

## Review

## Impact of plant growth-promoting rhizobacteria (PGPR) on plant nutrition and root characteristics: Current perspective<sup>☆</sup>

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## ARTICLE INFO

## Keywords:

PGPR  
Rhizosphere  
Root trait  
Phytohormones  
Plant nutrition

## ABSTRACT

Through a variety of mechanisms, including increasing the amount of readily available mineral nutrients, regulating phytohormone levels, and biocontrol of phytopathogens, plant growth-promoting rhizobacteria (PGPR) associated with the plant rhizosphere either directly or indirectly stimulates plant growth and development. The establishment, survival, and persistence of PGPR inoculants are widely acknowledged to be contingent upon these two parameters, in addition to the intricate network of interactions within the rhizosphere. In general, the soil is a moist environment with significant amounts of carbon that have been degraded and harbors a large population of soil microbes. The rhizo-microbiome is crucial to agriculture because a wide variety of root exudates and plant cell debris attract unique and distinct patterns of microbial colonization. The rhizo-microbiome plays a crucial role in the manufacture and regulation of extracellular molecules, including hormones, secondary metabolites, antibiotics, and various signaling chemicals. Additionally, the microbial composition within the rhizo-microbiome influences soil texture enhancement. Research has shown that PGPR can be used to treat plants or inoculate plants to promote plant development. PGPR alters the physiology of the entire plant, which enhances nutrient uptake and affects the effectiveness of root activity. The specific biochemical processes of plants involved in this phenomenon are often not well understood. Nevertheless, new studies have shed light on the mechanisms via which signaling by PGPR can induce various plant responses, both at the local and systemic levels. Insufficient information is available regarding the impact of the PGPR mechanism and molecules on metabolic pathways in root characteristics. Consequently, this review will concentrate on elucidating the PGPR mechanism and identifying the essential molecules that exert influence on root-microbe interactions.

## Introduction

A diverse yet substantial population of microorganisms requires the ecological niche known as the rhizosphere, which consists of the soil

surrounding a plant's roots, affected via root exudates, to grow and function (Bakker et al., 2013). Rhizosphere-colonizing bacteria called plant growth-promoting rhizobacteria (PGPR) have the capacity to stimulate plant growth in a number of direct and indirect ways

<sup>☆</sup> This article is part of a special issue entitled: "Role of Microorganisms in Plant Growth, Stress Amelioration and Phytoremediation" published at the journal *Plant Stress*.

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<https://doi.org/10.1016/j.stress.2023.100341>

Received 16 August 2023; Received in revised form 19 October 2023; Accepted 27 December 2023

Available online 28 December 2023

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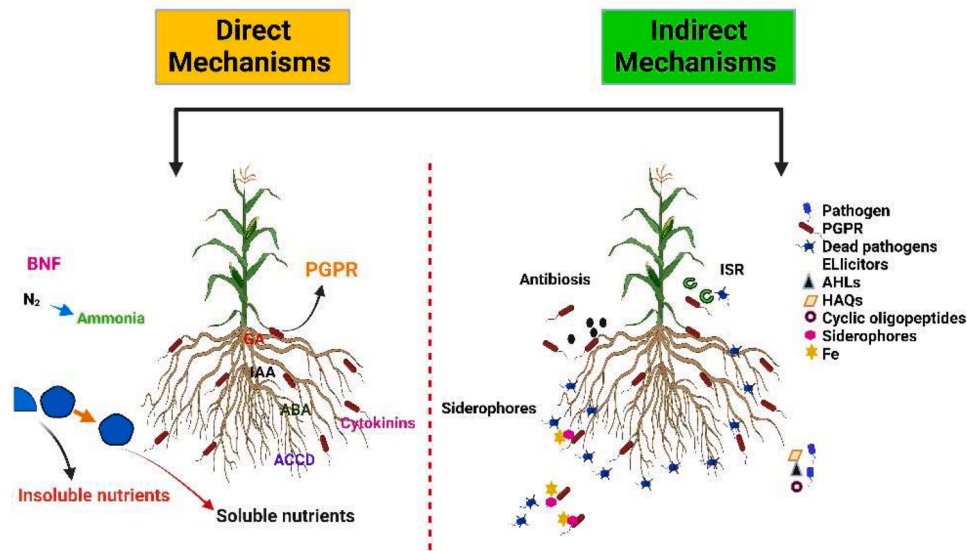


Fig. 1. Direct and indirect mechanisms promoting host-PGPR interactions and plant development.

(Hartman and Tringe, 2019). The root microbiome encompasses the advantageous bacterial communities residing in the microhabitats of the rhizoplane and root endosphere, which play a crucial role in facilitating plant growth. (Salwan et al., 2023). As a result, plants release carbon molecules into the surrounding soil, and microbial populations in the rhizosphere are larger (100–1000 times higher) than those in the main soil (Fazeli-Nasab et al., 2022; Goswami et al., 2016). Terrestrial photosynthetic plants play a pivotal role in the formation and structure of ecosystems. One notable contribution is their ability to establish unique microbiological ecological niches inside plant systems. This is especially true of the rhizosphere, the region of soil where plant roots develop (Ayilara et al., 2022; Courteney-Jones et al., 2022). The root system of a plant has multiple functions, including providing stability by anchoring the plant in the soil, facilitating the absorption of water and ions, storing essential nutrients, and supporting vegetative growth. Furthermore, it has a close interaction with numerous microbial populations present in the soil (Jafari et al., 2022). The root system and its rhizosphere have gotten much less attention from plant physiologists than the rest of the plant, despite their linkages to the biotic environment. In particular, microbial communities that can metabolize the compounds produced by plants and live in this microbial environment are attracted to organic nutrients from plant roots, such as organic acids, phyto-siderophores, sugars, vitamins, amino acids, nucleosides, and mucilage (Bazany et al., 2022; Castro, 2022).

The primary source of carbon in soil is via root exudates, and the rhizosphere is home to a wide range of taxa and a dense microbial community with up to  $10^{10}$  bacteria per gram of soil (Hao et al., 2022; Panchal et al., 2022). The rhizo-microbiome refers to the microbial community that is analogous to the one found in plant roots (Dhungana et al., 2023; Kumar et al., 2022a). Both direct and indirect PGPR pathways may have an impact on plant performance (Fig. 1). Producing substances that stimulate plant growth (phytohormones), increasing the availability and uptake of nutrients in the soil through biological nitrogen fixation, releasing fixed forms of nutrients into plant-useful systems (P, K, and Zn), chelating nutrients (Fe) through the production of siderophores, and other similar processes are examples of direct mechanisms (Kour et al., 2023; Upadhyay et al., 2022). An example of an indirect strategy is resistance to abiotic stress and control of plant pathogens (Gupta and Pandey, 2023). The genera *Acinetobacter*, *Agrobacterium*, *Arthobacter*, *Azotobacter*, *Azospirillum*, *Burkholderia*, *Bradyrhizobium*, *Rhizobium*, *Frankia*, *Serratia*, *Thiobacillus*, *Pseudomonads*, and *Bacillus* are among the bacteria that form a reliable group of PGPR

(Cordero et al., 2023).

There are two main types of beneficial interactions between plants and microbes, i.e. symbiotic alliances where plants and microbes share benefits and costs (Angulo et al., 2022; Astapati and Nath, 2023). A preliminary characterization of mutualistic interactions refers to a limited assemblage of host plants and microorganisms that possess compatibility and establish a closely intertwined relationship, occasionally displaying obligatory traits. They typically result in the development of a structure that is solely focused on the interaction (such as nodules in the relationship between Fabaceae and nodulating rhizobia, or arbuscules in the endomycorrhizal relationship) (Bastias et al., 2022; GOSS et al., 2023). Furthermore, cooperative links (also called associative symbioses) are more intentional and deliberate compared to symbioses (Sharp and Foster, 2022). Rhizobacteria are soil microorganisms that can colonize the surface of a plant's root system (and occasionally the tissue inside the root), promoting the growth and well-being of the plant (Sharma et al., 2023; Vocciante et al., 2022). PGPR are believed to engage in interactions with a diverse array of host plant species, displaying considerable taxonomic variation, particularly within the *Firmicutes* and *Proteobacteria* phyla. This is in contrast to mutualistic symbionts (He et al., 2023a; Lacava et al., 2022; Patwardhan et al., 2022). Both above-ground and below-ground plant parts have benefited from inoculation with PGPR. Nevertheless, greater emphasis has been placed on the aerial components due to their significant economic value as sources of sustenance and animal feed, as well as the convenience associated with collecting and documenting observations pertaining to them. Researchers have focused on the growing evidence about the importance of root traits to ecosystem functioning to understand and test how treatments based on root traits can improve ecosystem processes (Weemstra et al., 2022). A comprehensive comprehension of root system growth and function could facilitate the realization of the second Green Revolution, which is vital for the preservation of global food security. This will allow us to identify root traits that influence crop yields in different contexts and the mechanisms by which they are enhanced (Liu et al., 2022). Investigating PGPR-mediated modulations of root traits can increase the efficiency of agroecosystems (Nagrle et al., 2023). The utilization of PGPR has the potential to facilitate the development of desirable root characteristics that enhance the efficient utilization of soil resources, hence enabling the achievement of sustainable agricultural output (Backer et al., 2018; Li et al., 2023b; Mashabela et al., 2022).

**Table 1**  
Examples of plant nutrition substances secreted by PGPR that promote growth.

PGPR strains	Plant species	Growth substances	References
<i>Acinetobacter</i> spp.	Alfalfa ( <i>Medicago sativa</i> L.)	IAA, phosphate solubilization, and siderophores	Tafaraji et al. (2022)
<i>Azospirillum amazense</i>	Rice ( <i>Oryza sativa</i> L.)	Nitrogenase activity and IAA	dos Santos Ferreira et al. (2022)
<i>Azospirillum</i>	Strawberry ( <i>Fragaria x ananassa</i> )	Siderophores production	Sivasakthivelan et al. (2023)
<i>Azotobacter chroococcum</i>	Canola ( <i>Brassica napus</i> L.)	Gibberellin, kinetin, IAA, phosphate, and antioxidant activity	Abdel Latef et al. (2021), Bhadrecha et al. (2023)
<i>Azotobacter salinestris</i> ASM	Tomato ( <i>Solanum lycopersicum</i> L.)	IAA, ammonia, ACC deaminase, and exo-polysaccharides	Danish et al. (2022)
<i>Azotobacter vinelandii</i>	Common duckweed ( <i>Lemna minor</i> )	Nitrogenase activity and phosphate solubilization	Jain et al. (2021)
<i>Azotobacter</i> (SR-4)	Calabash ( <i>Lagenaria siceraria</i> ) & Okra ( <i>Abelmoschus esculentus</i> )	Nitrogen fixation	Pandove et al. (2022)
<i>Bradyrhizobium</i> sp.	Chickpea ( <i>Cicer arietinum</i> L.)	HCN, IAA, ammonia, siderophores, and exo-polysaccharides	Kiruthika and Arunkumar (2021)
<i>Bradyrhizobium</i> sp.750	Rice ( <i>Oryza sativa</i> L.)	Heavy metals	Fagorzi et al. (2018)
<i>Bacillus subtilis</i>	Tomato ( <i>Solanum lycopersicum</i> L.)	Antifungal activity, osmoregulation, ion homeostasis, antioxidant defense, and methylglyoxal detoxification	Hasanuzzaman et al. (2022); Mahapatra et al. (2022)
<i>Bacillus subtilis</i> DR2	Coriander ( <i>Coriandrum sativum</i> )	Siderophores production	Singh et al. (2022a)
<i>Bacillus subtilis</i> SL-44	Maize ( <i>Zea mays</i> )	Siderophores, IAA, and phosphate solubilization	Xiang et al. (2023)
<i>Bacillus</i> spp. PSB10	Chickpea ( <i>Cicer arietinum</i> L.)	IAA, ammonia, siderophores, and HCN	Wani et al. (2007)
<i>Bradyrhizobium japonicum</i>	Mung bean ( <i>Vigna radiata</i> )	IAA	Zveushe et al. (2023)
<i>Burkholderia</i>	<i>Calendula officinalis</i>	Siderophore, heavy metal solubilization, phosphate solubilization, ACC deaminase, and IAA	Han et al. (2021)
<i>Brevibacillus</i> spp.	Peanut ( <i>Arachis hypogaea</i> L.)	Zn resistance and IAA	Li et al. (2022b)
<i>Bravibacterium</i> sp.	Scots pin ( <i>Pinus sylvestris</i> )	Siderophore	Lutfullin et al. (2022)
<i>Bradyrhizobium japonicum</i>	<i>Glycine max</i> (L.)	IAA	Miljaković et al. (2022)
<i>Enterobacter asburiae</i>	Chickpea ( <i>Cicer arietinum</i> L.)	IAA, siderophores, phosphate solubilization, HCN, ammonia, and exo-polysaccharides	Saikia et al. (2023)
<i>Enterobacter</i> sp.	<i>Cajanus cajan</i>	Phosphate solubilization and ACC deaminase, IAA, and siderophores	Singh et al. (2022c)
<i>Flavobacterium</i>	Common bean ( <i>Phaseolus vulgaris</i> L.)	IAA and siderophores	Feng et al. (2023)
<i>Klebsiella oxytoca</i>	Maize ( <i>Zea mays</i> )	Phosphate solubilization, IAA, and nitrogenase activity	Khalifa and Aldayel (2022)
<i>Mesorhizobium</i> sp.	Chickpea ( <i>Cicer arietinum</i> L.)	Exo-polysaccharides, IAA, siderophores, ammonia, and HCN	Yadav et al. (2022b)
<i>Pseudomonas putida</i>	Scots pine ( <i>Pinus sylvestris</i> L.)	Exo-polysaccharides, ammonia, siderophores, HCN, IAA, and phosphate solubilization	Pinisetty et al. (2022)
<i>Pseudomonas aeruginosa</i>	Maize ( <i>Zea mays</i> L.)	Exo-polysaccharides, ammonia, siderophores, HCN, IAA, and phosphate solubilization	Parvin et al. (2022)
<i>Pseudomonas</i> sp.	Onion ( <i>Allium cepa</i> L.)	Phosphate solubilization	Priya et al. (2022)
<i>Pseudomonas</i> sp. A3R3	Apple ( <i>Malus × domestica</i> )	Siderophores production and IAA	Tirry et al. (2021)
<i>Pseudomonas aeruginosa</i>	Indian Mustard ( <i>Brassica juncea</i> L.)	Siderophores production	Rajkumar and Freitas (2008)
<i>Pseudomonas aeruginosa</i> OSG41	Chickpea ( <i>Cicer arietinum</i> L.)	Salicylic acid, 2, 3-dihydroxybenzoic acid siderophores, phosphate-solubilization, EPS synthesis, and IAA	Pereira (2019)
<i>Pseudomonas jessenii</i>	<i>Sulla flexuosa</i> ( <i>Hedysarum flexuosum</i> L.)	Siderophores, IAA, ACC deaminase, phosphate solubilization, and antifungal activity	Ali et al. (2020)
<i>Pseudomonas fluorescens</i>	Tea	Antifungal activity, siderophores, IAA, ACC deaminase, and phosphate solubilization	Khan et al. (2022)
<i>Pseudomonas chlororaphis</i>	Apple ( <i>Malus × domestica</i> )	Antifungal activity	Wang et al. (2021)
<i>Pseudomonas</i> sp. K32	Rice ( <i>Oryza sativa</i> L.)	Pb and Cd stress	Rai et al. (2023)
<i>Pseudomonas putida</i>	Chamber bitter ( <i>Phyllanthus urinaria</i> )	Pb, Cd resistance, and siderophores	Lopes et al. (2022)
<i>Pseudomonas fluorescens</i> PRS9, GRS1	Maize ( <i>Zea mays</i> L.)	IAA, phosphate solubilization, and siderophores	Ahemad and Khan (2012)
<i>Rhizobium</i> E20-8	Maize ( <i>Zea mays</i> L.)	Antioxidant, siderophores, and IAA	Cruz et al. (2023)
<i>Rhizobium</i> sp. pea	Chickpea	IAA, HCN, siderophores, exo-polysaccharides, and ammonia	Banjare et al. (2023)
<i>Rhizobium</i> sp. lentil	Lentil ( <i>Lens culinaris</i> ssp. <i>Culinaris</i> )	Ammonia, IAA, siderophores, and HCN	Alinia et al. (2022)
<i>Rhizobium phaseoli</i>	Common bean ( <i>Phaseolus vulgaris</i> L.)	IAA	Maslennikova et al. (2022)
<i>Rhizobium leguminosarum</i> bv phaseoli	Common bean ( <i>Phaseolus vulgaris</i> L.)	IAA, ACC deaminase, and siderophore	Kamran et al. (2017)
<i>Rhizobium leguminosarum</i> Thy2	Wheat ( <i>Triticum aestivum</i> )	Siderophores, nitrogen fixation, and cd stress	Nofal and Attia (2023)
<i>Stenotrophomonas maltophilia</i>	Rice ( <i>Oryza sativa</i> L.)	Nitrogenase activity, ACC deaminase, IAA, and phosphate solubilization	Li et al. (2023a)
<i>Serratia marcescens</i>	Sunflower ( <i>Helianthus annuus</i> ) & Maize ( <i>Zea mays</i> )	IAA, siderophores, and HCN	Sriwati et al. (2023)
<i>Sphingomonas paucimobilis</i> ZJSH		IAA	Asaf et al. (2020)
<i>Sphingomonas</i> sp.	Tomato ( <i>Solanum lycopersicum</i> L.)	IAA	Nadeem et al. (2016)
<i>Variovorax paradoxus</i>	Cucumber ( <i>Cucumis sativus</i> )	Siderophores and IAA	Flores-Duarte et al. (2022)
<i>Xanthomonas</i> sp. RJ3	Rapeseed ( <i>Brassica napus</i> )	IAA	He et al. (2023b)

### Impact of plant nutritional rhizobacteria on plant growth

The effects of PGPR on plant nutrition can affect how well plants take up nutrients or how quickly plants develop (Etesami and Adl, 2020; Jalal et al., 2023). The augmentation of root surface area through the application of PGPR has been observed to result in enhanced nutrient absorption. However, the ion transporters in the roots are controlled by regulatory mechanisms that change their behavior depending on the

nutrient demand of the plant (Bhat et al., 2022; Saghafi et al., 2019). The coordination of root growth regulators and ion transporter activities is essential in order to maintain a regular intake of nutrients (Suliman, 2019). Plant growth and nutrient absorption rate increase must be accelerated by PGPR, which must intervene in the pathways that coordinate plant growth and nutrition (Guan et al., 2023; Ortiz-Castro et al., 2020). Rhizobacteria that enhance plant development have the capacity to either activate ion transport systems inside roots or directly enhance

nutrient availability in the rhizosphere. (Carreiras et al., 2023). There are two fundamental forms of bacterial activity that can be taken into consideration when aiming to enhance the nutrition supply. One of the primary impacts of PGPR on plant nutrition is the solubility of phosphate. Soil phosphorus levels are often relatively high; yet, only a tiny fraction of the phosphorus that accumulates from repeated fertilizer applications is used by plants (Office, 2019). Monobasic and dibasic phosphates can be absorbed by plants without the need for mineralization or dissolution by microbes, in contrast to organic or insoluble forms of phosphate (Ding et al., 2021).

Several PGPR can dissolve insoluble forms of phosphate, including *Pseudomonas*, *Bacillus*, and *Rhizobium*. The release of low molecular weight organic acids (such as gluconic acid) and the creation of phosphatases and phytases, which break down organic forms of phosphate compounds, make the external medium more acidic. These acids chelate the cations bound to the phosphate (Dhole et al., 2023; Díaz et al., 2022). Furthermore, a significant percentage of the bacteria associated with plants possess the ability to perform nitrogen fixation, so enabling them to give nitrogen to the plant. Extensive research has been conducted to showcase the role of PGPR in facilitating the nitrogen supply to various plant species, with a special emphasis on sugarcane (Turan et al., 2021). Though, the contribution of N<sub>2</sub> fixation via PGPR to the promotion of plant development is still controversial and hardly acknowledged (Wang et al., 2023b). Moreover, it has been demonstrated that non-fixing rhizobacteria can enhance plant growth, so indicating that this phenomenon is not contingent upon nitrogen supply. For example, *Phyllobacterium brassicacearum* STM196 promotes growth of *Arabidopsis* and oilseed rape, but is probably unable to fix N<sub>2</sub> (Kechid et al., 2022). The effects of PGPR on nutrient absorption systems have only been the subject of a small number of investigations. After being injected with the *Achromobacter* sp. strain U80417, canola plants exhibited higher net influx rates of NO<sup>-2</sup> and K<sup>+</sup> per unit root surface area (Calvo et al., 2019; Turan et al., 2021). When measuring the uptake of NO<sup>-3</sup> in *Arabidopsis* in response to PGPR, inconsistent results can be obtained over time: A 24-h inoculation with *Phyllobacterium brassicacearum* STM196 increased NO<sup>-3</sup> influx in seedlings; a 7-day follow-up showed a decrease in NO<sup>-3</sup> influx (Aluko et al., 2023; Kechid et al., 2022). Since the net uptake rate of NO<sup>-3</sup> was unknown, it is challenging to make a firm conclusion even though ion efflux was not quantified in these studies (Trinder et al., 2021).

Dynamic microbial ecologies and soils rich in organic matter typically need less fertilizer than soils that have undergone conventional treatment (Bender et al., 2016; Costantini and Mocali, 2022). For instance, while controlling the application of organic nitrogen sources, soil microbial mass activity is frequently taken into account. Research on the phyto-microbiome is revealing certain plant-microbe interactions that directly improve plant nutrition (Shah et al., 2022). Several bacterial functions, such as increasing the surface area available to plant roots, nitrogen fixation, P-solubilization, siderophore synthesis, and HCN production, contribute to the facilitation of nutrient acquisition by plants (Farhat et al., 2023; Kumar et al., 2022b; Uzma et al., 2022). For this reason, control of microbial activity has significant potential for providing nutrients to plants. The N-fixing symbiosis between rhizobia and legumes is the most studied and utilized link between plants and bacteria. Rhizobia play a crucial role in this symbiotic association by providing leguminous plants with readily available nitrogen and creating a suitable anaerobic environment necessary for the optimal functioning of nitrogenase (Raj et al., 2021). This interaction leads to significant changes in both the rhizobia and the legume, in the tuber and the new organ that the legume develops. The free-living, rod-shaped rhizobia transform into a branching, N-fixing bacteroid (Khumairah et al., 2022; Mahmud et al., 2020).

The first commercially available microbial products in agriculture, rhizobial inoculants for legumes, are still the most extensively applied agricultural inoculants (Orozco-Mosqueda et al., 2023). Genetic advances in N-fixing symbiosis between rhizobia and crop plants have

proven difficult to achieve. Due to the substantial energy demand associated with the conversion of atmospheric nitrogen to ammonia, the bacterial cell must allocate precedence to oxidative phosphorylation of carbon sources as opposed to glycogen production, in order to enhance the process of nitrogen fixation (Goyal et al., 2016). It was investigated that the application of *Rhizobium tropici* glycogen synthase deletion mutants did not survive in the soil environment, even though bean plants were infected with more nodules and dry matter (Albicoro et al., 2023; Redondo-Gómez et al., 2022). Since the first decade of the twenty-first century, there has been increased interest in commercial inoculants made from free-living N-fixing bacteria such *Azoarcus* species, *Burkholderia* species, *Gluconacetobacter* species, *Diazotrophicus* species, *Herbaspirillum* species, *Azotobacter* species, *Bacillus polymyxa*, and especially *Azospirillum* species (Patra and Mandal, 2022; Picoli et al., 2022). Similar to P, other essential nutrients for example Fe and Zn, may be abundant in soil but inaccessible for plants, which can reduce crop yields (Moon and Ali, 2022). Several bacterial strains produce siderophores or organic acids that act as inhibitors of harmful pathogens and increase the availability of Fe (Roskova et al., 2022; Yankey et al., 2022) (Table 1).

### PGPR as producers of phytohormones and other substances

The root system consists of postembryonic and embryonic roots, unlike many dicotyledonous plants that depend on the primary root and branching lateral roots. Cereal plants, including rice, wheat, and barley, exhibit the growth of a compact and intricate root system characterized by the presence of crown roots and nodular structures (Viana et al., 2022; Kořínková et al., 2022). Complex genetic networks control root traits such as number of branches, branching patterns, length, orientation, angle, and diameter. These networks are also involved in how plants respond to environmental influences (Jung and McCouch, 2013; Singh et al., 2022d). Investigating the relationship between plant phytohormone pathways and the root is a valuable endeavor. Given that the root system serves as the foundation for plant growth and productivity, the potential for hormone disturbance across a significant number of roots is not only theoretically plausible but also very pertinent in terms of adaptation considerations. It holds the plant firmly in place, absorbs nutrients and water, and communicates with soil microbes (Nile et al., 2022). The main characteristics of the geographic distribution of roots or the "root system" are determined by three main developmental processes: (i) the rate of proliferation and differentiation, the two main factors affecting the rate of root development; (ii) the direction of root growth, which indicates the direction in which the root system spreads; (iii) the development of lateral roots, which determines the lateral extent of the root system. Multiple phytohormone pathways exert influence over these many functions (Fig. 2) (Motte et al., 2019; Satbhai et al., 2015).

### Auxin effect on plant growth

Total root surface area may increase due to auxin-induced changes in plant root architecture, which is one of the main reasons PGPR strains accelerate plant development. The enhanced expansion of the root surface area has the potential to promote improved nutrient and water absorption, hence offering advantageous prospects for plant growth and development (Etesami et al., 2015; Hmaeid et al., 2019; Noori et al., 2018). In PGPR, the synthesis of indole-3-acetic acid (IAA) is one of the most crucial methods for promoting plant development (Park et al., 2021). IAA can be produced by more than 80 % of rhizosphere-associated bacteria, including *Azospirillum* species, *Azotobacter* species, *Enterobacter* species, *Pseudomonas* species, and *Staphylococcus* species (Bag et al., 2022; Park et al., 2017). The biosynthesis of auxin is well conserved in plants, wherein the primary sites of auxin production are developing seeds, young leaves, and leaf bases. The transportation of substances occurs through the phloem, whereby they



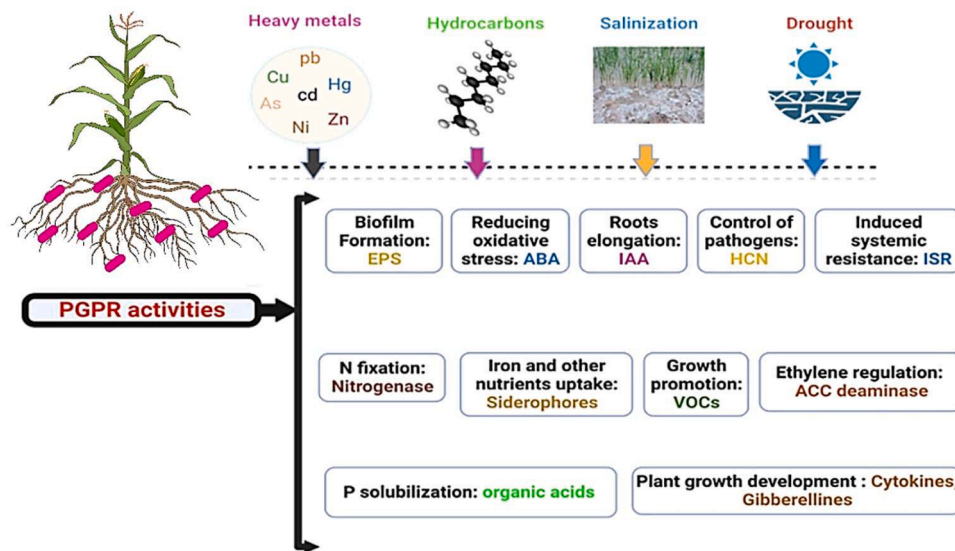


Fig. 2. PGPR's highly effective network of functional interactions supports plant health and performance in response to environmental stressors and abiotic threats. Abbreviations: EPS (exopolysaccharides); ABA (abscisic acid); IAA (indole-2-3-acetic acid); HCN (hydrogen cyanide); VOCs (volatile organic compounds); ACC (1-aminocyclopropane-1-carboxylic acid).

are conveyed from the site of synthesis to the intended destination, either over long distances or through adjacent cells if the target is in close proximity (Chai and Subudhi, 2016). Plant cells and tissues are divided, enlarged, and differentiated by auxins, and it is known that auxins also accelerate the production of xylem and roots (Pasternak et al., 2023). Promoting lateral root growth while preventing root elongation is a concise and simple description of how auxin functions in root formation. During the process of lateral root formation, the activated endoderm/pericycle cells undergo a series of cell divisions, leading to the development of root primordia and subsequent differentiation into new lateral roots (Garg et al., 2022; Hassan et al., 2022; Singh et al., 2023).

Auxin biosynthesis, transport, and signaling control all of these lateral root development activities, including their initiation, growth, emergence, and elongation (Zhang et al., 2022). PGPR partially promote root development due to their ability to release indoleacetic acid (IAA). Several PGPR have been discovered to synthesize auxins, which play a crucial role in modulating root architecture and development. (Pantoja-Guerra et al., 2023a). When wheat plants were inoculated with auxin-producing PGPRs like *Pseudomonas extremaustralis* IB-13-1A and *Paenibacillus illinoisensis* IB 1087, the root biomass and auxin concentration increased (Bargaz et al., 2021; Grover et al., 2021; Kudoyarova et al., 2017). The roots of plants, particularly during their first growth phases, exhibit heightened sensitivity to an excessive presence of auxins. The PGPR strain *Bacillus toyonensis* Bt04 produces IAA due to its function in the phytostimulation of maize. There is no doubt that the production of IAA by rhizobacteria is essential for plant growth (Pantoja-Guerra et al., 2023b; Zerrouk et al., 2020). Furthermore, there exists empirical evidence indicating that these microorganisms exert an influence on plant growth promotion (PGP). When wheat seedlings were inoculated with the mutant strain of the minor IAA producer *Azospirillum brasilense*, strain SPM7918, results showed that SpM7918 had a lower ability than the wild-type strain Sp6 to promote root system growth (Duca and Glick, 2020). It was discovered that *Pseudomonas* sp. UW4 (WT-UW4) produced excessive amounts of IAA after being transformed with the pRK415 plasmid. The process involved in this study involved the recombination of the nit gene, which is responsible for encoding the enzyme nitrilase. This enzyme plays a crucial role in modifying indole-3-acetonitrile into IAA. This demonstrates the importance of the indole-acetonitrile biosynthetic pathway for IAA synthesis and highlights the role of IAA in canola growth promotion by the UW4 strain. The

canola seedlings that were subjected to inoculation with mutant strains exhibited a notable stimulation in the formation of lateral roots, as well as a substantial increase in root length as compared to the wild strains (Duca et al., 2018). IAA-attenuated mutants may serve as compelling evidence to support the notion that IAA plays a significant role in enhancing root development induced by PGPR (Mohanty and Mohapatra, 2023). It was observed that the increase in IAA and indole-3-butyric acid concentrations (IBA) in the presence of *Azospirillum* spp. positively correlated with the enhancement of cell membrane activity in plant roots.

Additionally, the bacteria deliver additional compounds to their host plant, such as indole-3-acetaldehyde, indole-3-lactic acid (ILA), indole-3-ethanol (tryptophol, TOL), and indole-3-acetamide (IAM), that regulate plant development (Bartolini et al., 2023; Keswani et al., 2020). It has been hypothesized that *Paenibacillus polymyxa* and *Azospirillum* species produce tryptophan and substances that resemble auxins, such as TOL, into the rhizosphere (Rosier, 2022). Bacterial auxins have been seen to facilitate the development of primary plant roots at low concentrations. However, higher concentrations of bacterial auxins have been found to promote the growth of lateral and adventitious roots as well. This phenomenon can potentially enhance mineral uptake and stimulate the generation of root exudates, thereby fostering bacterial proliferation. (Mann et al., 2023). Compared to plants inoculated with an IAA-deficient *P. putida* mutant, canola (*Brassica napus*) seeds treated with *Pseudomonas putida* strain GR12-2 were found to produce more roots (Singh et al., 2022b). Bacterial-produced auxins have the capacity to ameliorate adverse environmental circumstances, including soil contamination, salinity, and drought (Phour and Sindhu, 2022). In contrast to plants inoculated with the IAA-deficient mutant of *Ensifer meliloti*, *Medicago truncatula* treated with the IAA overexpression strain DR-64 showed a better salt tolerance (Kudoyarova et al., 2019). It has been suggested that tryptophan and auxin-like substances, including TOL, are released into the rhizosphere by *Paenibacillus polymyxa* and *Azospirillum* species (Begum et al., 2019). The *Leifsonia xylis* strain SE134 produced more IAA when exposed to copper (Kang et al., 2017). The increased growth and salt tolerance of *Solanum lycopersicum* is caused by the IAA-producing halophilic *Leclercia adecarboxylata* strain MO1 (Kang et al., 2019b). Proline and pinitol, two low molecular weight osmolites that prevent *Medicago sativa* from drying out, are produced by the IAA overproducing *Rhizobium* strain RD64 in particular. A temperature gradient was discovered to promote the production of IAA in both

*B. cereus* strain So3II and *B. subtilis* strain Mt3b (Wagi and Ahmed, 2019). While the gene expression of certain bacteria can be affected by indole-3-acetic acid (IAA), its primary role lies in serving as a signaling molecule that facilitates interactions between bacteria and plants within an ecological context, ultimately leading to advantageous effects on plant growth and development.

### Impact of cytokinins on plant growth

It is known that certain parts of plants are stimulated by cytokinins, a subclass of phytohormones, to promote cell division, cell enlargement, and tissue growth (Osugi and Sakakibara, 2015). Along with continuously responding to environmental cues through root and shoot meristem activity, vascular development, root elongation, lateral root, nodule creation, and apical dominance (Chen et al., 2022). Cytokinins play a crucial role in plant growth by regulating cellular division and differentiation, often in collaboration with other phytohormones. Balanced auxin and cytokinin levels are often considered to be critical regulators of plant organogenesis and root architecture (Hussain et al., 2021). Cytokinins have a crucial role in stimulating the activity of apical and axillary meristems, as well as facilitating cell division in the shoot. Moreover, an increase in cytokinin levels inside the shoot has been observed to correlate with enhanced yield (Wang et al., 2023a). In contrast to their stimulatory influence on shoot growth, cytokinins impose limitations on root development. This phenomenon can be attributed to their facilitation of cell differentiation and regulation of root branching inside the root apical meristem. Cytokinins control root architecture and root activities, including nutrient transport and protein absorption, by preventing lateral root initiation and primary root elongation (Mok, 2019). Under in vitro conditions, 90 % of rhizobacteria have been found to produce and release growth stimulants resembling cytokinins. The rhizobacteria associated with *Coleus forskohlii*, including *Pseudomonas putida* MTP50, *Stenotrophomonas maltophilia* MTP42, and *Pseudomonas stutzeri* MTP40, produce cytokinins that promote plant development (Patel and Saraf, 2017).

In addition, cytokinins and auxins work together to regulate plant growth, with cytokinins promoting the phloem and auxins developing the xylem through a series of often antagonistic compounds (Hussain et al., 2021). There have been multiple occurrences of PGPR, which encompass the synthesis of cytokinins. (especially zeatin) by *Arthrobacter*, *Azospirillum*, *Bradyrhizobium*, *Bacillus*, *Pseudomonas*, and *Paenibacillus* (Kaur and Pandove, 2023; Vaghela and Gohel, 2023). Cytokinins influence apical dominance, axillary bud development, and leaf withering, in addition to increasing root surface area by accelerating adventitious and lateral root formation. Cytokinins play a role in inter-organ communication, specifically in transmitting signals from the roots to the shoots, within the context of environmental conditions (Burr et al., 2020). In plants treated with cytokinin-producing bacteria, shoot development is accelerated and the root-to-shoot ratio is reduced (Chetverikov et al., 2023). Furthermore, a multitude of PGPRs have the ability to synthesize cytokinins, which act as stimulants for the secretion of root exudates by plants. This subsequently augments the interactions between the PGPRs and the plant. Auxin and cytokinin have been found to play a role in controlling the symbiotic nitrogen-fixing relationship between Rhizobium (Sibponkrung et al., 2020). Cytokinins regulate the differentiation of the root meristem and promote the growth of root hairs, but also prevent the growth of lateral roots and the spread of main roots (Akhtar et al., 2020).

Recently, bacterial cytokinins have been shown to play a dual role in pathogen-infected plants, enhancing nutrient availability and controlling host immunity (Großkinsky et al., 2016). For example, in *Arabidopsis*, cytokinins of bacterial origin promoted resistance to bacterial infection. Furthermore, the discovery of plant cytokinins was the reason

for the beneficial properties of *B. megaterium* for plants in the *Arabidopsis Bacillus megaterium* system. To stop *P. syringae* infection in *Arabidopsis*, cytokinins were used to regulate *P. fluorescens* strain G20-18 (Liu et al., 2023; Singh et al., 2022b).

### Growth effects of ABA on plants

According to a comprehensive body of study, it has been noted that the utilization of PGPR has the capacity to stimulate the production of ABA, thereby aiding in the modulation of this hormone's levels within plants. The significance of the phytohormone abscisic acid (ABA) in the context of drought stress has been extensively described in academic literature (Karnwal et al., 2023). The stomata close as ABA levels rise during dehydration, minimizing water loss. After being inoculated with *Azospirillum brasilense* Sp245, ABA levels in *A. thaliana* increased, especially when the plant was under osmotic stress, but it is also understood that the hormone behaves differently when lateral roots grow (Mariotti et al., 2021). The elevation in abscisic acid (ABA) concentrations during the state of dehydration induces the closure of stomata, hence diminishing the rate of transpiration. An increase in ABA levels in *A. thaliana* was observed upon inoculation with *Azospirillum brasilense* Sp245, particularly under osmotic stress conditions. However, it is also known that the hormone works differently during lateral root growth (Kang et al., 2014).

PGPRs and stress applications on cucumber plants were used to assess endogenous modulation of phytohormones. The results showed that the plants containing *B. cepacia*, *A. calcoaceticus*, and *Promicromonospora* sp. exposed had significantly lower levels of stress-responsive ABA than control plants, compared to PGPR treatments, control plants had 27 % higher ABA levels (Belimov et al., 2014). Nevertheless, quantifying the precise impact of an individual hormone on plant development poses challenges due to the co-production of many phytohormones by bacterial strains. Moreover, these hormones interact with other regulatory variables, further complicating their effects on plant systems. Plant development and metabolic processes are significantly inhibited by the hormone ABA. This sesquiterpenoid is necessary for a number of critical processes, including the synthesis of proteins and the required osmolytes, senescence processes, seed growth and maturation, the beginning of seed and bud dormancy, and many more. It also plays a key role in regulating plants' resilience to abiotic and biotic stressors that cause them to be exposed to harsh and unpredictable environments (Pal et al., 2023).

### Impact of gibberellins on plant growth

Gibberellins (GAs) play a number of different roles in the development of plants, including regulating seed dormancy, germination, flowering, fruit ripening, encouraging root growth, and increasing root hair density (Nagel et al., 2018). The presence of GA1, GA4, GA9, and GA20 was shown in gnotobiotic cultures of *Rhizobium meliloti* in the first investigation to describe gibberellin in bacteria (Keswani et al., 2022; Tudzynski, 2005). Since then, research has revealed that some rhizospheric bacteria, including *Acetobacter diazotrophicus*, *Herbaspirillum seropedicae*, *Bacillus* spp., or *Azospirillum* spp., generate GA (Hershey et al., 2014; Mia, 2022). Currently, 136 different chemical compounds fall under the category of naturally occurring gibberellins, with GA3 (gibberellic acid) being the one that bacteria make the most frequently. Gibberellins, which are synthesized by bacterial organisms, are hypothesized to facilitate the stimulation of plant growth and enhance crop productivity. For instance, increasing the level of GA3 in the roots and promoting their development was accomplished by inoculating maize roots with different *Azospirillum* strains. It has been demonstrated that the *Enterococcus faecium* strain LKE12 works in conjunction with a

variety of gibberellins (GA1, GA3, GA7, GA8, GA9, GA12, GA19, GA20, GA24, and GA53) generated with IAA to lengthen and enhance the biomass of rice grains and oriental melon. Gibberellins have also been discovered to work in plants as thermotolerance agents. Under extreme temperature stress, *Bacillus tequilensis* strain SSB07 generated GA1, GA3, GA5, GA8, GA19, GA24, and GA53 with the assistance of soybeans and improved shoot length and host plant biomass (Kang et al., 2019a; Revolti et al., 2018).

### Influence of VOCs on characteristic plant root pathways

PGPR live together in dynamic groups and excrete VOCs that help them survive in their environment (Bhadrecha et al., 2023; Vlot and Rosenkranz, 2022). Low molecular weight chemicals and easily vaporized molecules have the ability to disperse in intricate matrices, including biological membranes, water, soil, and air (Lemfack et al., 2014; Mhlongo et al., 2022). The effective colonization of plant roots by PGPR is the result of multiple signals in an intricate process regulated by molecules from the two species involved. The *Lysinibacillus sphaericus* (T19), *Paenibacillus alvei* (T22), *Pseudomonas koreensis* (N19), and *Ps. fluorescens* (N04) are four bacterial strains that exhibit PGPR activity (Hassen and Labuschagne, 2010). These PGPRs successfully colonize the roots of tomato, wheat, and maize plants and encourage their growth, according to prior research. Research has demonstrated that plant roots possess the ability to detect and respond to quorum-sensing signals, hence influencing the architecture of their root systems. Plant roots can detect the volatiles released by the related microbes with great speed and accuracy (Gutiérrez-Luna et al., 2010). A split petri dish experiment highlighted the significance of VOCs in plant growth control and showed the favorable benefits of certain rhizobacteria isolated from citron (*Citrus limon* L.) on root morphogenesis and biomass production in *A. thaliana* seedlings. The exposure of plants to volatile organic compounds (VOCs) can induce alterations in root architecture, which in turn may have ecological implications for root colonization and the interactions between plants and their associated microbial communities (Konappa et al., 2020). The architecture of the root system of *A. thaliana* changed after inoculation with *Bacillus megaterium* UMCV1, with primary root growth being suppressed and lateral roots germinating more frequently and longer (Vasant et al., 2023).

The volatiles of *B. subtilis* GB03 stimulated plant growth through cytokinin and ethylene signaling. In contrast, the volatiles of *B. amyloliquefaciens* IN937a had an independent effect in the absence of cytokinin or ethylene, highlighting the significance of various volatiles in phytostimulation (Meldau et al., 2013). Tobacco plants (*Nicotiana attenuata* L.), which are influenced by dimethyl disulfide generated by *Bacillus* sp., grow more quickly when grown in low-sulfur environments. Type BG55 Dimethyl sulfoxide's absorption and assimilation were major contributors to the observed effect, suggesting VOCs from *Microbacterium* sp. In *A. thaliana* plants, strain EC8 increased root biomass and lateral root density (Cordovez et al., 2018). A new avenue to sustainably increase crop yield could be revealed by identifying bioactive volatiles generated by PGPR and characterizing their ecological roles.

### The function of the siderophore produced by PGPR

The trivalent hydroxide form of iron ( $\text{Fe}^{+2}$ ) normally found in soil is difficult for plants to absorb. To help plants absorb iron, fungi, bacteria, and plants make and release tiny siderophore molecules. Siderophores can be categorized into four distinct groups, which are delineated based on their chemical composition. These groups include catecholates, phenolates, hydroxamates, and carboxylates. Combinations of the different groups also occur rather frequently (Yadav et al., 2022a). Siderophores function as strong, soluble chelators for  $\text{Fe}^{+3}$  and are small, high-affinity iron chelators secreted by plants and microbes. The restricted solubility of iron at high pH levels prompts several bacteria to exhibit a response to iron deficiency by synthesizing these compounds, a

phenomenon commonly observed in soils with neutral to alkaline pH values (Li et al., 2022a). Because bacteria compete for iron with other rhizosphere bacteria by invading plant roots, it is critical for bacteria to acquire Fe through the creation of siderophores. Iron is necessary for cell growth and metabolism, and by securing  $\text{Fe}^{3+}$  close to the root, PGPR can inhibit the growth of harmful microorganisms (Dhankhar et al., 2022).

Numerous bacterial siderophores have the potential to serve as iron sources for various plants, however their overall concentration may not be substantial enough to significantly influence plant iron uptake. Dicotyledons achieve this through the formation of phytosiderophores, another mechanism by which plants take up iron. Monocots do this by using a protein in the root membrane called root membrane reductase, which converts the insoluble  $\text{Fe}^{3+}$  ion to the more soluble  $\text{Fe}^{2+}$  ion (Myo et al., 2019). Numerous investigations have identified siderophore-producing bacteria of the types *Bradyrhizobium*, *Bacillus*, *Enterobacter Pseudomonas*, *Rhizobium*, *Serratia*, and *Streptomyces* (Verma et al., 2013). Iron ions ( $\text{Fe}^{+3}$ ) are reduced to iron ions ( $\text{Fe}^{2+}$ ) by the siderophore complex, which can easily enter the cells (Tamariz-Angeles et al., 2021). Furthermore, siderophores have the ability to form complexes with many metals, including molybdenum, manganese, cobalt, and nickel. This process enhances the accessibility of these metals to plants and other microorganisms. Plant diseases can be effectively managed by utilizing PGPR. These beneficial bacteria play a crucial role in enhancing agricultural productivity by sequestering iron from the pathogen's food source, resulting in increased crop output. Numerous studies have shown evidence for the positive impact of PGPR on plant growth and development, as well as their ability to produce highly effective extracellular siderophores. In addition to other undesirable metals, including Al, Cd, Cu, Ga, In, Pb, and Zn, siderophores are capable of forming stable complexes with iron. The presence of heavy metals has been shown to stimulate the synthesis of bacterial siderophores (Ghosh et al., 2014; Rubio-Santiago et al., 2023). Contrarily, iron deficiency in plants is common in soils polluted with metals, and bacteria may aid in iron uptake via plants. Microbial siderophores function as metal-chelating agents in order to regulate the availability of iron inside the plant rhizosphere. Based on available information regarding the uptake of arsenic by various plant species, it has been observed that this process contributes to the mitigation of the harmful impacts of metallic substances on plants. In contrast, iron deficiency in plants is common in soils contaminated with metals, and bacteria can support iron uptake by plants. To control the availability of iron in the plant rhizosphere, microbial siderophores act as metal chelators. In turn, the uptake of arsenic by many plants has been reported to help plants mitigate the toxic effects of metals (Garg et al., 2021; He et al., 2020).

Iron is an important micronutrient that bacteria consume and need for proper metabolism. Ferrous iron ( $\text{Fe}^{+3}$ ), which is prevalent in nature, cannot be directly absorbed by microorganisms because it is poorly soluble and not at a sufficient concentration to support microbial development in the soil. Soil microorganisms emit small molecular weight iron-binding compounds as a means of sustenance. The main stream of  $\text{Fe}^{+3}$  in the rhizosphere is bound by siderophores, which effectively arrest the growth of fungal pathogens by denying them access to accessible iron (Sarkar et al., 2022; Wang et al., 2022). The suppression of pathogens occurs due to the inhibitory effects of iron deficiency, which include growth inhibition, decreased nucleic acid synthesis, sporulation inhibition, and alterations in cell structure. Iron is prone to oxidation following its reduction and subsequent release into the periplasm and subsequent entry into the cytoplasm. This iron ion is easily trapped in a carrier molecule and held in its newly reduced state to prevent it from entering the cell's cytoplasm (Cain and Smith, 2021). Alternatively, this reduced iron state can be used directly in metabolic processes instead of being oxidized. Bacteria that are better able to obtain iron are better able to compete since iron is important for survival and growth. Rivalry for iron takes place at two different levels: competition for iron (III) and competition for complex iron



siderophores. The former depends on the properties of the siderophores, while the latter is a feature of the iron siderophore receptor on the outer membrane (Rahul et al., 2022).

### Solubilization of phosphate by PGPR

Although phosphorus (P) is an essential element for plant development, it is infrequently present in soil. Phosphorus occurs naturally in both inorganic (Pi, average 50 %) and organic (Po, average 50 %) forms (Brewin, 2004). The roots are unable to absorb any of them since they are just marginally soluble (often a little over 5 %). In order for the process of P dissolution and mineralization to occur, it is imperative that soil microorganisms possess the capability to execute designated functions (Jindo et al., 2023). Due to the growth of low molecular weight organic acids, the pH of the soil frequently drops, making Pi soluble. Both the monobasic ion ( $\text{H}_2\text{PO}_4^{-24}$ ) and the dibasic ion ( $\text{HPO}_4^{-24}$ ) can be taken up by plants. In contrast, phosphatase enzymes catalyze the hydrolysis of phosphoric acid esters, resulting in the process of mineralization of organic phosphorus (Alori et al., 2017). When sufficient phosphorus (P) is made accessible through the activity of phosphate-soluble bacteria (PSB), the need for chemical fertilizers can be significantly reduced. The benefits of heavy metals to plants allow for more efficient phytoextraction or phytostabilization.

It is widely accepted that soil microorganisms have a variety of beneficial effects that significantly affect plant growth and soil P availability. Research has demonstrated that the utilization of high-performance liquid chromatography (HPLC) purified PGPR with a high phosphorus solubilization capacity (PSC) can effectively enhance plant growth and increase crop output. This positive impact has been observed not only when these PGPR are linked with plant roots, but also when they are in contact with other plant components, such as leaves (Kumar, 2016; Tang et al., 2020). Both rice and sunflower yielded higher yields in response to the simultaneous application of different mineral phosphates such as Triple Superphosphate (TSP) and inoculation with different PSB isolates such as *Bacillus*, *Rahnella aquatilis*, *Enerobacter sp.*, *Pseudomonas fluorescens*, and *Pseudomonas putida*. The advantageous use of both resources was observed throughout the physiological and crop developmental phases of plants, encompassing a diverse range of functional characteristics. Among these are plant height, the quantity of panicles and stems, grain weight, biological yield, seed oil production, and nutrients present in seeds and oils. It also contains the photosynthetic pigments chlorophyll (Chl)a, (Chl)b, (Chl)s, and carotenoids growth factors. In the presence of heavy metals, the positive effect on plants also leads to better effectiveness of phytoextraction or phytostabilization (Gavrilescu, 2022).

### Nitrogen fixation by PGPR

Nitrogen (N), an essential element, is required for all life forms. It is the most crucial nutrient for plant growth as well as a key ingredient in nucleotides, membrane lipids, and amino acids (Altaf, 2021). The quantity of vegetation present in the area constitutes the fourth biggest amount of dry matter. The process of biological nitrogen-fixing is of utmost importance for microorganisms in sustaining life on our planet. Nitrogenase, a highly sophisticated oxygen-labile enzyme retained in free-living symbiotic diazotrophs, is responsible for this process, which involves turning atmospheric nitrogen into ammonia (Nag et al., 2022). An  $\text{H}_2$  molecule is created throughout the process in addition to the hydrolysis of 16 equivalents of adenosine triphosphate (ATP). When examining the two distinct forms of nitrogen fixation, namely symbiotic and non-symbiotic, which are contingent upon the plant and its related organism group, it is widely acknowledged that non-symbiotic bacteria generally exhibit a lower capacity for nitrogen fixation compared to root nodule bacteria, also known as rhizobia (Bellés-Sancho et al., 2023). The majority of PGPRs have been shown to be especially effective in accelerating this process, making the scarce nutrient (nitrogen) accessible to

plants despite their weak fixation capacity. Furthermore, the growth-promoting capabilities of each isolate are influenced by the availability of nitrogen, which in turn affects plant height and root length (Khumairah et al., 2018). The ability of rhizobacteria to enhance plant growth is contingent upon the specific type of rhizobacteria and their distinct characteristics. Every rhizobacteria isolate has a different capacity for fostering plant development, and those that create more metabolites and do so at higher levels give the plants more nutrients to support their growth. The rhizobacteria that are capable of boosting plant growth and yield depend on their type (Gupta et al., 2019).

The halotolerant strains of *Hihengliuella*, A1B62, and *Brachy bacterium sp.*, B0sh64, had longer fresh roots and a heavier fresh shoot weight than the other strains and the control (Alishahi et al., 2020). It was discovered that *Pseudomonas stutzeri* and *K. pneumoniae* strains could produce IAA, nitrogenase enzyme, P-solubilization, ammonia, and siderophore to support plant growth and reduce salt stress in plants. These outcomes support PGPR's capability to assist plants in a number of ways (Baba et al., 2021). One instance of stimulating plant development involves the production of phytohormones that facilitate nitrogen fixation, phosphorus release, ammonia production, and siderophore production (Kusale et al., 2021). It was examined how nitrogen fixation and nutrient uptake were impacted by co-inoculating white clover (*Trifolium repens*) with Rhizobium and PGPR. White clover plants were either infected with just one of the two *Rhizobium* strains, CHB1120 or CHB1121, or they were co-inoculated with either of the two PGPR strains, *Bacillus aryabhattai* strain Sb or *Azotobacter vinelandii* strain G31. White clover infected with CHB1120 or CHB1121 alone and co-inoculated with either *Rhizobium* strain and the PGPR exhibited noticeably more nodules than the uninoculated control (Sharma et al., 2016). When CHB1120 or CHB1121 and Sb were administered together instead of separately, the nitrogenase levels were significantly greater. Furthermore, in conditions of phosphorus deficiency, the nitrogen content of both the roots and shoots was significantly enhanced by a single inoculation of either CHB1120 or CHB1121, as well as by their simultaneous inoculation with PGPR. Co-inoculation of CHB1121 and G31 revealed the highest N content in the shoots (Matse et al., 2020). The physiological fixation of nitrogen by bacteria like *Azotobacter spp.* and *Azospirillum lipoferum* results in the production of ammonia, which is required for the synthesis of amino acids, the building blocks of protein in plants. The bacteria under consideration have a notable capacity for nitrogen fixation owing to their ability to synthesize the enzyme nitrogenase. This enzymatic activity enhances the ability of cereal plants to assimilate nitrogen (Niewiadomska et al., 2018).

When nitrogen-fixing bacteria (*Azospirillum lipoferum* and *Azotobacter chroococcum*) were utilized, the protein output and content were reduced, according to the studies that are currently available. It was demonstrated that the spring barley grains that had the maximum yield and total protein content were those that had been co-administered with PGPR (*Bacillus subtilis* and *Pseudomonas fluorescens*) and nitrogen-fixing bacteria (*Azotobacter chroococcum*) (Renoud et al., 2022). Furthermore, it has been observed that the initial seed inoculation facilitates the development and sprouting of maize, while also influencing the rhizomicrobiota. These include microbial functional groups in the maize model system PGPR *Azospirillum lipoferum* CRT1 that regulate plant growth. In three fields, seeds were inoculated with *A. lipoferum* CRT1 at either conventional (105-6) cells per seed or reduced (104-5) cells per seed inoculation levels. The two PGPR formulations affected corn development and the microbial functional groups nifH (2,4-diacetylphloroglucinol production), acdS (ACC deaminase activity), and phlD (2,4-diacetylphloroglucinol production) were evaluated. In another study, the salt-tolerant PGPR strain *P. endophytica* SK1 was shown to stimulate nitrogen-fixing mechanisms that led to a reduction in salt stress and increased trigonelline concentration biosynthesis in *fenugreek* (Sharma et al., 2022).



**Table 2**  
Examples of rhizobacteria that support plant growth.

PGPR strains	Plants	Role in plant growth and development	Reference
<i>Azospirillum</i> , <i>Pseudomonas putida</i> , and <i>Azotobacter</i>	Artichoke ( <i>Cynara cardunculus</i> var. <i>scolymus</i> )	In plants, the combination of phosphorus-solubilizing bacteria and nitrogen-fixing bacteria increased radicle and shoot length, shoot weight, coefficient of velocity of germination, seedling vigor index, and significantly decreased mean time of germination.	Allahdadi and Raei (2017)
<i>Pseudomonas</i> sp. PS1	Mung bean ( <i>Vigna radiata</i> )	Plant dry weight, nodule counts, total chlorophyll content, leghaemoglobin, nitrogen in the roots and shoots, phosphorus in the roots and shoots, seed yield, and protein in the seeds were all significantly higher.	Hussain et al. (2020)
<i>Bradyrhizobium</i> MRM6	Mung bean ( <i>Vigna radiata</i> )	The herbicide-resistant Rhizobium strain MRP1 improved growth metrics at all herbicide doses examined (quizalafop-p-ethyl and clodinafop).	Naz et al. (2022)
<i>Pseudomonas</i> sp. A3R3	Indian Mustard ( <i>Brassica juncea</i> L.)	Increased noticeably the Ni content ( <i>A. serpyllifolium</i> ) and biomass ( <i>B. juncea</i> ) of plants cultivated in Ni-stressed soil.	Pandita (2022)
<i>Pseudomonas</i> sp.	Soybean ( <i>Glycine max</i> L.) & Wheat ( <i>Triticum aestivum</i> L.)	Enzyme activity, soil productivity, and nitrogen absorption have all dramatically increased.	Kumawat et al. (2022)
<i>Psychrobacter</i> sp. SRS8	Castor bean ( <i>Ricinus communis</i> ) & Sunflower ( <i>Helianthus annuus</i> )	Both plant species growth and Ni accumulation were improved by higher plant biomass, chlorophyll, and protein contents.	Bortoloti and Baron (2022)
<i>Rhizobium</i> strain MRP1	Common pea ( <i>Pisum sativum</i> )	The growth, symbiotic features (nodulation and hemoglobin content), amount of N and P nutrients in plant organs, seed yield, and protein content of pea plants were all significantly increased.	Dasgupta et al. (2023)
<i>Rhizobium phaseoli</i>	Mung bean ( <i>Vigna radiata</i> L.)	Tryptophan helped Rhizobium minimize the negative effects of salt while also increasing plant height, nodule density, biomass, grain production, and nitrogen content in the grain.	Dhole et al. (2023)
<i>Bacillus</i> PSB10 SP.	Chickpea ( <i>Cicer arietinum</i> )	Significantly increased seed output, nodulation, chlorophyll content, leghemoglobin, grain protein, decreased chromium absorption in roots, shoots, and grains.	Verma et al. (2019)
<i>Paenibacillus polymyxa</i>	Black Pepper ( <i>Piper nigrum</i> )	Significantly more plant biomass was produced, and untreated plants developed systemic resistance to the bacterial spot pathogen <i>Xanthomonas axonopodis</i> pv. <i>Vesicatoria</i> .	Kralova and Jampilek (2023)
<i>Pseudomonas fluorescens</i> strain R-93, <i>Pseudomonas putida</i> strain R-168	Maize ( <i>Zea mays</i> L.)	Plant height, seed number, weight, area of the leaves, and dry weight of the shoots all increased noticeably.	Velasco-Jiménez et al. (2022)
<i>Psychrobacter</i> sp. SRS8, <i>Bacillus</i> sp. SN9, <i>Pseudomonas</i> sp. SR12,	Indian mustard ( <i>Brassica oxyrrhina</i> ) & Chinese mustard ( <i>Brassica juncea</i> )	The biomass of the test plants exhibited an increase, leading to an enhancement in the accumulation of nickel inside the plant tissues.	Alves et al. (2021)
<i>Psychrobacter</i> sp. SRA1 <i>Bacillus</i>	Chinese mustard ( <i>Brassica juncea</i> )	Considerably enhanced measurements of plant roots, shoots, fresh weight, and dry weight in addition to enhanced copper uptake by plants.	Benizri et al. (2021)
<i>Ralstonia metallidurans</i> , <i>Pseudomonas fluorescens</i> , and <i>Pseudomonas aeruginosa</i>	Maiz ( <i>Zea mays</i> L.)	Higher soil metal mobilization, enhanced plant development, and increased absorption of Cr and Pb.	Mudgal et al. (2022)
<i>Klebsiella pneumonia</i>	Wheat ( <i>Triticum aestivum</i> )	Boosted the root and shoot lengths significantly.	Noman et al. (2021)
<i>Pseudomonas</i> sp.	Chickpea ( <i>Cicer arietinum</i> )	Plant fresh and dry weight increased with a nickel dosage of 2 mM.	Lyu et al. (2022)
<i>Azospirillum amazonense</i>	Rice ( <i>Oryza sativa</i> L.)	Increased numbers of panicles (3–18.6 %), grain dry matter accumulation (7–11.6 %), and nitrogen buildup (3.5–18.5 %) at grain maturity.	Namdeo et al. (2020)
<i>Pseudomonas</i> sp., <i>Bacillus</i> sp., and <i>Mucilaginibacter</i> sp.	Cannabis ( <i>Cannabis sativa</i> )	Plant height, node number, branch number, & leaf area all increased as compared to the control, increasing the flower's fresh weight by (5.13 %, 6.94 %, and 11.45 %).	Boyer (2023)
<i>Bacillus licheniformis</i> A21, <i>Bacillus haynesii</i> EN43, <i>Paralicheniformis</i> EN107	Rice ( <i>Oryza sativa</i> )	Plants treated with PGPR produced more grain, showed less stress & accumulated more biomass. Compared to the un-inoculated control, plants treated with bacterial inoculum showed a 24 %, 20.5 %, and 20 % decrease in the antioxidant enzyme activity of SOD, CAT, and GPOX, respectively.	Joshi et al. (2020)
<i>P. capsici</i> HydPak1 MF322868 and HydPk2 MF322869	Chili pepper ( <i>Capsicum annuum</i> )	Decreased seedling mortality and <i>P. capsici</i> disease severity in the chili pepper.	Hyder et al. (2020)
<i>Peribacillus</i> sp. P10, <i>Pseudomonas</i> sp. P8, and <i>Streptomyces</i> sp. X52	Maize ( <i>Zea mays</i> L.)	Having PGP traits and managing the bacterial population in the rhizosphere may help plants grow better in salty environments.	Peng et al. (2021)
<i>Pseudomonas</i> sp. G22, <i>Rhizobium</i> sp. IC3109, and <i>Enterobacter</i> sp. C1D.	Maize ( <i>Zea mays</i> L.) & Pigeon pea ( <i>Cajanus cajan</i> )	Effect of distinct beneficial bacterial strains' chemotaxis, root colonization behavior on root exudates made of a legume (pigeon pea) and a grain (maize).	Vora et al. (2021)
<i>Brevundimonas vesicularis</i> (A40), <i>Lysinibacillus Bacillus safensis</i> (S7), <i>Bacillus pumilus</i> (A26), <i>Bacillus sphaericus</i> (T19), <i>Paenibacillus alvei</i> (T29), & <i>Lysinibacillus safensis</i> .	Maize ( <i>Zea mays</i> L.)	Increases in <i>Zea mays</i> yield ranged from 24 % to 34 %.	Breedt et al. (2017)
<i>Burkholderia ambifaria</i> (RZ2MS16) <i>Bacillus</i> sp (RZ2MS9)	Maize ( <i>Zea mays</i> L.) & Soybean ( <i>Glycine max</i> L.)	Shoots showed increases of more than 47 % for both strains and crops, which was substantially greater than those of un-inoculated plants.	Batista et al. (2018)
<i>Atlantibacter</i> sp., <i>megaterium</i> , and <i>A. calcoaceticus</i>	Tomatillo ( <i>Physalis philadelphica</i> )	Excellent biofertilizer choices for the cultivation of tomatillo crops, in comparison to the control, the bacterially treated seedlings had greater leaf weight (>349 %) and root length (>11 %).	Ramírez-Cariño et al. (2023)
<i>Bacillus</i> ( <i>B. subtilis</i> , <i>B. velezensis</i> , and <i>B. amyloliquefaciens</i> )	Sugar beet ( <i>Beta vulgaris</i> )	Potential to synthesize antifungal metabolites and for their abilities as plant growth-stimulators.	Farhaoui et al. (2022)

## Function ACC deaminase produced by PGPR

A vital metabolite for the growth and development of plants is ethylene. Almost all plants naturally produce this plant growth hormone. Furthermore, it is generated inside the soil by a diverse range of biotic and abiotic mechanisms. It plays a pivotal role in eliciting many physiological alterations in plants (Dehghanian et al., 2022). Ethylene has been shown to be a stress hormone and plant growth regulator. In stressful environmental conditions, such as salt, drought, waterlogging, heavy metals, and pathogenicity, there is a significant increase in the endogenous ethylene levels. This elevation in ethylene levels adversely affects the overall growth of the plant. For instance, a significant amount of ethylene may encourage defoliation and other cellular processes that lower crop production (Gupta et al., 2022). Furthermore, ACC (1-aminocyclopropane-1-carboxylate) deaminase has the capacity to decrease ethylene concentrations in plants, while also enhancing their salt tolerance and mitigating the effects of drought stress. The *Acinetobacter*, *Achromobacter*, *Agrobacterium*, *Alcaligenes*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Pseudomonas*, *Ralstonia*, *Serratia*, and *Rhizobium* are only a few of the plant-development-promoting genera of rhizobacteria that have been found to possess ACC deaminase activity (Rafique et al., 2023). These rhizobacteria consume the ethylene precursor ACC, which is then converted to 2-oxobutanoate and  $\text{NH}_3$ . The results of microbes that cause plant disease (such as bacteria, fungi, and viruses). Resistance to stressors brought on by polyaromatic hydrocarbons, heavy metals, radiation, injury, insect damage, high salinity, drafts, extremely cold temperatures, intense light, and flooding is produced by ACC deaminase (Shabaan et al., 2022).

The ethylene precursor ACC is consumed by these rhizobacteria, who then transform it into 2-oxobutanoate and  $\text{NH}_3$  (Shahid et al., 2023; Tanveer et al., 2023). Consequently, the principal effects of seed and root inoculation with rhizobacteria that produce ACC deaminase in diverse crops encompass the promotion of root elongation, acceleration of shoot growth, enhancement of rhizobial node formation, facilitation of N, P, and K absorption, and augmentation of mycorrhizal colonization (Shahid et al., 2023). The presence of ACC deaminase enzymatic activity in PGPR is a notable factor in promoting plant growth. This enzymatic activity contributes to the development of plants and their ability to tolerate stress, regardless of whether they are exposed to normal or challenging conditions (Gupta and Pandey, 2019). Stress-induced ACC (secreted as root exudates) is converted by the microbial enzyme ACC deaminase to ammonia and beta-ketobutyrate instead of ethylene, which has detrimental effects on plant physiology, growth, and development (Roy Choudhury et al., 2023). As a result, the role of microbial ACC deaminase manufacturers is crucial in today's agricultural system, which is growing more and more susceptible to climate change (Table 2).

## Conclusions and future perspectives

One of the most effective and safest ways to increase productivity in agriculture is to use bio-fertilizers (PGPRs). This is a practical solution to the demand for better crop yields. Due to their capacity to improve plant growth and development, PGPR are regarded as essential elements of rhizosphere engineering. In the last two to three decades, a considerable number of PGPR strains have been identified, analyzed, and utilized to facilitate optimal growth and development in many plant species, both under normal conditions and in the presence of stresses. The impacts of PGPR inoculations on the subsurface microbial population have drawn increased attention from researchers as they learn more about the roles that various PGPRs play in plant growth. Rhizobacteria, which promote plant development, have shown remarkable results in several agricultural studies. The bacteria exhibit a diverse range of functions that facilitate the growth and development of plants, while also possessing the capacity to neutralize a wide array of contaminants and regulate many types of plant diseases. The productivity of a given PGPR can be

further increased by optimizing and adapting it to local soil conditions. They are expected to eventually replace the synthetic growth regulators, herbicides, and chemical fertilizers that have a number of negative impacts on sustainable agriculture.

More research and understanding of the processes involved in PGPR-mediated phytostimulation would help to create more effective rhizobacterial strains that could function in a variety of agroecological settings. In an ever-evolving context, it is imperative to generate sufficient quantities of plant biomass. A multitude of microorganisms present in the soil surrounding the roots and at the interface between the roots and rhizosphere have the potential to enhance plant growth and increase biomass production. The capacity of rhizobacteria to support plant growth, development, and health, which is essentially a result of bacterial activities to boost nutrient availability, produce phytohormones, and lower pathogenic infections, is particularly significant in circumstances of abiotic stress.

Under bad climatic conditions, microorganisms have the ability to enhance and improve plant development, but this potential is currently underutilized. This knowledge could lead to the development of novel biotechnological products and methods that utilize microbes beneficial to plants in order to biologically manage plant diseases. (biopesticides) and stimulate plant growth (biofertilizers), thereby assisting in phytoremediation and sustainable agricultural practices. The productivity of agriculture has experienced an improvement due to the implementation of various methods and procedures using PGPR. Subsequent to that period, notable advancements have been observed in the realm of soil fertility, plant tolerance, plant productivity, and the preservation of a harmonious nutrient cycle. The utilization of contemporary methodologies and advanced technologies plays a crucial role in the advancement of PGPR, as they are indispensable for the establishment of sustainable agricultural practices.

## Funding

This work was supported by grants from the Jiangxi Provincial Natural Science Foundation of China (20224BAB215002 to Fen Liu), Jiangxi Provincial Introduced Intelligence Program (20212BCJ25024 to Fen Liu), and Jiangxi Provincial International Science and Technology Cooperation Program (S2023KJHZH0040 to Fen Liu).

## Declaration of competing interest

The authors declare no potential conflict of interest.

## Data availability

No data was used for the research described in the article.

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