

From Rhizosphere to Crop Production: Evolutionary and Molecular Insights into Plant Growth Promoting Rhizobacteria (PGPR)

Pedro Lezama-Asencio ¹, Edinson Larco-León ¹, Pablo Chuna-Mogollón ¹, Martha Lezama-Escobedo ², Cynthia Ramos ², Cecilia Bardales-Vasquez ², Percy Asmat ² and Manuel Hidalgo ^{2*}

¹ Departamento Académico de Ciencias, Universidad Privada Antenor Orrego, Trujillo 13008, Peru

² Programa de Estudio de Medicina Humana, Universidad Privada Antenor Orrego, Trujillo 13008, Peru

*(e-mail: jemhidalgor@gmail.com)

(Received: 3 September 2025; Revised: 22 October 2025; Accepted: 10 November 2025; Published: 21 November 2025)

ABSTRACT

Plant growth-promoting rhizobacteria (PGPR) are key components of the plant microbiota that coevolved with hosts as an entity called holobiont, acquiring traits for chemotaxis, root adhesion, high-affinity nutrient capture, and antagonism of phytopathogens. By integrating evolutionary, molecular, and multi-omics perspectives, this review aims to synthesize how these adaptations drive direct (biofertilization, phytohormone modulation) and indirect (biocontrol, stress tolerance) benefits that enhance crop productivity and ecosystem services. Multi-omics studies are revealing conserved PGPR functions, including induction of nitrogenase, ACC deaminase, siderophore biosynthesis, exo/endometabolites among others, that coordinate colonization and plant signaling. Also, PGPR activate induced systemic resistance (JA/ET pathways) and interact with systemic acquired resistance to improve immunity. Agronomic applications span biofertilizers, biostimulants, biological control agents, improving nutrient use efficiency, root architecture, and resilience to abiotic/biotic stress. Nonetheless, field performance is context dependent, shaped by environmental factors, host genotype, management, competition with native microbiota, and among others imposing challenges to PGPR use. Thus, a framework including multi-omics, ecological modeling, and machine learning is needed to predict their functions, design synthetic consortia and tailor bioinoculants to crops and soils. Embedding PGPR within climate-smart and precision agriculture can reduce inputs, stabilize yields, and support long-term soil health, advancing sustainable, resilient food systems globally.

Key words: microbiota, rhizosphere, plant growth promoting rhizobacteria, sustainable agriculture, rhizobacterium

INTRODUCTION

Throughout evolution and due to their sessile nature, plants have had to overcome the challenges imposed by abiotic and biotic environmental factors. The latter group, includes the set of viruses, prokaryotes (archaea and bacteria) and eukaryotes (fungi, protists including oomycetes, algae), that interact with plant surfaces and inner parts, are collectively known as microbiota (Tharanath et al., 2024). To survive, these microorganisms use the carbon compounds generated by plants (Mesny et al., 2024), and through specialized adaptations, they participate in nutrient absorption, providing plants with new metabolic capabilities (Mohamed, 2020).

For plants, these interactions can induce deleterious (pathogenic relationships), neutral (commensalism) or positive (mutualism) effects (Bauer et al., 2020). Thus, while some microorganisms can be detrimental or neutral to plant survival, some others can form a complex microbial

consortium that carry beneficial effects including disease suppression, immune system activation, induction of systemic resistance, increased nutrient absorption, enhanced tolerance to biotic and abiotic stress, adaptation to environmental variations, among others (Singh et al., 2025).

In agroecosystems, these mutualistic relationships impact on the regulation of carbon dynamics, greenhouse gases, soil acidity, the mediation of the cycling of nutrients and the mitigation of soil erosion and pollutants, and are associated with improvements in crop yield, productivity, and efficiency in the use of resources (Berg et al., 2023). In particular, a group termed Plant-Growth-Promoting Rhizobacteria (PGPR) has become of vital importance to achieving the efficient and sustainable management of modern farming systems.

PGPR are being extensively studied to understand their ecological roles and agronomical applications as biofertilizers that improve physiological parameters in the plant. Most of the research has focused on the analysis



of the physiological benefits of PGPR or their application as biofertilizers (Kurt, 2025), often overlooking how evolutionary processes and genomic adaptations are related to these functions. Thus, there is a research gap in our understanding of how the evolutionary principles, molecular mechanisms, and agronomic potential of PGPR are linked in sustainable agricultural systems. This review aims to integrate evolutionary, molecular, and omics-based evidence to explain how PGPR evolved and diversified as key drivers of plant adaptation and sustainable crop productivity. Providing a novel conceptual framework connecting fundamental microbial evolution with applied agricultural innovation.

To prepare this review the authors made a comprehensive literature search using PubMed, Scopus, and Web of Science databases. Keywords included “plant growth-promoting rhizobacteria (PGPR),” “rhizosphere,” “plant-microbe interactions,” “metabolomics,” and “sustainable agriculture.” Articles published between 2018 and 2025 in English were prioritized, focusing on peer-reviewed research and review papers relevant to PGPR mechanisms and agricultural applications.

EVOLUTIONARY ADAPTATION OF PGPR

The nature of the molecular principles that govern the interaction between plants and PGPR has been developed through years of evolution. Viruses, bacteria, and archaea originated approximately 3500 million years ago (Mya), followed by the appearance of protists (~1500 Mya), fungi (~1000 Mya), green plants (~1000 Mya), and terrestrial plants (~450 Mya). These evolutionary events established a framework for multiple interaction networks in which plants serve as hosts for their microbiomes, forming a functional entity called the holobiont (Bettenfeld et al., 2022), which combines the plant and microbiome genomes to form a hologenome. This entity allows holobionts to adapt in morphological, developmental, behavioral, physiological and disease resistance aspects (Lyu et al., 2021).

In this context, PGPR have coevolved with their hosts, acquiring different adaptive traits for root colonization (adhesion, extracellular polymeric substances EPS/biofilm formation), chemotaxis toward root exudates, and high-affinity resource acquisition (iron via siderophores, nitrogen via biological fixation, phosphate via solubilization), that have all been progressively selected within the plant holobiont (Santoyo et al., 2021). These traits

enable efficient arrival to the rhizosphere, stable persistence on or within root tissues, and rapid metabolic responses to plant-derived cues, thereby linking microbial evolution to host performance under fluctuating edaphic conditions (Mashabela et al., 2022). Functionally, such adaptations translate into enhanced nutrient mobilization and hormone modulation, as well as competitive exclusion and antagonism against phytopathogens, which collectively support plant growth and stress tolerance (Sharma et al., 2025). These capabilities are conserved and have emerged in evolution from repeated selection due to the interaction between different organisms and have been established within agroecosystems, consistent with the holobiont/hologenome framework. Among them, bacteria-bacteria interactions, include nutritional interdependence, biofilm formation, quorum sensing, resource competition, contact-dependent competition, and secretion of antimicrobial compounds. Bacteria-micro-eukaryote interactions, are characterized by nutritional interdependence, biofilm formation, fungal displacement, endosymbiosis, production of volatile organic compounds (VOCs), quorum sensing interception, resource competition, contact-dependent competition, and antimicrobial secretion. Micro-eukaryote-micro-eukaryote interactions encompass nutritional interdependence, molecular quorum sensing, resource competition, antimicrobial compound secretion, and predation. Microorganism-plant interactions, involve plant growth promotion, nutrient exchange and solubilization (nitrogen, phosphate, and carbon), biocontrol activities, microbial diseases, and competition for nutrients (Figure 1).

At the same time, the holobiont is affected by abiotic factors such as soil pH, organic carbon quality and quantity, nitrogen availability, temperature, and redox status, which are the primary determinants of soil microbiota composition and functioning (Grzyb & Szulc, 2024). In agroecosystems, these environmental factors are further influenced by agricultural practices including fertilizer application, pesticide use, crop genotype, and rotation systems, which can further modify the interactions and functional potential of the rhizospheric microbiota (Meena et al., 2020). The aforementioned practices work as selective pressures, imparting ecological filters that determine community structure and drive the retention of microbial traits to optimize nutrient acquisition and stress resistance within the holobiont (Dutta et al., 2022).

Some adaptative responses have been reported in soils exposed to nutrient depletion, salinity, or drought. These include, the selection of siderophore-producing strains under iron-limited conditions, which enhances microbial competitiveness and iron uptake within the rhizosphere (Deb & Tatung., 2024), or the enrichment of 1-aminocyclopropane-1-carboxylate (ACC)

deaminase-containing bacteria improves the response to abiotic stress, modulating plant ethylene levels for improved root elongation and stress tolerance (Ferreira et al., 2025). These adaptations reflect the evolutionary and ecological filtering processes that favor microbial genotypes with traits conferring both survival advantages and plant-beneficial effects.

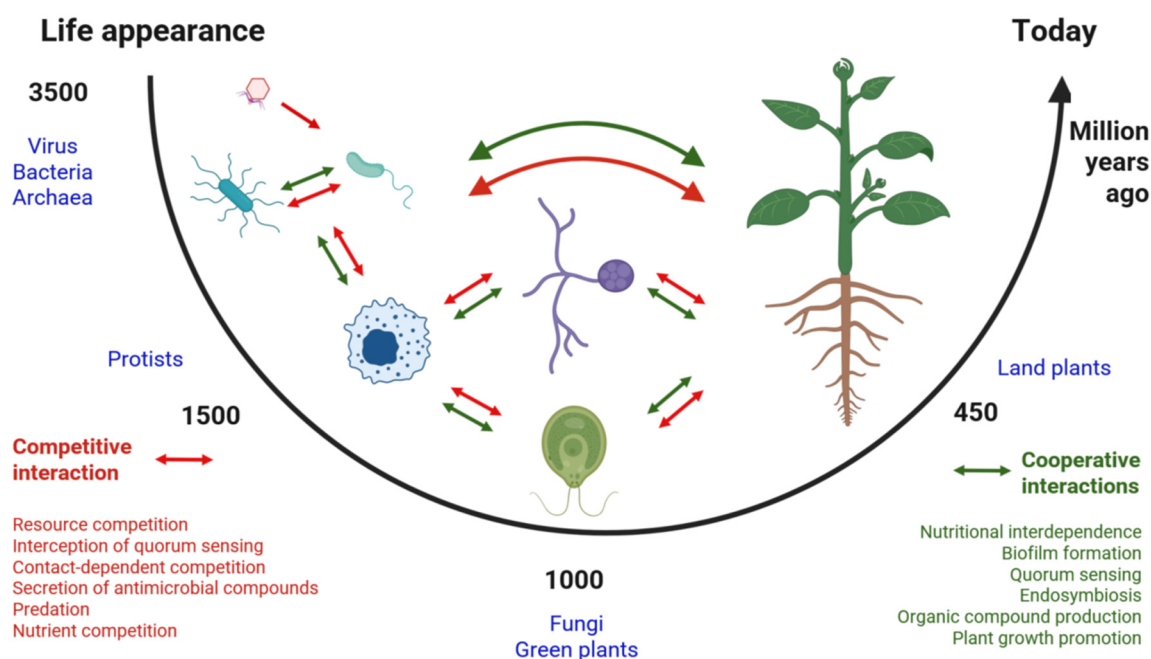


Fig. 1. Evolutionary timeline of the development of biological organisms and the emergence of interactions between them. Adapted with permission from Hassani et al. (2018). Licensed under the Creative Commons Attribution (CC BY) license. Created with BioRender.com.

Indeed, in agroecosystems, the interactions among multiple organisms generate a complex and dynamic network that is continually influenced by fluctuating environmental conditions including soil management, leading to modifications in the gene expression of both plants and their associated microbiota to produce specific adaptive traits (Du et al., 2025). These interaction networks underpin key processes such as induced systemic resistance, nutrient mobilization, and competitive exclusion, which are characteristic of the functional role of PGPR within the rhizosphere. Through these mechanisms, PGPR contribute to maintaining ecosystem stability and enhancing plant performance under biotic and abiotic stress conditions (Palermo et al., 2025; Al-Turki et al., 2023).

Currently, near 50,000 species are regarded as part of the plant microbiota, although this number might be underestimated because a large proportion of microorganisms cannot be isolated or cultured using conventional

techniques (Seabloom et al., 2023). To overcome this limitation, several techniques, including shotgun metagenomics and the reconstruction of metagenome-assembled genomes (MAGs) allow the discovery of PGPR taxonomic diversity, the understanding of community composition and their relation with functional attributes such as nutrient cycling, phytohormone biosynthesis, and secondary metabolite production relevant to rhizospheric bacteria (Kifle et al., 2024).

Moreover, functional gene annotation and comparative genomics from MAGs have uncovered the presence of key PGPR-associated genes such as ACC deaminase, the nitrogenase enzyme complex for nitrogen fixation, and siderophore biosynthetic clusters. These findings highlight the evolutionary conservation and ecological significance of these traits across diverse plant-associated taxa (Al-Turki et al., 2023). Moreover, they demonstrate how genomic technologies are deepening our understanding of PGPR

evolution, adaptation, and their potential for sustainable crop management.

MOLECULAR MECHANISMS OF PGPR FUNCTION

The establishment of PGPR symbiosis involves a multistage signaling and recognition process mediated by specific chemical, genetic, metabolic and cellular interactions that play critical roles in shaping microbial communities and their interactions with plants (Figure 2) (Fan & Smith, 2021). Physical and ecological interactions, include biomass turnover driven by predation (e.g., bacteriophage infection of bacteria); encapsulation via lipopolysaccharides (LPS), which facilitates adhesion and protection; competitive exclusion for shared substrates, leading to spatial and resource-based

competition. On the other hand, Molecular-level interactions include syntrophic interactions, where distinct microbial species share and exchange metabolic intermediates (S1, S2, S3), including directional or commensal nutrient flow; quorum sensing mediated by signaling molecules, coordinating microbial behavior such as biofilm formation or secondary metabolite production; production of antimicrobial compounds that regulate population balance; division of labor among microbial consortia, optimizing substrate use and metabolic efficiency. These interactions are actively being studied through a multi-omics perspective, integrating genomics, transcriptomics, proteomics, and metabolomics to analyze and elucidate the complex mechanisms by which PGPR influence plant growth and development (Sahil et al., 2025).

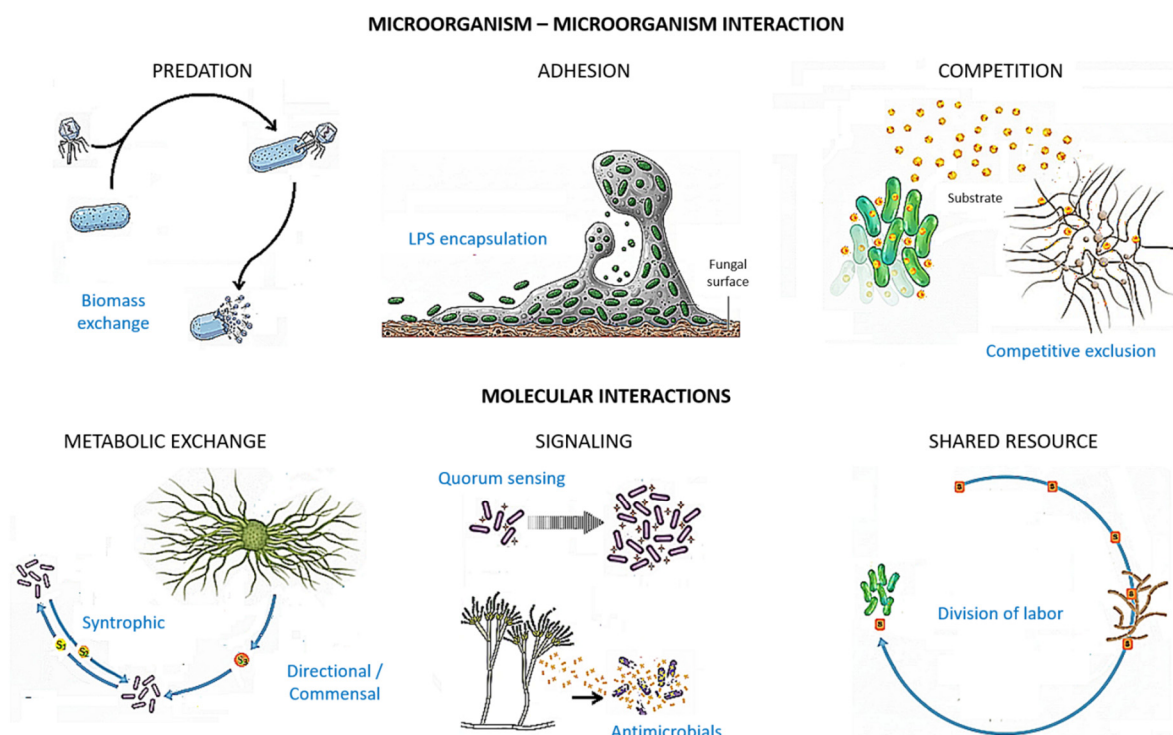


Fig. 2. Microorganism-microorganism interactions and their molecular mechanisms in soil ecosystems. Adapted with permission from Jansson & Hofmockel (2018). Licensed under the Creative Commons Attribution (CC BY) license. Created with BioRender.com. LPS: lipopolysaccharides, S1, S2, S3: exchange metabolic intermediates.

Plants actively exude signaling molecules including flavonoids, sugars, and phytohormones, which act as chemotactic signals and transcriptional modulators of bacterial traits. These compounds are recognized by bacterial sensor systems. Gram-negative PGPR employ LuxI/LuxR-type quorum-sensing circuits (Soto-Aceves et al., 2023), whereas Gram-positive PGPR use

peptide pheromones and two-component regulators to synchronize gene expression for chemotaxis, extracellular polymeric substances (EPS) secretion, and exoenzyme production (Chen et al., 2024). In response to plant exudates, PGPRs synthesize specific signaling molecules that serve as molecular signatures of the symbiotic bacterium, and as these communication process intensifies, signals

such as acyl homoserine lactones (AHLs), volatile organic compounds (VOCs), and cyclic lipopeptides coordinate biofilm formation and secondary-metabolite production (Sibanyoni et al., 2025). Specific VOCs including 2,3-butanediol and acetoin can prime plant defenses, while lipopeptides (e.g., surfactin, fengycin, iturin) facilitate swarming, root attachment, and pathogen membrane disruption (Badri et al., 2025). In later stages, signal turnover is tempered by quorum-quenching enzymes (AHL lactonases/acylases), which help stabilize community structure (Jacobson et al., 2025). The changes also include a genetic regulation, with the participation of several loci, including nonribosomal peptide synthetase (NRPS) and polyketide synthase (PKS) clusters, quorum-sensing genes, and siderophore biosynthetic genes that can be detected in shotgun metagenomes and metagenome-assembled genomes, linking community membership to function. Collectively, this signaling architecture governs colonization hierarchies, cooperative metabolic handoffs, and competitive exclusion, thereby shaping rhizosphere assembly and plant fitness (Imchen et al., 2022; Zhou et al., 2021). These processes are further affected by soil type, plant compartment, genotype, immune system, and stage of development (Hanif et al., 2024). Thus, in agroecosystems, individual species establish specific interrelationships that sustain the trophic network comprising thousands of interacting taxa (Copeland et al., 2025).

Plant Growth-Promoting Rhizobacteria (PGPR)

The rhizosphere, the soil region surrounding roots, is strongly influenced by the root system and is enriched in organic compounds released through exudation, secretion, and rhizodeposition, which provide carbon and energy for rhizobacteria (Santoyo et al., 2021; Upadhyay et al., 2023). Some act as decomposers of residual agents and agricultural waste, whereas others positively influence plant growth and development and are termed plant growth-promoting rhizobacteria (PGPR) (Azizoglu et al., 2021). At this interface, three mechanisms including chemotaxis toward exudates, adhesion via EPS/LPS, and coordinated biofilm formation enable effective and stable root colonization (Iqbal et al., 2024). Recent imaging studies with fluorescently tagged PGPR highlight enhanced colonization efficiency linked to

these mechanisms and show that biofilm matrix components contribute to root surface attachment and microbial aggregation (Lazarus & Easwaran, 2024)

PGPR promote plant growth directly or indirectly and are commonly grouped into biofertilizers, biostimulants, biopesticides, and biological control agents, as well as modulators of tolerance to biotic and abiotic stress (Zhang et al., 2025). On the direct side, they improve nutrient availability through atmospheric nitrogen fixation, production of iron-chelating siderophores, mineralization of organic matter, phosphate solubilization, and production of plant growth hormones and stress regulators such as 1-aminocyclopropane-1-carboxylate (ACC) deaminase, the nitrogenase enzyme complex (nifHDK), and biosynthetic clusters for siderophores and organic acids (Gamalero et al., 2023). These interrelationships may be restricted to the rhizosphere—colonizing the rhizosphere, rhizoplane, surface intercellular spaces, or dead layers of root cells—or may be endophytic, occupying the apoplastic space with or without specialized structures such as nodules (Yusuf et al., 2025). Therefore, classification schemes distinguish extracellular PGPR (e-PGPR), limited to the rhizoplane, from intracellular PGPR (i-PGPR), which colonize spaces between cortical cells or form nodules. The colonization begins when bacteria are directed to root entry routes such as lateral root emergence sites and wounds, with EPS-mediated adhesion facilitating persistence in these niches (Iqbal et al., 2024).

Rhizosphere Interactions and Metabolomics Potential

Our understanding of the plant–plant and plant–microorganism interactions has advanced considerably in recent years, revealing that they are mediated by a wide array of chemical compounds that regulate physiological processes between above- and below-ground tissues. Nonetheless, the precise nature of this molecular communication is still being elucidated through metabolomics approaches that focus on the characterization of exometabolites and endometabolites to determine their roles in specific biochemical interactions (Yusuf et al., 2025). More recently, analytical platforms such as LC–MS/MS, GC–MS, NMR, and MALDI-TOF have enabled the detection of phytohormones (e.g., IAA), volatile organic compounds (VOCs), cyclic lipopeptides, and other metabolites that influence root architecture, defense signaling, and ultimately, the identification and classification of PGPR.

These metabolomic tools have also facilitated the development of strategies for sustainable crop production, including the induction of systemic resistance against foliar pathogens (Mhlongo et al., 2020), reinforcement of structural barriers against pathogen entry and herbivory, and the activation of immune responses mediated by microbe- or pathogen-associated molecular patterns (MAMPs). Information derived from these metabolomic analyses further clarify how plants differentiate between microorganisms, triggering distinct physiological outcomes. Depending on the molecular signals perceived, microorganisms may be recognized as non-pathogenic, pathogenic, or beneficial,

resulting in successful symbiotic interactions. Non-pathogenic microorganisms do not affect preformed plant barriers. Pathogenic microorganisms are able to penetrate preformed barriers, inducing responses of susceptibility and disease, or tolerance and resistance. Beneficial microorganisms also cross the preformed plant barriers, but do not trigger induced barriers, causing a beneficial response in the plant (Figure 3) (Pang et al., 2021). At the physiological level, these outcomes are orchestrated through complex changes in metabolite composition and the coordinated regulation of signaling molecules such as salicylic acid (SA), jasmonic acid (JA), and ethylene (ET) (Verma et al., 2024).

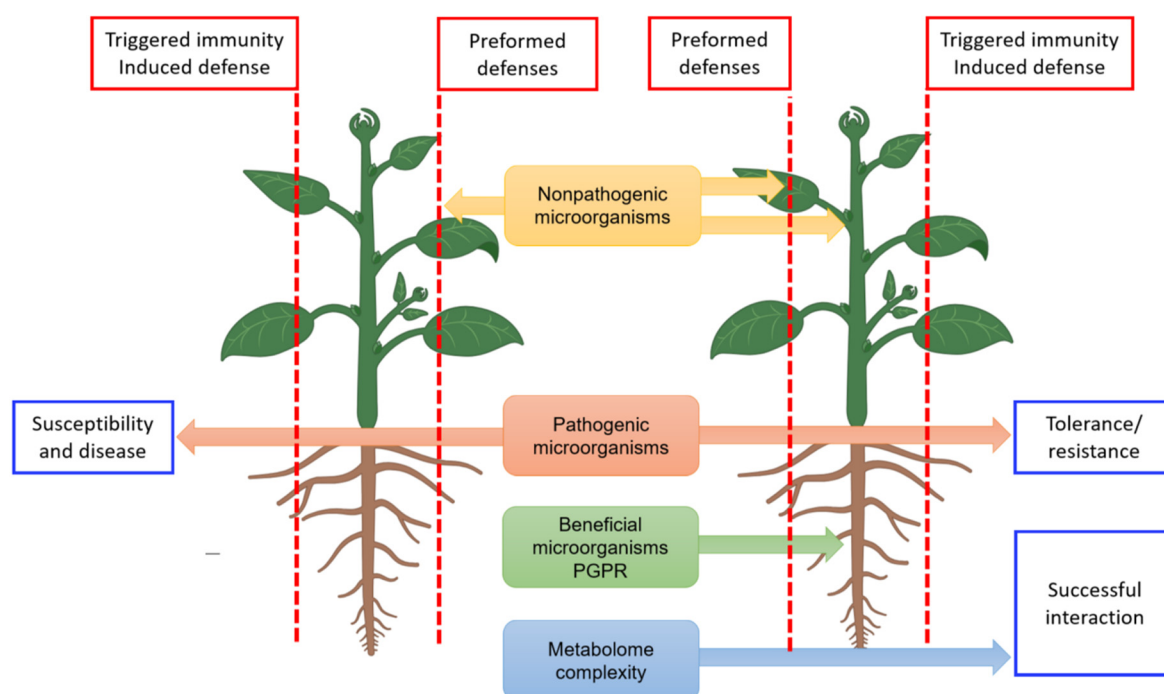


Fig. 3. Plant-microorganism interactions in relation to plant defenses. Adapted with permission from Mhlongo et al. (2018). Licensed under the Creative Commons Attribution (CC BY) license. Created with Biorender.com.

Indeed, PGPR enhance plant defense by activating Induced Systemic Resistance (ISR), which is typically mediated through JA and ET signaling pathways, which coordinate defense responses against necrotrophic pathogens and certain herbivores. ISR does not rely on the accumulation of pathogenesis-related (PR) proteins but instead prepares the plant for a faster and stronger activation of defense mechanisms upon subsequent pathogen attack (Mazuecos-Aguilera et al., 2025). In contrast, Systemic Acquired Resistance (SAR) is usually triggered following a localized infection by a pathogen and is primarily mediated by the salicylic acid (SA) pathway. SAR is characterized by the systemic

expression of PR genes, accumulation of SA, and long-lasting protection against a broad spectrum of biotrophic and hemibiotrophic pathogens (Zhao et al., 2024). Although ISR and SAR are governed by distinct hormonal pathways, cross-talk between JA/ET and SA signaling enables plants to fine-tune their immune responses according to the nature of the threat and environmental context. Consequently, beneficial PGPR act not only as growth promoters but also as key modulators of the plant immune system, contributing to sustainable protection in agroecosystems. The microorganisms composing the plant microbiome are being studied through different -omics perspectives, and the information

derived from their genomes shows genetic mechanisms involved in plant growth promotion, including ACC deaminase, auxins, pyoverdine, and rhamnolipids which are important in hormone modulation, iron acquisition, and biosurfactant-aided colonization, illustrating how genomic traits underpin PGPR function in hosts. Among rhizobacteria, the family Rhizobiaceae has long been of special interest for its role in symbiotic nitrogen fixation, primarily with members of the Fabaceae, where nodules are established. Through phenotypic, biochemical, physiological, and genetic characterizations, the original genus *Rhizobium* has been divided into several genera including *Allorhizobium*, *Azorhizobium*, *Bradyrhizobium*, *Mesorhizobium*, *Rhizobium*, and *Sinorhizobium* and others that are now regarded as PGPR (Koskey et al., 2018).

In the case of legumes, the symbiotic establishment is governed by nodulation (nodABC) and nitrogen-fixation (nifHDK) genes, which coordinate host recognition, nodule organogenesis, and nitrogenase complex expression. The nod genes are primarily responsible for the synthesis of lipochitooligosaccharide Nod factors, which mediate host recognition and trigger early plant responses such as root hair curling, cortical cell division, and the initiation of nodule organogenesis. Once nodules are formed, the nif genes, together with associated fix genes, encode the components of the nitrogenase complex responsible for biological nitrogen fixation (BNF), converting atmospheric nitrogen (N₂) into ammonia that can be assimilated by the plant (Paulitsch et al., 2020). Thus, through this molecular coordination, the symbiosis generates benefits for both organisms, the plant receives biologically available nitrogen, while the bacterium gains access to carbon sources from the host.

Understanding the structure, regulation, and expression of nod and nif gene clusters has been fundamental to improving legume productivity and is currently inspiring biotechnological approaches to transfer nitrogen-fixing capabilities to non-leguminous crops, expanding the potential applications of PGPR in sustainable agriculture (Han et al., 2023). By knowing these mechanisms, scientists will have more information to adapt new biotechnological tools that further improve the application of PGPR and could enable the rational design of PGPR strains with enhanced functionality (Argente-Martínez et al., 2024). Hence, genome editing tools such as

CRISPR–Cas systems allow precise modification of genes involved in nitrogen fixation, phytohormone biosynthesis, and stress adaptation, while synthetic biology could facilitate the construction of regulatory modules and metabolic pathways that optimize biosurfactant, siderophore, and volatile compound production (Singh and Ramakrishna, 2021). These improvements, have the potential to generate strains with the ability to modulate quorum sensing, improve root colonization, and deliver stress-alleviating molecules, contributing to greater resilience under adverse environmental conditions. Together, these strategies represent a transition from natural strain selection toward programmable bioinoculants tailored for sustainable and climate-resilient agriculture.

AGRONOMIC POTENTIAL AND SUSTAINABILITY

As detailed in the previous section, the PGPR effects include nitrogen fixation, phosphorus solubilization, phytohormone modulation, and induced systemic resistance, which collectively enhance plant performance. In the plant, these mechanisms improve nutrient use efficiency, stimulate plant growth, and strengthen tolerance to abiotic and biotic stresses, which significantly increase crop yield and soil fertility under both conventional and stress-prone conditions (Ehinmitan et al., 2024). When PGPR are established, their effects become permanent and contribute to sustainable farming systems balancing productivity, ecosystem health, and resource conservation. Thus, these mechanisms make PGPR crucial biofertilizers and biocontrol agents in precision and sustainable agriculture, reducing the need for synthetic fertilizers and pesticides while boosting plant productivity and resilience (Alzate et al., 2024). As a consequence, they reduce dependence on synthetic inputs, improving in soil health and efficiency in the use of resources. However, PGPR effects are also subjected to interactions with biotic factors such as nematodes, fungi, bacteria, and herbivorous arthropods, that are associated to the rhizosphere and under selective pressure from the plant (Park et al., 2023).

At the same time, PGPR function is subjected to plant genotypes with traits that directly or indirectly influence the composition, activity, or structure of the associated microbiome (Zhao et al., 2025). These microorganisms promote plant growth through direct (biofertilizer/biostimulant) and indirect (biocontrol/stress tolerance) pathways.

Biofertilizers promote biological nitrogen fixation and phosphorus solubilization. Phytostimulators increase the production of phytohormones, including auxins, cytokinins, and gibberellins. Biopesticide and biological control agents induce systemic resistance, production of cellulolytic enzymes,

siderophores, HCN, and antifungal metabolites, as well as competitive exclusion. Tolerance to biotic and abiotic stress: synthesis of ACC deaminase, antioxidants, antifreeze proteins, proline, and quaternary amines, processes associated to *Methylobacterium*, *Paenibacillus*, *Exiguobacterium* (Figure 4).

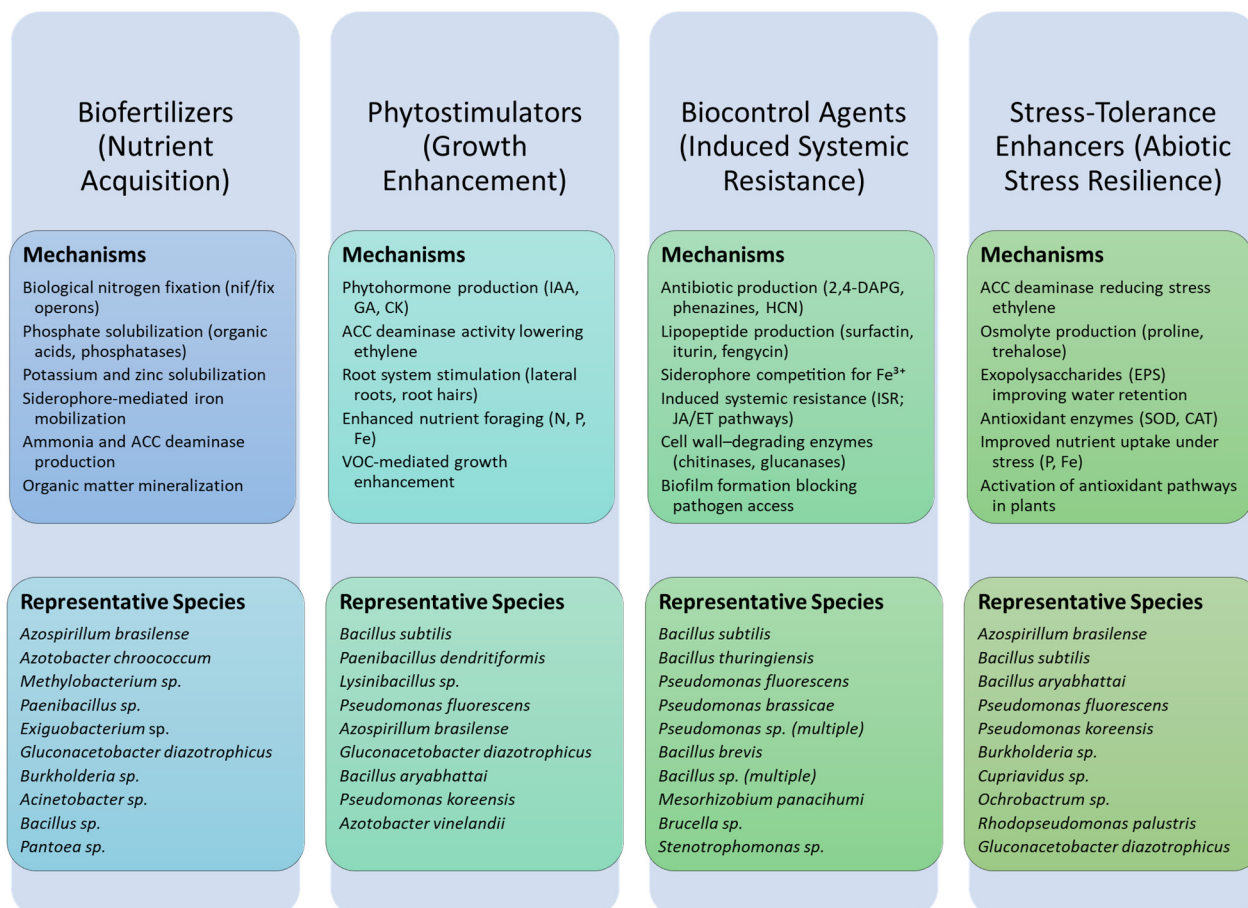


Fig. 4. Main functional traits of plant growth-promoting rhizobacteria (PGPR), grouped into four areas: biofertilizers, phytostimulators, biocontrol agents and stress tolerance enhancers. Nif: nitrogen fixation genes, Fix: nitrogen fixation regulatory genes, IAA: indole-3-acetic acid, GA: gibberellins, CK: cytokinins, ACC: 1-aminocyclopropane-1-carboxylic acid, ACC deaminase: enzyme that degrades ACC, VOC: volatile organic compounds, ISR: induced systemic resistance, SAR: systemic acquired resistance, 2,4-DAPG: 2,4-diacetylphloroglucinol, HCN: hydrogen cyanide, ROS: reactive oxygen species, SOD: superoxide dismutase, CAT: catalase, POD: peroxidase, EPS: exopolysaccharides, APase: acid or alkaline phosphatase.

Direct effects improve the plant's internal status via biological nitrogen fixation, phosphate solubilization, mineralization of organic matter, siderophore-mediated iron acquisition, and production of growth regulators and ACC deaminase that modulate ethylene (Gamalero et al., 2023). In practice, there is numerous evidence that PGPR enhance root system architecture by promoting lateral root formation and root hair development, which increases the root surface area available for absorption. As a result, plants exhibit improved uptake of essential nutrients such as nitrogen, phosphorus, and

iron, along with better water acquisition and retention under variable environmental conditions. Collectively, these effects translate into greater resource-use efficiency, enabling plants to achieve higher productivity with reduced input requirements (Lee et al., 2025). On the other hand, biopesticides and biological control agents act indirectly by modifying the rhizosphere environment—limiting pathogens through niche exclusion, hydrolyzing harmful molecules, producing enzymes targeting fungal cell walls, synthesizing hydrogen cyanide (HCN), and promoting beneficial symbioses with rhizobacteria and/or mycorrhizae; they also

contribute to insect or pathogen control (Chauhan et al., 2015; Santoyo et al., 2021). These indirect effects are consistent with the activation of Induced Systemic Resistance (ISR), inducing the immune system without causing disease symptoms (Mazuecos-Aguilera et al., 2025). Through ISR, plants respond more rapidly and effectively to subsequent pathogen attacks, resulting in lower pathogen pressure across the crop cycle. Consequently, these mechanisms contribute to reduced dependence on chemical pesticides in well-managed systems, promoting safer and more sustainable agricultural practices.

PGPR can impact productivity continuously because most of their life cycle remains associated with the rhizosphere (Helal et al., 2022). Consequently, several commercial PGPR products are available, including strains of *Agrobacterium*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Burkholderia*, *Delftia*, *Paenibacillus* macerans, *Pantoea* agglomerans, *Pseudomonas*, *Serratia*, *Rhizobium*, *Bradyrhizobium*, and mycorrhizae (Alzate et al., 2024). They are present in common formulations including peat-based inoculants, liquid suspensions, and polymer-encapsulated carriers, each designed to maintain microbial viability and facilitate application to seeds, soil, or nutrient solutions. However, due to the biological nature of this relationship, the field performance of these bioinoculants can vary significantly depending on soil physicochemical properties, climatic conditions, crop genotype, and agronomic management (Fadiji et al., 2024). Therefore, local validation and adaptation are essential to ensure consistency, efficacy, and compatibility within specific agricultural systems.

Other applications of PGPR use include: improved heavy-metal removal and growth of *Agrostis capillaris* with phytoremediation potential (Robas et al., 2021); IAA production, phosphorus solubilization, siderophore production, and antifungal activity by *Bacillus* spp. in wheat (*Triticum aestivum*), maize (*Zea mays*) and peanut (*Arachis hypogaea*) (Zhang et al., 2025) intercropping systems; enhanced oil removal of soils cultivated with *Festuca arundinacea* with the presence of a bacterial community composed by a proteobacteria and bacteroides consortium (Lee et al., 2022); P solubilization/mobilization by *Bacillus cereus* in soybean greenhouse cultivation, significantly improving nodulation and nitrogen fixation rate (Joshi et al., 2023); zinc-solubilization by PGPR such as *Priestia megaterium*, *Staphylococcus succinus*, and *Bacillus cereus* participate in nutrient

acquisition, enhancement of growth, yield, and oil content of canola (Jalal-Ud-Din et al., 2024). Also, the use of *Pseudomonas* strains as inoculants for biocontrol, fertilization, and phytostimulation has also been investigated and has become an alternative to reduce pesticide and fertilizer inputs in peanut (Bigatton et al., 2024);

In the rhizosphere of *Curcuma longa*, diverse strains of *Bacillus*, *Burkholderia thailandensis*, *Agrobacterium tumefaciens*, *Klebsiella*, *Pseudomonas*, and *Azotobacter* have been evaluated, demonstrating growth-promoting activity, salt tolerance, antibiotic sensitivity, and antimicrobial properties (Khan et al., 2023). These cases highlight that environmental and management context including soil salinity, contaminant levels, and cultivation conditions strongly influences the extent and consistency of plant responses to PGPR inoculation. Thus, variations in these factors can alter microbial survival, root colonization, and metabolite activity, ultimately shaping the magnitude of agronomic benefits observed under different production systems.

The agricultural potential of PGPR is related to the indirect regulation of physiological processes via nutritional balance and hormone modulation, increasing growth-regulator production and nutrient solubilization (Berg et al., 2023). Of particular interest is the flowering process, which is controlled by an evolutionarily conserved genetic network with direct consequences for crop productivity (Hidalgo et al., 2022). Besides, PGPR-mediated modulation of hormonal signaling involving auxin and ethylene, can influence key developmental stages such as flowering, fruit initiation, and maturation (Sharma et al., 2025). By adjusting hormone balance, PGPR may accelerate or delay these processes, leading to measurable effects on yield components like grain number, fruit set, or biomass accumulation, with outcomes that vary according to the crop species and growth conditions.

PGPR also display synergistic and antagonistic interactions with other microorganisms, which is critical for sustainable agriculture (Singh et al., 2023). They can induce resistance against pathogens or associate with other beneficial organisms. A notable synergy occurs with mycorrhizae, fungal organisms that enhance P and other nutrient uptake with substantial effects on plant growth and development (Hidalgo et al., 2024). Indeed, coinoculation of mycorrhizae with PGPR such as *Rhizobium* can increase plant productivity and improve food quality (Hidalgo Rodríguez et al., 2019). These

findings support the development of synthetic microbial consortia combining PGPR, arbuscular mycorrhizal fungi (AMF), and complementary bacterial species to enhance plant growth and resilience. Such multispecies inoculants can provide synergistic benefits, improving nutrient acquisition, stress tolerance, and disease suppression, while increasing the stability and consistency of performance across variable environmental and soil conditions (Zeng et al., 2025).

Moreover, embedding Plant Growth-Promoting Rhizobacteria (PGPR) within climate-smart and precision agriculture frameworks offers a synergistic strategy to enhance productivity while minimizing environmental impact (Zhang et al., 2025). By integrating PGPR inoculants with data-driven irrigation, nutrient management, and soil monitoring systems, farmers can reduce reliance on chemical fertilizers and pesticides, stabilize yields under variable climatic conditions, and improve soil structure and fertility over time (Khawula et al., 2025). This alignment not only promotes resource efficiency and carbon sequestration, but also contributes to the resilience of agroecosystems, advancing the transition toward sustainable and climate-adaptive global food systems (Grover et al., 2021).

Despite the extensive evidence supporting the beneficial effects of PGPR, several knowledge gaps and methodological limitations remain. One of the most common problems are the inconsistencies observed among laboratory or greenhouse results and field-scale outcomes, largely due to uncontrolled environmental variables, soil heterogeneity, and plant genotype differences. Also, many studies rely on single-strain inoculants or simplified conditions that do not fully represent the complexity of the rhizosphere microbiome, leading to limited reproducibility and variable efficacy under real agricultural settings. Another limitation is the dependence of PGPR performance on environmental factors such as soil physicochemical properties, nutrient availability, and competition with native microbial communities, which may outcompete introduced strains. Moreover, large-scale commercialization is constrained by challenges in strain formulation stability, shelf life, and delivery methods, as well as by the absence of harmonized biosafety and regulatory frameworks for microbial biofertilizers. Addressing these limitations through multi-omics-guided field validation, ecological modeling, and standardized biosafety guidelines is essential to fill the gap

between experimental research and the sustainable agricultural implementation

CONCLUSIONS

Plant Growth-Promoting Rhizobacteria (PGPR) utilization represents a promising and sustainable alternative to improve agricultural productivity while reducing dependence on chemical fertilizers and pesticides. The evidence reviewed highlights their ability to enhance plant growth, nutrient acquisition, and stress tolerance through direct mechanisms such as nitrogen fixation, phosphate solubilization, and phytohormone modulation, as well as indirect mechanisms that include induced systemic resistance, antioxidant regulation, and pathogen suppression; providing ecological benefits to processes such as soil aggregation, nutrient cycling, and phytoremediation, long-term soil health support and ecosystem restoration.

Despite these benefits, field-scale applications remain inconsistent due to environmental variability, soil physicochemical constraints, and competition with native microbiota. Successful PGPR implementation requires selecting context-adapted strains, improving formulation stability, and developing delivery systems suited to local agroecosystems. Thus, integrating multi-omics and machine learning approaches will be essential to predict PGPR functions, identify metabolic signatures linked to plant-microbe communication, and design synthetic microbial consortia tailored to specific crops or soil conditions. Furthermore, embedding PGPR technologies within climate-smart and precision agriculture frameworks can enhance resilience to drought, salinity, and heat stress.

Finally, the growing commercialization of PGPR-based bioinoculants highlights the need for clear regulatory guidelines to ensure biosafety, quality control, and efficacy under diverse field conditions. Continued interdisciplinary research, combined with policy support and technology transfer to farmers, will be key to translating PGPR potential into practical solutions that promote climate-resilient, productive, and sustainable agriculture that provides food security.

AUTHORS CONTRIBUTIONS

P.L.-A.: conceptualization, collection of the information; M.L.-E. and C.R.: data curation, writing-original draft preparation; E.L.-L. and C.B.-V.: visualization, investigation; P.C.-M.: supervision; M.H. and P.A.: software, writing—reviewing and editing. All authors have read

and agreed to the published version of the manuscript.

FUNDING

This research received no external funding.

CONFLICTS OF INTEREST

The authors declare no conflict of interest.

USE OF AI AND AI-ASSISTED TECHNOLOGIES

During the preparation of this work, the authors used ChatGPT to correct spelling mistakes and verify the reference formatting. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

REFERENCES

- Al-Turki, A., Murali, M., Omar, A. F., Rehan, M. and Sayyed, R. Z. (2023). Recent advances in PGPR-mediated resilience toward interactive effects of drought and salt stress in plants. *Front. Microbiol.* **14**: 1214845. <https://doi.org/10.3389/fmicb.2023.1214845>.
- Alzate Zuluaga, M. Y., Fattorini, R., Cesco, S. and Pii, Y. (2024). Plant-microbe interactions in the rhizosphere for smarter and more sustainable crop fertilization: The case of PGPR-based biofertilizers. *Front. Microbiol.* **15**: 1440978. <https://doi.org/10.3389/fmicb.2024.1440978>.
- Argentel-Martínez, L., Peñuelas-Rubio, O., Herrera-Sepúlveda, A., González-Aguilera, J., Sudheer, S., Salim, L. M., Lal, S., Pradeep, C. K., Ortiz, A., Sansinenea, E., Hathurusinghe, S. H. K., Shin, J. H., Babalola, O. O. and Azizoglu, U. (2024). Biotechnological advances in plant growth-promoting rhizobacteria for sustainable agriculture. *World J. Microbiol. Biotechnol.* **41**(1): 21. <https://doi.org/10.1007/s11274-024-04231-4>.
- Azizoglu, U., Yilmaz, N., Simsek, O., Ibal, J. C., Tagele, S. B. and Shin, J. H. (2021). The fate of plant growth-promoting rhizobacteria in soilless agriculture: Future perspectives. *3 Biotech* **11**(8): 382. <https://doi.org/10.1007/s13205-021-02941-2>.
- Badri, K., Sharifi, R. and Hosseini, S. (2025). Effectiveness of defense-inducing volatile compounds against *Xanthomonas translucens*, bacterial leaf streak pathogen of wheat. *Physiol. Mol. Plant Pathol.* **139**: 102738. <https://doi.org/10.1016/j.pmpp.2025.102738>.
- Bauer, J. T., Koziol, L. and Bever, J. D. (2020). Local adaptation of mycorrhizae communities changes plant community composition and increases aboveground productivity. *Oecologia* **192**(3): 735–744. <https://doi.org/10.1007/s00442-020-04598-9>.
- Berg, G., Schweitzer, M. and Abdelfattah, A. (2023). Missing symbionts—emerging pathogens? Microbiome management for sustainable agriculture. *Symbiosis* **89**: 163–171. <https://doi.org/10.1007/s13199-023-00903-1>.
- Bettenfeld, P., Cadena, I., Canals, J., Jacquens, L., Fernandez, O., Fontaine, F., van Schaik, E., Courty, P.-E. and Trouvelot, S. (2022). The microbiota of the grapevine holobiont: A key component of plant health. *J. Adv. Res.* **40**: 1–15. <https://doi.org/10.1016/j.jare.2021.12.008>.
- Bigatton, E. D., Verdenelli, R. A., Haro, R. J., Ayoub, I., Barbero, F. M., Martín, M. P., Dubini, L. E., Jorrín Novo, J. V., Lucini, E. I. and Castillejo, M. Á. (2024). Metagenomic analysis to assess the impact of plant growth-promoting rhizobacteria on peanut (*Arachis hypogaea* L.) crop production and soil enzymes and microbial diversity. *J. Agric. Food Chem.* **72**(40): 22385–22397. <https://doi.org/10.1021/acs.jafc.4c05687>.
- Chauhan, H., Bagyaraj, D. J., Selvakumar, G. and Sundaram, S. P. (2015). Novel plant growth promoting rhizobacteria—Prospects and potential. *Appl. Soil Ecol.* **95**: 38–53. <https://doi.org/10.1016/j.apsoil.2015.05.011>.
- Chen, A.-Q., Long, Z.-Q., Xiao, Y., Feng, Y.-M., Zhou, Y., Yang, S., Liao, Y.-M., Zhou, X., Liu, L.-W., Wu, Z.-B. and Yang, S. (2024). Application of natural product-based quorum sensing inhibitors in plant pathogen control: A review. *Arab. J. Chem.* **18**: 106050. <https://doi.org/10.1016/j.arabjc.2024.106050>.
- Copeland, C., Schulze-Lefert, P. and Ma, K. W. (2025). Potential and challenges for application of microbiomes in agriculture. *Plant Cell* **37**(8): koaf185. <https://doi.org/10.1093/plcell/koaf185>.
- Deb, C. R. and Tatung, M. (2024). Siderophore producing bacteria as biocontrol agent against phytopathogens for a better environment: A review. *S. Afr. J. Bot.* **165**: 153–162. <https://doi.org/10.1016/j.sajb.2023.12.031>.
- Du, J., Gao, Q., Sun, F., Liu, B., Jiao, Y. and Liu, Q. (2025). Agricultural soil microbiomes at the climate frontier: Nutrient-mediated adaptation strategies for sustainable farming. *Ecotoxicol. Environ. Saf.* **295**: 118161. <https://doi.org/10.1016/j.ecoenv.2025.118161>.
- Dutta, P., Muthukrishnan, G., Gopalasubramaniam, S. K., Dharmaraj, R., Karuppaiah, A., Loganathan, K., Periyasamy, K., Pillai, M. A., Upamanya, G. K., Boruah, S., Deb, L., Kumari, A., Mahanta, M., Heisnam, P. and Mishra, A. K. (2022). Plant growth-promoting rhizobacteria (PGPR) and

- its mechanisms against plant diseases for sustainable agriculture and better productivity. *Biocell* **46**(8): 1843–1859. <https://doi.org/10.32604/biocell.2022.019291>.
- Ehinmitan, E., Losenge, T., Mamati, E., Ngumi, V., Juma, P. and Siamalube, B. (2024). BioSolutions for green agriculture: Unveiling the diverse roles of plant growth-promoting rhizobacteria. *Int. J. Microbiol.* 2024: 6181491. <https://doi.org/10.1155/2024/6181491>.
- Fadiji, A. E., Xiong, C., Egidi, E. and Singh, B. K. (2024). Formulation challenges associated with microbial biofertilizers in sustainable agriculture and paths forward. *J. Sustain. Agric. Environ.* **3**(4): e70006. <https://doi.org/10.1002/sae2.70006>.
- Fan, D. and Smith, D. L. (2021). Characterization of selected plant growth-promoting rhizobacteria and their non-host growth promotion effects. *Microbiol. Spectr.* **9**(2): e00279-21. <https://doi.org/10.1128/spectrum.00279-21>.
- Ferreira, J. P., Vidal, M. S. and Baldani, J. I. (2025). Exploring ACC deaminase-producing bacteria for drought stress mitigation in Brachiaria. *Front. Plant Sci.* **16**: 1607697. <https://doi.org/10.3389/fpls.2025.1607697>.
- Gamalero, E., Lingua, G. and Glick, B. R. (2023). Ethylene, ACC, and the plant growth-promoting enzyme ACC deaminase. *Biology* **12**(8): 1043. <https://doi.org/10.3390/biology12081043>.
- Grover, M., Bodhankar, S., Sharma, A., Sharma, P., Singh, J. and Nain, L. (2021). PGPR mediated alterations in root traits: Way toward sustainable crop production. *Front. Sustain. Food Syst.* **4**: 618230. <https://doi.org/10.3389/fsufs.2020.618230>.
- Grzyb, T. and Szulc, J. (2024). Deciphering molecular mechanisms and diversity of plant holobiont bacteria: Microhabitats, community ecology, and nutrient acquisition. *Int. J. Mol. Sci.* **25**(24): 13601. <https://doi.org/10.3390/ijms252413601>.
- Han, K., Li, Y., Zhang, Z., Sun, L., Wang, E. T. and Li, Y. (2023). Comparative genome analysis of *Sesbania cannabina*-nodulating *Rhizobium* spp. revealing the symbiotic and transferrable characteristics of symbiosis plasmids. *Microb. Genom.* **9**(5): e001004. <https://doi.org/10.1099/mgen.0.001004>.
- Hanif, M. S., Tayyab, M., Baillo, E. H., Islam, M. M., Islam, W. and Li, X. (2024). Plant microbiome technology for sustainable agriculture. *Front. Microbiol.* **15**: 1500260. <https://doi.org/10.3389/fmicb.2024.1500260>.
- Hassani, M. A., Durán, P. and Hacquard, S. (2018). Microbial interactions within the plant holobiont. *Microbiome* **6**: 1–17. <https://doi.org/10.1186/s40168-018-0445-0>.
- Helal, D. S., El-Khawas, H. and Elsayed, T. R. (2022). Molecular characterization of endophytic and ectophytic plant growth promoting bacteria isolated from tomato plants (*Solanum lycopersicum* L.) grown in different soil types. *J. Genet. Eng. Biotechnol.* **20**(1): 79. <https://doi.org/10.1186/s43141-022-00361-0>.
- Hidalgo Rodríguez, J. E. M., Ramos Otiniano, C. C., Lezama Asencio, P. B., Chuna Mogollón, P. and Chaman Medina, M. E. (2019). Coinoculación de *Rhizophagus irregularis* y *Rhizobium* sp. en *Phaseolus vulgaris* L. var. canario (Fabaceae) “frijol canario”. *Arnaldoa* **26**(3): 991–1006. <https://doi.org/10.22497/arnaldoa.263.26309>.
- Hidalgo, M., Ramos, C., Luis-Alaya, B., Vera-Vega, M., Linares-Huapaya, S., Pedro, J., Lezama-Asencio, P. and Chaman, M. (2024). *Rhizophagus irregularis* y la fertilización con P inducen el crecimiento de Carica papaya después de la fase de aclimatación. *Cienc. Tecnol. Agropecu.* **25**(1). https://doi.org/10.21930/rcta.vol25_num1_art:3371.
- Hidalgo, M., Ramos, C., Vázquez-Regalado, J. and Zolla, G. (2022). Closing the gap in the “ABC” model in legumes: A review. *Legume Res.* **45**(12): 1465–1475. <https://doi.org/10.18805/LRF-694>.
- Imchen, M., Anju, V. T., Busi, S., Mohan, M. S., Subhaswaraj, P., Dyavaiah, M. and Kumavath, R. (2022). Metagenomic insights into taxonomic, functional diversity and inhibitors of microbial biofilms. *Microbiol. Res.* **265**: 127207. <https://doi.org/10.1016/j.micres.2022.127207>.
- Iqbal, M. Z., Singh, K. and Chandra, R. (2024). Recent advances of plant growth promoting rhizobacteria (PGPR) for eco-restoration of polluted soil. *Clean. Eng. Technol.* **23**: 100845. <https://doi.org/10.1016/j.clet.2024.100845>.
- Jacobson, R., Castonguay, C. and Elias, M. H. (2025). Durable formulations of quorum quenching enzymes. *Sci. Rep.* **15**: 27435. <https://doi.org/10.1038/s41598-025-12623-1>.
- Jalal-Ud-Din, S., Elahi, N. N. and Mubeen, F. (2024). Significance of zinc-solubilizing plant growth-promoting rhizobacterial strains in nutrient acquisition, enhancement of growth, yield, and oil content of canola (*Brassica napus* L.). *Front. Microbiol.* **15**: 1446064. <https://doi.org/10.3389/fmicb.2024.1446064>.
- Jansson, J. K. and Hofmockel, K. S. (2018). The soil microbiome—From metagenomics to metaphenomics. *Curr. Opin. Microbiol.* **43**: 162–168. <https://doi.org/10.1016/j.mib.2018.01.013>.
- Joshi, S., Gangola, S., Jaggi, V. and Sahgal, M. (2023). Functional characterization and molecular fingerprinting of potential phosphate solubilizing bacterial candidates from

- Shisham rhizosphere. *Sci. Rep.* **13**: 7003. <https://doi.org/10.1038/s41598-023-33217-9>.
- Khan, S., Ambika, R., Rani, K., Sharma, S., Kumar, A., Singh, S., Thapliyal, M., Rawat, P., Thakur, A., Pandey, S., Thapliyal, A., Pal, M. and Singh, Y. (2023). Rhizobacterial mediated interactions in *Curcuma longa* for plant growth and enhanced crop productivity: A systematic review. *Front. Plant Sci.* **14**: 1231676. <https://doi.org/10.3389/fpls.2023.1231676>.
- Khawula, S., Daniel, A. I., Nyawo, N., Ndlazi, K., Sibiya, S., Ntshalintshali, S., Nzuza, G., Gokul, A., Keyster, M., Klein, A., Niekerk, L.-A. and Nkomo, M. (2025). Optimizing plant resilience with growth-promoting rhizobacteria under abiotic and biotic stress conditions. *Plant Stress* **17**: 100949. <https://doi.org/10.1016/j.stress.2025.100949>.
- Kifle, B. A., Sime, A. M., Gemed, M.T. and Woldeamayrat, A. A. (2024). Shotgun metagenomic insights into secondary metabolite biosynthetic gene clusters reveal taxonomic and functional profiles of microbiomes in natural farmland soil. *Sci. Rep.* **14**: 15096. <https://doi.org/10.1038/s41598-024-63254-x>.
- Koskey, G., Mburu, S. W., Kimiti, J. M., Ombori, O., Maingi, J. M., Njeru, E. M. (2018). Genetic Characterization and Diversity of Rhizobium Isolated From Root Nodules of Mid-Altitude Climbing Bean (*Phaseolus vulgaris* L.) Varieties. *Front. Microbiol.* **15**(9): 968. <https://doi.org/10.3389/fmicb.2018.00968>.
- Kurt, P. O. (2025). Field-based evaluation of multi-strain PGPR to improve Zea mays yield and soil nutrient dynamics in semi-arid of Türkiye. *Sci. Rep.* **15**: 22553. <https://doi.org/10.1038/s41598-025-07643-w>.
- Lazarus, H. P. S. and Easwaran, N. (2024). Molecular insights into PGPR fluorescent Pseudomonads complex mediated intercellular and interkingdom signal transduction mechanisms in promoting plant's immunity. *Res. Microbiol.* **175**(7): 104218. <https://doi.org/10.1016/j.resmic.2024.104218>.
- Lee, S., Kim, Y. K., Nie, H., Ahn, J., Kim, N., Ko, S. R., Choi, A. H., Kwon, H., Peng, Y., Kwon, S. Y. and Shin, A. Y. (2025). Functional characterization of a novel plant growth-promoting rhizobacterium enhancing root growth and salt stress tolerance. *Sci. Rep.* **15**: 30405. <https://doi.org/10.1038/s41598-025-14065-1>.
- Lee, Y. Y., Lee, S. Y., Lee, S. D. and Cho, K. S. (2022). Seasonal dynamics of bacterial community structure in diesel oil-contaminated soil cultivated with tall fescue (*Festuca arundinacea*). *Int. J. Environ. Res. Public Health* **19**(8): 4629. <https://doi.org/10.3390/ijerph19084629>.
- Lyu, D., Msimbira, L. A., Nazari, M., Antar, M., Pagé, A., Shah, A., Monjezi, N., Zajonc, J., Tanney, C. A. S., Backer, R. and Smith, D. L. (2021). The coevolution of plants and microbes underpins sustainable agriculture. *Microorganisms* **9**(5): 1036. <https://doi.org/10.3390/microorganisms9051036>.
- Mashabela, M. D., Piater, L. A., Dubery, I. A., Tugizimana, F. and Mhlongo, M. I. (2022). Rhizosphere tripartite interactions and PGPR-mediated metabolic reprogramming towards ISR and plant priming: A metabolomics review. *Biology* **11**(3): 346. <https://doi.org/10.3390/biology11030346>.
- Mazuecos-Aguilera, I., Anta-Fernández, F., Crespo-Barreiro, A., Martínez-Quesada, A., Lombana-Larrea, L. and González-Andrés, F. (2025). Plant growth-promoting rhizobacteria enhanced induced systemic resistance of tomato against Botrytis cinerea phytopathogen. *Front. Plant Sci.* **16**: 1570986. <https://doi.org/10.3389/fpls.2025.1570986>.
- Meena, R. S., Kumar, S., Datta, R., Lal, R., Vijayakumar, V., Brtnicky, M. and Marfo, T. D. (2020). Impact of agrochemicals on soil microbiota and management: A review. *Land* **9**(2): 34. <https://doi.org/10.3390/land9020034>.
- Mesny, F., Bauer, M., Zhu, J. and Thomma, B. P. H. J. (2024). Meddling with the microbiota: Fungal tricks to infect plant hosts. *Curr. Opin. Plant Biol.* **82**: 102622. <https://doi.org/10.1016/j.pbi.2024.102622>.
- Mhlongo, M. I., Piater, L. A., Madala, N. E., Labuschagne, N. and Dubery, I. A. (2018). The chemistry of plant-microbe interactions in the rhizosphere and the potential for metabolomics to reveal signaling related to defense priming and induced systemic resistance. *Front. Plant Sci.* **9**: 112. <https://doi.org/10.3389/fpls.2018.00112>.
- Mhlongo, M. I., Piater, L. A., Steenkamp, P. A., Labuschagne, N. and Dubery, I. A. (2020). Metabolic profiling of PGPR-treated tomato plants reveal priming-related adaptations of secondary metabolites and aromatic amino acids. *Metabolites* **10**(5): 210. <https://doi.org/10.3390/metabo10050210>.
- Mohamed, Y. (2020). Impact of some growth stimulants in cooperation with arbuscular mycorrhizal fungi on growth, productivity and chemical constituents of Dutch fennel plant. *Sci. J. Flowers Ornam. Plants* **7**(3): 303–319. <https://doi.org/10.21608/sjforp.2020.114567>.
- Palermo, J. S., Palermo, T. B., Cappellari, L. D. R., Balcke, G. U., Tissier, A., Giordano, W. and Banchio, E. (2025). Influence of plant growth-promoting rhizobacteria (PGPR) inoculation on phenolic content and key biosynthesis-related processes in *Ocimum basilicum* under Spodoptera frugiperda herbivory. *Plants* **14**(6): 857. <https://doi.org/10.3390/plants14060857>.
- Pang, Z., Chen, J., Wang, T., Gao, C., Li, Z., Guo, L., Xu, J. and Cheng, Y. (2021). Linking plant secondary metabolites and plant

- microbiomes: A review. *Front. Plant Sci.* **12**: 621276. <https://doi.org/10.3389/fpls.2021.621276>.
- Park, I., Seo, Y. S. and Mannaa, M. (2023). Recruitment of the rhizo-microbiome army: Assembly determinants and engineering of the rhizosphere microbiome as a key to unlocking plant potential. *Front. Microbiol.* **14**: 1163832. <https://doi.org/10.3389/fmicb.2023.1163832>.
- Paulitsch, F., Delamuta, J. R. M., Ribeiro, R. A., da Silva Batista, J. S. and Hungria, M. (2020). Phylogeny of symbiotic genes reveals symbiovars within legume-nodulating Paraburkholderia species. *Syst. Appl. Microbiol.* **43**(6): 126151. <https://doi.org/10.1016/j.syapm.2020.126151>.
- Robas, M., Jiménez, P. A., González, D. and Probanza, A. (2021). Bio-mercury remediation suitability index: A novel proposal that compiles the PGPR features of bacterial strains and its potential use in phytoremediation. *Int. J. Environ. Res. Public Health* **18**(8): 4213. <https://doi.org/10.3390/ijerph18084213>.
- Sahil, R., Pal, V., Kharat, A. S. and Jain, M. (2025). A multi-omics meta-analysis of rhizosphere microbiome reveals growth-promoting marker bacteria at different stages of legume development. *Plant Cell Environ.* <https://doi.org/10.1111/pce.15429>.
- Santoyo, G., Urtis-Flores, C. A., Loeza-Lara, P. D., Orozco-Mosqueda, M. D. C. and Glick, B. R. (2021). Rhizosphere colonization determinants by plant growth-promoting rhizobacteria (PGPR). *Biology* **10**(6): 475. <https://doi.org/10.3390/biology10060475>.
- Seabloom, E. W., Caldeira, M. C., Davies, K. F.; et al. (2023). Globally consistent response of plant microbiome diversity across hosts and continents to soil nutrients and herbivores. *Nat. Commun.* **14**: 3516. <https://doi.org/10.1038/s41467-023-39179-w>.
- Sharma, N., Mahawar, L., Mishra, A. and Albrechtsen, B. R. (2025). Microbial contributions to plant growth and stress tolerance: Mechanisms for sustainable plant production. *Plant Stress* **17**: 100966. <https://doi.org/10.1016/j.stress.2025.100966>.
- Sibanyoni, N. R., Piater, L. A., Kerchev, P., Madala, N. E. and Mhlongo, M. I. (2025). Metabolomic insights into cross-feeding interactions between *Priestia megaterium* PM and *Pseudomonas fluorescens* NO4: Unveiling microbial communication in plant growth-promoting rhizobacteria. *Microb. Ecol.* **88**(1): 76. <https://doi.org/10.1007/s00248-025-02577-2>.
- Singh, A., Yadav, V. K., Chundawat, R. S., Soltane, R., Awwad, N. S., Ibrahim, H. A., Yadav, K. K. and Vicas, S. I. (2023). Enhancing plant growth-promoting rhizobacterial activities through consortium exposure: A review. *Front. Bioeng. Biotechnol.* **11**: 1099999. <https://doi.org/10.3389/fbioe.2023.1099999>.
- Singh, B. K., Hu, H.-W., Macdonald, C. A. and Xiong, C. (2025). Microbiome-facilitated plant nutrient acquisition. *Cell Host Microbe* **33**(6): 869–881. <https://doi.org/10.1016/j.chom.2025.05.005>.
- Singh, S. and Ramakrishna, W. (2021). Application of CRISPR-Cas9 in plant–plant growth-promoting rhizobacteria interactions for next Green Revolution. *3 Biotech* **11**(12): 492. <https://doi.org/10.1007/s13205-021-03041-x>.
- Soto-Aceves, M. P., Diggle, S. P. and Greenberg, E. P. (2023). Microbial primer: LuxR-LuxI quorum sensing. *Microbiology* **169**(9): 001343. <https://doi.org/10.1099/mic.0.001343>.
- Tharanath, A. C., Upendra, R. S. and Rajendra, K. (2024). Soil symphony: A comprehensive overview of plant–microbe interactions in agricultural systems. *Appl. Microbiol.* **4**(4): 1549–1567. <https://doi.org/10.3390/applmicrobiol4040106>.
- Upadhyay, S. K., Rajput, V. D., Kumari, A., Espinosa-Saiz, D., Menendez, E., Minkina, T., Dwivedi, P. and Mandzhieva, S. (2023). Plant growth-promoting rhizobacteria: A potential bio-asset for restoration of degraded soil and crop productivity with sustainable emerging techniques. *Environ. Geochem. Health* **45**(12): 9321–9344. <https://doi.org/10.1007/s10653-022-01433-3>.
- Verma, K. K., Joshi, A., Song, X.-P., Liang, Q., Xu, L., Huang, H.-r., Wu, K.-C., Seth, C. S., Arora, J. and Li, Y.-R. (2024). Regulatory mechanisms of plant rhizobacteria on plants to the adaptation of adverse agroclimatic variables. *Front. Plant Sci.* **15**: 1377793. <https://doi.org/10.3389/fpls.2024.1377793>.
- Yusuf, A., Li, M., Zhang, S.-Y., Odedishemi-Ajibade, F., Luo, R.-F., Wu, Y.-X., Zhang, T.-T., Yunusa Ugya, A., Zhang, Y. and Duan, S. (2025). Harnessing plant–microbe interactions: Strategies for enhancing resilience and nutrient acquisition for sustainable agriculture. *Front. Plant Sci.* **16**: 1503730. <https://doi.org/10.3389/fpls.2025.1503730>.
- Zeng, W., Xiang, D., Li, X., Gao, Q., Chen, Y., Wang, K., Qian, Y., Wang, L., Li, J., Mi, Q., Huang, H., Xu, L., Zhao, M., Zhang, Y. and Xiang, H. (2025). Effects of combined inoculation of arbuscular mycorrhizal fungi and plant growth-promoting rhizosphere bacteria on seedling growth and rhizosphere microecology. *Front. Microbiol.* **15**: 1475485. <https://doi.org/10.3389/fmicb.2024.1475485>.
- Zhang, S., Li, F., Chang, L., Zhang, Q., Zhang, Z., Wu, T., Wu, Y., Wang, Z., Su, Y., Yang, X., Gao, W., Li, M., Wu, Y. and Jiang, Y. (2025). Broad-spectrum applications of plant growth-promoting rhizobacteria (PGPR) across diverse crops and intricate planting

- systems. *Microbiol. Spectr.* **13**(3): e01879-24. <https://doi.org/10.1128/spectrum.01879-24>.
- Zhao, S., Li, M., Ren, X., Wang, C., Sun, X., Sun, M., Yu, X. and Wang, X. (2024). Enhancement of broad-spectrum disease resistance in wheat through key genes involved in systemic acquired resistance. *Front. Plant Sci.* **15**: 1355178. <https://doi.org/10.3389/fpls.2024.1355178>.
- Zhao, T., Jia, X., Liu, X., Nepal, J., Guyoneaud, R., Treder, K., Pawłowska, A., Michałowska, D., Berg, G., Stocker, F. and Cernava, T. (2025). Harnessing microbiome-plant synergies: Microbiome-interactive traits enhance plant growth and support sustainable agriculture. *NPJ Sustain. Agric.* **3**: 50. <https://doi.org/10.1038/s44264-025-00093-x>.
- Zhou, Z., Hu, R., Ni, Y., Zhuang, W., Luo, Z., Huang, W., Yan, Q., He, Z., Zhong, Q. and Wang, C. (2021). Genetic elucidation of quorum sensing and cobamide biosynthesis in divergent bacterial-fungal associations across the soil-mangrove root interface. *Front. Microbiol.* **12**: 698385. <https://doi.org/10.3389/fmicb.2021.698385>.