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REVIEW ARTICLE

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The role of plant-associated rhizobacteria in plant growth, biocontrol and abiotic stress management

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Abstract

The rhizosphere is the region around the plant roots where maximum microbial activities occur. In the rhizosphere, microorganisms' beneficial and harmful activities affect plant growth and development. The mutualistic rhizospheric bacteria which improve plant growth and health are known as plant growth-promoting rhizobacteria (PGPR). They are very important due to their ability to help the plant in diverse ways. PGPR such as *Pseudomonas*, *Bacillus*, *Azospirillum*, *Azotobacter*, *Arthrobacter*, *Achromobacter*, *Micrococcus*, *Enterobacter*, *Rhizobium*, *Agrobacterium*, *Pantoea* and *Serratia* are now very well known. Rhizomicrobiome plays critical roles in nutrient acquisition and assimilation, improved soil texture, secreting and modulating extracellular molecules such as hormones, secondary metabolites, antibiotics and various signal compounds, all leading to the enhancement of plant growth and development. The microbes and compounds they secrete constitute valuable biostimulants and play pivotal roles in modulating plant stress responses. In this review, we highlight the rhizobacteria diversity and cutting-edge findings focusing on the role of a PGPR in plant growth and development. We also discussed the role of PGPR in resisting the adverse effects arising from various abiotic (drought, salinity, heat, heavy metals) stresses.

KEYWORDS

abiotic stress, inorganic fertilizers, PGPR, rhizosphere, sustainable agriculture

INTRODUCTION

Plant growth-promoting rhizobacteria (PGPR) is a group of bacteria found in the soil surrounding the roots of plants known as the rhizosphere (Santoyo et al., 2021). The rhizosphere is the soil environment where the plant root is available and is a zone of optimum microbial activity resulting in a constricted nutrient pool in which necessary macro and micronutrients get extracted (Bhatt & Bhatt, 2021). The microbial population in the rhizosphere is significantly distinct from its surrounding area due to root exudates that function as a nutrient source for microbial growth (Zhao et al., 2021). Ryan (2009) confirmed that the small rhizosphere region is abundant in microbial nutrients relative to the bulk soil; this is seen by the number of bacteria present around the roots of the plants, typically 10 to 100 times higher than in the bulk soil

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(Ryan et al., 2009). Microflora found in the rhizosphere is dominated by bacteria, followed by fungi, protozoa, algae and actinomycetes (Kour et al., 2019; Poria et al., 2021). Various studies confirm the role of the microbial population in enhancing plant growth (da Silva et al., 2021; Fincheira et al., 2021). Kloepper et al., (1980) referred to such advantageous rhizobacteria as growth-enhancing rhizobacteria (PGPR) (Kloepper et al., 1980). The definition of PGPR is limited to bacterial strains that may satisfy at least two conditions, such as vigorous invasion, stimulation of plant growth and biocontrol (Arjumend et al., 2022; More et al., 2022). Phytomicrobiome has recently emerged as a primary plant trait that affects crop production. The phytomicrobiome also acts as an essential modifying factor in plant root exudation and vice versa, resulting in better plant health and crop yield both in terms of quantity and quality. Not only supports better plant growth but also involved in the degradation of toxic materials (Akhtar et al., 2021, 2022) alleviating the stress conditions (Ilyas et al., 2022) that adversely affect plant development (Bhat, Tariq, Mir, et al., 2022; Bhatt, Verma, et al., 2020). The role of these PGPR is not only restricted to plant development but also to controlling the growth of phytopathogenic microorganisms (Gouda et al., 2018; Gupta et al., 2015; Sudha et al., 2022; Sukmawati et al., 2021). They reflect the importance of PGPR as one of the active ingredients in the formulation of biofertilizers. Rhizobacteria can be divided into two major groups according to their relationship with the host plants: (1) symbiotic rhizobacteria and (2) free-living rhizobacteria (Saharan & Nehra, 2011; Turan, 2022), which could invade the interior of cells and survive inside intracellular PGPR (e.g., nodule bacteria), or remain outside the plant cells, extracellular PGPR (e.g., *Bacillus*, *Pseudomonas*, *Azotobacter*, etc.) (Sagar, Rai, et al., 2022; Sagar, Sayyed, et al., 2022). These microorganisms affect plant growth in three different ways (1) by synthesizing and providing particular compounds to the plants (Qu et al., 2020), by facilitating the uptake of certain nutrients from the environment (Mohanty et al., 2021; Qu et al., 2020), and (2) protecting plants from certain diseases (Sofy et al., 2019).

Generally, rhizobacteria improve plant growth by synthesizing phytohormones precursors (Dodd et al., 2010; Tsukanova et al., 2017), vitamins, enzymes, siderophores, antibiotics (Prakash et al., 2022) and inhibiting ethylene synthesis. Plant growth-promoting rhizobacteria (PGPR) promote plant development through a broad range of mechanisms, such as biological nitrogen fixation, phosphate solubilization, rhizosphere engineering, siderophore output, 1-Aminocyclopropane-1-carboxylate deaminase (ACC) output, quorum sensing (QS) signal intervention, production of phytohormone and inhibition of biofilm production (Kapadia, Kachhdia, et al., 2022; Kapadia, Patel, et al., 2022), having antifungal activity, synthesis of volatile organic compounds (VOCs), promoting beneficial plant-microbe symbioses, systemic resistance induction (Prakash et al., 2022), etc. In the present review, we highlight recent studies addressing the role of PGPR as a biofertilizer, biopesticides and photostimulation used in equitable agriculture. Meanwhile, the molecular and physiological mechanism behind plant growth promotion by rhizobacteria and combating abiotic stress will also be discussed.

INSIGHTS INTO THE RHIZOBACTERIA

Various plants can have explicit predominant PGPR genera and species. The root microbiome of plants relies upon different ecological (biotic and abiotic) factors, for example, plant species, root type, soil type, plant age and sort of plant species. PGPR has been classified in numerous gatherings based on their capacities and taxonomical status. PGPR strains broadly have a place with five primary taxa: Actinobacteria, Firmicutes, Cyanobacteria, Bacteroidetes and Proteobacteria (Figure 1; Parray & Shameem, 2019; Singh et al., 2020).

Among these five primary taxa reported PGPRs to include *Azotobacter*, *Arthrobacter*, *Aeromonas*, *Acinetobacter*, *Allorhizobium*, *Agrobacterium*, *Azoarcus*, *Azorhizobium*, *Azospirillum*, *Bradyrhizobium*, *Bacillus*, *Burkholderia*, *Caulobacter*, *Chromobacterium*, *Delftia*, *Enterobacter*, *Frankia*, *Flavobacterium*, *Gluconacetobacter*, *Klebsiella*, *Micrococcus*, *Mesorhizobium*, *Pseudomonas*, *Paenibacillus*, *Pantoea*, *Rhizobium*, *Streptomyces*, *Serratia*, *Thiobacillus* (Olson, 2006; Singh et al., 2016, 2017, 2020). Some of the main PGPRs and their functions are explained further below (Table 1).

Azotobacter species

Martinus Beijerinck (1851–1931), a Dutch scientist, discovered the *Azotobacter* genus in 1901 (Gurikar et al., 2016). *Azotobacter* spp. is a Gram-negative diazotrophic bacterium with pleomorphic forms ranging from spherical to bacillary (Gurikar et al., 2016). *A. vinelandii*, *A. paspali*, *A. chroococcum*, *A. beijerinckii*, *A. armeniacus*, *A. insignis*, *A. nigricans*, *A. Brasiliense*, *A. salinestris* and *A. tropicalis* have been investigated extensively in the previous two decades (Shelat et al., 2017). *A. vinelandii* and *A. chroococcum* are the most common in rhizospheric soils. The population of *Azotobacter* is mainly determined by other soil microbes and other variables such as organic matter, pH, phosphate, potassium and calcium (Billah et al., 2019;

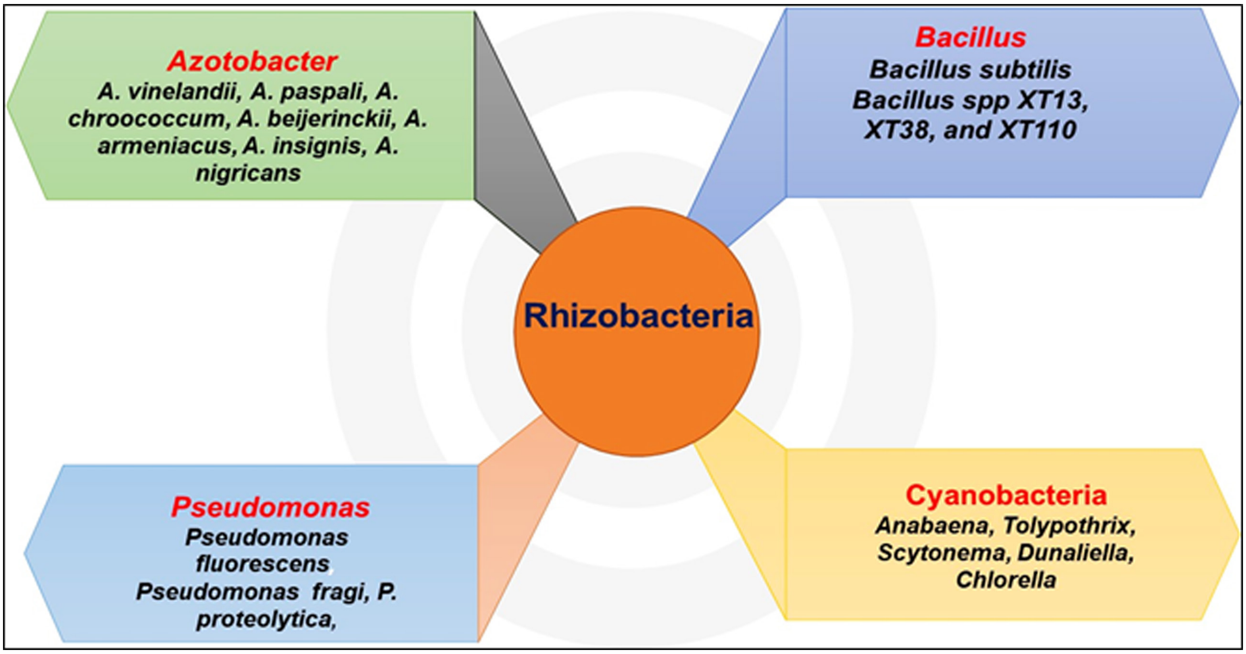

FIGURE 1 The existing rhizobacteria of a plant.

Itelima et al., 2018; Sattar et al., 2019). Bagyaraj and Patil found *Azotobacter* in ragi, sugarcane, cereals, soybeans and rice. *Azotobacter* spp. produces melanin, making food additives, biopolymers and biofertilizers (Itelima et al., 2018). *Azotobacter* spp. can fix atmospheric-free nitrogen (Backer et al., 2018; Chennappa et al., 2019). These growth-promoting chemicals influence shoot and root length and seed germination.

Bacillus species

Bacillus species are a prominent PGPR group that may form spores and persist in soil long (Bhatti et al., 2017; Paul et al., 2019; Radhakrishnan & Hashem, 2017). PGPR induces systemic tolerance, antibiotics and competitive omissions (Hashem & Tabassum, 2019; Wang et al., 2018). *Bacillus* species like *Bacillus subtilis* use direct and indirect biological control to keep pathogens at bay (Fira et al., 2018). These bacteria can produce stress-tolerant spores and compounds that help plants thrive and prevent pathogen infestation. *Bacillus subtilis* also increases biotic stress resistance (Hashem & Tabassum, 2019). The expression of genes and hormones, such as ACC, has a role in developing disease susceptibility. *Bacillus* spp. produce siderophores and exopolysaccharides that help regulate ion balance, transport water in plant tissues, and inhibit pathogenic microbe growth (Bhandari & Garg, 2019; Patel et al., 2018; Shaikh et al., 2016). *Bacillus* is harmless bacteria that produce chemicals beneficial to agriculture and chemical research. These species synthesize antimicrobial metabolites that can be utilized to manage plant diseases instead of artificial pesticides (Fira et al., 2018; Wang et al., 2018).

Pseudomonas species

Pseudomonas species are currently receiving a lot of attention from researchers studying sustainable agriculture due to their role in promoting plant growth and inducing systematic resistance (ISR) through a variety of mechanisms including the suppression of plant diseases, enhanced nutrient uptake and phytohormone production. *Pseudomonas* is a family of 191 diverse species of aerobic, gram-negative, *Gamma proteobacteria* called *Pseudomonadaceae*. *Pseudomonads* are common in the soil environment because of their adaptable metabolism and genetic plasticity. They frequently live in the rhizosphere of a variety of agricultural crop plants, where they contribute significantly to the encouragement of plant growth and the development of biocontrol agents that improve plant growth, yields and disease management (Jain & Pandey, 2016; Kumar et al., 2016; Lugtenberg & Kamilova, 2009; Pathma et al., 2011). Large amounts of carbohydrates, lipids and amino acids are found in the secretions of root exudates in the rhizospheric regions of plants, and these substances serve as chemoattractants for bacteria. Chemoattractants are important in the interactions between microbes. The previous study concluded that some carbohydrates or amino acids acted as potent chemoattractants for microorganisms. Chemoattractants

TABLE 1 Role of PGPR in regulating metabolism of crop plants

PGPR	PGPR Mechanisms	Crops	Application mode	Observation/Findings	References
Azoarcus	Nitrogen fixation	Rice	Plants were developed genotobiotically with a mutant of strain BH72 that expresses b-glucuronidase gene constitutively	The existence of *Azoarcus* in the stele, particularly in the stellar tissue of culms, represents that these bacteria may spread systemically in situ, and highlighting their endophytic life style	(Reinhold-Hurek & Hurek, 1998)
Azobacter	Cytokinin synthesis	Cucumber	-	-	(Aloni et al., 2006)
Azorhizobium	Nitrogen fixation	Wheat	2 ml of rhizobial culture was supplemented with four times to each wheat plant, once during the seed planting, and consequently three times after one-week interval	Five times more short lateral roots were observed in wheat each up to the length of 3 mm, when inoculated with *Azorhizobium caulinodans* IRBG314	(Sabry et al., 1997)
Azospirillum	Nitrogen fixation	Sugar cane	-	-	
Azotobacter	Nitrogen fixation	Wheat, Barley, Oats, Rice, Sunflowers, Maize, line, Beetroot, Tobacco, Tea, Coffee and Coconuts	-	-	(Wani et al., 2013)
Bacillus	Auxin synthesis	Potato	Seed-dipping (10^8 ml cfu)	Both the strains increased the amount of auxin in the inoculated plants up to 71.4% and 433%, respectively, in contrast to non-inoculated plants	(Ahmed & Hasnain, 2010)
Bacillus	Cytokinin synthesis	Cucumber	Seed-dipping 10^6 cells/ml (10^6 CFU/ml)	Enhancement in root development was found in cucumber seedlings which were subjected to bacterization	(Sokolova et al., 2011)
Bacillus	Gibberellin synthesis	Pepper	-	-	(Joo et al., 2005)
Bacillus	Potassium solubilization	Pepper, Cucumber	1 ml of inoculum containing approximately 10^8 cells was used to inoculate the seedling	The soils planted with pepper than with cucumber, had comparatively higher content of P and K	(Han & Lee, 2005)
Bacillus	Induction of plant stress resistance	Peanuts Maize	1 ml of a 10^8 cfu suspension Seed-dipping for 30 min was employed to inoculate the plants	Increase in the salt concentrations, biological nitrogen fixation may be competitive, becoming more economic and sustainable alternative to chemical fertilization. The bacterial inoculants resulted in the increase of total N, P, and K concentration of the maize shoots as well as in Calcisol soil between 16% and 85% considerably in contrast to the control	(Egamberdiyeva, 2007; El-Akhal et al., 2013)

Journal of Applied Microbiology sfam

TABLE 1 (Continued)

PGPR	PGPR Mechanisms	Crops	Application mode	Observation/Findings	References
Bacillus	Antibiotic production	Alfalfa	Inoculation of seedling	Culture filtrates suppressed alfalfa disease caused by *P. medicaginis* and inhibited the pathogen growth in an agar plate assay	(Silo-Suh et al., 1994)
Bacillus	Siderophore production	Maize, Pepper	-	-	(Bedmar et al., 2006)
Beijerinckia	Nitrogen fixation	Sugar cane	-	-	Dobereiner, 1961)
Burkholderia	Nitrogen fixation	Rice	-	-	(Elbeltagy et al., 2001)
Chryseobacterium	Siderophore production	Tomato	Soil drenched	Production of siderophores increased due to increase in bacterial biomass after 16 h of culture	(Radzki et al., 2013)
Gluconacetobacter	Nitrogen fixation	Sugar cane	Root-dipping of seedlings for 1 h	The endophytic establishment of *G. diazotrophicus* inside sugarcane stem was established by the scanning electron microscopy (SEM)	(Muñoz-Rojas & Caballero-Mellado, 2003)
Herbaspirillum	Nitrogen fixation	Rice	Inoculation of seeds	GFP-tagged cells of *Herbaspirillum* sp. strain B501gfp1 were apparently restricted to intercellular spaces of shoot tissues of 7-day-old seedlings of *O. officinalis* W0012	(Elbeltagy et al., 2001)
Mycobacterium	Induction of plant stress resistance	Maize	-	-	(Egamberdiyeva, 2007)
Paenibacillus	Indole acetic acid synthesis	Lodgepole pine	-	-	(Bent et al., 2001)
Paenibacillus	Potassium solubilization	Black pepper	-	-	(Bent et al., 2001; Sangeeth et al., 2012)
Phyllobacterium	Phosphate solubilization	Strawberries	Seedlings of strawberry were inoculated with 1 mL of 10^8 CFU/ml suspensions	Strain PEPV15 solubilizes moderate amounts of phosphate	(Flores-Félix et al., 2015)
Phyllobacterium	Siderophore production	Strawberries	10^8 CFU/ml suspensions were used to inoculate the strawberry seedlings	The strain grew on the CAS indicator medium in which colonies were surrounded by a yellow-orange halo (3.5 mm radius around colonies) indicating siderophore production	(Flores-Félix et al., 2015)
Pseudomonas	Chitinase and β-glucanases production	Several crops	-	-	(Arora et al., 2008)
Pseudomonas	ACC deaminase synthesis	Mung beans, Wheat	-	-	(Ahmad et al., 2013; Shaharoona et al., 2008)

(Continues)

TABLE 1 (Continued)

PGPR	PGPR Mechanisms	Crops	Application mode	Observation/Findings	References
Pseudomonas	Induction of plant stress resistance	Cotton, Maize	-	-	(Yao et al., 2010)
Pseudomonas	Antibiotic production	Wheat	-	-	(Mazzola et al., 1995)
Pseudomonas	Chitinase and β-glucanases production	Pigeon pea	Seed bacterization was done according to Weller and Cook (1983) method	*P. fluorescens* LPK2 and *S. fredii* KCC5 demonstrated chitinase activity on chitinase minimal medium. B-1, 3-glucanase activity was more prominent in the fluorescent pseudomonads strains	(Kumar et al., 2010)
Pseudomonas	Siderophore production	Potato, Maize	-	-	(Beneduzi et al., 2012)
Rhizobia	Nitrogen fixation	Legumes	-	-	(Peter et al., 1996)
Rhizobia	Induction of plant stress resistance	Peanuts	-	-	(El-Akhal et al., 2013)
Rhizobia	Hydrogen Cyanide Production	Legumes	-	-	(Thamer et al., 2011)
Rhizobium	Nitrogen fixation	Rice	-	-	(Yanni et al., 2001)
Rhizobium	Indole acetic acid synthesis	Pepper, Tomato, Lettuce, Carrot	Seed Inoculation Seedlings were inoculated with 250 μl plant of a bacterial suspension with a turbidity of 5 in McFarland standards (1.5×10^9 CFU/ml)	Dry weight of the inoculated shoots as well as roots was more than double of the un-inoculated seedlings. N, P and Ca contents were appreciably high in inoculated plants, representing that they had a higher potential for nutrient uptake in comparison to control plants	(Ahmad et al., 2013; Flores-Félix et al., 2015; García-Fraile et al., 2012)
Rhizobium	ACC deaminase synthesis	Pepper, Tomato Mung beans	-	-	(Ahmad et al., 2013; García-Fraile et al., 2012)
Rhizobium	Siderophore production	Tomato, Pepper, Carrot, Lettuce,	Seed Inoculation Seedlings were inoculated with 250 lL plant of a bacterial suspension with a turbidity of 5 in McFarland standards (1.5×10^9 CFU/ml).	Strain TPV08 colonies were enclosed by a yellow-orange halo (3.5 mm radium around colonies) indicating the production of siderophores	(Flores-Félix et al., 2015; García-Fraile et al., 2012; Kumar et al., 2010)
Sinorhizobium	Chitinase and β-glucanases production	Pigeon pea	-	-	(Kumar et al., 2010)
Sphingomonas	Gibberellin synthesis	Tomato	-	-	(Khan et al., 2014)
Streptomyces	Indole acetic acid synthesis	Indian lilac	-	-	(Verma et al., 2011)
Streptomyces	Siderophore production	Indian lilac	-	-	(Verma et al., 2011)

are important in the interactions between microbes. The previous study concluded that some carbohydrates or amino acids acted as potent chemoattractants for microorganisms. *P. fluorescens* demonstrated high chemoattractants toward certain amino acids, including cysteine, glycine, isoleucine, lysine, methionine, phenylalanine and serine in the case of tomato plants, which promoted successful root colonization (Oku et al., 2012).

Pseudomonas putida is a saprotrophic soil bacterium. Using 16S rRNA, *P. putida* was affirmed to be a Pseudomonas animal group and placed in the *P. putida* gathering, with which it shares its name. It can also degrade natural solvents like toluene (Volke et al., 2020; Wijte et al., 2011). This ability has been used in bioremediation or microbes to debase ecological toxins. *Pseudomonas putida* is a plant growth-promoting rhizobacterium (PGPR). There was less anthocyanin colour for all plants with *P. putida* strains, yet biomass was consistently more prominent with PGPR strains (Ali & Glick, 2019; Singh, 2019; Volke et al., 2020; Zulueta-Rodriguez et al., 2014). Plant growth promoting strain *P. putida* BSP9 and the rhamnolipid biosurfactant it produces is a novel technique for enhancing the productivity of *Brassica juncea*. It was observed that the combination of *P. putida* BSP9 and rhamnolipid BS showed the maximum enhancement in the growth parameters of *B. juncea*, including root and shoot length, total fresh and dry weight, number of pods, total oil content, total chlorophyll and flavonoid content (Mishra et al., 2020).

Streptomyces

Actinomycetes are gram-positive bacteria with a more G+C genome ratio (Bhatti et al., 2017; Subramani & Sipkema, 2019). They are primarily aerobic, although some are anaerobic. Actinomycetes are unusual among rhizosphere microorganisms in promoting plant growth (Javed et al., 2021; Olanrewaju & Babalola, 2019). The *Streptomyces* genus is a significant source of bioactive natural products (Hifnawy et al., 2020; Sarmiento-Vizcaíno et al., 2018). Actinobacteria create around two-thirds of natural antibiotics, with *Streptomyces* producing approximately 75 per cent (Moumbock et al., 2021). Most soil actinobacteria thrive in alkaline to neutral environments (Anilkumar et al., 2017). They are now called growth-promoting rhizobacteria (Anilkumar et al., 2017). Most plant growth-promoting actinomycetes have antifungal or antibacterial activity, indicating their potential as biological control agents (Ma et al., 2019). Recently, a relationship between endophytic Actinobacteria and medicinal plants from Northeastern India was described. It was proposed that this might be a source of bioactive compounds and antibacterial and plant growth-promoting uses (Passari et al., 2020). *Streptomyces* have evolved various compounds competing with hydroxyl ions for ferric iron (Khoshru et al., 2020; Varjani et al., 2020). Most nitrogen-fixing bacteria produce siderophores to get iron. Streptomyces activates the nitrogenase enzyme (Alawiye & Babalola, 2019). *Streptomyces MCR24* had the highest levels of siderophores production, whereas *Streptomyces MCR30* had the lowest amounts (Schütze et al., 2015). Most Streptomyces can invade the rhizosphere and rhizoplane. Endophytes colonize host plant inner tissues (Liu et al., 2017; Olanrewaju & Babalola, 2019; Vurukonda et al., 2018). Other factors that influence this process include quorum sensing, multiplication rate of amino acids and siderophores, antibiotic production and development of 1-glucanases and chitinases (Olanrewaju & Babalola, 2019; Sayyed et al., 2019; Vurukonda et al., 2018). The introduction of PGPS as biofertilizers or biocontrol agents has led to new advances in several areas where such bacteria may be valuable. Due to the high development of bioactive chemicals utilized as defense mechanisms, various studies have focused on these genera (Olanrewaju & Babalola, 2019).

The *Sesbania* rhizome

Sesbania plants and their associated rhizobia offer a non-polluting and more economically viable alternative to chemical fertilizers, herbicides and sewage sludge for enhancing soil fertility (Zainab et al., 2021). As a result of the leakage of chemicals from fertilizers and pesticides into the groundwater, the fertility of the soil is a serious cause for concern due to numerous worrisome health hazards (Zainab et al., 2021). *Sesbania* possesses a variety of characteristics that make them desirable as multipurpose plants and potentially valuable species in agricultural production systems (Evans & Rotar, 2020). *Sesbania* rhizobia are superior to other high-potential N_2-exchanging systems. Sesbania plants and their associated rhizobia are advantageous because they can adapt to acidic, alkaline and waterlogged soil conditions (Evans & Rotar, 2020). Seven unique genospecies of *Agrobacterium*, *Ensifer*, *Neorhizobium* and *Rhizobium* were identified among the *Sesbania cannabina* rhizobia, and they were all characterized as symbiovar sesbaniae due to their highly conserved symbiosis genes and nodulation test results (Cummings et al., 2009; Sindhu et al., 2019). Several *Sesbania* plant rhizobia capable of tolerating extreme conditions of alkalinity, acidity, salinity, drought, metal toxicity and fertilizer were identified. The existence of Rhizobium-tree legume symbiosis, capable of fixing the appreciable amount of N_2 under severe conditions, is fascinating. Thus, *Sesbania* represents the best source of ideal fertilizers in the present and subsequent crops, and therefore, commands great interest as the subject of future research. There is a need to implement the use of *Sesbania* plants and their respective rhizobia as biofertilizers from lab to field so that in the upcoming years, soil health is maintained and the problem of soil infertility can be diminished. Recent high-throughput tools and techniques in the future can also help to increase our understanding of the *Sesbania* plants and their associated microbes (Singh et al., 2021).

Azospirillum species

Bacteria belonging to the genus *Azospirillum* are free-living microbes that promote plant growth (PGPB). They affect the growth and yield of numerous plant species, many of agronomic and ecological importance (Pii et al., 2015). The most accepted theory regarding the mechanism of action of *Azospirillum* spp is its growth promotion, which includes nitrogen fixation (Machado et al., 1991; Santos et al., 2017) and phytohormone, polyamine and trehalose production (Bashan & De-Bashan, 2010). The mode of action of the *Azospirillum* is multiple, and the importance of each of these mechanisms can vary depending on soil and climate conditions and the solubilization of minerals such as iron and phosphorus, which the plant uses (Bashan & De-Bashan, 2010). These 1mechanisms eventually produce larger, and in many cases, more productive plants (Díaz-Zorita et al., 2015; García et al., 2017). *Azospirillum* has improved crop yields of wheat, corn, rice and sugar cane (Bashan & De-Bashan, 2010). It has also been used in chilli pepper, fruit trees and cacti (Bashan & De-Bashan, 2010). In the case of the genus *Azospirillum*, 25 species isolated from different niches have been reported (Table 1). Most of these species have been isolated from roots of wild plants (Dekhil et al., 1997; Xie & Yokota, 2005) and cultured (Beijerinck, 1925; Khammas et al., 1989) from aquatic environments (Lavrinenko et al., 2010; Wu et al., 2021; Yang et al., 2019) and contaminated areas (Zhou et al., 2013).

ROLE OF PGPR IN AGRICULTURE: AN OVERVIEW

The PGPR use is theoretically improved in organic farming because it can be used in synthetic nutrients and insecticides (Bhat et al., 2020; Ijaz et al., 2019; Thakur, 2017). The rhizobacteria develop many substances that, in any way, influence plant growth promotion. Increasingly, commercial biofertilizers containing the best strains of PGPR lead to a greater understanding of the role of PGPR (Figure 2; Riaz et al., 2021). Plant growth regulators may be classified into three groups, namely phytostimulators, biopesticides and biofertilizers. This has resulted in multi-functional regimens for commercial agriculture based on PGPR (Riaz et al., 2021).

PGPR as bioinoculant

The search for the best PGPRs strains and their action mechanism increases with each passing day due to their use as potential commercially available biofertilizers (Hamid et al., 2021; Mahanty et al., 2017; Pathania et al., 2020). Researchers have studied plants' growth, and development as living bacteria and fungi form colonies in the inner plant area after their injection into the soil or root seedlings (Bright et al., 2022; Choudhary et al., 2018; Khairnar et al., 2022; Riaz et al., 2020; Vafa et al., 2021). The microorganisms present in the biofertilizer employ several mechanisms to benefit the crop plants (Manasa et al., 2021; Mir et al., 2022; Nithyapriya et al., 2021). They can either be efficient in nitrogen fixation, phosphate solubilization and plant growth promotion or possess a combination of all such traits (Asaf et al., 2017; Mus et al., 2016). Biofertilizers can fix atmospheric nitrogen through the biological nitrogen fixation (BNF) process, solubilize and provides nutrients such as phosphate (Kusale, Attar, Sayyed, Enshasy, et al., 2021), zinc, and potassium (Baba et al., 2021) to the plants, and secrete plant growth-promoting substances (hormones) (Gurikar et al., 2016; Liu et al., 2017). Further, when applied as seed or soil inoculants, biofertilizers can multiply, participate in nutrient cycling and help crop production for sustainable farming (Basu et al., 2021; Shelat et al., 2017).

Some strains of PGPRs, such as *Azorhizobium*, *Bradyrhizobium*, *Mesorhizobium*, *Rhizobium*, etc., have been documented as potential biofertilizers (Keswani et al., 2019; Mącik et al., 2020). PGPR improves fertility in the rhizosphere across five distinct regions, such as improving nutritional status in exceptional roots proximity, facilitating the host plant symbiosis, increasing the root surface area, and integrating all of the above modes of action (Gupta et al., 2015; Mishra & Arora, 2019; Patel et al., 2019). Two potential methods for enhancing rhizosphere nutrient availability are nitrogen fixation and phosphate solubilization *via* beneficial living organisms.

Endosymbiotic rhizobacteria, including *Bradyrhizobium*, *Rhizobium*, *Mesorhizobium* and *Sinorhizobium*, cause nitrogen fixation in the legumes' root nodules and *Frankia* spp. in root nodules of non-leguminous plants (Mahmud et al., 2020; Raza et al., 2020; Thorman et al., 2020). Symbiotically, *Azotobacter* and *Bacillus* are considered two potential PGPR species

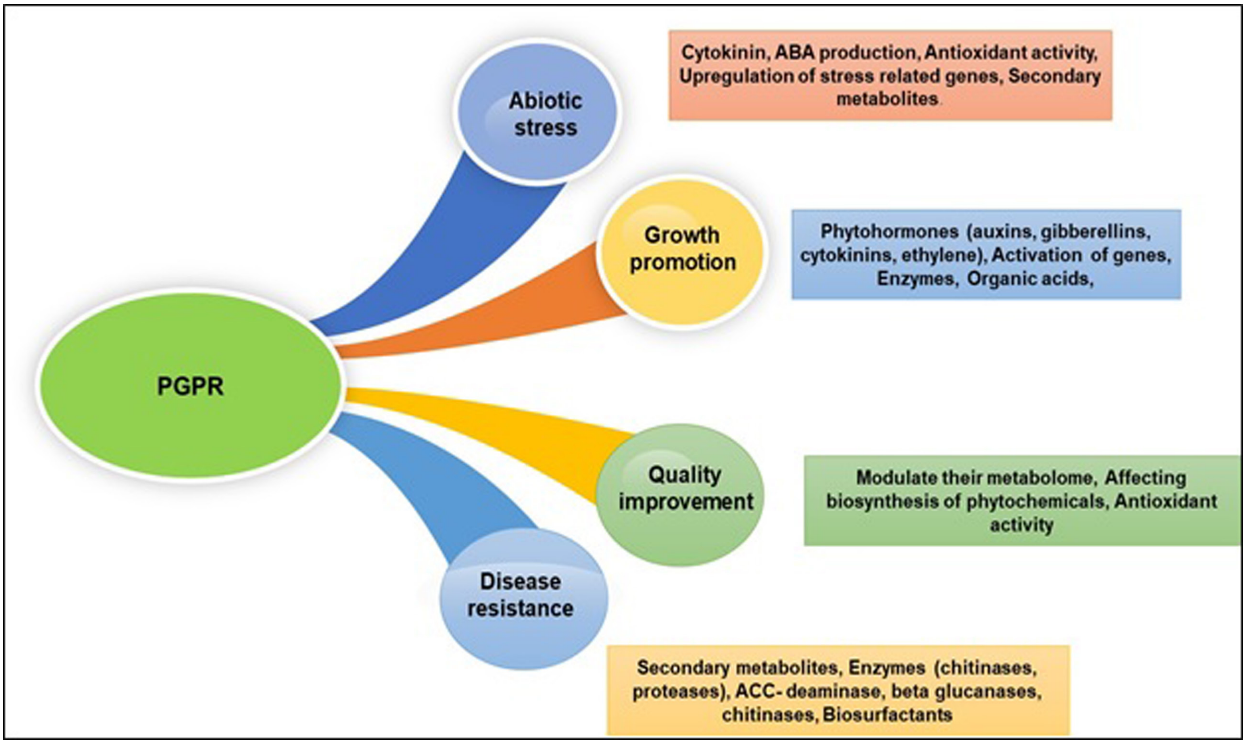

FIGURE 2 Plant-associated rhizobacteria and their role in plant growth and metabolism.

to fix atmospheric nitrogen upon inoculation to the leguminous crop plants. The non-symbiotic species' counterpart includes *Enterobacter*, *Gluconobacterium diazotrophicus*, *Azospirillium*, *Azoarcus*, *Pseudomonas*, *Azotobacter*, *Burkholderia Anabaena*, *cyanobacteria* and *Nostoc* (Arora & Tiwari, 2017; Bashandy et al., 2019). Phosphorous is the second essential plant growth macronutrient, as it contributes a lot to respiration, macromolecule biosynthesis, cell signalling, photosynthesis and energy transfer (Malhotra et al., 2018). It has been reported that PGPR plays a crucial role in the solubilization of precipitated phosphate and makes it accessible for the growth of the crop (Satyaprakash et al., 2017). The plants cannot use the phosphorous unless it is converted into insoluble organic types (soil phytate, inositol phosphate, phosphomono- and triesters) and inorganic minerals (iron phosphates, primarily apatite, calcium and aluminium (Satyaprakash et al., 2017)). Plants take two soluble forms, monobasic ions ($H_2PO_4^{-}$) and dibasic ions (HPO_4^{2-}). PGPRs solubilize insoluble phosphates via two different strategies

1. Hydrolysis of phosphoric esters that mineralize organic forms of phosphate via synthesis of extracellular enzymes (phytases/phosphatases)
2. Solubilization of inorganic phosphate compounds by releasing mineral dissolving agents or chelating agents containing hydroxyl or hydrogen ions, CO_2 and organic acid anions (Adnan et al., 2017; Verma et al., 2017).

Rhizobacterial strains are widely distributed among various genera like *Achromobacter*, *Bacillus*, *Acinetobacter*, *Alcaligenes*, *Agrobacterium*, *Rhizobium Azospirillum*, *Burkholderia*, *Pseudomonas*, *Enterobacter*, *Serratia*, *Klebsiella* and *Ralstonia* with ACC deaminase activity, that help in decreasing the ethylene accumulation due to which strong root structure is maintained in surviving abiotic stress (Kour et al., 2019; Sagar, Sayyed, et al., 2020; Verma, Mishra, & Arora, 2019). In canola plants, it has been documented that ACC-deaminase-producing bacteria reduced salt-induced ethylene, improved salt tolerance and increased plant growth and crop productivity (Etesami & Maheshwari, 2018; Win et al., 2018). For the growth and development of the plant, the presence of iron and detoxification of heavy metals from soil is of great importance to the production of siderophores by various PGPR species (Khatoon et al., 2020; Singh et al., 2019). Tripathi et al. (2018) elucidated that Fe translocation to plants is seriously disrupted by heavy metal stress, drought and saline. Bacterial siderophores are a potential source of Fe_3^{+} to plants under abiotic stress or decreased Fe conditions (Perez et al., 2019; Ramos et al., 2017).

PGPR as biocontrol agent

PGPR is a considerable concept since it includes bacteria that encourage observable plant growth and increase productivity by protecting the plant against disease attacks (Benizri et al., 2021; Benizri & Kidd, 2018). Phytopathogenic microorganisms are an essential and persistent barrier to organic agriculture and the ecosystem's health (Prasad et al., 2019; Prasad & Prasad, 2001; Varjani & Singh, 2017; Zope et al., 2019). The daily use of chemical pesticides and fungicides has contributed to environmental concerns and has led to disease resistance, leading to the continuous development of new agents (Ismail et al., 2017; Lengai et al., 2020). Environmental Protection Agency (EPA) regulates substances that could cause a danger to the environment (Kassotis et al., 2020). The EPA only requires confident chemicals/pesticides that are harmless in agricultural products; thus, it actively promotes biopesticides (DeJong, 2020; Kassotis et al., 2020). EPA has announced and commercialized some fungus taxa as biopesticides. Using PGPR to provide biochemical attributes that can reduce the magnitude of pathogens and diseases to the same degree as chemical pesticides, chemical pesticides can be altered (Prasad & Prasad, 2001; Ukhurebor et al., 2021). A significant number of pathways used by PGPR are involved in biocontrol, such as direct antagonism through the development of antibiotics, siderophores, HCN, hydrolytic enzymes (chitinases, proteases, lipases, etc.) or indirect mechanisms in which the biocontrol species function as a probiotic by competing with the niche pathogen (Rehman et al., 2020; Shaikh et al., 2018; Verma, Shelake, et al., 2019). Antibiosis is the most studied and commonly identified pathway for biological control agents (Köhl et al., 2019).

The most successful rhizobacteria belong to *Arthrobacter*, *Alcaligen*, *Azotobacter*, *Azospirillum*, *Bradyrhizobium*, *Bacillus*, *Enterobacter*, *Serratia*, *Burkholderia*, *Klebsiella*, *Mesorhizobium*, *Rhodococcus*, *Pseudomonas*, *Flavobacterium*, *Streptomyces*, etc. *Bacillus* and *Pseudomonas* are the two most relevant genera of all PGPR strains that have been widely investigated for antibiotic pathways in disease prevention activities (Fira et al., 2018). The *B. amyloliquefaciens* strains BPSRB4 and BPSR14 have been shown to have antagonistic activity and PGP potential that might be used to generate biofertilizers and biocontrol agents for the development of chilli seedlings (Passari et al., 2018). Due to the success of *Bacillus subtilis* and *Trichoderma* spp. as biocontrol agents, scientists have been looking for substitutes. Recently, filamentous actinobacteria have shown promising results as an alternative. One more research study revealed that *Acinetobacter lactucae* Strain QL-1, a novel quorum quenching candidate effectively degrades bacterial pathogen *Xanthomonas campestris pv. Campestris* (*Xcc*) diffusible signal factor (DSF)-mediated quorum sensing (QS) system.

PGPR as biostimulators

PGPR can act as a phytostimulators via the synthesis of various phytohormones such as cytokinin, indole acetic acid (IAA), ethylene and gibberellin. Phytostimulators or plant growth regulators are organic substances that encourage, impede or alter plant growth and development at low concentrations (1 mM) (Vejan et al., 2016). The ability to produce phytohormones is widely distributed across soil and plant-related microbes. Like cyanobacteria, diverse fungal and bacterial species may have phytohormones (Verma, Mishra, & Arora, 2019). Symbiotic, rhizospheric and epiphytic bacteria known as PGPR can secrete hormones. Ironically, the development of these phytostimulators can also be caused by certain bacteria, such as PGPR in plants. Phytostimulators IAA synthesized by PGPRs influence cell division, cell enlargement, root initiation, phototropism, growth rate, apical dominance, geotropism, etc., in plants (Kour et al., 2019; Rehman et al., 2020). The development of phytostimulators such as IAA, cytokinin and gibberellins or 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase, an enzyme that can lower plant ethylene levels that are usually enhanced by a wide range of environmental stresses such as floods, drought, heavy metals, organic pollutants (Arora & Jha, 2019; Prasad et al., 2019). The IAA development capability can enable bacteria to detoxify excess tryptophan/tryptophan analogues deleterious to the bacterial cell. Cytokinins promote plant cells' division and regulate root growth by inhibiting primary root elongation and lateral root formation (Márquez et al., 2019; Motte et al., 2019). PGPRs are associated with the development of phytostimulators, including the genera *Bradyrhizobium*, *Rhizobium*, *Bacillus*, *Pantoea*, *Rhanella*, *Burkholderia*, *Arthrobacter*, *Herbaspirillum*, *Pseudomonas*, *Enterobacter*, *Mesorhizobium* and *Brevundimonas* (Prasad et al., 2019). The rhizobacterial strains, namely *Proteus mirabilis*, *P. vulgaris*, *Halomonas desiderata*, *Klebsiella pneumonia*, *B. cereus*, *Bacillus megaterium*, *Escherichia coli* and *B. subtilis*, are known for cytokinin production (Prasad et al., 2019). *Actinomycetes*, a group of these microbes referred to as plant growth-promoting bacteria (PGPB), are a significant source of bioactive and antibacterial compounds and can manage a variety of phytopathogens (Marimuthu et al., 2020). Several agroactive chemicals and direct and indirect methods enable *Actinomycetes* as biostimulants, biopesticides, bioherbicides and biological control agents (Chaurasia et al., 2018; Vurukonda et al., 2018). The strains of *Nocardiopsis aegyptica* H14 and *Streptomyces albidoflavus* H12 also demonstrated the strongest in vitro biocontrol activity (Djebaili et al., 2021).

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MOLECULAR MECHANISM AND PHYSIOLOGICAL ROLE OF PLANT GROWTH PROMOTION BY RHIZOBACTERIA

PGPR comprises many bacterial strains from diverse taxonomic groups that populate plants' roots and rhizosphere (Mustafa et al., 2019). PGPR can enhance agricultural crop productivity and their resistance to pathogens by inducing intricate changes in the growth and development of plants (Kumar & Dubey, 2020). PGPR plays an essential role in promoting plant growth via a broad range of mechanisms (Etesami & Adl, 2020). These microorganisms can operate as biofertilizers, promoting plant growth and development by improving biotic and abiotic stress tolerance and supporting the host plant's nutritional needs (Mącik et al., 2020; Mahmud et al., 2020; Olanrewaju & Babalola, 2019; Sharma et al., 2013). The molecular foundation of plant-bacteria interaction mechanisms responsible for physiological changes is discovered, primarily due to the growing "omics" methodologies. The methods of action by which PGPRs enhance plant development have generally been divided into direct mechanisms occurring within the plant and indirect mechanisms occurring outside the plant (Rosenberg et al., 2008). Direct modes of action of the PGPR include improving plant nutrition by providing phytonutrients such as fixed nitrogen or solubilized minerals from the soil (such as Zn, P, Fe, K and other essential mineral nutrients) and/or stimulating plant growth and development by regulating plant hormone levels in the plant's environment (like gibberellins, auxins, cytokinins, ethylene and abscisic acid) (Bashandy et al., 2019; Singh et al., 2017; Figure 3 and Table 2) (Choudhary et al., 2011; García-Fraile et al., 2015).

Indirect effects of PGPRs on plant health include suppressing phytopathogens and other harmful microorganisms through parasitism, competing for nutrients and niches within the rhizosphere, producing antagonistic substances (such as hydrogen cyanide, siderophores, antibiotics and antimicrobial metabolites), and lytic enzymes (such as chitinases, glucanases and proteases), inducing systemic resistance in plants against a broad-spectrum range of root and foliar pathogens (Etesami et al., 2017; Jadhav et al., 2020; Reshma et al., 2018, 2020; Riaz et al., 2021; Vinay et al., 2016). Therefore, direct mechanisms affect plant growth regulators' stability by releasing growth regulators or hormones derived from plants, which promote the plant's metabolism and enhance its capacity to adapt. While indirectly contributing to defensive processes, plants are affected by signals derived from bacteria. Due to the direct and indirect impacts of PGPRs on host plants have emerged as suitable candidates for formulation and commercialization as bio inoculants and photo-protective microbial products. On the other hand, the manner and mechanism of PGPR activity differ depending on the host plant type (Gupta et al., 2015). PGPR action is also influenced by several other factors, including biotic factors such as plant genotype, developmental stages, plant defense mechanisms and the presence of other members of the microbial community, and abiotic factors such as soil type, structure, soil management history and the occurrence of prevalent environmental conditions (Bashandy et al., 2019).

Typically, rhizobacteria stimulate plant growth by synthesizing phytohormone precursors (Perveen et al., 2002), enzymes, vitamins, antibiotics and siderophores, hindering ethylene production. Besides, rhizobacterial strains can also solubilize inorganic phosphate; boost plant stress tolerance to metal toxicity, drought, salinity and organic phosphorus mineralization, leading to increased plant growth. Plant growth booster of rhizobacteria also stimulates plant growth by generating different enzymes that induce physiological changes in plants. Ethylene is critical in many developmental processes, such as leaf senescence, leaf abscission, epinasty and fruit ripening (Kusale, Attar, Sayyed, Malek, et al., 2021; Vogel et al., 1998). Ethylene synthesis also occurs at the time of plant infection with rhizobacteria. Symbiotic nitrogen fixers improve the growth of legumes by (1) raising the availability of nutrients in the rhizosphere, (2) supplying N to plants through N_2 fixation, (3) mitigating or blocking the negative impacts of phytopathogenic species, (4) by improving other advantageous symbioses of the host and (5) by raising the root surface region.

Various investigations demonstrate that bacteria directly affect plant auxins homeostasis by producing it. There is copious information indicating auxin synthesis by diverse PGPR strains in culture. Intriguingly, high auxin levels are synthesized by nonpathogenic rhizobacteria strains such as *Enterobacter* sp. I-3 could have an inhibitory result on plants. A study revealed an increase in the expression of IAA biosynthesis genes and the amount of endogenous IAA in the MR in the plants when inoculated with the PGPR strains *Phyllobacterium brassicacearum* STM196 and *Bacillus* sp. LZR216.PGPR can affect ethylene's homeostasis by influencing gene expression encoding enzymes for ethylene synthesis, ACC-synthase and ACC-oxidase. For example (*Burkholderia phytofirmans*) PsJN enhances ACS and ACO gene expression in *A. thaliana* (ACS5, ACO1 and ACO2) *Panicum virgatum*, while in *A. thaliana*, ACS7 and ACS11 gene was enhanced by PGPR *Phyllobacterium brassicacearum* STM196. Studies have shown that PGPR may regulate the concentration of plant cytokinin, and cytokinin can be produced by different PGPR strains. It has been demonstrated that cytokinin levels in the shoots of *Platycladus orientalis* plants

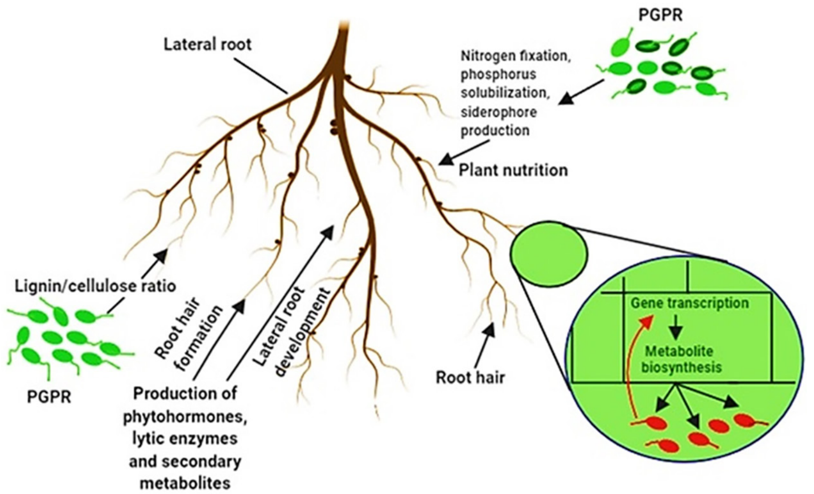

FIGURE 3 The molecular mechanism behind PGPR for plant growth and development.

TABLE 2 PGPRs on alleviating abiotic stresses in crop plants

Stress	Crop	Rhizobacteria	References
Salinity	*Arachis hypogea*	*B. licheniformis* K11	(Lim et al., 2011)
	Phaseolus vulgaris	*Aneurinibacillus aneurinilyticus*, *Paenibacillus* sp.	(Gupta & Pandey, 2019)
	Stevia rebaundiana	*Streptomyces* spp.	(Tolba et al., 2019)
	Abelmoschus esculentus	*Enterobacter* sp.	(Habib & Kausar, 2016)
Drought	*Zea mays*	*Klebsiella variicola* F2, *Pseudomonas fluorescens* YX2 *Raoultella planticola* YL2	(Gou et al., 2015)
	Oryza sativa	*Azospirillum brasilense* Az.39	(Ruíz-Sánchez et al., 2011)
	Helianthus annuus	*Achromobacter xylosoxidans* (SF2) *Bacillus pumilus* (SF3 and SF4)	(Castillo-Lorenzo et al., 2019)
	Vigna radiata	*Pseudomonas fluorescens* strain Pf1 *Bacillus subtilis* EPB5, EPB22 and EPB31	(Saravanakumar et al., 2011)
	Cucurbita pepo	*Bacillus circulans* ML2, *Bacillusmegaterium* ML3	(El-Meihy, 2016)
Heavy metal	*Solanum nigrum*	*Bacillus genus*	(Akhtar et al., 2021)
	Mentha piperita	*Alcalegenes faecalis*, *B. amyloliquefaciens*	(Zafar-ul-Hye et al., 2021)
	Lycopersicon esculentum	*Pseudomonas aeruginosa*, *Burkholderia gladioli*	(Khan et al., 2021)
	Triticum aestivum	*Bacillus siamensis*	(Awan et al., 2020)
	Pisum sativum	*V. paradoxus* 5C-2	(Belimov et al., 2003)
	Brassica nigra	*Bacillus cereus*	(Akhtar et al., 2021)
Heat	*Lycopersicon esculentum*	*Bacillus cereus*	(Khan, Asaf, et al., 2020)
	Triticum aestivum	*Bacillus velezensis* 5113	(El-Daim et al., 2019)
	Triticum aestivum	*Pseudomonas brassicacearum*, *Bacillus thuringiensis*, *Bacillus subtilis*	(Ashraf et al., 2019)

when inoculated with a cytokinin-producing PGPR strain *Bacillus subtilis* (AE016877)

ROLE OF PGPR IN COMBATING THE ABIOTIC STRESS

PGPR promotes plant growth by enhancing abiotic stress tolerance in plants, fixating nutrients for easy uptake by the plant, triggering the synthesis of plant growth regulators, forming siderophores, volatile organic compounds and protection enzymes glucanase, chitinase and ACC-deaminase for the prevention of plant diseases (Figure 4) (Bhat, Tariq, Nissar, et al., 2022; Choudhary et al., 2011; Khan et al., 2021; Tariq et al., 2022) (Table 2).

The mechanism of action of each PGPR varies depending on the kind of host plant (García-Fraile et al., 2015). Plant biostimulant treatment is recommended under stress conditions as an effective agronomic strategy to promote tolerance to poor soil and severe environmental

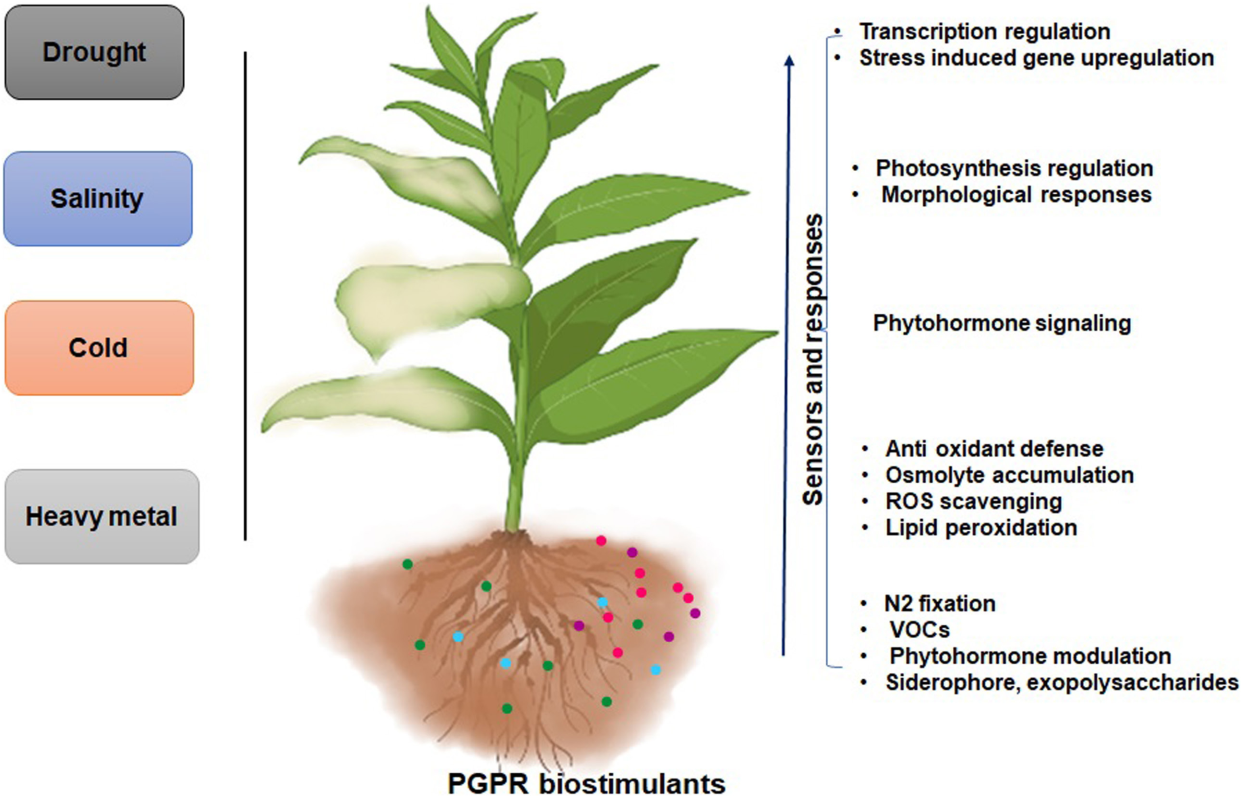

FIGURE 4 Role of PGPR in combating the abiotic stress in plants.

conditions and mitigate the negative impacts of suboptimal growing conditions on agricultural and horticultural crops (Haney et al., 2015). It has been shown that plant growth rhizobacterium (PGPR) may improve plant responses to abiotic stresses and can also stimulate physical, chemical and biological activities (Sharma et al., 2017) through a variety of mechanisms (Adnan et al., 2017; Gupta et al., 2015; Mahmud et al., 2020; Mustafa et al., 2019; Raza et al., 2020). A great deal of study has been done on bacterial isolates that can enhance abiotic stress mitigation in various crop species. By regulating osmolytes and stress-responsive genes and exacerbating changes in the roots, PGPR can increase drought tolerance by producing phytohormones, volatile chemicals, ACCD, exopolysaccharides and antioxidants as by regulating osmolytes and stress-responsive genes. By regulating osmolytes and stress-responsive genes, PGPR can augment drought tolerance in plants (Khan, Bano, et al., 2020; Rehman et al., 2020). Plants benefit from PGPR by enhancing nutrient absorption, achieving ion homeostasis, decreasing oxidative stress by increasing antioxidant activity, lowering volatile organic compounds (VOCs), and improving photosynthesis (Etesami & Maheshwari, 2018; Hamid et al., 2021; Kour et al., 2019). Genera with cold-adapted PGPR include *Pseudomonas*, *Bacillus*, *Exiguobacterium*, *Paenibacillus*, *Providencia* and *Serratia*. Psychrotolerant PGPR has various properties that make them valuable biostimulants for reducing cold stress. Examples are nutrient solubilization, Fe-chelating chemicals, ACC deaminase synthesis, IAA and bioactive molecules. PGPRs regulate plant health by improving nutrient uptake, guarding against phytopathogenic microorganisms and increasing tolerance to abiotic stressors (Milledge, 2011; Sattar et al., 2019). It stimulates plant development by increasing abiotic stress tolerance, fixing nutrients for easy absorption, activating plant growth regulator synthesis, producing siderophores, volatile organic compounds and protective enzymes glucanase, chitinase and ACC-deaminase (Choudhary et al., 2011). The manner of action of each PGPR varies depending on the host plant (García-Fraile et al., 2015).

Heat tolerance

Temperature stress alters hormone formation, especially ethylene, which can stifle plant growth (Young et al., 2006). Temperatures between 60 and 75°F are ideal for plant growth (Banerjee & Roychoudhury, 2018; Marchin et al., 2022). Abiotic stress reduces crop yields when temperatures rise over a safe threshold. Drought, salinity, heavy metal exposure and temperature affect plant metabolism and growth, but heat stress is the most damaging of these abiotic stresses. Heat stress occurs when the temperature rises above 75°F. Plant morbidity and mortality increase due to heat stress, and their quality declines (Bhat et al., 2020; dos Santos et al., 2022; Haider et al., 2022; Perrella et al., 2022). Plant cells may undergo permanent changes, like cellular death, if heat stress persists for an extended period. Weeding, leaf curling and fruit drop are just some symptoms plants exhibit when under too much heat stress (Faizan et al., 2022). In plants, heat stress damages cellular machinery and alters chromatin structure by increasing membrane fluidity, causing a reaction series to become uncoupled.

Plant cells accumulate reactive oxygen species and intermediate intermediates due to reaction decoupling. The cytoskeleton of plant cells is disrupted by heat stress that alters the fundamental dogma (Ali et al., 2020; Hassan et al., 2021; Shaffique et al., 2022). Photosynthesis in photosystem II (PSII) is impaired when the chloroplast thylakoid membrane detaches from the chloroplast in response to heat stress (Naik et al., 2019). High-temperature stress induces denaturation and accumulation of cellular proteins if left unchecked, leading to cell necrosis. Grain abortion may occur due to an imbalance between ABA and cytokinins resulting from excessive heat stress during the reproductive period (Hifnawy et al., 2020). Inhibition of standard transcription and translation, enhanced expression of genes coding for heat shock proteins, and thermotolerance induction are all heat responses (Moumbock et al., 2021).

On the other hand, low-temperature stress disrupts metabolic pathways, alters membrane properties and protein structure, and prevents enzymatic reactions (Salwan & Sharma, 2020). The cold will induce flower sterility by interfering with meiosis during spore formation (Anilkumar et al., 2017). The inoculation of microorganisms increases tolerance and resilience to heat stress. The cross-protection of plants would benefit significantly from the isolation and identification of helpful microorganisms. By synthesizing phytohormones and other metabolites, beneficial bacteria improve plant defense mechanisms while reducing the negative impacts of stress. Plant–microbial interactions activate the antioxidant defense system. They have also been found to improve ion homeostasis by maintaining osmoprotectant levels. Therefore, it is important to explore plant-associated microbial communities (Shaffique et al., 2022).

Osmotic stress

Osmotic stress in plants can be caused by dry and salty soils, resulting in cell dehydration due to a shortage of water (drought) or a lack of water supply (salinity). These two constraints are often agronomically significant since high salinity in the soil is primarily caused by irrigation, which is required for growing yields in many parts of the world where rainfall is scarce. If the amount of water needed to expel ions from the superficial soil layer is inadequate, they collect, increasing salinity (Alawiye & Babalola, 2019). Plants growing in such soils are often subjected to osmotic stress, decreasing water absorption and raising tissue ionic concentrations to dangerous levels (Vurukonda et al., 2018). PGPR reduces stress symptoms via several mechanisms, including the development of Na^+-binding exopolysaccharides (Liu et al., 2017), improved ion homeostasis (Ijaz et al., 2019), and reduction of ethylene levels in plants through ACC deaminase (Thakur, 2017), and IAA synthesis (Riaz et al., 2021).

Drought stress

Drought severity that has increased as a result of human activity and global warming poses a serious threat to agricultural productivity. The demand for environmentally friendly solutions to ensure the security of the world's food supply has increased as a result. Plant growth-promoting rhizobacteria (PGPR) application has potential benefits. The plant's survival during a drought is guaranteed by PGPR through a variety of mechanisms, including osmotic adjustments, increased antioxidant activity, phytohormone production, etc., and these mechanisms also promote the plant's growth. Additionally, new developments in omics technologies have improved our understanding of PGPR, which makes it easier to investigate the genes involved in colonizing plant tissue (Baba et al., 2021; Jabborova et al., 2021, 2022; Kapadia et al., 2021; Kapadia, Kachhdia, et al., 2022; Kapadia, Patel, et al., 2022; Khan et al., 2021; Khumairah et al., 2022).

Beneficial microorganisms that facilitate drought tolerance and boost plant water usage have recently gained much publicity. Technological advancements in next-generation sequencing and micro biomics have aided these attempts (Verma et al., 2017). Plant growth-promoting rhizobacteria (PGPR) are thought to be a long-term synergistic biological way of dealing with water scarcity in crop production (Khan, Bano, et al., 2020). By regulating osmolytes and stress-responsive genes and aggravating changes in the roots, PGPR can confer drought tolerance via releasing phytohormones, volatile compounds, ACCD, exopolysaccharides and antioxidants (Khan, Bano, et al., 2020; Rehman et al., 2020). *Pseudomonas putida* MTCC5279 ameliorated drought stress in chickpea (*Cicer arietinum*) plants by modulating membrane integrity, osmolyte accumulation (proline, glycine betaine) and ROS scavenging ability. Stress responses were positively modulated by the bacteria resulting in differential expression of genes involved in ethylene biosynthesis (ACO and

ACS), salicylic acid (PR1), jasmonate (MYC2) transcription activation, SOD, CAT, APX and GST (code for antioxidant enzymes), DREB1A (dehydration responsive element binding), NAC1 (transcription factors expressed under abiotic stress), LEA and DHN (dehydrins) (Tiwari et al., 2016).

Heavy metal stress

Environmentalists are concerned about the toxicity of heavy metals due to their limited degradability and high persistence in the environment. The toxicity of metals varies depending on their concentration or type. Certain heavy metals are hazardous at doses. Cd and Hg ions are harmful at 0.001 0.1 mg l21; however certain elements change their nature in response to their surroundings (Singh et al., 2019). Their buildup in the soil directly influences its texture and pH, reducing crop development by interfering with various biological processes (Benizri & Kidd, 2018; Sagar, Riyazuddin, et al., 2020). In plants, heavy metal stress has both direct and indirect consequences, including oxidative stress via a variety of indirect mechanisms (e.g., glutathione depletion or binding to proteins—sulphhydryl (SH) groups) or by inhibiting anti-oxidative enzymes, thereby inducing ROS-producing enzymes (e.g., Nicotinamide Adenine Dinucleotide Phosphate (NADPH) oxidases) (Varjani & Singh, 2017). Heavy metal-tolerant PGPR like *Pseudomonas*, *Streptomyces*, *Methylobacterium* and *Bacillus* can help mitigate heavy metals' adverse effects on crops while increasing their growth and productivity. PGPR biostimulants are incredibly efficient at reducing heavy metal toxicity in plants. They inhibit heavy metal translocation to various regions of the plant by modifying their mobilization via complexation, precipitation, redox processes, chelation and adsorption (Ismail et al., 2017; Lengai et al., 2020; Sayyed et al., 2015). Additionally, rhizospheric bacteria produce extracellular polymeric substances (EPS) (Nasab et al., 2022; Sheikh et al., 2022) such as polysaccharides, glycoproteins, lipopolysaccharides and soluble peptides that contain many anions binding sites and thus aid in the expulsion or recovery of heavy metals from the rhizosphere via biosorption. Furthermore, heavy metals mobilization and subsequent bioavailability in excess by siderophores, organic acids or bioleaching remain questionable in heavily polluted areas. The frequently employed microbial species include *Bacillus* spp., *Raoultella ornithinolytica*, *Pseudomonas flourescens*, *Brevibacterium* sp., *Acinetobacter* sp., *Aspergillus* sp., *Candida* sp., *Trichoderma* sp. and *Candia* spp., can effectively degrade pyrethroids toxic compounds into non-toxic compounds (Bhatt et al., 2019). The plant-associated microbial species augment the metal solubility due to the production of important enzymes such as pyrethroid hydrolase enzyme (pyrethroid catalysing esterase) which regulates pyrethroid degradation (Bhatt, Bhatt, et al., 2020). Several studies reveal that microbial and physicochemical paraquat degradation methods and pathways, analyse the potential of bioremediation in paraquat-contaminated environments (Huang et al., 2019).

Salinity stress

In the upcoming years, it is predicted that soil salinity will rise more quickly, which will harm agricultural production. It has been discovered that many conventional methods for reclaiming salt-affected lands are unsustainable and economically less feasible. PGPR has become a versatile tool for reclaiming salty soil. They also aid in reducing the negative effects of salt stress on plants. PGPR has several mechanisms for enhancing plant survival in salty environments. The biocontrol and plant growth-promoting properties of PGPR-based biostimulants against a variety of phytopathogens are well known.

Soil salinization affects more than 6% of global soil, putting 22% and 33% of total cultivated and irrigated agricultural land under threat, lowering crop production (Gupta et al., 2015). By 2050, almost half of all arable land will be affected by soil salinity, which grows at a rate of 10% each year due to several causes, including implausible irrigation activities, irrational fertilization, inadequate drainage and climate change (Verma, Mishra, & Arora, 2019; Yadav et al., 2017). PGPR can alleviate salinity stress in plants through many synergistic mechanisms, including osmotic regulation by prompting the accumulation of osmolytes and signalling of phytohormones, increasing nutrient uptake and attaining homeostasis of ions, and reducing oxidative stress through enhanced antioxidant activity (Najafi et al., 2021), volatile organic compounds (VOCs) (Sudha et al., 2022), and photosynthesis amelioration (Etesami & Maheshwari, 2018; Kour et al., 2019). Studies have shown that several actinomycetes isolated from Algerian salt soil have been found to exhibit good in vitro and planta (*Solanum lycopersicum* L.) plant growth-promoting (PGP) properties under normal circumstances (Sharma et al., 2019). These investigations showed salt tolerance up to 10% (i.e., 1.7 M). A decreased phosphate solubilization rate in a saline environment is also reported (Rangseekaew et al., 2022). Another mechanism for PGPB to induce plant tolerance against various environmental stresses is the regulation of phytohormones synthesis (Subramaniam et al., 2020). Phytohormones help plants tolerate salt stress by developing a protective response against stress promoting cell proliferation in the root system, and increasing the surface area for water and nutrient uptake through the overproduction of root hairs (Paul & Lade, 2014). Growth regulators, such as auxins, reduce salinity-induced dormancy in wheat seeds. Many PGPBs can produce IAA and participate in plant growth and development. Studies have shown that marine actinobacteria may boost plant development under salt stress, especially Dermacoccus (Rangseekaew et al., 2022). *Pseudomonas putida* and *Enterobacter cloacae* improvise the plant resistance to salt stress (Cheng et al., 2012). The plant biomass is enhanced through the inoculation of *Pseudomonas putida* under drought stress condition.

CONCLUSION AND FUTURE PERSPECTIVE

Demand for food production has increased due to the expanding world population. Nevertheless, the production of crops and food is seriously threatened by the growing negative impacts of climate change, environmental pollution, the introduction of aggressive viruses, and ancient traditional agricultural practices. For better and sustainable agricultural production, preservation of food security, greater yields, efficient plant protection and the agroeconomic industry, PGPR has become a prominent alternative to conventional farming methods during the past several decades. Interactions between plants and microbes in the rhizosphere have made it possible for plants and the PGPR they are linked with to exchange vital compounds. The commercialization of PGPR as biofertilizers should get illustrated. In this context, substantial development has been made worldwide in biofertilizer production for PGPR. PGPR has also been very efficient and necessary to improve crop production and soil fertility. In general, we can assume many advantages have been achieved by incorporating microbial biotechnology into agriculture. Still, many obstacles and opportunities for future sustainable agricultural development remain to be addressed. India, an agricultural country with a large population size, largely depends on its agroeconomy. Keeping this in mind, the need for research and improvement in agriculture is the need for an hour. The role of PGPR in providing beneficial services, such as bio fertilization, photostimulation, biopesticides and bioremediation, exhibit a substantial influence on crop production and sustainable agriculture. Therefore, we should facilitate their successful implementation in the core agricultural system for better crop production and sustainable agriculture. The use of PGPR will become a reality with more meticulous research and growth and will be conducive to basic processes that drive the sustainability and productivity of agroecosystems, resulting in an ideal agricultural system that is efficient, preserves and improves human health, benefits the environment and provides the world's population with adequate food. Finally, it may also be helpful to search for new PGPR strains for biofertilizers and create a microbial diversity map for any region, just like nutrient mapping. The demand for biostimulants as growth promoters has increased since 2000, and publications and research interest in employing beneficial microorganisms to handle heat stress are rising. The injection of microorganisms increases tolerance and resilience to various stresses. The cross-protection of plants would benefit significantly from the isolation and identification of helpful microorganisms. Appropriate technical calibrations and tests to boost the development and maintenance of sustainable agriculture and microbial diversity can also be used to build advanced simulation models related to microbes and their behavioural patterns in changing edapho-climatic conditions. Further studies on the selection of suitable rhizosphere microbes and the development of microbial species, together with the advancement of multidisciplinary research-integrating applications in agro-biotechnology, biotechnology, chemical engineering, nanotechnology and material sciences, and putting together various ecological and functional biological approaches, will provide new formulations and prospects Developing alternative compositions viz., liquid inoculants/granular, PGPR identification for biocontrol against numerous plant pathogens in bioassays is a prerequisite for sustainable agriculture.

CONSENT TO PARTICIPATE

All authors have given their consent for participation in this submission and possible publication of this study.

CONSENT FOR PUBLICATION

All authors are aware of this submission and have consented to the publication of this study.

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CONFLICT OF INTEREST

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