

## Original Research Article

### Leveraging plant growth promoting rhizobacteria for sustainable agriculture and environment

#### Abstract

The term "soil health" refers to specific qualities of soil that allow it to support crop growth and productivity over time without harming the environment. Healthy soil contains abundant microorganisms, including plant growth promoting rhizobacteria (PGPR), which perform various beneficial functions in the rhizosphere. PGPR aid in nutrient cycling and uptake prevents the growth of harmful plant pathogens, stimulates plant immunity, and directly enhances plant growth by producing hormones and other compounds. They also can clean up soil pollution through bioremediation. This review examines recent literature on how PGPR contributes to maintaining soil health and reducing the need for toxic agrochemicals. Ultimately, the goal is to promote more sustainable agriculture practices using PGPR as biocontrol agents, plant growth stimulators, and rhizoremediators.

Keywords: PGPR, biofertilizer, bioinoculant, rhizosphere, sustainable agriculture, sustainable environment, soil fertility

#### INTRODUCTION

One of the most significant barriers we face in feeding the growing global population is the need for high-quality, nutritious food from a balanced diet. However, the unwise use of chemical fertilizers to increase agricultural yields has harmed agroecosystems, as noted by (Alavaisha et al., 2019). Similarly, chemical pesticides used to control plant diseases and insect pests have had harmful effects on natural insect predators like bee populations, soil biota, and land and aquatic flora and fauna, as pointed out by (McLaughlin and Mineau, 1995). In addition, agrochemicals have various toxic effects on human health, as (Pelosi et al., 2014) noted. Consequently, agricultural practices that rely heavily on chemical pesticides have caused a depletion, modification, or even total loss of the beneficial and indigenous micro biodiversity.

Environmental sustainability is a critical issue worldwide, as human activities have caused significant environmental harm, including soil health and the destruction of plant habitats, growth, and development, as (Harte, 2007) noted. To address the problem of increasing demand and overuse of synthetic chemicals and their long-term negative impact on global agroecosystems, there is a need to develop, adopt, and promote sustainable approaches. Sustainable agriculture is vital in this era, as it offers the potential to meet future agricultural needs that cannot get accomplished through conventional and harmful agrarian practices that negatively impact the environment, as (Santoyo et al., 2017) highlighted. For instance, fertilizer runoff from traditional agriculture is a leading cause of creating dead zones with low oxygen levels, which makes it difficult for marine life to survive.

The heavy use of chemical fertilizers has acidified fertile soils (Slepetiene et al., 2020). This underscores the need to educate farmers and encourage innovative and suitable farming practices to address the challenge of increasing productivity while maintaining environmental stability.

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PGPR, or plant growth-promoting rhizobacteria, have gained attention through the years because of their capacity to enhance plant development and their potential role as stress management agents. As soil serves as the natural habitat for beneficial microorganisms for plant crops, they play a critical role in various soil processes that impact overall plant health, crop yields, and productivity, as noted by (Santoyo et al., 2017) and (Probanza et al. 2002). Extensive research is required to investigate indigenous soil microbial diversity, distribution, and behaviour in soil habitats to ensure the successful functioning of microbial inoculants and their impact on soil health, as highlighted by (Chenniappan et al. 2019). Growth-stimulating bacteria, such as PGPR, can improve soil health through various mechanisms, including nitrogen fixation, phosphate solubilization, heavy metal sequestering, phytohormone production (e.g., indole acetic acid, gibberellins, or cytokinins), mineralization of soil organic matter, decomposition of crop residues, suppression of phytopathogens, and more, making them useful for plants to grow in nutrient-deficient soils, according to (He et al. 2019; Shameer and Prasad 2018).

PGPR is essential for improving plant growth and stress management and holds significant value for the biotechnology industry due to its potential for producing valuable compounds. As such, PGPR has become a key player in agriculture (Etesami et al., 2018; Glick, 2012; Majeed et al., 2018). However, to fully harness the benefits of PGPR, it is crucial to understand their mechanisms of action in promoting soil health and sustainable agriculture. Thus, the primary objective of this study is to elucidate and illustrate the various tools employed by PGPR to sustainably enhance soil health and agricultural productivity.

### *1. Rhizosphere as an ecological system*

The rhizosphere is a term used to describe the zone surrounding the roots, which is directly influenced by plant root secretions (Hartmann et al., 2009). The activities of microbes in this zone are crucial for plant functioning as they aid in nutrient uptake and protect against pathogen attack (Kibbey and Strevett, 2019). The interaction between the plant, the soil, and the microbes are essential for various processes that contribute to plant health and productivity (Ahmed et al., 2019). Rhizobacterial association and communication with plant roots within the rhizosphere promote successful plant growth. PGPR increases the availability of nutrients in the rhizosphere during root colonization, promoting plant growth and development (Kumari et al., 2019). Plant roots directly influence the rhizosphere, and various compounds are released by plants in the form of root exudates, creating a unique environment. These exudates include sugars, amino acids, organic acids, flavonoids, proteins, and fatty acids (Badri et al., 2009). Some of these root exudates function as signals, either as repellents against various pathogens or as attractants for beneficial microbes, depending on the plant's physiological status, plant species, and the microorganisms present (Ahmed et al., 2019). Root exudates also act as messenger molecules between roots and rhizobacterial species in the rhizospheric soil (Lucini et al., 2019). As a result, root exudates are essential growth substrates for soil microbes, playing a vital role in plant growth promotion and inducing defences against phytopathogens. Rhizodeposition, which includes root border cells, root debris, root exudates, lysates, mucilage, and mucigel, is the soil's primary reservoir of organic carbon (Pausch and Kuzyakov, 2018). Rhizodeposits provide energy to soil microbes to solubilize essential nutrients in soil organic matter, thus increasing soil fertility and promoting plant growth. A wide range of nutrients in the rhizosphere creates an intensely competitive micro-environment, as all inhabitants strive to occupy the most favorable

root zones and ecological niches to ensure their survival. In this challenging environment, rhizobacteria have developed and refined various biological tactics to thrive.

## 2. Role of rhizobacteria in plant growth promotion and soil health

To enhance plant growth, yield, and disease resistance, plant growth promoting rhizobacteria (PGPR) form a healthy and competitive relationship with plant roots (Prasad et al., 2019). These bacteria play a crucial role in soil fertilization through bio solubilization and biofixation of essential nutrient elements, as well as the production of plant growth regulators (Compant et al., 2019). PGPR can also improve the nutritional value of important crops by increasing their antioxidant activities, phenolic contents, and photosynthetic pigments (Singh et al., 2019a). *Azotobacter*, *Pseudomonas*, and *Bacillus* species have been shown to improve the nutrient contents of crops such as lettuce and soybean (Alori and Babalola, 2018). PGPR uses direct and indirect mechanisms to regulate plant growth and improve soil health. Their ideal characteristics (Harish et al., 2019), such as high rhizosphere competence, ease of mass multiplication, and compatibility with other rhizobacterial species, make them suitable for enhancing plant growth and suppressing pathogens, and having a broad spectrum of action. Additionally, they are environmentally friendly (Santoyo et al., 2012).

**Comment [FS2]:** If there is no need for this letter "a", it is advisable to remove it from the text.

**Comment [FS3]:** Because they are genera of living beings, it is necessary to highlight them with an italic text font: *Azotobacter*, *Pseudomonas*, and *Bacillus*

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PGPRs are highly adaptable to various soil environments as they can metabolize natural and synthetic compounds due to their biochemical plasticity. The effectiveness and mode of action of PGPRs have led to the combination of different PGPR treatments being more efficient in pathogen inhibition than single treatments alone (Kumar et al., 2019). This is why PGPRs are considered the most active ingredients in biofertilizer formulations. Furthermore, PGPRs can be categorized based on their beneficial effects. Numerous forms and mechanisms of PGPRs are utilized to obtain desirable agricultural traits. Table 1 illustrates the names of various PGPR species that contain beneficial means and play vital roles as bioremediation, biostimulants, and bioprotectors of plant crops.

Plant growth promoting rhizobacteria thrive naturally in soil, playing a crucial role in soil processes and determining plant productivity. Their beneficial activities, such as reducing crop residues, synthesizing soil organic matter, breaking down soil organic matter, and fixing and solubilizing nutrients, all occur in the presence of other soil microbes. These activities ultimately enhance soil fertility and plant productivity (Chaparro et al., 2012). It is worth emphasizing that soil moisture and other pertinent factors play a vital role in the colonization of PGPR in the rhizosphere. (Vargas et al., 2019).

PGPR can connect with plant roots by producing different biomolecules that enhance soil fertility (Kumar and Verma, 2019). They can break down and mineralize complex organic molecules present in plant residues, thereby contributing to their decomposition. This results in the formation of mineralized organic compounds that blend with the soil, improving soil quality (Raheem et al., 2019). Additionally, PGPR also can produce various phytohormones, which have a significant impact on root structure.

Table 1 :List of Bacterial species with theirFunction

Bacterial species	Function	Mechanism	Effect on plant	Reference
Acetobacter diazotrophicus	Biofertilization	Nitrogen fixation	-	(Mehmood et al. 2018)
Azotobacter chroococcum	Biostimulation Bioprotection	Gibberellin production Siderophore production	Cereals	(Verma et al.,2001), (Zhang et al.,2019)
Advenellakashmirensis	Biostimulation	Cytokinin production	-	(Ibal et al., 2018)
Agrobacterium radiobacter	Bioprotection	Antibiotics	-	(Mohanram and Kumar 2019)
Achromobacterxylosoxidans	Biofertilization	Ammonia production	Agricultural fields	(Akbar and Sultan, 2016)
Azospirillum diazotrophicus	Biofertilization	Nitrogen fixation	Sugarcane (Saccharum officinarum)	(Steenhoudt and Vanderleyden 2000)
Azospirillum brasilense	Biofertilization Biostimulation Bioremediation	Nitrogen fixation IAA production Phosphate solubilization Reclamation of degraded land Heavy	Rice (Oryza sativa) Cereals	(Thomas et al.,2019) (Schillaci et al.,2019) (Hungria et al.,2016) (Kamnev et al., 2005)

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		metals uptake		
<b>Azospirillum lipoferum</b>	Biostimulation	Gibberellin production	Rice (Oryza sativa)	(Cassán et al. 2001)
<b>Bacillus aerius</b>	Bioprotection	HCN production	-	(San Fulgencio et al. 2018)
<b>Bacillus amyloliquefaciens</b>	Biostimulation Bioprotection Bioprotection	Gibberellin production Lipopeptides Antibiotics Bacteriocins	Rice (Oryza sativa) - Tomato (Solanum lycopersicum)	(Shahzad et al. 2016) (Gupta et al., 2015) (Abdallah et al., 2018) (Chowdhury et al. 2015)
<b>Bacillus atrophaeus</b>	Biostimulation	IAA production	Soybean (Glycine Max L.)	(Bai et al. 2002)
<b>Bacillus anthracis</b>	Bioprotection	Protease production	Wheat (Triticum aestivum L.)	(Verma et al. 2016)
<b>Bacillus aryabhatai</b>	Biofertilization	Zinc solubilization	Soybean (Glycine Max L.) and Wheat (Triticum aestivum L.)	(Ramesh et al. 2014)

<b>Bacillus circulans</b>	Biofertilization Bioprotection	Potassium solubilization Protease production Lipopeptides Acquired and induced systemic resistance Amylase production	Tomato (Solanum lycopersicum) - Bean (Phaseolus vulgaris) Tomato (Solanum lycopersicum) Soybean (Glycine Max L.)	(Mehta et al. 2015) (Contesini et al., 2018) (Ongena and Jacques, 2008) (Hashami et al. 2019) (Vaikundamorthy et al., 2018) (Rao et al. 2010)
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Rhizobacteria can enrich the nutrient content of the soil. Nitrogen is a crucial nutrient for all microorganisms, and it is a fundamental component of proteins, nucleic acids, and several other important organic compounds. Since it is not readily accessible in the soil, PGPR can gather atmospheric nitrogen through biological nitrogen fixation in the soil and plant roots.

Some of these bacteria can also dissolve phosphate in the soil, increasing the availability of phosphate ions that can be quickly taken up by the plant roots (Liu et al., 2019b). These processes will be discussed in detail below.

PGPR produces various volatiles and metabolites, such as antibiotics, hydrolytic enzymes, and proteins, that blend into the soil and serve as soil conditioners, enhancing soil health (Prasad et al., 2019). Rhizobacterial species from various genera, including *Agrobacterium*, *Arthrobacter*, *Bacillus*, *Burkholderia*, *Collimonas*, *Enterobacter*, *Paenibacillus*, *Pedobacter*, *Pseudomonas*, *Rahnella*, and *Serratia*, have been identified as producers of volatile compounds and other antimicrobial agents that inhibit the growth of soil-borne fungal pathogens, resulting in fertile and healthy soil (Kanchiswamy et al., 2015; (Chenniappan et al., 2019). Examples of such volatiles include dimethyl disulfide, 2,3-butanediol, furfural, dimethylhexadecylamine, propanoic acid, butanoic acid, 5-hydroxymethylfurfural,  $\beta$ -caryophyllene, geosmin, 2-methyl isoborneol, 1-octen-3-ol,  $\alpha$ -pinene, camphene, camphor, methanol, and acetaldehyde, among others. These volatiles play a vital role in the biocontrol of potential pathogens, stimulation of plant growth or the plant immune system, modulation of root-system architecture, and other functions (Hernández-León et al., 2015; Gutiérrez -Luna et al., 2010; Kanchiswamy et al., 2015; Rojas-Solis et al., 2018). In general, these mechanisms contribute to improving soil health. A healthy soil body is a potential reservoir of macro and micronutrients, contributing to good yields and long-term productivity (Summuna et al., 2019).

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**Comment [FS7]:** Because they are genera of living beings, it is necessary to highlight them with an italic text font: *Agrobacterium*, *Arthrobacter*, *Bacillus*, *Burkholderia*, *Collimonas*, *Enterobacter*, *Paenibacillus*, *Pedobacter*, *Pseudomonas*, *Rahnella*, and *Serratia*

### 3. Direct and indirect mechanisms exerted by PGPR

Rhizobacteria promote plant growth directly and indirectly through compounds that stimulate plant growth, enhance nutrient uptake, or protect plants from pathogens (Orozco-Mosqueda et al., 2018). These actions maintain soil and plant health by releasing various antimicrobial and growth-stimulating compounds, which may be excreted or diffused in solid media or volatilize. Numerous studies have investigated the mechanisms of action of such compounds (Glick, 2012). The discovery of indirect means of plant growth promotion has highlighted the vital role of PGPR in sustainable agriculture (Santoyo et al., 2019). As a result, several bioprotectant PGPR is now commercially produced by different companies worldwide (Galindo et al., 2013).

#### 4.1 Biological nitrogen fixation

Biological nitrogen fixation (BNF) refers to the process by which atmospheric nitrogen turns into forms that plants can use, carried out by nitrogen-fixing microorganisms through a complex enzyme system known as nitrogenase (Masson-Boivin & Sachs, 2018). BNF can occur in two main types: symbiotic nitrogen fixation, which involves members of the Rhizobiaceae family with leguminous plants (Dinnage et al., 2019), and nonsymbiotic nitrogen fixation, which involves various genera such as *Arthrobacter*, and *Acetobacter*, *Clostridium*, *Azotobacter*, *Bacillus*, *Pseudomonas*, and *Diazotrophicus* (Martins et al., 2019). A significant proportion of atmospheric nitrogen enters the soil naturally through beneficial soil microorganisms like PGPR, which fix nitrogen (Ji et al., 2019). Thus, plant-microbe interactions through biological nitrogen fixation play a significant role in organic fertilizer production (Kuypers et al., 2018).

Recent research has indicated that the *Azospirillum* species can provide adequate nitrogen to sunflowers and boost their yield and productivity (Fukami et al., 2018). These bacteria can fix nitrogen up to 15 kg/ha/year and produce indoleacetic acid (IAA). This plant growth hormone aids nutrient uptake and enhances plant growth and development (Aulakh et al., 2017). Using nitrogen-fixing bacteria can reduce the need for chemical fertilizers, resulting in lower production costs. PGPR, with nitrogen-fixing abilities, can supply more soil organic nitrogen and other vital nutrients, reducing the use of chemical nitrogen fertilizers and increasing nutrient availability.

Furthermore, combining various rhizobacterial species enhances soil health and promotes sustainable agriculture, unlike using a single species. Recent research has revealed that common nitrogen-fixing bacteria like rhizobia do not always infect the roots of leguminous plants but instead coexist with diverse PGPR in other nonleguminous plants. In some instances, the interaction of PGPR, such as *Pseudomonas* species, with *Rhizobium* may result in a synergistic process, potentially forming nodules and improving nitrogen fixation capacity (Tilak et al., 2006). Moreover, in some cases, horizontal transfer of important nodulation and nitrogen fixation genes from rhizobia to other bacterial groups like Gammaproteobacteria (*Pseudomonas*) and Betaproteobacteria (*Burkholderia*) may enable them to form nodules in *Robinia pseudoacacia* roots (Shiraishi et al., 2010). These findings highlight the crucial diverse interactions between common nitrogen-fixing bacteria like rhizobia and other saprophytic bacteria, commonly known as plant growth-stimulating species (Santoyo et al., 2012).

#### 4.2 Phosphate Solubilization

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Phosphorus (P) is a crucial nutrient for plants, as it is involved in various metabolic processes such as photosynthesis, respiration, biosynthesis of macromolecules, and signal transduction (Khan et al., 2010). P also helps in root growth, seed development, and crop maturity (Heydari et al., 2019). However, plants can only absorb low amounts of phosphatic fertilizers due to their fixation in the soil as insoluble complexes (Alori et al., 2017). The use of phosphatic fertilizers is not only expensive but also harmful to the environment. Hence, finding an eco-friendly and safe approach to enhance crop productivity in low P soils is necessary. Various PGPR has been identified to transform insoluble phosphate complexes using different mechanisms (Zaidi and Khan, 2005).

PGPR makes phosphorus available to plants by solubilizing and mineralizing complex P components (Kafle et al., 2019). Solubilization of phosphorus occurs due to the production of organic acids by soil bacteria. These organic acids chelate mineral ions and lower the pH of the medium, thereby bringing P into the soil solution (Zaheer et al., 2019). Mineralization is another mechanism responsible for P-solubilization, where complex organic P compounds are broken down into utilizable forms through the action of enzymes such as phosphatases and phytases secreted by soil microbes (Wu et al., 2018). Phosphatases are extracellular enzymes that use organic forms of P as a substrate and transform them into inorganic forms. At the same time, phytases play an essential role in releasing P from phytic acid, a significant component of organic phosphorus in soil (Puppala et al., 2019). Once P's organic and inorganic forms become simpler, they become readily available to plants for uptake. Developing bacterial inoculants that can produce these phosphate solubilizing enzymes is highly desirable, as they could be of great practical value in sustainable agriculture (Rathinasabapathi et al., 2018).

#### 4.3 Potassium solubilization

PGPR solubilizes potassium and has been able to increase the level of potassium in the soil, enhance the uptake of potassium by plants and promote the growth of economically significant crops such as cotton, rape, pepper, cucumber, peanut, and maize (Ashley et al., 2006). Potassium availability is essential for regulating cell growth, including the development of hair roots, the growth of pollen tubes, the management of plant cellular osmotic pressure, and the transportation of various compounds in plants (Ahmad et al., 2018). Potassium-solubilizing bacteria can convert insoluble potassium in the soil into forms that can be easily absorbed and utilized by plants (Etesami et al., 2017). Compared to bulk soil, many rhizobacteria that solubilize potassium (KSR) are present in rhizospheric soil. Potassium-solubilizing bacteria can release potassium from feldspar and aluminosilicate minerals in the soil (Bahadur et al., 2019).

Organic acids, such as citrate, oxalate, and acetate, can break down various minerals in the soil, including clay silicates, mica, feldspar, sandstones, granite, calcite, and dolomite from limestone. This breakdown converts insoluble potassium into a soluble form readily available to plants, increasing nutrient availability for crop plants. *Bacillus* species produce carboxylic acids that help solubilize potassium complexes in the soil, leading to increased soil fertility and crop productivity (Majeed et al., 2018; Saha et al., 2016). Based on this information, using potassium solubilizing rhizobacteria may significantly contribute to sustainable high yield, increased productivity, and improved soil fertility.

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#### 4.4 Production of *Phytohormones*

Phytohormones, also known as plant growth regulators, are substances produced by plants that act as signalling molecules and have a significant impact on various physiological processes at low concentrations, including cell elongation, apical dominance, tissue differentiation, cell division, and intracellular communication (Cassán et al., 2014). They can be classified into five major classes based on their structural composition and response to physiological processes in plants: auxins, gibberellins, cytokinins, ethylene, and abscisic acid. Under stressful environmental conditions, plants often maintain their levels of endogenous hormones to counteract the adverse effects of stress (Dimkpa et al., 2009). Phytohormones are widely produced by bacteria associated with plants and soil and play a fundamental role in plant growth and development. They are also crucial in alleviating biotic and abiotic stress conditions. Auxins, gibberellins, and cytokinins regulate plant growth and respond to various stress conditions (Syta et al., 2019). The article details the roles of different phytohormones produced by bacteria and their effects on plant development.

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##### 4.4.1 *Auxins*

Auxins are bioactive molecules that are engaged in a variety of plant physiological processes. Many research studies have shown that the growth rate of plants treated with PGPR-producing auxins is significantly greater than that of untreated plants (Mahmoud et al., 2020). Auxins are essential for cell elongation, cell division, and cell differentiation. Root hairs expand in response to the auxin gradient, i.e., auxins stimulate signalling pathways for root epidermal hair cells (Nascimento et al., 2020). According to an examination of transcriptome sequencing data, 90 percent of the genes associated with root growth are favourably regulated by auxins (Zhang et al., 2018). In addition, *auXin* synthesis by plant growth-promoting rhizobacteria can modify and enhance the antioxidant system in economically significant crops such as wheat (Acuña et al., 2019). *Rhizobium*, *Pantoea*, *Agrobacterium*, *Pseudomonas*, and *Bacillus* species have been identified as PGPR for auxin synthesis (Tabassum et al., 2017). Indole-3-acetic acid (IAA)-producing PGPR have also been involved in mitigating metal stressors by inhibiting metal sorption and boosting antioxidant enzymes (Salazar et al., 2016). In general, IAA generation by PGPR may be the most incredible option for enhancing crop and biofertilizer output in the future, given that there are various potential methods for mitigating stress conditions. IAA, the most significant auxin, is produced by multiple parallel routes. There are primarily four tryptophan-dependent mechanisms involved in the microbial production of IAA. These processes are called the indole-3-Acetamide pathway, the indole-3-pyruvic acid pathway, the indole-3-acetonitrile pathway, and the indole-3-tryptamine pathway, based on their intermediate compounds (Imada et al., 2017). In PGPR, the indole-3-pyruvic acid pathway is the primary route for IAA synthesis. Enzymes involved in IAA synthesis are typically encoded by huge gene families, making it difficult to identify and characterize distinct pathways. Both plants and bacteria utilize L-tryptophan as a significant precursor for IAA synthesis. The first stage of this route is the aminotransferase-catalyzed conversion of tryptophan to indole-3-pyruvate. In the second phase, indole-3-pyruvate is transformed into IAA by monooxygenases containing flavin (Matthes et al., 2019). This two-way conversion of tryptophan to IAA is the primary auxin biosynthesis route, which plays a crucial role in numerous plant developmental processes.

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#### 4.4.2 *Gibberellins*

They are a group of tetracyclic diterpenoid carboxylic acid derivatives involved in various developmental and physiological processes in plants. Gibberellins serve as signaling molecules for host plants during stressful and non-stressful conditions (Goswami and Suresh, 2020). Gibberellin-producing PGPR safeguards plants against biotic and abiotic stress by modulating antioxidant levels by decreasing superoxide dismutase, flavonoids, and radical scavengers (Goswami and Suresh, 2020). Gibberellins stimulate calcium ions and other nutrient absorption, which regulates salinity stress by reducing the peroxidation of lipid membranes (Carlson et al., 2020). In addition, the exogenous application of gibberellins increases soybean growth by increasing the level of daidzein and genistein, indicating the protective role of gibberellins under adverse conditions (Ahanger et al., 2018). Inoculation of GA-producing *Bacillus* and *Pseudomonas* species into crops increased dry weight, fresh weight, and moisture content compared to the untreated control.

Gibberellin synthesizes from geranyl-geranyl diphosphate (GCPP) and isopentenyl diphosphate, a 5-carbon precursor to all terpenoid compounds (Salazar-Cerezo et al., 2018). The basic isoprenoid unit (IPP) generates by two pathways in the chloroplasts of most plants: the Mevalonic acid pathway (Cytoplasm) and the Methyl erythritol phosphate pathway (Plasmid). The process divides into three phases based on the subcellular compartments and enzymatic activity. In the first step of ent-kaurene production, proplastid-located enzymes catalyze the reaction. In the subsequent step, ent-kaurene oxidize to GA12-aldehyde, the general GA precursor, catalyzed by monooxygenases at endoplasmic reticulum sites. In the final step, dioxygenases in the cell's cytosol catalyze the reaction (Zou et al., 2019).

Furthermore, gibberellins are responsible for seed germination, flowering, stem elongation, and fruit set in various higher plants (Martins et al., 2019). Sessile plants rely on finely tuned responses to their hormones and other signaling components to control their growth and development. Consequently, it is essential that plants tightly regulate their hormone signaling pathways.

#### 4.4.2 *Cytokinin*

Cytokinins are a class of growth regulators that can regulate multiple developmental processes throughout the life cycle of plants, including gametogenesis, root meristem specification, vascular development, shoot and root growth, meristem homeostasis, and senescence. In addition, they regulate responses to environmental stimuli such as light, stress, and nutrient conditions (Arkhipova et al., 2007). Most bacteria can synthesize cytokinins, increasing cytokinin concentrations in the soil and the plants (Zürcher & Müller, 2016). Therefore, inoculating the root environment with cytokinin-producing rhizobacteria stimulates plant growth, suggesting increased plant growth and improved soil health. Under stress, such as drought, the cytokinin content of plants decreases, and it has been demonstrated that the application of cytokinins promotes stomatal opening, most likely by acting in concert with accumulated abscisic acid (ABA) (Sahu et al., 2019). It is widely reported that microbes increase the level of cytokinin in plants (Selvakumar et al., 2018). Consequently, cytokinin-producing bacteria linked to plant growth promotion can be utilized as indicators in plant health management practices.

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#### 4.5 Siderophores

Natural soil health can be maintained only by applying PGPR, which can be an effective bioprotectants (Karthik et al., 2017). One of the first mechanisms described to inhibit phytopathogens is the production of iron-chelating compounds or siderophores (Kloepper et al., 1980). Since iron ( $\text{Fe}^{3\text{p}}$ ) is among the essential nutrients and is particularly deficient in plants under stressful and calcareous conditions, several PGPR produce siderophores (of different types, such as bacillibactins, pyoverdines, cephalosporins) in response to low iron levels in the soil, therefore, when it is limiting, PGPR can form  $\text{Fe}^{3\text{p}}$ -siderophores complexes, making it unavailable for other pathogenic microorganisms, such as pathogenic fungi. By contrast, the rhizobacterial (or plant) siderophores chelate iron and make it available to the plants (Sinha and Parli, 2020). Several studies have employed siderophores-producing rhizobacteria as potential biocontrol agents since these iron-chelating compounds have been involved in antifungal action by depriving the plant pathogens of this vital element (Fe) (Kour et al., 2019).

**Comment [FS25]:** If this topic refers to item (3. Direct and indirect mechanisms exerted by PGPR), then it should be numbered 3.5

#### 4.6 Volatile organic compounds (VOCs)

During interactions with plants and other rhizosphere microorganisms, PGPR (and other organisms) produce volatile organic compounds (VOCs) with distinct roles and functions (Bitas et al., 2013). There is substantial evidence that VOCs have dual direct and indirect action during plant growth promoting activities (Santoyo et al., 2019), i.e., rhizosphere VOCs can induce plant growth directly or indirectly by limiting the development of potential phytopathogens. The volatile N,N-dimethylhexadecylamine (DMHDA) produced by the rhizobacterium *Arthrobacter agilis* UMCV2 inhibits the growth of *Botrytis cinerea* and *P. cinnamomi* in vitro, thereby protecting plants from their attack. In addition, under Fe-deficient conditions, the DMHDA compound induces the Fe-uptake mechanisms of *M. truncatula* seedlings (Orozco-Mosqueda et al., 2013; Velázquez-Becerra et al., 2013). Other PGPR volatile compounds, such as dimethyl disulfide (DMSD), can promote plant growth by enhancing sulphur nutrition in *Arabidopsis* plants, as well as exerting an antagonistic action against major plant pathogens such as *B. cinerea* and simultaneously acting as an elicitor of defence responses in plants (Huang et al., 2012; Rojas-Sols et al., 2018). During interactions with plants and other rhizosphere microorganisms, PGPR (and other organisms) produce volatile organic compounds (VOCs) with distinct roles and functions (Bitas et al., 2013). There is substantial evidence that VOCs have dual direct and indirect action during plant growth promoting activities (Santoyo et al., 2019), i.e., rhizosphere VOCs can induce plant growth directly or indirectly by limiting the development of potential phytopathogens. The volatile N,N-dimethylhexadecylamine (DMHDA) produced by the rhizobacterium *Arthrobacter agilis* UMCV2 inhibits the growth of *Botrytis cinerea* and *P. cinnamomi* in vitro, thereby protecting plants from their attack. In addition, under Fe-deficient conditions, the DMHDA compound induces the Fe-uptake mechanisms of *M. truncatula* seedlings (Orozco-Mosqueda et al., 2013; Velázquez -Becerra et al., 2013). Other PGPR volatile compounds, such as dimethyl disulfide (DMSD), can promote plant growth by enhancing sulphur nutrition in *Arabidopsis* plants, as well as exerting an antagonistic action against major plant pathogens such as *B. cinerea* and simultaneously acting as an elicitor of defence responses in plants (Huang et al., 2012; Rojas-Sols et al., 2018).

**Comment [FS26]:** If this topic refers to item (3. Direct and indirect mechanisms exerted by PGPR), then it should be numbered 3.6

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In a groundbreaking study by (Ryu et al; 2003), the volatile compounds produced by beneficial *Bacillus* bacteria, particularly 2,3-butanediol and acetoin, play a crucial role in

promoting the growth of *Arabidopsis thaliana*. Conversely, the volatile compound hydrogen cyanide (HCN) has an antagonistic effect on pathogens. This compound helps to control pathogens by inhibiting the electron transport chain, resulting in cell death (Aloo et al., 2019). Many bacterial genera, including *Bacillus* spp. and *Pseudomonas* spp., can produce HCN (Santoyo et al., 2012). The HCN-producing trait in bacteria can greatly benefit plant establishment by controlling fungal diseases (Aarab et al., 2019). PGPR-produced HCN acts as a biocontrol factor against phytopathogens and plays a role in geochemical processes in the substrate, such as metal chelation. Consequently, this volatile organic compound indirectly increases phosphate availability in the rhizosphere, benefiting the associated plants (Kumari et al., 2018; Rijavec and Lapanje, 2016).

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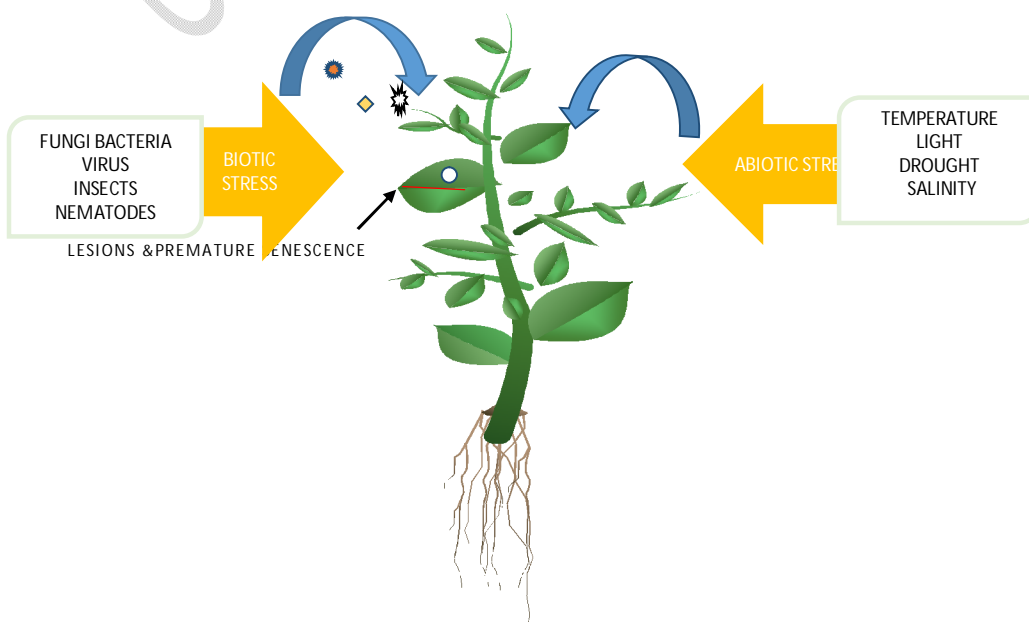
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#### 4.7 Hydrolytic enzyme production

**Comment [FS40]:** If this topic refers to item (3. Direct and indirect mechanisms exerted by PGPR), then it should be numbered 3.7

PGPR produces and expels various hydrolytic enzymes, including cellulases, pectinases, proteases, catalases, and chitinases. The defense-related activities of these enzymes against various phytopathogens have been demonstrated. Chitin is the vital structural component of the cell wall of fungi. Rhizobacteria that stimulate plant growth target fungal cell walls by secreting chitinases, resulting in chitin degradation. In this manner, chitinolytic bacteria inhibit fungal pathogens such as *Botrytis cinerea*, a phytopathogen capable of infecting more than 200 plant species. Thus, chitinolytic PGPR reduces the severity of plant diseases caused by fungal or oomycete pathogens, indirectly enhancing plant growth (Martnez-Absalón et al., 2014; Hao et al., 2017). Rhizobacteria that produce cellulase hydrolyze cellulose to glucose via the synergistic actions of enzymes, including glucanases, hydrolases, and glucosidases (Siqueira et al., 2020). It is well-established that cellulase-producing bacteria can be considered antifungal agents (Sadeghi et al., 2017). By degrading cellulosic residues, cellulosic bacteria also provide a carbon source in the rhizosphere to improve soil health and maintain nutrient balance (Behera et al., 2017). These bacteria that produce cellulase can also be used to convert biomass into biofuels (Siqueira et al., 2020). Compared to chemical conversions, cellulase-mediated conversions are green and environmentally friendly.

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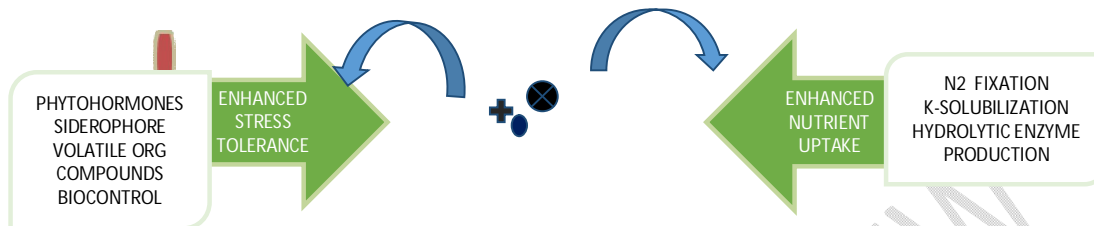


Fig.1 Potential of Plant Growth Promoting Rhizobacteria

#### 4. PGPR as Green bioinoculants

Bioremediation refers to using biological agents/biological processes to remove harmful substances from the environment (Sampaio et al., 2019). Bioremediation has provided an alternative to conventional methods for remediating soil contaminated with metals. In metal-contaminated soils, the natural role of metal-resistant plant growth-promoting rhizobacteria is more critical than in conventional agricultural practices for enhancing soil properties (Sharma and Archana, 2016). Most metals are classified as toxic, but their toxicity levels vary greatly. Cadmium (Cd) and Lead (Pb) harm soil organisms by binding to respiratory proteins and through oxidative damage, i.e., the production of reactive oxygen species (Ullah et al., 2019). Soil microorganisms are damaged by even the lowest concentration of these metals. Significant roles are played by bulk and rhizosphere bacteria in the biogeochemical cycling of heavy metals, resulting in the remediation of contaminated soil.

Comment [FS42]: I think this thread is the 4.8.

#### 5.1 Degradation of Pollutants by PGPR

The biodegradation of persistent organic pollutants (POPs) is studied from oxidative degradation by aerobic bacteria and dechlorination by anaerobic bacteria. In aerobic bioremediation, PGPR degrade contaminants using atmospheric oxygen (Murugan and Vasudevan, 2018). Bacteria have successfully utilized biphenyl to stimulate the aerobic remediation of polluted soil (Chakraborty and Das, 2016). During this process, polychlorinated biphenyl (PCB) is degraded by oxidation using multiple genes and their associated enzymes (Terzaghi et al., 2018). Major enzymes involved in POPs degradation are dehydrogenases, dioxygenases, hydrolases, hydratases, aldolases (Reddy et al., 2019). Bacterial strains that degrade POPs via aerobic oxidation include, to name a few, *Pseudomonas*, *Bacillus*, *Achromobacter*, *Rhodococcus*, *Ralstonia*, and *Corynebacterium* (Vergani et al., 2017).

Comment [FS43]: I think this thread is the 4.9.

Comment [FS44]: If there is no need for this letter "X" to be capitalized, it is advisable to put it in lowercase.

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In anaerobic degradation, anaerobic bacterial species break down chemical compounds in the soil to liberate the energy necessary for their metabolic processes. In unpolluted soils, anaerobic bacterial respiration occurs via electron acceptors such as sulfate and nitrates. PCB-contaminated soils change to reductive dehalorespiration (Field and Sierra-Alvarez, 2008). In dehalorespiration, bacterial species attack chlorine substituents at the para and meta positions, thereby replacing them with hydrogen atoms (Furukawa and Fujihara, 2008). Bacteria involved in

dechlorination convert more chlorinated compounds to less chlorinated ones, reducing their toxicity and making them more susceptible to aerobic degradation (Yim et al., 2008).

Due to a lack of timely degradation, intense and frequent pesticide use has resulted in pesticide persistence in soil (Rangasamy et al., 2018). These pesticides loaded in the soil's rhizosphere are responsible for adverse effects on the microbial community and plants (Rangasamy et al., 2018). Due to their long shelf life and nonbiodegradable nature, these toxin-containing chemicals persist in the environment and enter the food chain, posing grave health risks (Singh et al., 2008). These increased pesticide levels degrade the entire ecosphere via biomagnification (Morillo and Villaverde, 2017). Biotransformation, biomineralization, bioaccumulation, biodegradation, bioremediation, and cometabolism can break down pesticides (Liu et al., 2019a). Bacterial degradation is the bacterially mediated breakdown of pesticides into simple inorganic compounds on contaminated sites, soil rhizosphere, groundwater, and industrial systems (Subbanna et al., 2018). Therefore, the PGPR significantly removes pesticides from the environment and significantly improves soil health and promotes plant growth.

### 5. Conclusion and perspective

Leveraging the potential mechanisms of action in PGPR and its beneficial interactions with plants is essential to increase plant growth and production. PGPR is important because of the dire need to feed a continuously growing world population, expected to reach 10 billion by 2050 and peak in approximately 2070–2080 (Lutz et al., 1997). Hence, one of the aims of this endeavor is to... is to emphasize the different mechanisms of PGPR, as well as their enormous potential to generate optimal conditions for sustainable agricultural production, which includes a reduction in the environmental impact. Therefore, understanding rhizobacterial ecological roles in a micro-ecosystem like a rhizosphere is an essential first step to obtaining better results when inoculating PGPR (Santoyo et al., 2019). There are several critical aspects to determine the efficiency of a bioinoculant with stimulatory or protective effects, including regulation at the molecular level of genes involved in the production of diffusible and volatile compounds as well as enzymes in the rhizosphere; also the colonizing capacity of PGPR, interaction with other beneficial soil microorganisms, tolerance, and adaptive mechanisms to abiotic and biotic stresses, among others. However, discovering new bacterial strains (or even species) with plant growth-promoting activities emerged, unveiling the dark side of known and unstudied ecosystems with potential applications in agri- culture. In addition, novel molecular and genomic strategies are high- lighting the specific but essential roles of bacterial consortia in direct and indirect activities of plant growth promotion (Carrion et al., 2019). Despite all this knowledge, there is still an enormous gap in the transition from the laboratory to and field, which is usually the bottleneck that reduces the possibilities of expanding the use of PGPR in agriculture. In this phase, scientists and other business and political actors must create optimal and legal conditions to benefit agricultural and economic production without neglecting the aspect of sustainable agriculture and an environment healthy for the population, particularly in those developing countries.

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**Comment [FS46]:** If there is no need for this letter "a", it is advisable to remove it from the text.

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