



Unlocking the Secrets of Rhizosphere Microbes: A New Dimension for Agriculture

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Abstract

Rhizospheric microbes help plants to acquire and assimilate nutrients, improve soil texture and modulate extracellular molecules. Rhizosphere bacteria regularly encounter a copious number of variables, such as temperature, pH, nutrients, pest resistance mechanisms, etc. The extracellular concentration of chemical messengers fabricated by plant growth promoting bacteria (PGPB) in a system is directly proportional to the bacterial population. To dwindle the use of chemically synthesised pesticides, plant growth-promoting rhizobacteria (PGPR) are new arsenals of imperishable agricultural practises for managing plant pathogens and resistance. This review aims to harness the rhizosphere milieu to raise climate smart crops. The PGPB mediated hormonal control of plant stress management pathway could be potentially modified for the benefit of plants. Nutrient solubilisation strengthens the rhizomicrobiome for phytoremediation and pathogen control. Quorum sensing as well as the role of enzymes and siderophores in rhizo-microbiome has been discussed. With advent of metagenomics, the understanding of soil microbiome ecology has acquired new dimensions and has enabled us to modify the microbiome for sustainable agriculture and enhanced productivity.

Keywords Plant growth promoting bacteria · Rhizosphere · Biofertilizer · Biocontrol agents · Quorum sensor · Climate change

1 Introduction

A community of micro-organisms neighbouring plant roots is critical for verdure. The environmental conditions exhibit a temporal and spatial control over the cast and roleplay of

these microbes (Islam et al. 2020). Metabolites secreted by roots determine the type of microbiome of the rhizosphere. The plants being sessile, adapt to stress by altering the composition and amount of their metabolites during neighbour rivalry, pathogenic infections and herbivore attacks (Jan et al. 2021). Root tissue exudates, volatile chemicals along

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with carbon and nitrogen-rich rhizodeposits, contribute to the formation of rhizomicrobiomes (Jiang et al. 2022).

Plant-associated microbiota can be transferred vertically, as in endophytes, where they establish strong symbiotic relation directly with plants through the secretion of compounds responsible for plant growth, synthesis of metabolic products and rapid host adaptation under biotic and abiotic stress conditions. Similar to PGPR these endophytes synthesize different class of metabolic products, enzymes and molecules to degrade contaminants and helps host plant to breed even at polluted sites. Horizontal transfer of microbes occurs, by recruiting microbes from a pool of soil species into the rhizosphere. It affects plant's immune system, metabolism, and hormone balance. These plant-associated microorganisms modify pathways such as stress responses, and growth regulation, contributing to the smooth functioning of these essential processes (Meena et al. 2020; Anand et al. 2023). Constant secretion of low and high molecular weight natural substances from roots changes the chemical and biological conditions in the soil near the roots. Conductive intercommunications like nutrient availability, growth stimulation, and disease suppression between roots and rhizospheric bacteria lead to healthy growth of plants. Among the complex microflora, plants prefer bacteria the most for their growth by releasing organic compounds through root exudates (Adedeji and Babalola 2020; Chai and Schachtman 2022). Autogenetic disease suppression mechanisms mediated by rhizomicrobiomes proactively entail disease control (Jamil et al. 2022). With the advances in metagenomics, gene expression and metabolomics, the trend of comprehending

the plant microbiome has changed. The most recent findings in the field of plant microbiome research demonstrate an ongoing compatibility between plants and microbes in terms of nutritional availability. Such interaction is constantly taking place and has either a direct or indirect impact on plant health.

The present review summarizes a comprehensive description of mechanisms used by rhizobacteria for plant growth promotion resulting from soil–plant–microbe interactions. We also discuss the significant role of PGPR in the nutrient cycle, secretion of phytohormones, mineral solubilization, and biocontrol applications for further use in modern agriculture. Consequently, we compile the key strategies employed by PGPR to enhance soil health and shed light on functional genomics, aiming to broaden the sustainable utilization of these advantageous microorganisms. The potential target areas for future research and use of Rhizobacteria in agriculture have also been projected. The overview of plants and PGPR and their dynamics in nature has been depicted in Fig. 1.

2 Root exudates determine the diversity of Rhizospheric bacteria

Plant growth-promoting rhizobacteria (PGPR) reside intracellularly in nodules and extracellularly between the cellular region of root cortex and alter the entire microbial community in the pool by synthesising various chemicals (Behera et al. 2021; Pandita 2022).

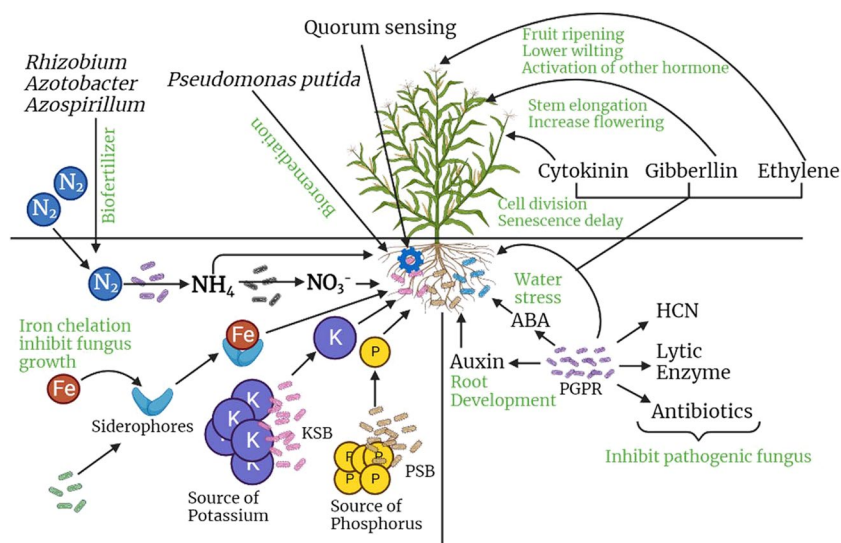


Fig. 1 Major roles of rhizospheric bacteria in plant growth promotion and defence. PGPRs produce signalling molecules like growth hormones for establishing advantageous rhizospheric interactions with the host, which helps to improve nutrient uptake, seed germination, root and shoot elongation, abiotic stress tolerance, and biocontrol

efficacy. Phytopathogen growth is constrained by the production of siderophores, HCN, antibiotics, and lytic enzymes. Quorum sensing results as cell-to-cell chemical communication between rhizospheric microbes through the synthesis, release, detection, and response to small biomolecules

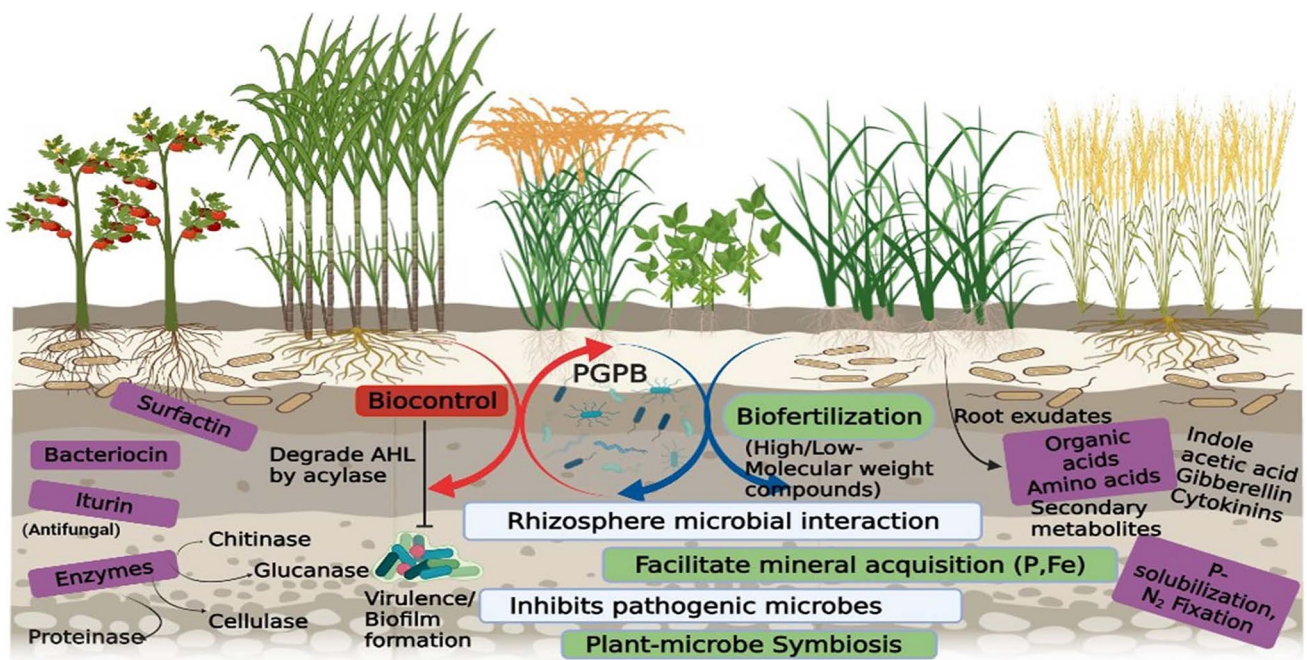


Fig. 2 Schematic diagram depicting significant strategies for stimulating plant development by PGPB. These strategies can be widely examined under biocontrol, biofertilization processes including min-

erals solubilization, enzymes production. Different low molecular weight compounds produced by root exudates attracts the PGPB to improve the fitness of plants under stress conditions

Antagonistic competition among PGPR, in which one microbe preys on other is crucial to impede the growth of phytopathogens through the secretion of bacteriocins and lytic enzymes. The function of PGPR as a biocontrol agent can be enhanced by studying the interactions between various microbes in the rhizosphere (Niu et al. 2020; Boro et al. 2022). The involvement of PGPR in plant development and defence against pathogen is illustrated in Fig. 2.

The majority of root exudates are composed of high and low molecular weight molecules, as well as carbon and secondary metabolites. The two main mechanisms of exudation are the 1) Root seep out the primary metabolites by concentration gradient diffusion process where plant and microbes are actively involved that depend on the nutritional availability in the soil; (2) The transuded metabolites concentrate at the tip of the root to direct the signal cascade process for development and alteration of the root structure (Canarini et al. 2019). These root exudates penetrate cell membranes and seep into the rhizosphere. The extent of these exudates is determined by the physiological condition, age, and availability of nutrients in the soil. The low molecular weight exudates released by the plants attract microbial consortia into the rhizosphere (Volkov and Schwenke 2020; Maurer et al. 2021). *Arthrobacter*, *Enterobacter*, *Azobacter*, *Pseudomonas* and *Azospirillum* are some of the beneficial bacteria that play a predominant role in plant growth. These bacteria act as biofertilizers by facilitating N, P and vital minerals that directly affect plant growth. On the other hand,

they also produce antibacterial substances, volatile compounds (HCN), siderophores and lytic enzymes in an indirect manner which works as biocontrol agents and prevent the spread of phytopathogens (Carballo-Sánchez et al. 2022). Rotting of root caused by *Bipolaris sorokiniana* is a major threat worldwide due to the long life of its spores in the soil. *Pseudomonas* and *Bacillus* spp. has been found to be effective against this cereal disease pathogen (Morales-Cedeño et al. 2021). *Pseudomonas fluorescens* inhibit the growth of *Pythium*, *Phytophthora*, and *Alternaria* (Ghadamgahi et al. 2022; Volynchikova and Kim 2022), *Bacillus amyloliquefaciens* produce antifungal compounds against *Botrytis cinerea* and *Rhizoctonia solani* (Liu et al. 2023), *Bacillus subtilis* induce systemic resistance (ISR) in plants against *Fusarium* and *Rhizoctonia* (Madhi and Jumaah 2020), *Serratia plymuthica* produces prodigiosin against *Botrytis cinerea* and *Colletotrichum* spp., (Trejo-López et al. 2022). Successful biocontrol applications may require proper formulation and application methods to ensure their efficacy in the field.

3 Rhizomicrobiome induces Plant Growth via molecular relaying

The molecular mechanisms underlying plant growth promotion are intricate and multifaceted processes influenced by various factors, including microbial interactions, nutrient availability, hormonal regulation, and environmental

conditions. Understanding these mechanisms provides valuable insights into harnessing nature's potential to optimize agricultural practices and foster sustainable plant growth. The various molecules secreted by plants in root exudates and by the rhizomicroorganisms are key messengers of signalling pathways.

3.1 Phytohormones

Phytohormones are structurally unrelated and are produced by rhizospheric bacteria to regulate plant growth. They act as chemical messengers of the plant and boost plant development. Phytohormones are co-produced by soil microbes, plants, and plant microbes. Plant hormones are divided into three categories: Auxins, Gibberellins (GA), and Cytokinins (Huang et al. 2020; Eichmann et al. 2021). Brassinosteroids, jasmonate, salicylic acid, nitric oxide, strigolactones, and other semi- and synthetic phytohormones are involved in plant defence, and auxin has a direct impact on root growth and development (Anfang and Shani 2021).

3.1.1 Auxin

Auxin is the most-used phytohormone fabricated in the shoot apical meristem of plants. Plant tissues release diffusible auxin (free auxin) after hydrolysis, autolysis, and enzymolysis (Primo et al. 2015). Indole acetic acid (IAA) hinders cell division, extension, differentiation, and tuber germination in plants. It regulates organogenesis, tropic reactions, and cellular responses such as cell expansion, gene regulation, lateral adventitious root formation, and stress resistance (Spaepen and Vanderleyden 2011).

The biosynthetic pathways for auxins production is different in the plants and microbes. More than 80% of rhizospheric soil bacteria can produce auxins. It can affect root growth by affecting endogenous levels (Spaepen et al. 2007). IAA improves root surface area and length, allowing the plant to obtain more nutrients from the soil and increasing the crop's growth and output. Auxins have concentration-dependent effects on plant seedlings, i.e., low amounts may stimulate development while large concentrations may restrict growth (Sarwar and Kremer 1995). *Rhizobium*, *Microbacterium*, *Sphingomonas*, and *Mycobacterium* produce IAA (Tsavkelova et al. 2007). IAA-producing microbes increase N, P, K, Ca, and Mg uptake in crops and stimulate plant growth. (Sivasakthi et al. 2014). IAA produced by beneficial microbes such as *Azospirillum*, *Rhizobium* and *Bacillus* stimulates root branching, enhance seed germination and ultimately promoting overall plant growth. *Pseudomonas* and *Bacillus* helps plants cope with stressed environment, mitigate nematode infestations by promoting root health and triggers systemic resistance that makes plants more resistant to disease in plants (Meena et al. 2020; Swarnalakshmi

et al. 2020). Certain *Trichoderma* species produce IAA, and besides promoting plant growth, they also act as mycoparasites, attacking and suppressing pathogenic fungi in the rhizosphere (Fazeli-Nasab et al. 2022).

3.1.2 Gibberellin

Gibberellins (GAs) are tetracyclic diterpenoid carboxylic acids that act as plant growth hormones. First identified as byproducts of the rice pathogen *Fusarium fujikuroi*, which causes overgrowth ("bakanae") in rice seedlings. Japanese scientists isolated GA₃, which restored normal growth to dwarf mutant plants, suggesting that GAs can improve the growth in higher plants (Tudzynski 2005). Gibberellins affect abiotic stress response, stem elongation, flowering, and other physiological effects (Gusmiaty et al. 2019). They promote root growth, root hair abundance, and plant cell ageing. Gibberellins break seed dormancy exogenously and endogenously. Gibberellins can replace temperature or light stimulus in some plant species. Gibberellins affect food reserves and the embryo's growth potential during germination (Debeaujon and Koornneef 2000). Gibberellins also affect the floral induction, floral bud differentiation, and flower development in woody angiosperms (Rub et al. 2004). Some strains of *Rhizobium*, *Bacillus*, *Azospirillum*, *Stenotrophomonas maltophilia*, *Pseudomonas* spp. and *Actinomyces* produce gibberellins. These well-known PGPRs influence the plant growth positively and suppress phytopathogens, however their effects on plant growth may differ depending on the specific bacterial strain and plant species involved (Adeleke et al. 2022; Kumar et al. 2022; Mitra et al. 2022; Tsotetsi et al. 2022).

3.1.3 Cytokinin

Plants use cytokinins, which are N₆-substituted aminopurines, as PGPRs to affect cell division, seed germination, root growth, synthesis of chlorophyll, leaf expansion, and the delay of senescence (Kieber and Schaller 2014). Root-produced cytokinins are transported to the shoots in the xylem. Their levels fluctuate with changes in root and soil conditions (Ko et al. 2014). Cytokinins are found in microorganism biomass (free or coupled to tRNAs) and in culture media as isoprenylated adenine derivatives or ribosides, such as 6-benzyladenine, N₆-isopentenyladenosine, and zeatinriboside. Inoculating droughted plants with bacteria producing cytokinin stimulates late shoot growth and lowers the root/shoot ratio (Hussain and Hasnain 2009). Stay-green genotypes may demonstrate higher stress tolerance, particularly during periods of water stress during grain loading. This was related to a rise in cytokinin levels in the xylem sap. This hormone can promote cell division and growth, which contribute to stress tolerance in plants (Zhang et al.

2010). Reduced carbon intake and assimilation are caused by ABA-induced stomatal closure, and under stressful circumstances, the up-regulation of cytokinin oxidase may also result in decreased carbon metabolism. Heavy metals hamper the seedling's growth. Rhizospheric microorganisms can indirectly impact plant health and responses to stressors by affecting nutrient availability, hormone levels, and carbon metabolism in the rhizosphere (Mohapatra et al. 2011).

3.1.4 ABA (Abscisic acid)

ABA is synthesised in the plastids (an organelle not found in fungi or animals) from 40-carbon carotenoid precursor molecules via the 2-C-methyl-D-erythritol 4-phosphate (MEP) pathway. (Finkelstein 2013). ABA in soil affects plant growth, resistance, and fitness. Plants may be able to grow in drier soil by accumulating ABA. Depending on concentration, exogenous ABA can either prevent or encourage the growth of well-watered plant roots (Yuzikhin et al. 2021). ABA is produced by higher plants, algae, fungi, and bacteria and its synthesis is increased by salinity, cold temperature, dehydration, and injury (Primo et al. 2015). ABA impacts pest resistance by controlling stomata closure to deny pathogens entry (Hewage et al. 2020). *Azospirillum* sp. might be helpful for maize plants to tolerate water stress

by producing ABA. *A. brasilense* Sp 245 in *Arabidopsis* and *A. lipoferum* USDA 59b in maize boost ABA levels (Casán et al. 2014). In lettuce, *B. subtilis* and *B. licheniformis* Rt4M10 in grapes also improves ABA level (Cohen et al. 2009). Several phytopathogenic fungi and PGPR species, including *Azospirillum brasilense* strains Cd, Az39, and Sp245 and *Azospirillum lipoferum* USA 59b, can synthesise ABA (Martins et al. 2018). From *Prosopis strombulifera* plants raised in very high salinity, the bacteria *Achromobacter xylosoxidans*, *Bacillus licheniformis*, *Bacillus pumilus*, *Brevibacterium halotolerans*, and *Lysinibacillus fusiformis* were recovered. Under osmotic stress, it was proposed that bacteria produce more ABA and this enhanced ABA levels empower the host plant to withstand higher sodicity of soil (Belimov et al. 2014).

3.1.5 Ethylene

Exposure to ethylene may lead to suppression of *Rhizobia* spp. nodule formation and hindering mycorrhiza-plant interaction, while boosting root initiation, fruit ripening, seed germination, leaf abscission, and responses to biotic and abiotic stresses (Kaur and Gera 2016). Volatile ethylene can infiltrate through soil pores that are filled with gas and water. It affects legume-rhizobia symbioses and arbuscular

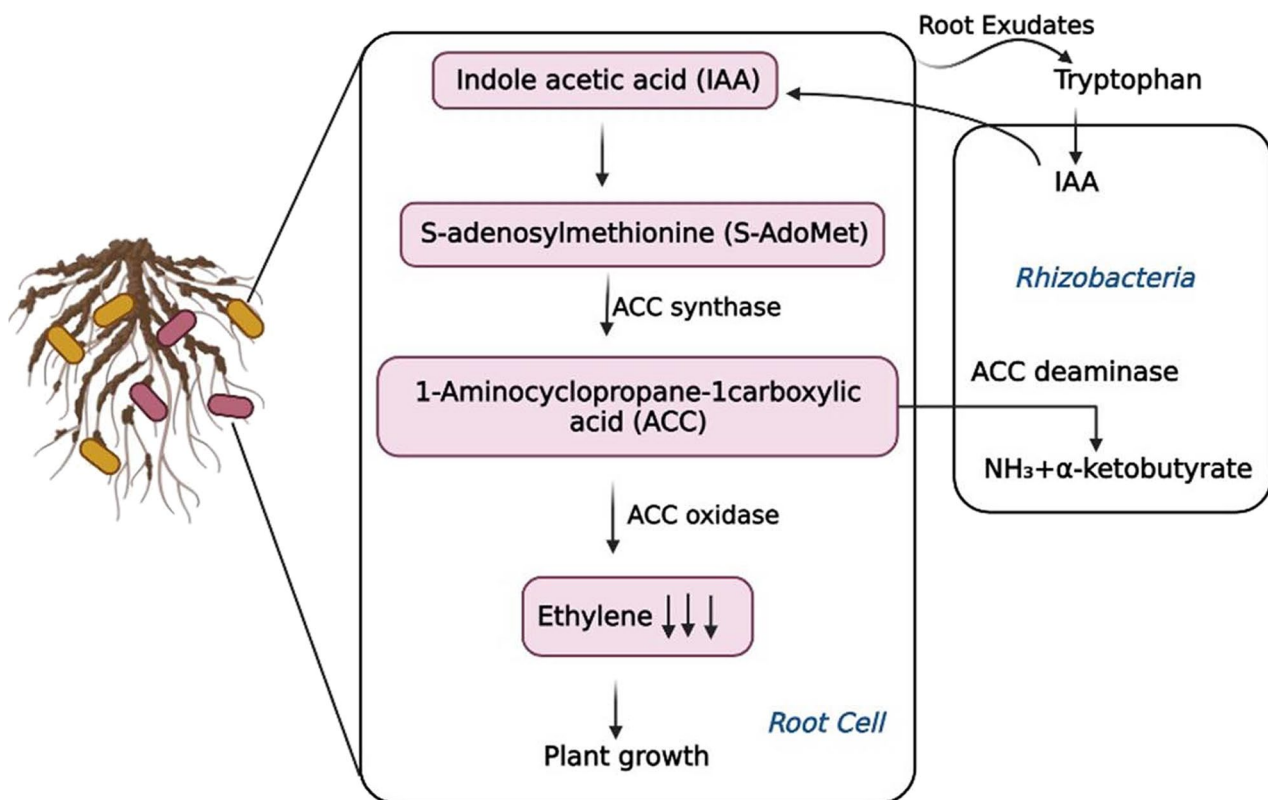


Fig. 3 Schematic diagram depicting the role of ACC deaminase producing Rhizobacteria in plant growth and development

mycorrhizal root colonisation. Ethylene interacts with soil-specific microbes near growing roots. Gaseous compounds attract bacteria to roots from far away in the soil (Schulz-Bohm et al. 2018). Plant physiology depends on precisely controlling cellular ethylene levels. Stress-derived ethylene triggers adaptive responses and affects hormonal signalling, such as growth inhibition and late flowering (Bleecker and Kende 2000). During normal plant development and stressed conditions, ethylene is produced from S-adenosyl-Met by ACC synthase in all higher plants. ACC deaminase regulate ethylene level and plays a crucial role in bacterial physiological activities that support plant growth under stress (Gamalero and Glick 2015). High ethylene levels can inhibit plant growth, cause chlorosis, or kill them. Thus, by converting ethylene's precursor (ACC) into NH_3 and β -ketobutyrate (Fig. 3) and reducing its effects brought on by waterlogging, bacterial ACC deaminase probably plays a crucial role in reducing ethylene (Ali and Kim 2018). Thereby it could be concluded that the rhizospheric bacteria provide ethylene mediated stress tolerance to the host plant and these microbes could potentially be harnessed to develop climate smart crops.

3.2 Nutrient Mobilization and Uptake

Beneficial microorganisms can influence nutrient availability by solubilizing nutrients present in the soil in forms that are more easily accessible to plants. Some key mechanisms of nutrient mobilization include:

3.2.1 Nitrogen fixation & Ammonia production

Plant species cannot convert dinitrogen directly into ammonia for growth (Egamberdieva and Kucharova 2008). Diazotrophic bacteria fix atmospheric nitrogen into NH_3 , the nitrification substrate (Mylona et al. 1995; Cheng 2008). Ammonia production is linked to nitrogen fixation in leguminous rhizobacteria. Biochemical reactions of organic nitrogen fixation occur via symbiotic bacteria with legumes that convert N_2 into ammonia (NH_3) (Upadhyay 2016). Symbiotic and non-symbiotic nitrogen-fixing bacteria boost plant growth. Biological nitrogen fixing (BNF) bacteria such as *Anabaena*, *Bradyrhizobium*, *Clostridium*, *Azospirillum*, *Frankia*, *Mesorhizobium* spp., benefits agroecosystems by transforming N_2 to NH_3 and help in stress tolerance (Nag et al. 2020; Cruz-Hernández et al. 2022). Symbiotic nitrogen fixation is a microbe-plant mutualism. Rhizobia are rhizobacteria that can build symbiotic partnerships with leguminous plants by inhabiting root nodules and linking nitrogen to ammonia. *Frankia* are free-living diazotrophs that can accelerate the growth of non-legume plants including rice and wheat (Ladha et al. 2022). A group of non-symbiotic nitrogen-fixing rhizospheric bacteria from the *Azoarcus*

and *Acetobacter* genera, as well as *Azospirillum* and *Burkholderia*, have no mutual relationship with plant roots. About 20% of the total fixed nitrogen is fixed by naturally occurring nitrogen fixing bacteria (Sivasakthi et al. 2014). *Azospirillum* species are aerobic heterotrophs that restore N_2 in microaerobic conditions (Hayat et al. 2010). There are two steps involved in nitrogen fixation. The oxidation process is catalysed by ammonium monooxygenase, which requires two electrons to decrease an O_2 atom in H_2O . Bacteria that oxidise ammonium create hydroxylamine oxidoreductase, which produces NO_2 . Second, chemolithoautotrophic nitrite-oxidizing bacteria use the chemical energy of nitrification to fix CO_2 (Science and Conservation 2016). Morphological transformation in the roots are because of Nod factors, resulting in the formation of a globular structure known as a "nodule." *Rhizobia* can fix atmospheric N_2 in nodules (Zhang et al. 2018). Rhizobia (*Rhizobium*, *Mesorhizobium*, and *Bradyrhizobium*) can create symbiotic relationships with legume roots. Legumes generate flavonoids that are recognised by rhizobia for the induction of nodulation factor synthesis (Dixon and Kahn 2004). Identification of the *nifH* gene, which encodes the nitrogenase Fe protein, helps to assess nitrogen-fixing capacity. As a result, nitrification and nitrogen fixation are essential processes in the nitrogen cycle as they serve a significant ecological function (Santoyo et al. 2021).

3.2.2 Phosphate solubilization

Phosphorus (P), the second-most crucial nutrient for plants after nitrogen, can be found in organic and inorganic soil types (Kumar et al. 2015). Most of this P is insoluble and cannot support plant growth (Rodríguez et al. 2006). It is involved in photosynthesis, energy transmission, signal transduction, cell division, respiration, and macromolecular biosynthesis (Vassileva et al. 2000). It can be found in two different forms and is degraded by bacteria or fungi. Inorganic phosphorus (30 to 50% of the total) can be found as inositol hexaphosphate or phytate. With Ca, Al, and Mn, inorganic phosphorus creates insoluble mineral complexes. Most soils have 1 mg/kg of soluble phosphorus, insufficient for plant growth (Khan et al. 2014).

Monobasic (H_2PO_4^-) and dibasic (HPO_4^{2-}) ions are plant-accessible forms of phosphorus. Flowers & microbes compete for this element through desorption, absorption, solubilization, and precipitation. Mineralization of organic phosphorus is possible as a byproduct of soil natural processes or by specialised enzymes regulated by nutrient demand (Khatoun et al. 2020) Organic acid synthesis and exudation by soil bacteria are key to solubilizing inorganic phosphate. These organic acids are made by oxidising glucose (Santoyo et al. 2021). Through direct phosphorus uptake or bioavailability, PGPR with phosphate-solubilizing

behaviour can reside in the rhizosphere and improve plant and root health (Hooker et al. 1994). PGPR solubilizes inorganic phosphate which is insoluble into its soluble form, such as orthophosphate, and makes it available to the plant. These P-solubilizing PGPR increase the crop yield by providing a sufficient amount of soluble phosphorus to the plant (Shukla et al. 2011). P-solubilizing PGPR bacteria are used as bio fertilizers to reduce agrochemical use and promote environmentally friendly crop production (Kour et al. 2020).

3.3 Enzymes

Production of lytic enzymes is an important method used by biocontrol agents to influence crop diseases. Rhizobacteria that stimulate plant development use enzymatic activity as a growth strategy. These enzymes breakdown or deform cell wall components of fungal pathogens. This is one of the most important mechanisms for controlling soil pathogens in an environment-friendly manner (Hyder et al. 2022). Chitinases, dehydrogenases, glucanases, lipases, phosphatases, proteases, and other enzymes produced by PGPR strains have hyperparasitic activity. The lytic enzymes produced by myxobacteria are effective against fungal plant diseases. With the lytic behaviour of these enzymes, PGPR reduce pathogenic fungi such as *Rhizoctonia solani*, *Pythium ultimum*, *Fusarium oxysporum*, *Sclerotium rolfsii*, *Phytophthora* sp., and *Botrytis cinerea* (Babalola et al. 2021; Boro et al. 2022). *Bacillus* spp., *Trichoderma virens* are used to promote plant growth and due to broad range of lytic enzymes producing abilities these strains are widely used against *R. solani*, *F. oxysporum* (Shameer and Prasad 2018; Mazrou et al. 2020). *Lysobacter* can develop glucanase, which aids in the treatment of diseases associated with *Bipolaris* and *Pythium* sp. *Pseudomonas stutzeri* produces chitinase and laminarinase extracellularly that digest and lyse *Fusarium solani* mycelia, preventing crop damage from root rot caused by this fungus (Meena et al. 2020; Xu et al. 2021).

3.4 Siderophores

A wide variety of bacterial, fungal, and plant species produce siderophores (Ahmed and Holmström 2014). Low-molecular-weight molecules that chelate Fe^{3+} ions and transport it into microbial cells on iron scarcity, are siderophores. PGPR has been associated with a number of benefits, especially in limiting circumstances during iron uptake in rhizosphere. In addition, it may prevent the spread of pathogens that harm the plant and shield it from harmful weather conditions. (Crowley 2006). In rhizospheres with minimal iron, PGPR that creates siderophores can hitch accessible iron and lessen the pathogens' access to it, inadvertently promoting plant growth (Alberto and Jose 2012). Siderophore-producing bacteria are mostly found in the genus *Pseudomonas*, with the siderophores

pyochelin and pyoverdine being produced by *Pseudomonas fluorescens* and *Pseudomonas aeruginosa*, respectively (Buysens et al. 1996). When iron is low, pyoverdines as constructive siderophore reduce the growth rate of bacteria and fungi in vitro. Pseudomonads have been discovered to control soil-borne plant diseases like chickpea and wheat root rot disease (Santos et al. 2011). *Pseudomonas* strain colonised the roots of numerous crops quickly after producing a specific siderophore, resulting in enhanced output. Pseudomonad-induced plant growth was typically accompanied by a decrease in pathogen populations on the roots (Singh and Jha 2017). As a result of the iron chelation, siderophores are efficient in lowering phytopathogen proliferation and boosting plant development through increased iron uptake (Olanrewaju et al. 2017).

A number of enzymes involved in critical physiological activities, such as nitrogen fixation and photosynthesis, use iron as a cofactor (Lankford 1994). The oxidised form of Fe^{+3} is the most common chemical form that interacts with organic matter to generate insoluble oxides and hydroxides (Goswami et al. 2016). Iron-chelating chemicals are released into the rhizosphere by some rhizospheric bacteria such as *Pseudomonas fluorescens*, *Bacillus subtilis*, *Azospirillum brasilense*, *Azotobacter chroococcum* and *Streptomyces* spp., drawing iron to the rhizosphere and allowing it to be absorbed by the plant (Trapet et al. 2016; Marastoni et al. 2019; Chen et al. 2023). Dual methods have been developed by plants for efficiently absorbing iron. First method involves the release of organic molecules that chelate iron, making it soluble and allowing it to penetrate into the plant, where it is reduced and captivate by an enzyme system located in the cell membrane (Ahmed and Holmström 2014). Other way involves the intake of organic component and Fe^{+3} complex, which reduces and easily absorbs iron (Colombo et al. 2014). Rhizobacteria boosts plant growth by multiple routes. PGPR fixes nitrogen, produces plant hormones, and delivers iron to iron-deficient plants (Rosier et al. 2018). Bio-antagonism involves rivalries for space or resources (iron), anti—fungal secondary metabolites (HCN), and hydrolytic enzymes (chitinases, glucanases) (Gull and Hafeez 2012). By creating siderophores, some bacterial strains can operate as biocontrol agents. In this situation, PGPR siderophores can prevent phytopathogens from obtaining enough iron, restricting their ability to multiply (Kloepper et al. 1980). Due to the lack of iron, PGPR creates siderophores that have a greater propensity for iron than pathogenic fungi, which inhibits their establishment in the host plant's rhizosphere. This is because they efficiently compete with fungi for available iron (Glick 2012). Since most plants can grow at far lower concentrations than most bacteria, they are unaffected by the iron depletion in the rhizosphere brought on by biocontrol PGPR siderophores. Numerous plants can attach to, take up, and utilise the iron siderophore complex (O'Sullivan and O'Gara 1992). In the rhizosphere, microbially produced siderophores may give iron to crops connected with

siderophore-producing PGPR (Santoyo et al. 2021). Chemicals called iron-chelating polycyclic organic compounds generated by plant growth promoting bacteria can be used to gain an advantage over organisms that are unable to synthesise them (Poonam Pandurang 2021).

4 Rhizosphere is a site for biocontrol of pathogens

The rhizosphere is a pool of microbial interplay, wherein the rhizospheric microbes may function as biocontrol agents (Chase et al. 2016). Rhizobacteria limit the growth of phytopathogens by producing siderophores, bacteriocins, antibiotics, and lytic enzymes (Sindhu et al. 2009). This antagonistic pursuit of PGPR's where one bacterium acts as a predator of another bacteria is of fundamental importance because it interferes with pathogen growth (Jaiswal et al. 2019).

Various microbiological control agents have proven effective in controlling plant diseases. The EPA (Environmental Protection Agency) approved *Agrobacterium radiobacter* strain K84 for the treatment of crown gall in 1979. *Trichoderma harzianum* ATCC 20476 was approved ten years later for plant disease control. There are 14 bacteria and 12 fungi registered for plant disease control at EPA (Samada and Tambunan 2020; Ahmed et al. 2022). Pseudomonads have received the most attention as potential biocontrol agents. These bacteria can successfully compete with soil microorganisms and produce a large amount of antifungal secondary metabolites. More than 100 aromatic antibiotics and antibiotic-like compounds have been discovered in *Pseudomonas* species. VSMKU3054, an isolate of *P. fluorescens* proved effective for the seed germination of the tomato seedlings with antagonistic effect towards phytopathogens (Suresh et al. 2021; Lahlali et al. 2022). The number of biocontrol products used in plant disease control is increasing. Some of the major antibiotics produced by PGPB are listed in Table 1. However, they account for only 1% of agricultural control measures, while fungicides account for 15% of all agricultural pesticides.

4.1 Antimicrobial compounds

The potential of PGPB's to function as antagonistic agents against phytopathogens is most typically related to the production of one or more antibiotics (Glick et al. 2007). The essentials of antibiosis, or biocontrol that solely relies on the release of chemicals that either kill or restrict the growth of target pathogen, have improved over the preceding decades (Beneduzi et al. 2012). Fungal and bacterial

remnants have yielded antibiotics with varied mechanisms of action, including those that impair pathogen cell wall assembly, modify cell membrane architecture, and block ribosome initiation complex formation (Maksimov et al. 2011). They might affect the cell membrane, membrane integrity, zoospores linked to fungal diseases, and the electron transport chain (PRN, PHZ) (Whipps 2001). Genes involved in antibiotic production are highly conserved across bacterial species (Fernando et al. 2006). Fluorescent Pseudomonads produce 2,4-diacetylphloroglucinol (DAPG), an antifungal, antibacterial, and phytotoxic antibiotic (Bangera and Thomashow 1999) (Jan et al. 2011). DAPG helps *Pseudomonas* sp. prevent plant diseases and reduces *Gaeumannomyces graminis* var. *tritici*'s wheat disease (Mishra and Arora 2018). Pyoluteorin (PLT) is a polyketide antibiotic produced by *Pseudomonas* with a resorcinol ring and a bichlorinated pyrrole moiety (Figueiredo et al. 2010). It controls pathogenic fungus-caused plant disorders and possesses bactericidal and herbicidal properties. PLT is synthesised from proline by a series of linked condensation, chlorination, and oxidation steps catalysed by at least 10 enzymes encoded by 10 PLT operon genes (plt L, M, R, A-G) (Nowak-Thompson et al. 1999). The PLT production is connected to oomycete fungal inhibition, including *Phythium ultimum*, the causative microbe of Phythium damping disease (Weller et al. 2007). Circulin, polymyxin, and colistin are antibiotics produced by *Bacillus* spp. (Amin et al. 2012). Antibiotics produced by *Bacillus subtilis*, such as fengycin and iturins, suppress the growth of fungi, such as *Podosphaera fusca*. Antibiotics, which have been used as biocontrol agents but have their limits, are vital in the treatment of infections and infection management (M 2017).

The biocontrol abilities of *Pseudomonad* are critical for aggressive root colonisation, antifungal antibiotic production and the induction of systemic resistance in plants. Fungal antibacterials have varied mechanisms of action. Polymyxin, circulin, and colistin, antibiotics produced by most *Bacillus* species, are potent against G+ve and G-ve bacteria along with fungi (Beneduzi et al. 2012).

4.2 HCN

Hydrogen cyanide (HCN) is a volatile molecule that is detrimental to plants and prevents key metabolic enzymes from working, and it's one of the most common characteristics of rhizobacterial isolates. It is a secondary metabolite generated by soil bacteria with an ecological function that gives selection advantage to the producing strains. HCN inhibits fungal development and brings about Sagar antagonism (Sagar et al. 2018). It doesn't participate in growth, energy storage, or primary metabolism (Ahemad and Kibret 2014). In solution, cyanide exists as free cyanide, consisting of the

Table 1 List of Major antibiotics produced by PGPB's

| Antibiotics | PGPR strain | Target organisms | Mode of action | References |
|---|--|---|--|---|
| Kanamamine | <i>Bacillus cereus</i> | <i>Saccharomyces cerevisiae</i> <i>Phytophthora medicaginis</i> <i>Candida albicans</i> | Inhibits the activity of Glucosamine-6-phosphate synthetase | (Prasertanan and Palmer 2019; Tran et al. 2022) |
| 2,4-diacetylphloroglucinol (2, 4-DAPG) | <i>P. fluorescens</i> | <i>Pythium</i> spp. <i>Thielaviopsis basicola</i> <i>Pythium ultimum</i> | Produces secondary metabolites that inhibit pathogen | (Fernando et al. 2006) |
| Oligomycins A | <i>Streptomyces</i> spp. | <i>Gaeumannomyces graminis</i> var. <i>tritici</i> <i>Plasmodiopsis viticola</i> <i>Magnaporthe oryzae</i> <i>Triticum</i> | Mitochondrial F1F0 ATP synthase inhibitors that cause apoptosis in a different cell types | (Chakraborty et al. 2020) |
| Pyrrrolnitrin (Pm) | <i>B. pyrrocinia</i> <i>Pseudomonas pyrrrocinia</i> | <i>Saccharomyces cerevisiae</i> , <i>Penicillium atrovenetwn</i> <i>P. oxalicwn</i> <i>Fusarium oxysporum</i> | Acts on electron transport system, Reduces NADPH and CoQ10 | (Tripathi and Gottlieb 1969; Uzair et al. 2018) |
| Zwittermycin A | <i>Bacillus cereus</i> | <i>Phytophthora medicaginis</i> | Disruption of cell wall, inhibition of RNA synthesis | (Silo-Suh et al. 1998) |
| Viscosinamide | <i>Pseudomonas fluorescens</i> | <i>Pythium ultimum</i> | Zoospore production inhibited and encystment of zoospore was strongly stimulated | (Thrane et al. 2000) |
| Pyoluteorin (Pit) | <i>Pseudomonas putida</i> <i>P. fluorescens Pf-5</i> <i>Pseudomonas protegens</i> | <i>Glomerella tucumanensis</i> <i>Heterobasidium irregulare</i> <i>Pantoea ananatis</i> | Induces the production of reactive oxygen species | (Gu et al. 2022; Pellicciaro et al. 2022) |
| Phenazines phenazine-1-carboxylic acid (PCA) | <i>Pseudomonas</i> , <i>Burkholderia</i> , <i>Brevibacterium</i> , and <i>Streptomyces</i> <i>P. fluorescens</i> <i>P. aureofaciens</i> <i>P. aeruginosa</i> | <i>G. graminis</i> var. <i>tritici</i> <i>Fusarium oxysporum</i> <i>f. sp. radicis-lycopersici</i> <i>Aspergillus fumigatus</i> | Enhances the production of ROS and Reactive nitrogen species | (Briard et al. 2015) |
| Pyocyanin (1-hydroxy-5-methyl phenazine) | <i>P. aeruginosa</i> | <i>Aspergillus flavus</i> , <i>A. fumigates</i> , <i>A. niger</i> , <i>Fusarium oxysporum</i> , <i>S. rolfisii</i> and <i>Colletotrichum falcatum</i> | Cause the production of anion radicals and cause toxicity | (Marrez and Mohamad 2020) |
| phenazine-1-carboxamide (PCN) | <i>P. chlororaphis</i> PCL1391 and <i>P. aeruginosa</i> MML2212 <i>P. aeruginosa</i> PNA1 <i>Bacillus velezensis</i> | <i>Rhizoctonia solani</i> Kühn and <i>Xanthomonas oryzae</i> pv. <i>Oryzae</i> <i>Fusarium oxysporum</i> | Affects the function of chitin synthetase along the with complex I on electron transport chain | (Xiang et al. 2018) |
| Surfactin | <i>Bacillus velezensis</i> | <i>Ralstonia solanacearum</i> <i>Fusarium oxysporum</i> | Cause disintegration of cell membrane Inhibits protein synthesis Restricts cell reproduction | (Chen et al. 2022) |
| Bacilysin | <i>B. subtilis</i> <i>B. amyloliquefaciens</i> FZB42 | <i>Phytophthora infestans</i> <i>Microcystis aeruginosa</i> | Inhibits the activity of glucosamine 6-phosphate synthase | (Islam et al. 2022) |

Table 1 (continued)

| Antibiotics | PGPR strain | Target organisms | Mode of action | References |
|--|---|---|--|---|
| Bacitracin | <i>B. licheniformis</i> | <i>Streptococcus mutans</i> | Restricts the dephosphorylation of undecaprenyl pyrophosphate (C55-PP) to undecaprenyl phosphate (C55-P) and ultimately cause the destruction of peptidoglycan layer | (Tran et al. 2022) |
| Fengycin | <i>Bacillus subtilis</i> | <i>Rhizoctonia solani</i> and <i>Paecilomyces variotii</i> | Cause the disruption and solubilization of lipid bilayer | (Kaspar et al. 2019) |
| Iturin | <i>Bacillus amyloliquefaciens</i> | <i>Micrococcus luteus</i> and <i>Fusarium graminearum</i> | Improves the electrical conductance of artificial lipid membranes via ion conducting pores | (Crane et al. 2013; Gong et al. 2015) |
| Surfactin (lichenysin and pumilacidin) | <i>B. licheniformis</i> <i>B. pumilus</i> | <i>Pseudomonas syringae</i> <i>Ralstonia solanacearum</i> , <i>Rhizoctonia solani</i> , <i>Pythium aphanidermatum</i> , and <i>Sclerotium roffsii</i> | Cause leakage of K ⁺ ions Inhibits protein synthesis | (Th  atre et al. 2021) |
| Mycosubtilin | <i>Bacillus subtilis</i> | <i>Fusarium graminearum</i> and <i>Fusarium verticillioides</i> | Inhibits biosynthesis of Fumonisin (mycotoxin) | (Yu et al. 2021; Yang et al. 2022) |
| Viscosinamide | <i>P. fluorescens</i> DR54 | <i>Rhizoctonia solani</i> AG2-2 and <i>Pythium myriofolium</i> CMR1 | Cause the hyphal distortion and disintegration | (Oni et al. 2020; Bonaterra i Carreras et al. 2022) |

cyanide anion (CN) and the non-dissociated HCN (Upadhyay 2016). HCN, which is created in the rhizosphere of seedlings with the help of selected rhizobacteria, is a manageable and eco-friendly way to organically reduce weeds while minimising negative effects on favoured plant growth (Gusain et al. 2015). Many plant-associated fluorescent pseudomonads employ HCN to biologically manage root disease.

Certain rhizobacteria's plasma membrane is connected to the HCN synthetase enzyme which converts glycine to HCN (Shameer and Prasad 2018). Numerous bacterial genera can manufacture HCN, including *Alcaligenes*, *Aeromonas*, *Bacillus*, *Pseudomonas*, *Enterobacter*, and *Rhizobium* species (Kumar et al. 2015). According to some studies, *Pseudomonas* isolated from potato and wheat rhizospheres may produce HCN in vitro (Ghadamgahi et al. 2022). Biocontrol ability could be attributed to HCN's ability to bind iron in the rhizosphere, despite phytopathogen competition. Iron and cyanide have also been known to improve plant phosphate availability (Sagar et al. 2018).

4.3 Quorum sensing

The method of native cell-to-cell communication known as quorum sensing (QS) occurs in the community of bacteria and is used to exchange information (Shrestha et al. 2020). The QS controls the sporulation, bioluminescence, pathogenicity, conjugation, and biofilm formation in rhizospheric bacteria (Baltenneck et al. 2021). The QS regulates several transcription factors and genes in bacteria that are important for their growth, defence, and adaptability to changing environmental conditions (Li et al. 2021; Thakur et al., 2023). Versatile signalling molecules known as auto inducers play a crucial role in communication between bacterial species (Stephens and Bentley 2020).

QS is critical for plant-bacteria interactions and is mediated by a number of important chemical compounds (Ma et al. 2021; Paasch and He 2021; Thoms et al. 2021). The function of quorum sensing molecule N-acyl-homoserine lactone (AHL), for plant growth and interaction with bacteria has been thoroughly studied. The two components of AHL are an acyl side chain with 4 to 18 C-atoms and a homoserine lactone ring which plays a role in gene expression in plant defence mechanisms as well as in auxin and cytokinin signalling pathways. AHL is important for enhanced stomata closure and callose and lignin deposition in the cell wall, which helps plants resist infections caused by *Pseudomonas syringae* and *Blumeria graminis*. This role is demonstrated in a recent study in *Arabidopsis* (Shrestha et al. 2020; Wang et al. 2021; Babenko et al. 2022). A combination

of four AHL molecules interacting with *Arabidopsis thaliana* was successfully used to show how the AHL complex was confirmed in nature as a disease-resistant and plant growth promoting factor. Similarly, a recent study showed that benzoxazinoids secreted by maize root influences the microbial community present in the root rhizosphere (Cadot et al. 2021). Nanogypsum, which refers to nano-sized particles of gypsum (calcium sulfate dihydrate), has gained interest in agriculture due to its potential benefits in promoting plant growth and soil health. Nanogypsum enhance soil structure by promoting flocculation, reducing aluminum toxicity by binding with aluminum ions and reducing soil dispersion making plants more resilient to diseases. In the presence of nanogypsum the contribution of bacterium *Pseudomonas taiwanensis* to plant growth was demonstrated (Chaudhary et al. 2021). Metagenomic analysis demonstrated the possible contribution of nanogypsum to the proliferation of many bacteria that aid in plant growth, including Proteobacteria, Bacterioidetes, Planctomycetes, Acidobacteria, and Nitrospirae.

5 Rhizobacteria for Bioremediation

An enticing and less expensive method of cleaning contaminated soil and water is bioremediation (Singha and Pandey 2021). Overuse of pesticides, insecticides, hazardous chemicals in agricultural fields and increased anthropogenic activities leads to high level of pollutants in the environment. Bioremediation mainly includes the use of biological processes to remove, reduce, or transform these pollutants. Pollutant-degrading rhizobacteria colonize near roots and use root exudate as their main food source. PGPB and other rhizosphere-dwelling bacteria are used in rhizoremediation, a type of phytoremediation (Medfu Tarekegn et al. 2020; Yadav and Thakur 2021). The bacterium *Pseudomonas putida* PCL1444 utilises root exudate to break down the naphthalene surrounding the root and shield seeds from its hazardous effects. Phytoremediation although reduces chemical risks from organic and inorganic contaminants, but has limitations that hinder large-scale use in the field. Stress caused by contamination reduces seed germination. Soil can be contaminated by industrial pollution, petrochemical spills, hazardous wastes, leaded gasoline, mine tailings, chemical products, industrial wastes, atmospheric deposition, and the burning of coal residues having huge amount of metalloids and trace metals (Saeed et al. 2021; Oladoye et al. 2022). PGPR changes harmful chemical compounds into nontoxic ones. Microbial species have the potential to work along with plants to break down both organic and inorganic contaminants (Katiyar et al. 2020). Complex pollutants can be removed with the help of PGPR and pollutant-degrading bacteria.

6 Biofertilizer

Agriculture is one of the human activities that contribute most to the increase in chemical pollution due to extensive use of synthetic fertilizers as well as pesticides, which negatively affect the environment and threaten human health. Farmers use large amounts of agrochemicals to meet nutrient needs and to protect crops from phytopathogens (Maçik et al. 2020). Superfluous use of chemicals in the form of herbicides, insecticides, and fungicides provokes potentially harmful biological effects such as acute and chronic toxicity, mutagenicity, and carcinogenesis. The alternative to agrochemicals is biofertilizers that contain PGPB (Amenyogbe et al. 2021; Basu et al. 2021). Utilization of chemical fertilizers leads to eutrophication and consequent pollution of air and ground water. This practice also harms the roots of the crops as they can no longer absorb nutrients. Due to improved knowledge about the relationship of the plants with soil microbes, the use of microbes-based fertilizers has increased worldwide. A biofertilizer possesses microbes that populate the rhizosphere and boosts growth by escalating nutrient supply to the host plant (Ortiz and Sansinenea 2021; Nur Maisarah Mohamad Sarbani and Yahaya 2022).

PGPBs are commonly used as biofertilizers. They are used as substitutes for synthetic fertilizers, which are becoming more common (Kang et al. 2021). *Rhizobium*, *Azotobacter*, *Azospirillum*, and blue-green algae are examples of biofertilizers that have been used for a long time. Endophytic and rhizospheric relationships are the two most common types of PGPR-host relationships. Endophytic means that the PGPB live inside the host plants (Basu et al. 2021). Biofertilizers can dissolve plant nutrients like phosphate, zinc, and potassium, fix atmospheric N₂ through nitrogen fixation (BNF), and release hormones that stimulate plant growth (Aasfar et al. 2021). They colonize the plant's rhizosphere, which increases mineral accessibility and uptake. Some biofertilizers are specific for crops such as *Rhizobium* (Pea, soybean, pulses legumes), *Azospirillum* (sugarcane, millet), *Blue-green algae* (rice), *Azotobacter* (Mustard, banana, tomato), and *Arbuscular mycorrhizal fungi* (wheat, corn) (Nosheen et al. 2021; Daniel et al. 2022). They are "eco-friendly" organic agro-inputs that convert unavailable essential elements into usable forms (Asoegwu et al. 2020).

7 Impact of climate change on rhizospheric bacterial diversity and their colonization

Soil microbes have an important function to resist the adverse environmental conditions and enriching the organic matter, carbon and nitrogen cycles (Chen et al. 2021; Macabuhay et al. 2022; Sandrini et al. 2022). Since

soil microbes make all these significant contributions to the ecosystem, their importance is underlined.

Global climate change decreases productivity owing to adverse environmental conditions such as temperature rise, precipitation, imbalance in carbon and nitrogen cycles, shift in vegetation, melting of glaciers, use of chemicals and pesticides, etc. It is imperative to investigate the effect of climate change on the health of soil microbes and the dynamics of their communities (Tiedje et al. 2022). Climate change may favour the growth of some soil microbes and at the same time can inhibit the growth of other microbiota or change the metabolism to adapt (Naylor et al. 2020). In addition, the development of an ecological model based on climate change will help to understand that climate change has the first impact on microbial communities throughout the ecosystem (Dwivedi et al. 2022).

The temperature affects microbial metabolism, particularly soil mineralization and ATP generation. The mycorrhiza decreases with an increase in temperature. The rising atmospheric carbon dioxide and soil moisture affects the microbial population, in particular the ammonium oxidizing bacteria. The fungi's ability to colonize deeper soil layers increases with increase in soil carbon dioxide level. The temperature can be a potential game changer in the area of plant and microbial diversity (Nottingham et al. 2022). Bardgett and Shine 1999, demonstrated that increased temperatures have an impact on the microbial communities found in *Cardamine hirsute*, *Poa annua*, *Senecio vulgaris*, and *Spergula arvensis* over the course of three plant generations. The microbial biomass in the previous generation of plants was greater mostly due to fast-growing bacteria, but it afterwards decreased primarily due to slow-growing fungi and bacteria (Finlay et al. 2020; Adingo et al. 2021; Meena et al. 2022). The changing temperature can help the community stability and impact the soil productivity, biotransformation and disease control as studied in three bacterial species: *Pseudomonas koreensis*, *Flavobacterium johnsoniae* and *Bacillus* (Burman and Bengtsson-Palme 2021). Even a slight rise in temperature can affect the diversity of the phyllospheric bacteria present in the plant leaves. The impact is such that plant beneficial bacteria such as *Sphingomonas* spp. and *Rhizobium* spp. community reduce significantly whereas the plant pathogenic bacteria community increase manifold (Aydogan et al. 2018).

Current research has inadequate data to understand the effect of climate change on soil microbes. The analysis of two years' data from a temperate mountain soil microbial community showed a considerable rise in microbial metabolic activity. However, microbial stress biomarkers got regulated significantly (Schindlbacher et al. 2011). Rudgers et al. 2014 reported 20 years of experimental study on the effect of warming on graminoid and soil fungi. They reported the increased root colonization by AM fungi in

the two grass species but no effect on other three graminoids species. Suseela et al. 2014 reported that warming and precipitation significantly regulate enzyme activity which modifies the chemical reaction during litter decomposition. Similar activity showing that climate change may have direct physiological change in enzyme mediated decomposition have been reported by Sorouri and Allison 2022. To understand more about the enzyme activity with climatic factor. In southwest China, the impact of seasonal shift on soil microorganisms and enzymes was studied. A total of 36 distinct phospholipid fatty acids were found, with 16:0 fatty acid being the most prevalent throughout all seasons. In contrast, the levels of invertase and catalase were high and low in the autumn and winter. In a similar manner, the activity of the enzymes urease and phosphates acid was shown to be high and low in the spring and winter, respectively. The reliance of microorganisms' enzyme activity on temperature and season suggests that they play a controlling function in the microbial population in response to changes in the environment (Luo et al. 2020).

8 Functional metagenomics to explore endophytic symbiosis

The endophytic or rhizospheric bacteria associated with the plants have a critical impact on plant growth either directly or indirectly (Saeed et al. 2021; Shah et al. 2021). Most of these bacteria fail to grow in an axenic environment. Therefore, the metagenomics approach could suitably be taken to comprehend their diversity, abundance, and function. These bacteria regulate gene expression and the production of proteins and bioactive chemicals in such a way that they are critical to the plant's ability to adapt to harsh environment. The microbial ecology of the *Datura* plant was studied using a metagenomic technique that revealed the presence of 14 bacterial families, belonging to mainly Sphingomonadaceae, *Flavobacterium* and *Pedobacter* (Senn et al. 2022). An intriguing discovery about the microbial ecology in the rhizospheric soil associated with roots during root growth from the root tip, hairy root, to lateral root was made by (Rüger et al. 2021). They discovered a complex relationship between the root microbiome, lateral roots, and the nutrients in the soil, as well as the pattern of microbiome community formation. Compared to lateral roots, where beta-diversity is limited and deterministic, root tips and root hair zone exhibit high variation in beta diversity. This may be due to the availability of abundant food resources in root tips and root hair zone from the soil as compared to the lateral roots. Therefore, the lateral roots develop a community that is deterministic due to low resources. The co-occurrence pattern of prokaryotic community and deterministic (competitor and predators) was strongest in the lateral roots. Such

microbiome assembly in the root system is very important to understand a healthy root microbiome for plant growth and development. Plant host gene and their interaction may influence the dynamic of microbiotic components which need to be understood with further research and innovation. In this regard, the research must be carried out in the native environmental condition which has been least explored. Roux et al. (2023) studied the genome-environmental association of plant microbiota of 141 whole-genome sequences of wild *Arabidopsis thaliana* to explore bacterial communities residing in leaf and roots in two different seasons (autumn and spring). The study revealed that most of the bacterial community was governed by host genetics than any other factor. Moreover, the bacterial community was able to the plant tissue regardless of seasons due to the polygenic effect. Their finding indicates the plant's health and growth is the major factor for genetic variation that helps in bacteria assembly in *A. thaliana*. Zhang et al. (2022) demonstrated the recruitment of highly conserved endophytic bacteria dominated by Gammaproteobacteria in the stem xylem of maize plants from the soil or roots or leaves. About 25 bacterial taxa carrying nitrogenase gene (*nifH*) are actively involved in nitrogen fixation in the stem xylem. The core endophytic bacteria contribute to the nutrient supply to plant development.

9 Conclusion

Root exudates serve as a central orchestrator in shaping the intricate web of microbial interactions within the rhizosphere, the specialized zone of soil directly influenced by the root system of plants. This interplay gains complexity from the diverse and thriving community of microorganisms that call the rhizosphere home. These microorganisms actively contribute to this dynamic ecosystem by secreting phytohormones and engaging in intricate biomolecular exchanges, which go well beyond the conventional understanding of roots as mere anchors for plants and conduits for water and nutrient uptake. Recent scientific explorations have uncovered the immense potential of PGPR in revolutionizing sustainable agricultural practices. These beneficial microorganisms have emerged as formidable allies in the quest to bolster crop productivity while simultaneously reducing the reliance on chemical pesticides. This aligns perfectly with the growing global emphasis on adopting eco-friendly and environmentally conscious farming methods. To gain a comprehensive understanding of the intricate microbial ecology within soil, researchers advocate for a synergistic approach that combines axenic culture techniques and metagenomic analyses. Such an approach promises a more holistic perspective on soil health and fertility, providing invaluable insights for farmers as they make informed decisions about

soil quality before embarking on cultivation. Ultimately, this integrated approach holds the potential to fortify agricultural sustainability by fostering healthier soils and promoting environmentally-friendly farming practices.

The exploration of the phytomicrobiome represents a frontier rich with potential for the development of novel and sustainable crop management techniques. Nevertheless, further in-depth research is imperative to unravel the intricacies of PGPR interactions with native PGPR and other microbial inhabitants within the plant rhizosphere. Additionally, as climate change continues to exert its influence, it is paramount to investigate how this phenomenon impacts the well-being and community dynamics of soil bacteria. Future studies must delve into the changing states of soil microbes and how microbial communities dynamically respond to adverse climate conditions. Furthermore, the creation of an ecological model that considers the impact of climate change will enhance our comprehension of how microbial communities within ecosystems are often the first to bear the brunt of these environmental shifts.

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Declarations

Conflict of interest Authors declare that they have not any known conflict of interest.

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