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REVIEW ARTICLE

Direct mechanism of PGPR for promoting plant growth: Current perspective

Salman Khan & Avinash Pratap Singh*

Microbiology and Plant Pathology Laboratory, Department of Botany, Chaudhary Mahadev Prasad (C M P) Degree College, University of Allahabad, Prayagraj 211 002, India

*Correspondence email - avinashsinghau@gmail.com

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Abstract

PGPR, a plant growth-promoting rhizobacterium in the rhizosphere, stimulates growth and development through various mechanisms such as mineral nutrient availability, phytohormone regulation and phytopathogen control. PGPR inoculant's establishment, survival and persistence depend on these characteristics and a complex chain of interactions in the rhizosphere. Soil is a damp habitat containing decomposed carbon and abundant microorganisms. Agriculture relies heavily on the rhizo-microbiome, as root exudates and plant cell detritus create specific microbial colonization patterns. Secondary metabolites, antibiotics, hormones and signalling chemicals are the extracellular molecules produced and regulated by the rhizomicrobiome. The microbial composition of rhizomes affects soil texture. Research indicates that PGPR inoculates plants, promotes their growth and development. PGPR modifies plant physiology and improves nutrient intake and root activity. The plant biochemical pathways that contribute to this phenomenon are not yet fully understood. New research has revealed how PGPR signaling triggers plant responses at both local and systemic levels. There is limited understanding of how PGPR mechanisms and chemicals affect metabolic pathways in the roots. This review focuses on understanding the PGPR mechanism and the chemicals that affect root-microbe interactions.

Keywords: PGPR; phytohormone; rhizomicrobiome; rhizosphere; secondary metabolites

Introduction

Plant growth-promoting rhizobacteria that colonize the rhizosphere can directly or indirectly increase plant growth and development (1). The root microbiome refers to beneficial bacterial populations in the rhizoplane and root endosphere that aid plant growth (2). Microorganisms thrive in the rhizosphere and the soil around the roots of plants is directly influenced by root exudates (3). Plants emit carbon molecules into the soil, increasing the microbial populations in the rhizosphere (100-1000 times higher than that in the normal soil) (4). An important addition is their ability to create novel microbial niches in plant systems. This is especially true for the rhizosphere, where plant roots grow (5). The plant root system has several objectives including anchoring it to the soil, absorbing water and ions, storing nutrients and promoting plant development. It interacts closely with soil microbial populations (6, 7). Plant roots contain organic nutrients, such as sugars, acids, phyto-siderophores, amino acids, vitamins, nucleosides and mucilage which attract microbial communities (8). Fig. 1 shows the mechanisms of both direct and indirect support plant development and host-PGPR interactions (9).

Both the direct and indirect PGPR pathways affect plant performance. Direct mechanisms include producing phytohormones, increasing nutrient availability through biological nitrogen fixation, releasing unavailable nutrients into plant-useful systems (e.g. P, K, Zn), chelating heavy metals (e.g. Fe, Cu) through siderophores and other similar processes (10, 11). Two types of positive interactions have been reported between plants and microorganisms: symbiotic and mutually cooperative (12). Symbiotic mutualistic associations, in which plants and microbes are compatible with each other are closely related to some obligatory traits. Some specific structures are formed only because of such associations, such as the formation of root nodules in the members of the Fabaceae family (symbiotic interaction between Fabaceae and Rhizobia) and arbuscules in the endomycorrhizal symbiosis. In this association, microbes invade the host tissue. Cooperative links are also known as associative symbiosis, which is like symbiosis and generally colonizes the surface of plants and roots (very rarely develops inside the host tissue). Rhizobacteria are good examples of this association including plant growth and development and provide better adaptability to plants under different biotic and abiotic stresses. In contrast to the symbiotic association, PGPR have a wide range of host tissues, in which most

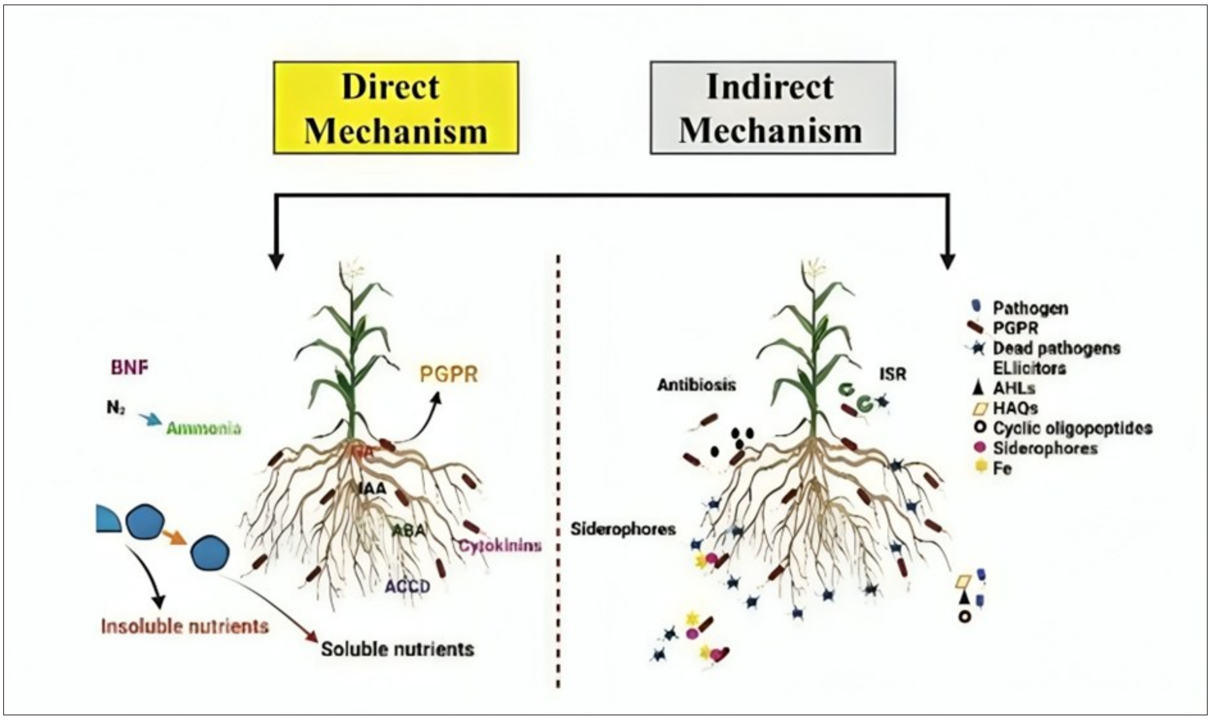

Table 1. Examples of rhizobacteria that support plant growth

bacteria belong to Firmicutes and Proteobacteria (13). Plants both above and below-ground benefited after PGPR inoculation. However, the aerial part is an economically important component and has received more attention because of its economic value as a food source for animals and ease of collecting and documenting observations. The impact of root properties on ecosystem functioning and tested measures based on these features can improve ecosystem processes (14). Understanding root system growth and functions can help achieve the next Green Revolution and ensure global food security. Hence, our objective was to uncover the root system and its impact on yields under different conditions and to help in studying the mechanism behind it (15). PGPR can help create the desired root features, improve soil resource consumption and lead to sustainable agricultural output (16).

PGPR: Plant growth promoting rhizobacteria

PGPR may influence plant nutrition and growth rate (34). Lorenz Hiltner, a German microbiologist coined the term “rhizosphere” in 1904 to describe how plant root exudates affect soil microorganisms (35). Rhizosphere microorganisms mostly include bacteria, actinomycetes, fungi, algae and viruses (36, 37). PGPR in the plant rhizosphere refer to helpful bacteria that live in the soil and attach to plant roots (37). PGPR is defined as a group of microorganisms that infiltrate the plant rhizosphere and stimulate plant growth (38). Table 1 shows the examples of rhizobacteria that support plant growth.

Role of PGPR for nutritional benefits in plants

It was found that inoculation of PGPR enhances plant growth by enhancing the absorption of nutrients the absorption of nutrients and transport is according to the demand for nutrients in the plant and controlled by ion transporters which are present in the roots (39, 40). It is a regulatory process that alters behaviour based on nutrient requirements. Proper coordination between root growth regulators and ion transporters is required for continuous intake of nutrients (41). PGPR are involved in this pathway and accelerate the rate of nutrient absorption. Rhizobacteria enhance plant growth and development by either activating the transport of ions in the roots or directly enhancing the availability of nutrients in the rhizosphere.

PGPR: Direct mechanism for plant growth and promotion

Biological nitrogen fixation by PGPR

Nitrogen is one of the most important macronutrients in dry plant biomass. It is a crucial component of genetic material, membrane lipids, amino acids enzymatic and structural proteins (42). Biological nitrogen fixation uses microbes such as blue-green algae, eubacteria and actinomycetes, to transform atmospheric nitrogen into ammonia via a reduction process.

Symbiotic nitrogen fixation

Some nitrogen-fixing microbes are symbiotically associated with plant roots and microorganisms. Symbiotic nitrogen-fixing microorganisms can fix atmospheric nitrogen and provide access to plants. Mutualistic interactions begin when the plant begins to secrete flavonoids and isoflavonoids in its rhizosphere, as recognized by *Rhizobium* (43). *Rhizobium, Sinorhizobium, Bradyrhizobium* and *Mesorhizobium* form symbiotic relationships with leguminous plants, whereas *Frankia* is associated with non-leguminous plants and shrubs (44).

Nonsymbiotic or free-living nitrogen fixation

Free-living nitrogen-fixing bacteria are in the root zone of plants; obtain food and nutrients from them while returning fixed nitrogen. Diazotrophs, which promote the growth of non-leguminous plants, such as rice and radish, also fix nitrogen without symbiotic relationships. The non-symbiotic nitrogen fixers are *Azoarcus, Azospirillum, Azotobacter, Burkholderia, Herbaspirillum, Azospirillum, Acetobacter* and *Diazotrophicus*, which are nitrogen-fixing

Table 1. Examples of rhizobacteria that support plant growth

PGPR Strain	Plants	Role in plant growth and development	Ref.
Bradyrhizobium MRM6	Mung bean (*Vigna radiata*)	The herbicide-resistant Rhizobium strain MRP1 improved growth metrics at all herbicide doses examined (quizalafop-p- ethyl and clodinafop).	(17)
Pseudomonas sp. A3R3	Indian Mustard (*Brassica juncea* L.)	Increased noticeably the Ni content (A. serpyllifolium) and biomass (*B. juncea*) of plants cultivated in Ni-stressed soil.	(18)
Pseudomonas sp.	Soybean (*Glycine max* L.) & Wheat (*Triticum aestivum* L.)	Enzyme activity, soil productivity and nitrogen absorption have all dramatically increased.	(19)
Psychrobacter sp. SRS8	Castor bean (*Ricinus communis*) & Sunflower (*Helianthus annuus*)	Both plant species growth and Ni accumulation were improved by higher plant biomass, chlorophyll and protein contents.	(20)
Rhizobium strain MRP1	Common pea (*Pisum sativum*)	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.	(21)
Rhizobium phaseoli	Mung bean (*Vigna radiata* 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.	(22)
Paenibacillus polymyxa	Black Pepper (*Piper nigrum*)	Significantly more plant biomass was produced and untreated plants developed systemic resistance to the bacterial spot pathogen *Xanthomonas axonopodis* pv. Vesicatoria.	(23)
Pseudomonas fluorescens strain R-93, *Pseudomonas putida strain* R-168	Maize (*Zea mays* L.)	Plant height, seed number, weight, area of the leaves and dry weight of the shoots all increased noticeably.	(24)
Psychrobacter sp. SRA1 *Bacillus*	Chinese mustard (*Brassica juncea*)	Considerably enhanced measurements of plant roots, shoots, fresh weight and dry weight in addition to enhanced copper uptake by plants.	(25)
Ralstonia metallidurans, Pseudomonas fluorescens and *Pseudomonas aeruginosa*	Maiz (*Zea mays* L.)	Higher soil metal mobilization, enhanced plant development and increased absorption of Cr and Pb.	(26)
Klebsiella pneumonia	Wheat (*Triticum aestivum*)	Boosted the root and shoot lengths significantly.	(27)
Pseudomonas sp.	Chickpea (*Cicer arietinum*)	Plant fresh and dry weight increased with a nickel dosage of 2 mM.	(28)
Pseudomonas sp., *Bacillus* sp. *and Mucilaginibacter* sp.	Cannabis (*Cannabis sativa*)	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 %).	(29)
Peribacillus sp. P10, *Pseudomonas* sp. P8 and *Streptomyces* sp. X52	Maize (*Zea mays* L.)	Having PGP traits and managing the bacterial population in the rhizosphere may help plants grow better in salty environments.	(30)
Pseudomonas sp. G22, *Rhizobium* sp. IC3109 *and Enterobacter* sp. C1D.	Maize (*Zea mays* L.) & Pigeon pea (*Cajanus cajan*)	Effect of distinct beneficial bacterial strains' chemotaxis, root colonization behavior on root exudates made of a legume (pigeon pea) and a grain (maize).	(31)
Atlantibacter sp., megaterium and A. calcoaceticus	Tomatillo (*Physalis philadelphica*)	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 %).	(32)
Bacillus (B. subtilis, B. velezensis and *B. amyloliquefaciens)*	Sugar beet (*Beta vulgaris*)	Potential to synthesize antifungal metabolites and for their abilities as plant growth-stimulators.	(33)

bacteria that coexist with members of the Poaceae family plant root cells. *Azospirillum* is a nitrogen-fixing bacterium that lives in C_4 plants including maize, sugarcane, bajra, sorghum and cereals such as rice, barley and wheat (45). It is an aerobic, non-nodulating, gram-negative bacterium. *Gluconacetobacter, Pseudomonas, Diazotrophicus, Enterobacter* and Cyanobacteria (*Anabaena* and *Nostoc*) in the rhizosphere (46).

Phosphate Solubilization by PGPR

PGPR have a significant impact on plant nutrition, which affects phosphate solubility. Despite high soil phosphorus levels, plants use only a small fraction of the phosphorus accumulated by fertilizer applications (46). Plants may absorb monobasic (HPO_4^-) and dibasic (HPO_4^{2-}) phosphates without mineralization or microbial breakdown, unlike organic or insoluble phosphates (47). *Pseudomonas, Bacillus* and *Rhizobium* are PGPRs that are capable of dissolving insoluble phosphate. The external media become more acidic due to the breakdown of organic forms of phosphate compounds by phosphatases and phytases, as well as the release of low molecular weight organic acids, such as gluconic acid. These acids chelate cations that are bound to phosphates were found by early researchers (48, 49). Research has shown that HPLC-purified PGPR with a high phosphorus solubilization capacity (PSC) can improve plant development and agricultural yield. Research indicates that PGPR favourably affects plant roots and leaves (50).

Siderophore produced by PGPR

Plants have difficulty absorbing the trivalent hydroxide form of iron (Fe^{2+}), which is prevalent in the soil. Fungi, bacteria and plants produce small siderophore molecules that aid in iron absorption. Depending on their chemical properties, siderophores can be classified into four classes: These categories include catecholates, phenolates, hydroxamates and carboxylates. A high frequency of combinations between distinct groups has been reported (51). Siderophores released by plants and microorganisms are tiny, high-affinity iron chelators that bind strongly to Fe^{3+}. Soil bacteria with alkaline to neutral pH levels synthesize chemicals in response to iron scarcity because of their limited solubility (52). Bacteria compete for iron with other rhizosphere bacteria by infecting the plant roots. To obtain Fe bacteria create siderophores. Iron is essential for cell growth and metabolism. PGPR can restrict the growth of pathogenic microbes by securing Fe^{3+} near the roots (53), while several bacterial siderophores can serve as iron sources for plants and their concentration may not be sufficient to significantly affect iron uptake. Numerous ions lead to an increased solubility. Siderophore-producing bacteria such as *Bacillus, Bradyrhizobium, Enterobacter, Rhizobium, Pseudomonas, Serratia, Streptomyces* etc were identified (54). The siderophore complex converts Fe^{3+} to Fe^{2+}, which is easily absorbed by the cells (55). Siderophores can form stable complexes with iron even with undesired elements including Al, Cd, Cu, Ga, In, Pb and Zn. Heavy metals promote the synthesis of bacterial siderophores (56, 57).

Phytohormones production by PGPR

Unlike many dicotyledonous plants, the root system of this plant includes both post-embryonic and embryonic roots. Cereal plants such as wheat, rice and barley develop a complex root system with root crowns and nodular structures (58, 59). Studying the connection between plant phytohormone pathways and roots is worthwhile. The root system is crucial for plant growth and productivity; thus, hormone disruption over many roots is a serious concern for plant adaptability. This structure stabilizes plants, absorbs water, nutrients and facilitates communication with soil bacteria (60).

Auxin effect on plant growth

PGPR strains enhance plant development by increasing total root surface area through auxin-induced root architectural modifications. Increasing the overall root surface area can improve water absorption and nutrient availability, leading to better plant growth and development (61). PGPR rely heavily on the synthesis of indole-3-acetic acid (IAA) to promote plant development (62). IAA is produced by over 80 % of rhizosphere-associated bacteria, including *Azotobacter, Enterobacter, Azospirillum, Staphylococcus* and *Pseudomonas* (63). Plants conserve auxin biosynthesis, with production primarily occurring in the developing seeds, young leaves and leaf bases. The phloem transports molecules from the synthesis source to the intended destination either over large distances or through nearby cells (64). PGPR promote root development by releasing IAA. Several PGPRs produce auxins that affect the root architecture and development (65). Inoculating wheat plants with auxin-producing PGPRs, such as *Pseudomonas extremaustralis* IB-13-1A and *Paenibacillus illinoisensis* IB 1087, led to increased root biomass and auxin concentration (66, 67). *Bacillus toyonensis* Bt04, a PGPR strain, produces IAA induces phytostimulation in maize. Rhizobacteria play an important role in plant growth by producing IAA (68). IAA-attenuated mutants play an important role in PGPR-induced root growth. *Azospirillum* boosted IAA and IBA levels, leading to improved cell membrane function in plant roots (69). Bacteria transfer chemicals to plants, including indole-3-acetaldehyde, indole-3-lactic acid (ILA), indole-3-ethanol (TOL) and indole-3-acetamide (IAM), which regulate plant growth and development (70). *Azospirillum* and *Paenibacillus* species may produce tryptophan and auxins in the rhizosphere (71). Bacterial auxins promote the growth of main plant roots at low concentrations. Bacterial auxins at higher concentrations can also encourage the formation of adventitious and lateral roots. This phenomenon can increase mineral intake and generate root exudates, leading to bacterial proliferation (72).

Cytokinin effect on plant growth

Cytokinin (CTK) is a hormone found in plants, algae and bacteria. It is the second most important phytohormone after IAA (73). CTK promotes cell division, tissue growth, chloroplast development and plant bud differentiation (74). Plants continuously respond to environmental stimuli through root and shoot meristem activity, vascular growth, root elongation, lateral root nodule formation and apical dominance (75). In shoots, increasing CTK levels correlate with higher yields (76). Rhizobacteria associated with *Coleus forskohlii*, such as *Stenotrophomonas maltophilia* MTP42, *Pseudomonas putida* MTP50 and *Pseudomonas stutzeri* MTP40, generate CTK that promote plant development (77). CTK and auxins govern plant growth by promoting the phloem and developing xylem through antagonistic chemicals (78). PGPR has been linked to CTK production on many occasions (79, 80). CTK influence axillary bud development, apical dominance and leaf withering. They also increased the surface area of the root by accelerating lateral and adventitious root formation. CTK facilitate inter-organ communication by delivering signals from the roots to shoots based on environmental variables (81). Treating plants with CTK-producing bacteria accelerates shoot development and reduces the root-to-shoot ratio (82). Many PGPRs produce cytokinins that stimulate the release of plant root exudate. This enhances the interactions between plants and PGPRs. Auxin and CTK regulate *Rhizobium* nitrogen-fixing symbiosis (83). CTK govern root meristem differentiation, increase root hair growth, inhibit the formation of lateral and main roots (84).

Abscisic Acid (ABA) effect on plant growth

Research suggests that PGPR can increase ABA production in plants, thereby helping to regulate its levels. The literature extensively describes the role of the phytohormone ABA during drought stress (85). As ABA levels increase during dehydration, the stomatal closure reduces water loss. Inoculating *A. thaliana* with *Azospirillum brasilense* Sp245 increased ABA levels, particularly during osmotic stress. However, hormones work differently when lateral roots grow (86). Inoculating *Arabidopsis thaliana* with *Azospirillum brasilense* Sp245 led to an increase in ABA levels, especially during osmotic stress. Hormones operate differently during lateral root growth (87). ABA plays a role in protein and osmolyte production, senescence, seed development, dormancy and other functions. It regulates plant tolerance to abiotic and biotic stresses, including harsh and unpredictable conditions (88).

Gibberellins (GAs) effect on plant growth

GAs regulates seed dormancy, germination, fruit ripening, root growth and root hair density (89). Gibberellin was discovered in *Rhizobium meliloti* gnotobiotic cultures, including GA1, GA4, GA9 and GA20 (90). Research has shown that certain rhizosphere bacteria such as *Herbaspirillum seropedicae, Acetobacter diazotrophicus, Bacillus sp., Azospirillum sp.* and *Bacillus sp.* produce GA (91). Naturally occurring gibberellins include 136 compounds, of which GA_3 is most produced by bacteria. Gibberellins produced by bacteria can stimulate plant growth and increase crop output. Inoculation of maize roots with several *Azospirillum* strains led to increased GA_3 levels and root growth. The *Enterococcus faecium* (LKE12) collaborates with IAA-generated gibberellins such as GA_1, GA_3, GA_7, GA_8, GA_9, GA_{12}, GA_{19}, GA_{20}, GA_{24} and GA_{53} to increase biomass in rice grains and oriental melon. Gibberellins can act as thermotolerant agents in plant. *Bacillus tequilensis* (SSB07) produced GA_1, GA_3, GA_5, GA_8, GA_{19}, GA_{24} and GA_{53} with soybeans, resulting in increased shoot length and host plant biomass (92).

Function of 1-aminocyclopropane-1-carboxylate (ACC) deaminase produced by PGPR

Ethylene is a crucial metabolite for plant growth and development. Almost all plants naturally produce this plant growth hormone. It is also produced by many biotic and abiotic processes in the soil. It has a significant effect on plant physiological changes. Ethylene has been identified as a stress hormone and plant growth regulator (93). Stressful environmental factors, such as salt, drought, waterlogging, heavy metals and pathogenicity, can significantly increase endogenous ethylene levels. Elevated ethylene levels reduce plant development. High levels of ethylene can lead to defoliation and decreased crop yield (94). Several plant-growth-promoting rhizobacteria, including *Acinetobacter, Achromobacter*, *Agrobacterium, Alcaligenes, Azospirillum, Bacillus, Burkholderia, Enterobacter, Pseudomonas, Ralstonia, Serratia* and *Rhizobium* have ACC deaminase activity (95). Inoculating seeds and roots with rhizobacteria that produce ACC deaminase in various crops can promote root elongation; accelerate shoot growth; enhance rhizobial node formation; facilitate N, P and K absorption and increase mycorrhizal colonization (96). ACC deaminase activity in PGPR promotes plant development. Enzymatic activity helps plants to develop and adapt to stress under normal or demanding conditions (97).

Conclusions and future perspectives

Bio-fertilizers (PGPRs) are a highly effective and safe technique for boosting agricultural yield. This practical method addresses the need for higher crop yield. PGPR are crucial for rhizosphere engineering as they enhance plant growth and development. Over the past few decades, numerous PGPR strains have been identified and used to promote optimal growth and development in various plant species, both under normal and stressful conditions. Researchers are studying how PGPR inoculations affect subsurface microbial populations to better understand their involvement in plant growth. Rhizobacteria, which enhance plant development, have demonstrated excellent results in several agricultural studies. Bacteria play multiple roles including promoting plant growth and development, neutralizing pollutants and controlling plant diseases. PGPR production can be further boosted by adjusting and customizing it to specific soil conditions in the area. They are intended to eventually replace chemical fertilizers, herbicides and synthetic growth regulators, which negatively impacts sustainable agriculture. Further research on phytostimulation can lead to the generation of more potent rhizobacterial strains suitable for various agroecological settings. Producing sufficient plant biomass is crucial in today's dynamic environments. Microorganisms in the soil around roots and in the rhizoplane can improve plant growth and increase biomass production. Rhizobacteria play a crucial role in plant growth, development and health by increasing nutrient availability, producing phytohormones and reducing pathogenic infections. This is particularly important under abiotic stress. Recent developments have improved soil fertility, plant tolerance, productivity and nutrient cycle balance. Modern methodologies and technologies are vital for advancing PGPR and for establishing sustainable agricultural practices.

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Author's contributions

All authors made substantial contributions to the conception and design, acquisition of data and analysis and interpretation of data, agreed to submit to the current journal, gave final approval of the version to be published and agreed to be accountable for all aspects of the work.

Compliance with ethical standards

Conflict of interest: The authors declare that no financial or any other conflicts of interest exist in this work.

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