total biomass, harvest index, grain yield, and Zn concentration in rice, while alleviating Zn deficiency symptoms. Similarly, Rehman *et al.,* 2018 demonstrated that P*seudomonas* sp., a ZSB, was particularly effective in boosting wheat productivity. Selvaraj *et al.,* 2016, have shown that ZSB inoculation enhances crop yields by regulating the expression of Zn transporter genes.

Sulfur oxidizing bacteria

Sulfur is a part of essential structural components such as disulfide bonds in proteins, amino acids, vitamins, and various cofactors. Additionally, sulfur is integral to the synthesis of numerous secondary metabolites, which are important for various physiological functions in plants (Narayan *et al.,* 2023). The oxidation of sulfur within the soil environment results in the generation of sulfuric acid (H_2SO_4), which decreases the pH of the rhizosphere. This acidification enhances the solubilization of calcium carbonate, zinc, and phosphorus. In addition to their sulfur-oxidizing capabilities, these bacteria produce ACC deaminase, solubilize rock phosphate, synthesize indole-3-acetic acid (IAA), generate ammonia, and produce siderophores. They also release antimicrobial agents, such as Hydrogen Cyanide (HCN) and other antimicrobial compounds, all of which contribute to enhanced plant growth and development (Chaudhary *et al.,* 2019; Kapadia *et al.,* 2021; Yadav *et al.,* 2022).

Sulfur-Oxidizing Bacteria (SOB) play an emerging role in helping plants cope with drought stress. Etienne *et al.,* 2018 highlight the importance of sulfur in plant growth and its impact on nutrient cycling and crop resilience under drought stress. Narayan *et al.,* 2023 discussed sulfur metabolism's role in antioxidant production, such as glutathione, which protects plants from oxidative stress during drought. The application of SOB has been demonstrated to improve drought stress tolerance in plants by directly producing growth-promoting substances or indirectly enhancing the production of sulfur-containing compounds. These compounds, such as glutathione, play a vital role in reducing oxidative stress and improving nutrient availability, which strengthens plant resilience under drought conditions. Additionally, plant-microbe interactions involving SOBs help modulate root systems and increase water uptake, further contributing to improved drought tolerance (Anandham *et al.,* 2007; Joshi *et al.,* 2021).

According to Reddy *et al.,* 2018; Joshi *et al.,* 2021; Kapadia *et al.,* 2021, the incorporation of Sulfur-Oxidizing Bacteria (SOB) into sulfur-based fertilizers significantly enhances plant development. Multiple bacterial strains, including *Thiobacillus acidianus*, *Arthrobacter*, *Citrobacter*, *Bacillus*, *Flavobacterium*, *Paracoccus*, *Pseudomonas*, *Paenibacillus*, *Streptomyces*, *Sulfolobus*, *Thiosphaera*, *Thiomicrospira*, and *Xanthobacter*, have demonstrated potential for oxidizing sulfur-rich compounds (Chaudhary *et al.,* 2019; Malviya *et al.,* 2022; Meier *et al.,* 2017; Reddy *et al.,* 2018). Similarly, certain fungi belong to genera *Aspergillus*, *Alternaria*, *Epicoccum*, *Scolecobasidium*, *Mucoraceae*, and *Penicillium* also contribute to sulfur oxidation (Anandham *et al.* 2007; Kulczycki, 2021; Vidyalakshmi *et al.,* 2009).

INDIRECT METHODS

There are several indirect mechanisms by which PGPR enhance plant growth, including their ability to control phytopathogens, release of antibiotics, siderophore and HCN production and trigger systemic resistance.

Pathogenicity

During drought stress, the plant's primary adaptive mechanism involves stomatal closure to minimize water loss through transpiration. However, this response can be compromised in the presence of pathogen infection,

potentially leading to yield reductions of up to 30%, depending on the specific crop and environmental conditions (Pandey *et al.,* 2015; Savary *et al.,* 2019). Fungal pathogens are a significant biotic stressor, particularly during extended or severe drought conditions, which can exacerbate disease outbreaks. Research has demonstrated that plants infected with fungal pathogens under drought conditions experience more pronounced reductions in dry biomass, leaf area, height, and survival rates compared to those subjected to drought alone (Ghanbary *et al.,* 2017). Numerous studies have also reported notable physiological changes when plants face both drought stress and pathogen infection, including reduced stomatal conductance, lower photosynthetic rates, declines in chlorophyll content, decreased Relative Water Content (RWC), and reduced water use efficiency (Ghanbary *et al.,* 2017).

Various species of rhizobacteria belonging to the genera *Alcaligenes*, *Arthrobacter*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Bradyrhizobium*, *Burkholderia*, *Enterobacter*, *Flavobacterium*, *Klebsiella, Mesorhizobium*, *Pseudomonas, Rhodococcus, Streptomyces*, *Serratia* have been reported to antagonist against plant pathogens (Ahmad *et al.,* 2008; Tariq *et al.,* 2014; Gupta *et al.,* 2016). In addition to promoting plant growth and development, PGPRs exhibit antagonistic effects on pathogenic microbes by excluding and reducing rhizosphere-dwelling pathogens, while making soil nutrients more accessible to plants.

Release of antibiotics

PGPRs are the best environment friendly component towards the disease management in plants and are best alternatives of chemical pesticides against the plant pathogens like bacteria, fungi, viruses, bug irritations, and nematode. The use of plant growth-promoting rhizobacteria (PGPR) to alleviate or prevent the damaging impact of phytopathogens is known as biological control. Among the various mechanisms PGPR employ the production of antibiotics stands out as one of the most effective strategies for suppressing the growth and metabolic functions of phytopathogens.

Some potential PGPR strains identified are *Pseudomonas, Bacillus, Azospirillum, Rhizobium*, and *Serratia* species, produces antibiotics against pathogenic microbes to inhibit their growth (Anith *et al.,* 2004). These antibiotics, such as phenazines, phloroglucinols, pyoluteorin, pyrrolnitrin, and cyclic lipopeptides, are a diverse group of low molecular weight organic compounds (Duffy *et al.,* 2003).

As reported by Maksimov *et al.,* 2011, Beneduzi *et al.,* 2012, Mihalache *et al.,* 2018, and Radovanovic *et al.,* 2018, the bacterial strains *P. fluorescens* BL915, *Pseudomonas spp.,* and *Bacillus sp.* are releasing 2, 4-DAPG, phenazine, fengisin and iturins etc. against the phytopathogenic fungi *Rhizoctonia solani, Fusarium oxysporum* and *Podosphaera fusca* respectively. Some other major antibiotics antagonistic against pathogenic fungi *in vitro* produced from PGPRs are surfactin, kanosamine, bacillomycin D, mycosubtilin, Martinez-Viveros oligomycin A, butyrolactones, xanthobaccin zwittermycin A, and viscosinamide (Viveros *et al.,* 2010). However, 2, 4-DAPG is recorded as one of the most efficient antibiotics to control pathogens produced by various strains of *Pseudomonas* (Rezzonico *et al.,* 2007).

Bouskill *et al.* (2016) recorded drought-impacted soils have elevated levels of antibiotics, which are likely produced by drought-resistant bacteria. This production may serve as a competitive strategy for resource acquisition or as signalling molecules to activate drought-adaptation mechanisms, such as biofilm development.

Production of siderophore

Iron is a crucial element for plant growth and development, particularly in processes such as respiration, nitrogen fixation, and photosynthesis. However, in its insoluble Fe^{3+} form, it becomes unavailable for plant uptake, leading to deficiencies that cause chlorosis and ultimately reduce crop quality and yield (Ferreira *et al.,* 2019). Under iron-limiting conditions, microbes, including endophytic bacteria, produce siderophores small organic molecules with a high affinity for ferric iron. Saha *et al.,* 2016 observed siderophores produced by microorganisms and some plants, help extract iron from the environment even in low availability conditions, as shown in recent researches.

PGPRs also produce siderophores to help plants overcome drought stress, either directly or indirectly, by improving nutrient absorption, stimulating root proliferation, and generating phytohormones like IAA and GA (Gowtham *et al.,* 2020). The generation of siderophores is crucial for limiting the growth of phytopathogens by sequestering iron, while simultaneously promoting plant growth through improved iron absorption (Siddiqui, 2006). Additionally, siderophores can act as biosensors to detect iron availability in various environments (Saha *et al.,* 2016). Bacteria such as *Pseudomonas*, *Enterobacter*, *Bacillus*, and *Rhodococcus* are known producers of siderophores which play a key role in iron uptake, pathogen inhibition, and fungal growth suppression (Glick, 1995; Wong *et al.,* 2015).

Hydrogen cyanide

Drought stress has been shown to trigger the production of the secondary metabolite HCN by identified PGPR, which aids in protecting plants from a range of biotic and abiotic stresses. They also promote plant growth by neutralizing pathogens, though more recent evidence suggests it may also

enhance phosphorus availability via metal chelation (Rijavec, 2016). Several bacterial species including Alcaligenes, Aeromonas, Bacillus, Pseudomonas, and Rhizobium, are capable of producing cyanide as a secondary metabolite, (Subramanian & Satyan 2014; Anand *et al.,* 2020). Bakker and Schippers 1987 reported that approximately 50% of pseudomonads isolated from potato and wheat rhizospheres produce HCN *in vitro*.

The nematode control efficacy of certain bacterial strains has been linked to their HCN production, where direct contact between HCN-producing bacteria and nematodes is critical for successful control (Siddiqui *et al.,* 2006). HCN can also enhance plant establishment and help prevent plant diseases, with significant potential for controlling bacterial infections in plants. It has been found effective in suppressing root-knot and black rot in tomato and tobacco, caused by the nematodes *Meloidogyne javanica* and *Thielaviopsis basicota*, respectively (Siddiqui *et al.,* 2006). Furthermore, HCN has been used to manage agricultural pests such as the subterranean termite *Odontotermes obesus*, a key threat to crops in India (Devi *et al.,* 2007).

However, some studies have highlighted adverse effects of HCN on plants, including inhibition of energy metabolism in potato roots (Bakker & Schippers, 1987) and restricted root growth in lettuce (Alstrom & Burns, 1989). Additionally, HCN produced by rhizospheric *Pseudomonas* has been found to suppress primary root growth in *Arabidopsis* through the inhibition of an auxin-responsive gene (Rudrappa *et al.,* 2008).

CONCLUSION

Plant-microbe interactions, particularly through beneficial microbial consortia in the root microbiome, offer an eco-friendly approach in enhancing stress tolerance in crops. These microorganisms improve plant growth and resilience by regulating phytohormones, facilitating nutrient uptake, and enhancing antioxidant defenses thus imparting tolerating ability of the plant to several insect pests and diseases. Recent agricultural practices have shown that microbial bio-inoculants, especially when used in the consortium, can effectively mitigate abiotic and biotic stresses while improving soil health and crop yields. However, there is a need for further molecular research to fully understand the mechanisms of stress tolerance conferred by these microbial communities and to develop more effective biostimulants tailored for field application, ultimately addressing the challenges of food security in a changing environment.

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