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Beneficial Soil Microorganisms: Role in Plant Growth and Soil Fertility: A Review

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ABSTRACT

The soil microorganism promotes soil fertility, plant productivity and ecosystem services. Recent molecular research suggests that the soil microorganism has been significantly underestimated. In addition to metagenomic analyses. Metatranscriptomic and Metaproteomics studies targeting the functional part of the microbiome are becoming more common and microorganism functional role and plant-microbe interactions require better understanding. These are crucial for understanding the microbiome's functional role and for figuring out how microbes and plants interact. Plant growth-promoting rhizobacteria (PGPRs) are helpful bacteria that colonize the roots of plants to stimulate plant growth. They benefit plants in several ways, including enhancing nutrient synthesis and uptake, as well as preventing disease. Understanding plant-microbe interactions in natural and agroecosystems can improve soil fertility and high-yield food production.

Key words: Agroecosystems, Metagenomics, Microorganism, PGPR, Soil fertility.

Global population expansion has led to a rise in demand for agricultural products. Increased production depletes topsoil, reduces organic matter content and negatively impacts soil ecology. Soil bacteria play a crucial role in maintaining soil ecology and ensuring stability under disturbance. Inadequate land usage can contaminate groundwater, plant disease outbreaks and air pollution. The population's awareness of environmental issues highlights the need for sustainable and healthy food choices. Therefore, environment-friendly alternatives for sustainable agriculture are gaining popularity. Sustainable agroecosystems as extremely resilient, adaptive and varied (Suresh *et al*., 2025: de Corato and Towards, 2020). These challenges are interconnected, with variety providing greater adaptability and adaptation is an important component of resilience in agroecosystems. The variety of soil bacteria, which plays an important role in nutrient recycling and soil formation, are a critical issue in sustainable agriculture. The essential issue to be examined is the functional diversity of soil bacteria, not their taxonomic organization. A better knowledge of the role of microorganisms in agroecosystem functioning, particularly in plant development and soil fertility, is critical for sustainable agricultural output.

Soil microorganisms

Distribution

Microorganisms comprise roughly 17% of the world's biomass (Bar-On *et al*., 2018). Soil is the most complicated environment for microbial life, with around 4-5 $\times$ 10^{30} cells (Dubey *et al*., 2019). The soil microorganism primarily consists of bacteria, archaea, fungi, protozoa and viruses *etc.* According to Mendes *et al*. (2013), 1gm of soil contains approximately 10^8-10^9 bacteria, 10^7-10^8 viruses and 10^5-10^6 fungal cells. Soil microbial communities provide ecological services such as nutrient recycling, carbon sequestration, water retention, plant growth promotion and defense (O'Brien *et al*., 2016; Jansson *et al*., 2019; Thakur *et al*., 2019). The rhizosphere is a biological hotspot that influences microbial community composition through interactions between plants-microbes and microbes-microbes. Plant roots produce organic chemicals that promote microbial activity (Fan *et al*., 2017). Bacterial community composition varies significantly across bulk and rhizospheric soils, resulting in reduced diversity from bulk soil to roots (Fan *et al*., 2017; Unnikrishnan *et al*., 2023). Tobacco and *Arabidopsis* plants have a significantly higher number of microorganisms in their rhizosphere compared to bulk soil (Bakker *et al*., 2013). The soil microbiome's geographical heterogeneity is affected by both environmental factors and population processes (Ettema *et al*., 2002). Plant root exudates in the rhizosphere and environmental conditions influence soil microbial colonization, which can be biotic or abiotic. Li *et al*. (2014) conducted studies in corn fields. The study found that *Proteobacteria*, *Actinobacteria*

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and Bacteroidetes, dominated the rhizosphere soil microbiota, accounting for 73-80% of total reads compared to 46-56% in bulk soil. The rhizosphere had lower abundances of *Acidobacteria, Firmicutes, Gemmatimonadetes, Nitrospira and Chloroflexi,* compared to the bulk soil (Li *et al*., 2014). Fan *et al*. (2017) examined the microbial population in wheat fields, focusing on three soil compartments: Firmly and loosely attached soil and bulk soil. The study found that *Proteobacteria, Actinobacteria* and *Acidobacteria* dominated all soils. *Actinobacteria, Alphaproteobacteria, Bacteroidetes* and *Verrucomicrobia* were more abundant, while *Chloroflexi, Gammaproteobacteria* and *Deltaproteobacteria* were less abundant in tightly bound soils compared to others. *Actinobacteria* were found to be more abundant in closely bound soil due to their ability to produce antibiotics, while *Alphaproteobacteria* were present due to their rapid proliferation. Rchiad *et al*. (2022) found that in a semiarid agroecosystem, soil microbiota diversity does not decrease with depth, although microbial profiles differed. The study identified 43 microbial phyla, with 12 impacted by soil depth. Microbial communities transitioned from top (0-15 cm) to deep (30-60 cm) at the phylum/family level. The abundance of *Verrucomicrobia* and *Bacteroidetes* decreased with soil depth. Depth affects the quantity of soil functional genes, with the majority of functional categories found in the top or deepest layers (Rchiad *et al*., 2022).

Beneficial interactions between plant-microbes

Bio-stimulant microbes

In nature, microbes and plants coexist, but they can be free-living, attached or form a symbiotic relationship with the host plants. Various relationships exist, including parasitism, mutualism and commensalism. Plants have interacted with a wide variety of plant growth-promoting rhizobacteria (PGPR) throughout their evolutionary history. Bacterial rhizobiome mapping is advancing fast due to novel identification methods, huge genome-sequencing strategies and current developments in metagenomics. These findings identified new bacterial species and how they promote plant growth and serve as biocontrol (Tabish Akhtar *et al*., 2020; Khan, 2019). By fixing atmospheric nitrogen, producing siderophores, plant growth hormones (cytokinin's, auxins and gibberellins), volatile compounds and solubilizing nutrients and minerals (phosphorus, potassium, zinc, *etc*.), microorganisms that live in soil can indirectly stimulate plant growth. Certain PGPR species also contribute to a plant's ability to with stand stress. They can boost the plant's ability to absorb heavy metals or other harmful substances and assist the host plant in overcoming salinity and drought stress (Li *et al*., 2014; Aira *et al*., 2010; Husna *et al*., 2023). PGPRs are crucial bacteria for agriculture because they promote plant growth. Biological nitrogen fixation through raising nitrogen content, biomass, germination rate and chlorophyll. These can increase crop productivity, hydraulic activity, shoot and root length and leaf area. In addition to giving plants resistance to biotic (pathogen fungi, bacteria, yeast, insects, pests, *etc*.) and abiotic (flood, drought, salinity, heavy metals, temperature, *etc*.) stress, they can also make nitrogen from the soil available to plants in inorganic forms (ammonium, nitrate) (Yadav *et al*., 2018). *Aspergillus, Rhizoctonia, Penicillium, Talaromyces* and *Trichoderma* are the genera that contain fungi that stimulate plant growth. Of these, *Trichoderma* sp. (*T. harzianum* and *T. viride*) and *Penicillium chrysogenum* are the most promising for increasing plant growth (Adedayo *et al*., 2023).

Biological nitrogen fixation

Plants can use nitrogen from soil in both inorganic (nitrate, ammonium) and organic forms (amino acids, urea and short peptides). Organic forms can only be exploited under specific conditions (Eva *et al*., 2019). Plants cannot utilize the abundant elemental dinitrogen (N_2) found in the Earth's atmosphere. Computed 473 Tg N of physiologically accessible nitrogen from 4×10^9 Tg N of dinitrogen gas (Flower *et al*., 2015; Ladha *et al*., 2022).

Bacteria having biological nitrogen fixation (BNF) capacity are classified into three types: Associated, free-living and symbiotic bacteria. Free-living N_2-fixing bacteria from several genera, including *Gluconacetobacter, Azospirillum* and *Azotobacter* spp., contribute minimally to the total BNF. *Rhizobia*, a type of symbiotic bacteria that fixes nitrogen, accounts for the majority of BNF (Ladha *et al*., 2022). *Rhizobium* are the symbiotic bacteria found in leguminous plants. Non-symbiotic N_2-fixing bacteria include cyanobacteria (*Anabaena, Nostoc* and other blue-green algae), as well as other genera including *Azotobacter, Beijerinckia* and *Clostridium*. Nitrogen-fixing bacteria, including *Azospirillum* sp. (rice, maize and wheat), *Azotobacter* sp., *Klebsiella* sp. and *Alcaligenes* sp., reside in the rhizospheric zone and transport fixed nitrogen to plants. Endophytic nitrogen-fixing microbes are found in cereals, grasses, sugarcane, *Azoarcus* sp. (sorghum, rice, kallar grass), *Gluconacetobacter diazotrophicus* (sugarcane, sorghum), *Herbaspirillum* sp. (rice, sugarcane, sorghum) and *Burkholderia* sp. (rice) (Eva *et al*., 2019; Ladha *et al*., 2022; Turan *et al*., 2016).

Phytohormone production

Phytohormones are chemical molecules that affect plant physiological processes, even in low quantities. Soil bacteria can create phytohormones, making them a possible source of these compounds. Microorganisms produce plant growth hormones, including auxins (indole-3-acetic acid), cytokinins, gibberellins, ethylene and abscisic acids. Synthesis requires significant amounts of metabolic energy and nutrients (Ladha *et al*., 2022; de Bruijn *et al.,* 2022: Anjum *et al*., 2007). Stress-related regulators of plant immunity, such as jasmonic acid, ethylene and salicylic acid, provide a core signaling backbone to coordinate defense responses against phytopathogens (Matilla *et al*., 2018). Bacteria from the *Rhizobium, Sinorhizobium, Bradyrhizobium, Azospirillum, Bacillus, Paenibacillus* and *Pseudomonas* genera can produce

phytohormones such as auxins, ABA, gibberellins and cytokinins, which enhance plant growth and productivity in natural conditions (Galler and Levy, 2023; Ladha *et al*., 2022).

While all plant-associated bacteria produce auxins all PGP microorganisms cannot produce gibberellin. This capability is linked to root-associated microorganisms. Approximately 80% of rhizospheric bacteria produce auxins, primarily indole-3-acetic acid (IAA). Tryptophan is the primary precursor for IAA production in bacteria. Bacteria that increase IAA production can consume tryptophan found in root exudates. *Azospirillum brasilense* has five distinct tryptophan-dependent and independent routes, with unknown biosynthesis intermediates (Matilla and Krell 2018). IAA, a bacterial phytohormone that promotes lateral root formation and root elongation is the most widely studied. Plant hormones are particularly effective during stressful situations. Bacterial auxins can help plants cope with stress when they cannot make enough (Ahmad *et al*., 2019). Bacterial species capable of producing IAA include *Pseudomonas fluorescens, Pseudomonas syringae, Agrobacterium tumefaciens, Pantoea agglomerans, Azospirillum brasilense, Bacillus cereus, Bacillus amyloliquefaciens, Bradyrhizobium* sp. and *Rhizobium* sp. (Matilla and Krell, 2018). Shahzad *et al*. (2017) found that inoculating rice plants with *Pantoea dispersa* RWL-3, *Micrococcus yunnanensis* RWL-2, *Staphylococcus epidermidis* RWL-7 and *Micrococcus luteus* RWL-3 led to significant increases in dry biomass, root and shoot length, protein and chlorophyll content (Chaudhary *et al*., 2022; Shahzad *et al*., 2017). Fungi that produce IAA include *Aspergillus, Mortierella, Talaromyces, Trichoderma* spp., *Fusarium, Penicillium. Penicillium janczewskii* suppresses the phytopathogen *Rhizoctonia solani,* which causes stem rot (Adedayo *et al*., 2023).

Abscisic acid (ABA) is a stress hormone that triggers photoperiodic blooming and promotes plant growth and development. It affects plant responses to different environmental stresses such cold, salt and desiccation (Ahmad *et al*., 2019). Plant-associated bacteria can create ABA, which boosts phytohormone levels in plants. Plant with altered ABA production or insensitivity are more resistant to infections than wild-type plants, as ABA plays an important role in modifying plant defense mechanism (Matilla and Krell, 2018). Endophytic bacteria that produce ABA include *Achromobacter xylosoxidans, Brevibacterium halotolerans, Bacillus pumilus, Bacillus licheniformis* and *Lysinibacillus fusiformis* (Salazar-Cerezo *et al*., 2018).

Gibberellin (GA) is a phytohormone that promotes stem elongation and leaf expansion. Exogenous GA can enhance parthenocarpy in fruits, cause bolting, break tuber dormancy and increase fruit size and bud count. Gibberellin production by soil microorganisms can affect nodulation and plant growth, either positively or negatively. These microorganisms can cause nodule organogenesis and prevent nodulation during infection (Ahmad *et al*., 2019). *Rhizobium phaseoli*, the first known bacterium capable of producing GA, generates both GA1 and GA4. *Acetobacter diazotrophicus, Azospirillum lipoferum* and *Herbaspirillum seropedicae* produce biologically active GA1 and GA3, as reported in (Salazar-Cerezo *et al*., 2018). Adedayo and Babalola (2023) discovered that GA-producing fungi, such as *Cladosporium* sp., enhance tomato plant growth and contribute to pea plant colonization.

Cytokinin (CK) stimulates root development, plant cell division and hair creation, activate dormant buds and promotes seed germination. These plant hormones regulate nodulation, apical dominance and nitrogen fixation. PGPRs in *Pseudomonas* and *Bacillus* produce cytokinin, particularly zeatin (Yadav *et al*., 2018; Ladha *et al*., 2022). *Rhizobium* spp. and *Pseudomonas fluorescens* are bacteria that produce cytokinin (de Garcia Salamone *et al*., 2006).

Major nutrients solubilization

Soil microorganisms play an important part in nutrient cycling. Crops that remain in the soil provide carbon, energy and nutrients to microorganisms. *Rhizobium* bacteria can solubilize nutrients like phosphorus, potassium, iron and zinc, boosting their availability for plants (Ramadan *et al*., 2016). Phosphorus (P) is crucial for the overall growth and development of plants. Soil has copious P in both organic and inorganic forms (apatite and secondary minerals like Fe, Al and Ca phosphates). Despite its abundance in soil as an insoluble nutrient, P is a significant growth-limiting factor. Soluble phosphorus in soil regulates its availability to plants (Matilla and Krell, 2018; Sakure and Bhosale, 2019). PGP bacteria act as a biological rescue mechanism by solubilizing insoluble inorganic P in soil and making it available to plants in the form of orthophosphate. The primary mechanism of P solubilization is the formation of organic acids. As a result, insoluble P is converted to its soluble form. Organic acids generated in soil can lower pH and bind mineral ions, leading to phosphate solubilization (Matilla and Krell, 2018). Gram-negative PGPRs mostly generate gluconic and 2-ketogluconic acids. Phosphate-solubilizing PGPRs create several organic acids, including isobutyric, lactic, isovaleric, glycolic, acetic, oxalic, malonic and succinic acids (Matilla and Krell, 2018). PGP microbes capable of phosphate solubilization include *Arthrobacter, Azotobacter, Bacillus, Beijerinckia, Burkholderia, Citrobacter, Enterobacter, Erwinia, Flavobacterium, Halolamina, Microbacterium, Pantoea, Paenibacillus, Pseudomonas, Rhizobium, Rhodococcus, Serratia* and *Thiobacillus* (Yadav *et al*., 2018; Matilla and Krell, 2018; Chaudhary *et al*., 2022). Potassium (K) is the third important macronutrient for plant growth and agricultural output. Soil contains about 90% potassium in the form of insoluble rocks and silicate minerals. The soluble form of potassium is found in soil in low concentrations. Inadequate fertilizer application can lead to potassium shortage, a severe limitation in crop productivity. Potassium deficiency leads to underdeveloped roots, tiny seeds, decreased agricultural yields and slower growth. Soil bacteria can solubilize potassium, providing an

alternate supply for plants. Potassium-solubilizing microorganisms (KSMs) produce and secrete organic acids to convert insoluble potassium into a form that plants can absorb. Many bacteria, including *Acidithiobacillus ferrooxidans, Bacillus edaphicus, Bacillus mucilaginosus, Bacillus circulans, Paenibacillus* sp., *Burkholderia* sp. and *Pseudomonas* sp., can solubilize K^+ in into an accessible form. These bacteria improve K^+ availability in agricultural soils (Mathur *et al*., 2019). Adedayo and Babalola found that *Ceriporia lacerata*, *Aspergillus awamori and Penicillium digitatum* can solubilize phosphate using organic acids and phytase (Adedayo and Babalola, 2023). *Trichoderma* sp. boosted mineral and nutrient absorption (N, K and P), while *T. viride* fungus increased soil nitrogen content (Adedayo and Babalola, 2023).

Iron solubilization and siderophore production

The soil limits the availability of essential micronutrients. Soil bacteria create siderophores, which are essential for iron-feeding in plants. These substances have a strong affinity for iron (III), the most prevalent type of iron in nature and are low molecular weight chelators. The iron solubilization method is based on the production of a stable siderophore. The Fe^{+3} complex can be absorbed by plants (Matilla and Krell, 2018; Mathur *et al*., 2019). Currently, there are roughly 500 siderophores known to exist. *Pseudomonas fluorescens* promotes plant development by producing pyoverdine and other siderophores. Microorganisms can create siderophoric chemicals such as catechol, carboxylate, hydroxamate and phenolate, which help protect plants from infections. Bacteria having iron chelation characteristics include *Azotobacter, Bacillus, Enterobacter, Arthrobacter, Nocardia* and *Streptomyces* (Ramadan *et al*., 2016). Siderophores increase the plant's iron nutritional status and promote growth. Bacterial siderophores may chelate Fe^{+3} from soil, making it available to phytosiderophores. However, the specific method remains uncertain. Plants can incorporate Fe^{+3}-pyoverdine complexes, increasing the iron content of their tissues. Bacterial siderophores indirectly promote plant growth by reducing the availability of iron for phytopathogens (Matilla and Krell, 2018). Environmental factors affecting siderophore synthesis include pH, iron levels, trace elements and sufficient phosphorus, carbon and nitrogen supplies (Mathur *et al*., 2019). Siderophores transfer iron into bacteria through a system of ferric-specific ligands and membrane receptors, which operate as chelating agents. Siderophores inhibit pathogen growth by sequestering a restricted supply of iron (III) in the rhizosphere (Ramadan *et al*., 2016).

Soil microbes biocontrol activity

Excessive use of chemicals in agriculture, including pesticides, insecticides, herbicides and fertilizers, harms consumer health, biomagnification and economic loss (Tandon and Vats, 2016; Vats *et al*., 2017). Biological control organisms are non-disease-resistant organisms that inhibit the activities of plant diseases in soil (Saxena *et al*., 2019). Agents of microbiological control can protect plants through both direct and indirect interactions with diseases. Indirect mechanisms include ISR (microbial-induced systemic resistance), nutrition and space competition, which do not require pathogen interaction. Lytic enzymes and antibiotics are directly inhibiting pathogens (Kohl *et al*., 2019). Numerous bioactive compounds are produced by bacterial isolates with biocontrol agents, including antibiotics, volatiles, siderophores and growth-promoting compounds. With other microbes, these bacteria can compete and adapt quickly to environmental stress (Saxena *et al*., 2019). *Trichoderma* spp. generates antifungal volatile organic compounds (VOCs), including 6-pentyl-2H-pyran-2-one (PP) (Adedayo and Babalola, 2023). Various bacteria, such as *Agrobacterium, Pseudomonas, Bacillus, Pantoea, Serratia, Stenotrophomonas, Streptomyces* and *Trichoderma*, have been studied for antibiotic manufacturing capacity (Ramadan *et al*., 2016; Kohl *et al.,* 2019). Some bacterial species and strains for producing agroinoculants, including *Agrobacterium tumefaciens, Streptomyces lydicus, Bacillus subtilis, Burkholderia cepacia, Alcaligenes* sp., *Serratia marcescens* GPS5, *Erwinia amylovora* and *Streptomyces griseoviridis.* Biocontrol strains produce a variety of antibiotics, including polyketides, phenazine, heterocyclic nitrogenous compounds, phenylpyrroles, aminopolyols, cyclic lipopeptides and volatile antibiotics (Saxena *et al*., 2019; Arseneault and Filion, 2017; Glick, 2020). Several studies have found that biocontrol bacterial strains produce antibiotics to target diseases (Ram *et al*., 2018; Glick, 2020; Kenawy *et al*., 2019). Ongena and Jacques (2008) studied the formation of fengycin, iturin and surfactin by *Bacillus* sp. Raaijmakers and Mazzola (2012) studied the formation of antibiotic metabolites (phenazine, 2, 4-diacetylphloroglucinol and pyrrolnitrin) in *Pseudomonas* sp. Adedayo and Babalola (2023) found that *T. harzianum* inhibited the growth of phytopathogen fungus including *F. oxysporum, Phythium* sp. and *R. solani*. *Gliocladium virens* generates gliovirin, an antibiotic that prevents the growth of *F. oxysporum, Pythium ultimum*.

Quorum sensing interference with virulence

Bacteria use quorum sensing (QS), which includes autoinducers that are extracellular signaling molecules to communicate cell density. As the bacterial population grows, gene expression changes due to the advantages of certain processes that are exclusive to this group. QS controls processes like as antibiotic synthesis, biofilm development and virulence factor secretion. The expression of bacterial pathogenicity in plants depends on quorum sensing (QS). Plant pathogenic strains such *Pseudomonas syringae, Pantoea stewartii, Erwinia chrysanthemi* and *Burkholderia glumae* require QS to colonize and express virulence proteins (Quiñones *et al*., 2005; Koutsoudis *et al*., 2006; Hussain *et al*., 2008; Kang *et al*., 2018). Plant and microbe extracts with QS inhibitory action have been employed to treat multi-drug-resistant bacteria and in the food packaging industry (Mookherjee *et al*., 2018).

Quorum quenching (QQ), or interference with pathogen QS, is a viable biocontrol method (Mookherjee *et al*., 2018; Noorashikin *et al*., 2016; Torabi Delshad *et al*., 2018). QQ interference can occur in three ways: stopping signal molecule manufacturing, degrading signal molecules and blocking signal corpuscle receptors (Torabi Delshad *et al*., 2018). BCAs can disrupt QS against pathogens by blocking the formation of enzymatic breakdown molecules such as lactonases, pectinases and chitinases that cause infections (Brígido *et al*., 2019; Panpatte *et al*., 2020). AHLs (Acyl-homoserine lactones), autoinducers, degrading bacteria include *Bacillus* sp., *Acinetobacter* sp., *Burkholderia* sp., *Serratia* sp., *Lysinibacillus* sp., *Pseudomonas* sp., *Strepsporangium* sp., *Rhodococcus* sp., *Myroides* sp. and *Enterobacter* sp. (Noorashikin *et al*., 2016; Chan *et al*., 2011; Ma *et al*., 2013). It has been demonstrated that AHL-degrading *Lysinibacillus* reduces the amount of potato soft rot disease caused by *Pectobacterium carotovorum* subsp. *carotovorum* (Garge *et al*., 2016; Jose *et al*., 2019).

Lytic enzymes

The generation of lytic enzymes is one potential pathogen-killing strategy. PGPRs inhibit fungal pathogens (*Fusarium oxysporum, Sclerotinia sclerotiorum* and *Botrytis cinerea*) and other soil-borne pathogens by secreting enzymes like chitinases, proteases, hydrolases and glucanases (Ramadan *et al*., 2016; Mathur *et al*., 2019). BCAs primarily inhibit the growth of soil-borne pathogens by producing and secreting cell wall lytic enzymes (CWLEs) (Singh *et al*., 2017). CWLEs damage the structural integrity of the target pathogen's cell wall. The cell wall of fungi is pathogenic and consists primarily of chitin and β-1,4-N-acetyl glucosamine. CWLEs, including β-1,3-glucanase and chitinase, are involved in the majority of BCAs. CWLEs neutralize the pathogen inhibitory effect by lysing cell walls (Goswami *et al*., 2016). PGPRS inhibits well-known phyto-pathogens such as *Rhizoctonia solani* and *Phytophthora capsici* (Kannojia *et al.,* 2019; Islam *et al*., 2016).

Induced systemic resistance

Beneficial bacterial strains manage diseases by inducing systemic resistance (ISR). Biocontrol agents and Microbial metabolites can trigger a plant's immune response, leading to disease resistance (Ramadan *et al*., 2016). Plants identify microbial molecules (exopolysaccharide, lipopolysaccharide and chitin oligosaccharide) generated by helpful microbes. Bacterial species such as *Bacillus amyloliquefaciens, B. atrophaeus, B. cereus, B. megaterium, B. subtilis, Paenibacillus alvei, Pseudomonas fluorescens, Pseudomonas aeruginosa* and *Streptomyces pactum* are effective against viral, fungal, bacterial, infections *via* ISR (Yu *et al*., 2022). ISR involves plant hormones such as ethylene, jasmonic acid and salicylic acid. Plant defense against phytopathogens involves the ethylene and jasmonic acid signaling pathways. ISR manifests as changes in cell wall integrity, biochemistry and physiology. Bacterial strains having ISR-eliciting characteristics have been shown to effectively combat a variety of fungal infections. Bacteria such as *Pseudomonas fluorescens, Pseudomonas aeruginosa, Bacillus amyloliquefaciens, B. subtilis, B. pumilus, B. pasteurii, B. cereus, B. sphaericus* and *B. mycoides*, have been identified (Panpatte *et al*., 2020; Kannojia *et al*., 2019). Cotton plants treated with *P. chrysogenum* exhibited ISR against *T. viride, Verticillium dahlia, P. simplicissimum, T. harzianum* and *Acremonium sclerotigenum* effectively induced ISR in agricultural plants including cucumber and tomato (Adedayo and Babalola, 2023).

Synergistic microbial mechanisms

Plants were more effectively inoculated with bacterial consortia compared to single strains. IAA and ACC deaminase synthesis have been shown to have synergistic effects on N_2 fixation (Ma *et al*., 2004; Serova *et al*., 2017; Defez *et al*., 2016; Defez *et al*., 2019; Nascimento *et al*., 2012; Nascimento *et al*., 2019; Alemneh *et al*., 2020), stress tolerance (Defez *et al*., 2019; Nascimento *et al*., 2012; Nascimento *et al*., 2019; Alemneh *et al*., 2020; Orozco-Mosqueda *et al*., 2020) and phosphate solubilization (Alemneh *et al*., 2021). IAA and ACC deaminase play multiple roles in BNF fixation, including enhancing nodule formation, increasing rhizobia competitiveness, suppressing nodule senescence and upregulating genes linked with legume-rhizobia symbiosis (Alemneh *et al*., 2020). Knockout and overproducing strains of the ACC deaminase gene were used to study its role in nodule formation (Alemneh *et al*., 2021). In terms of plant colonization and nodulation, the mutant strain of *Mesorhizobium loti* ACC deaminase that overproduces the enzyme performed better than the wild type (Ma *et al*., 2004). In *Mesorhizobium loti*, the acdS gene is located in the symbiotic island and its expression is controlled by the N_2 fixation regulator NifA2 (Nukui *et al*., 2006). Senescent nodules have enhanced expression and transcription of PsACS2, which encodes ACC synthase, an enzyme implicated in ethylene production (Serova *et al*., 2017). PGP bacteria produce ACC deaminase can improve nitrogen fixation by increasing the lifespan of functioning nodules. Comparing 31-day-old nodules of a transformed *Mesorhizobium* sp. expressing ACC deaminase to its parental strain devoid of this activity, Nascimento *et al*. (2012) discovered nitrogenase activity. Compared to the ACC deaminase mutant strain, Nascimento *et al*. (2019) discovered that the *Pseudomonas fluorescens* YsS6 strain that produces ACC deaminase enhanced the nodulation capacity of alpha- and beta-rhizobia. Free-living ACC deaminase-producing bacteria promote rhizobia nodulation. IAA, a biomolecule, plays a role in legume-rhizobia interactions by regulating nodule primordium formation and cell division. IAA affects the expression of genes involved in rhizobia and nodule formation in plant cells (Alemneh 2020). Camerini *et al*. (2008) found a link between IAA and nodulation, with IAA-negative *Rhizobium leguminosarum bv. viciae* producing fewer nodules than the parent strain. Additionally, using IAA-producing nodule-enhancing rhizobacteria as a

co-inoculum promoted rhizobia colonization due to their production of caproic acid (Alemneh *et al*., 2020). *Ensifer meliloti* RD64-induced 45-day-old nodules with IAA overproduction showed a longer nitrogen-fixing zone and a lower senescent zone compared to the wild-type strain (Defez *et al*., 2016). Scientists investigated the impact of ACC deaminase and IAA on the stress response (Defez *et al*., 2019; Orozco-Mosqueda *et al*., 2019). Interaction between the two properties was shown when *Pseudomonas* sp. UW4 trehalose (treS) and ACC deaminase (acdS) mutant strains (mutated at one or both features) were used as bioinoculant on tomato plants under salt stress. The impact of single gene mutations is greater than that of multiple ones (Orozco-Mosqueda *et al*., 2019). Alemneh *et al*. (2021) found ACC deaminase-producing bacteria capable of phosphate solubilization, indicating ACC deaminase-mediated P solubilization. Inoculating chickpeas with ACC expressing *Burkholderia* sp. 12F led to increased P nutrition and enhanced nodulation rates. Metabolomic investigations of the soil microbiome are crucial for understanding plant-soil-microbe interactions, as synergy can occur between bacteria, arbuscular mycorrhizal fungi and bacterial ACC deaminase (Orozco-Mosqueda *et al*., 2020).

CONCLUSION

The soil system's complexity, including stratification and microhabitats, promotes the growth of a diversified microbial community. The most difficult task at the moment is analyzing data from microbial communities. Understanding bacterial functional groups and community dynamics is crucial for knowing how soil ecosystems work, in addition to taxonomy. The rhizosphere is a hotspot for the microorganism and microbial gene transfer and contains a wealth of genetic capabilities, making PGPR genetic engineering a valuable tool for sustainable agriculture. What impact do environmental changes have on soil ecology and how may sustainable agriculture methods maintain this function? It is unclear how they are shaped by plant-microorganism interactions. Plant genome engineering is a tool for sustainable agriculture that utilizes unique plant-microbe communication. Sustainable agriculture requires a better understanding of soil-microbe-plant systems and their impact on short- and long-term sustainability. Future research should focus on utilizing genetically engineered plants and microorganisms for sustainable agriculture.

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Author's contribution

All authors made substantial contributions to the conception and design, acquisition of data, or analysis and interpretation of data.

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