

Review

Microbial contributions to plant growth and stress tolerance: Mechanisms for sustainable plant production

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ABSTRACT

Plant growth-promoting rhizobacteria (PGPRs) play a crucial role in enhancing plant development through a variety of direct and indirect mechanisms. These include the production of phytohormones, nitrogen fixation, phosphate solubilization, siderophore-mediated iron acquisition, and biocontrol of plant pathogens. Predominantly inhabiting the rhizosphere, PGPRs interact with plant roots via complex molecular and ecological processes involving signalling molecules, metabolite exchanges, and modulation of plant immune responses. Such interactions enhance nutrient uptake and stress tolerance but also contribute to long-term plant health and productivity across diverse environmental conditions. This review focuses on the genera *Pseudomonas* and *Bacillus*, which are extensively studied for their strong colonization abilities, metabolic versatility, and demonstrated potential in improving crop resilience. Advances in microbial genomics, metagenomics, and high-throughput phenotyping have greatly enhanced our ability to identify, characterize, and apply beneficial microbes across a range of crop systems. However, key challenges remain, including limited understanding of native soil microbiotas, the functional outcome of microbiome-soil-plant interactions, and the development of agricultural practices that efficiently integrate microbial solutions. With potato (*Solanum tuberosum*) as a model crop, this review synthesizes current knowledge on PGRP-mediated growth promotion - primarily by *Pseudomonas* and *Bacillus* acting alone or in microbial consortia, identifies critical research gaps, and outlines future directions for the application of PGPRs in sustainable crop production.

1. Introduction

The plant microbiome possesses a wealth of associations, of which many are still unknown to science. However, it is becoming more and more clear that the microbiome is a stepping stone for human exploitation of natural resources in the service of plant health and development (Naik et al., 2019). *Agrobacterium* is a well-established example of a microorganism capable of manipulating plant genetic structures to the extent, that it has become a cornerstone in molecular plant research. In transgenic plant transformation, multiple strains derived from the tumor-inducing (Ti) plasmids of *Agrobacterium tumefaciens* and the root-inducing (Ri) plasmids of *Agrobacterium rhizogenes* are widely used. These strains are engineered by first removing pathogenic genes from the plasmids, and then using the plasmids' machinery to transfer target DNA into plants (Gelvin, 2003). Another example is *Bacillus thuringiensis*

a bacterium known for producing crystalline proteins (Cry proteins or Bt toxins), that are toxic to many insect pests. Bt has been applied as pest control, either as a microbial pesticide or through genetically modified plants (like Bt corn or Bt cotton) that are engineered to express the Bt toxins (Azizoglu et al., 2023).

The engineered success stories are however relatively few, and a main problem is a lack of specific insight into the way plants sense and respond to the microorganisms that surround them. Beneficial microorganisms are especially cryptic and difficult to study, leaving our understanding of them particularly underdeveloped (Omomowo and Babalola, 2019; Lyu et al. 2021). However, it is well established that mutualism plays a crucial role in helping plants survive and thrive under adverse conditions. Due to their sessile nature, plants can only combat unfavorable conditions through metabolic responses and through collaboration with surrounding organisms. For instance, plant

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growth-promoting rhizobacteria (PGPR), mycorrhizal fungi, and bacterial and fungal endophytes establish mutually beneficial relationships with plants, improving soil nutrient availability, enhancing plant health, and increasing yields (Akinola and Babalola, 2021). These microbes also help mitigate various abiotic stresses, such as salinity, drought, extreme temperatures, heavy metal toxicity, and harmful ultraviolet radiation (Zhu et al., 2018; Zhang et al., 2019; Arkhipova et al., 2020; Ramasamy and Mahawar, 2023; Gouli et al., 2024; Tang et al., 2024). Additionally, they combat biotic stresses caused by pathogenic bacteria, fungi, viruses, and plant-consuming organisms like nematodes, arthropods, and vertebrate herbivores (Terra et al., 2023).

Microbial relationships that support plant growth have evolved over millions of years and are conserved in the fossil record. The sequence of unicellular colonization of terrestrial environments remains debated, and oxygen is now proposed to originate from terrestrial cyanobacteria (Strullu-Derrien, 2018; Lyu et al., 2021), that paved the way for plant growth promoting microorganisms and their coevolving vascular plants (Rensing, 2018; Delaux and Schornack, 2021; Mesny et al., 2023). Whereas the microbiota unquestionably played a critical role for the colonization of terrestrial environments, the supportive role of plant-associated microbiomes has sadly been overlooked in modern agriculture as farming practices became increasingly industrialized (Omomowo and Babalola, 2019; Lyu et al., 2021). As the chemical-intensive methods of the Green Revolution face mounting challenges, such as environmental degradation and declining effectiveness, microbial associations with crops are now being recognized as a promising and underexplored pathway for sustainable agriculture (Naik et al., 2019; Akinola and Babalola, 2021; Christel et al., 2021; Voccianti et al., 2022; Maitra et al., 2023).

Using potato (*Solanum tuberosum*) as a model, this review examines PGPR-mediated growth promotion, focusing on *Pseudomonas* and *Bacillus* as key taxa, both individually and in consortia. We highlight their potential as cornerstone bioinoculants for sustainable agriculture, emphasizing the advantages of microbial consortia in terms of functional diversity, resilience, and consistency. Integrated strategies - including bioformulation technologies, - are also discussed as pathways for advancing field application and research.

2. Plant-microbe interactions

Plant-microbe interactions encompass a wide spectrum of associations, ranging from loose epiphytic colonization on surfaces such as roots and leaves, to more intimate endophytic lifestyles within intercellular spaces and vascular tissues, and extending to the formation of specialized structures like nitrogen-fixing nodules, haustoria, and Hartig nets. These relationships can be mutualistic, antagonistic, or neutral. While neutral interactions do not directly impact plant health, they contribute to the diversity of the soil microbiome, which in turn helps buffer the effects of both mutualistic and pathogenic impacts (Buyer and Leong, 1986; Schulz and Boyle, 2005; Rensing, 2018; Contreras-Liza et al., 2022; Mesny et al., 2023). Indeed, a recent meta-analysis suggests that microbial diversity in soils provides a more stable and favorable growth environment than fertilizer application (Christel et al., 2021). The mechanisms by which each microbial community member support plant production are similarly diverse.

2.1. Growth promoting mechanisms

There are numerous examples of PGPR strains enhancing plant growth by regulating phytohormones, facilitating nutrient uptake, and improving stress tolerance.

2.1.1. Enhanced nutrient mobilization

Microbes assist plants in acquiring essential nutrients, particularly by fixing nitrogen, solubilizing phosphorus, and chelating iron (Pattnaik et al., 2021). These processes are driven by a broad spectrum of microbial

strategies, from highly specialized *Rhizobium* and *Bradyrhizobium* symbionts that form nodules with legumes to free-living nitrogen fixers without plant specificity (Flora et al., 2021; Goyal et al., 2024). Phosphate solubilization by for example *Pseudomonas*, *Bacillus*, and *Penicillium*, involve the release organic acids to mobilize insoluble phosphates (Sharma et al., 2013), and iron availability under limiting conditions is enhanced through siderophore-mediated iron chelation by *Pseudomonas* and *Azotobacter* (Saha et al., 2016).

Nitrogen-fixing rhizobacteria primarily belong to the class of *Alphaproteobacteria* including orders such as *Rhizobiales* and *Rhodospirillales*, but they can also be found among *Actinobacteria* (e.g. *Frankia*) (Koirala et al., 2021; Ramond et al., 2022). A defining feature of nitrogen-fixing bacteria is nitrogenase, a universal enzyme that converts inert dinitrogen (N_2) into bioavailable nitrogen (Bellenger et al., 2020). Although nitrogenase is structurally and functionally conserved across taxa, differences in metal cofactors (molybdenum, vanadium or iron) and mechanisms that protect the enzyme from oxygen inactivation reflect species-species ecological adaptations (Mus et al., 2019).

In contrast, arbuscular mycorrhizal fungi (AMF) belonging to *Glomeromycota* do not possess nitrogenase, but they still form symbioses that significantly enhance plant nutrient uptake. By expanding the root's absorptive surface area, AMF improve the mobilization of nutrients that are otherwise poorly accessible to the plant (e.g. phosphorous, zinc, magnesium, Kalik et al., 2022; Wahab et al., 2023). Besides expanding the root-fungal network and increase the uptake surface area, the changed root structure also facilitates recruitment and colonization by other nitrogen-fixing microbes (Lee et al., 2015).

2.1.2. Phytohormone biosynthesis and regulation

In addition to aiding nutrient acquisition, microorganisms possess a remarkable ability to influence and mimic the plant's internal metabolic processes (Bellenger et al., 2020). One of the most visually striking and well-studied examples of phytohormonal mediation by microbes is the formation of specialized host structures initiated by obligate symbionts. These structures arise through complex crosstalk between multiple plant hormone signaling pathways (Swapnil et al., 2023; Hernández Fresno, 2024). For instance, nitrogen-fixing *Rhodospirillales* produce nod factor molecules that trigger the activation of cytokinin pathways, stimulating root hair cell division in the host (Reid et al., 2017). As nodule development progresses, the bacteria release auxins (particularly indole-3-acetic acid, IAA, which promotes cell elongation in the host), along with other hormones (e.g. ethylene and gibberellins), ultimately orchestrating the formation of root nodules (Park et al., 2017; Timofeeva et al., 2024). Cytokinin and auxin are frequently produced by PGPR species and largely studied within the genera *Pseudomonas* and *Bacillus*, (e.g. Großkinsky et al., 2016; Lata et al., 2024). Phytohormone production has further been reported from screenings of novel indigenous rhizobacteria such as *Ignatzschineria* spp. (Park et al., 2021; Minhas et al., 2024). This suggests: 1) that exchange of phytohormonal signals commonly occur between plants and PGPRs, and 2) that PGPRs directly manipulate plant metabolism.

2.1.3. Modulation of photosynthetic efficiency

Microbial associations directly impact plant physiological processes. The arbuscular mycorrhizal fungus *Rhizophagus intraradices*, widely used in commercial formulations, is well known to enhance photosynthesis and biomass accumulation across various crops and environments (Zhu et al., 2014, 2018; de Andrade et al., 2015; Porcel et al., 2015; Chen et al., 2017; He et al., 2017).

Compared to AMF, PGPRs are less extensively studied for their potential to enhance photosynthetic efficiency. However, in *Sedum alfredii*, *Pseudomonas fluorescens* treatment improved carbon fixation and photosynthetic efficiency (Wu et al., 2020). Inoculation with *P. fluorescens* was also reported to enhance photosynthesis and yield in tomato (García-Villaraco et al., 2021) and in peanut (Wang et al., 2025). In *Arabidopsis thaliana*, network analyses linked inoculation with two

P. fluorescens strains (Pf-5 and GM30) to altered expression of photosynthetic light-reaction genes and changes in sugar and nutrient signaling. However, these effects were accompanied by reduced overall carbon gain (Weston et al., 2012). Pathogenic microbes such as *Pseudomonas syringae* further downregulate photosynthetic genes and affected photosystem II (PSII) activity, leading to reduced photosynthetic efficiency, chlorophyll degradation, and impaired carbon fixation (Bonfig et al., 2006).

Together these findings suggest complex species and strain-specific impacts of the *Pseudomonas* genera on photosynthesis and plant metabolism.

2.1.4. Root exudation and microbiome recruitment

Plant roots release a wide array of chemical compounds, known as root exudates, that, depending on their composition, shape interactions with microbes (Ankati and Podile, 2019; Hu et al., 2018). These exudates vary by plant species, development, and environmental stress, influencing the rhizosphere microbiome. Low-molecular-weight compounds (e.g., sugars, amino acids, organic acids) are passively secreted, while high-molecular-weight molecules (e.g., proteins, polysaccharides) are selectively released (Upadhyay et al., 2022).

Exudates also serve as info-chemicals (Kendall and Sperandio, 2016) guiding microbial recruitment. For instance, *Arachis hypogaea* secretes distinct compounds that selectively attract specific PGPR strains (Ankati and Podile, 2019), and legume flavonoids initiate symbiosis with *Rhizobia* via nod gene activation (Upadhyay et al., 2022). Such exudate-mediated interactions are key to PGPR colonization and may also moderate stress associations. For example, *Pseudomonas chlororaphis* upregulates stress-responsive genes when colonizing *Arabidopsis* roots under drought (Cho et al., 2013), and in maize, antimicrobial benzoxazinoids suppress pathogens (Hu et al., 2018) highlighting root exudates as central to plant-microbe communication and productivity.

2.2. Stress mitigation mechanisms

The stabilizing effects of diverse and well-balanced soil microbiomes are comparable to those of gut-associated microbiomes in human health. Similarly, soil and PGP-microbiomes play a crucial role in enhancing plants' adaptation to their environment as well as their tolerance and resistance to sudden environmental challenges (Adeleke and Babalola, 2021; Christel et al. 2021; Maitra et al. 2023).

Plant stress is commonly categorized into two types: abiotic and biotic stress (Voccianti et al. 2022). Abiotic stress refers to one-way impacts from non-living factors on the plant, such as drought, salinity, and temperature extremes. In contrast, biotic stress arises from interactions between at least two living organisms, where both can perceive, produce, and respond to chemical signals, allowing them to sense and react to each other's presence (Kalariya et al. 2024). Microbial interactions may aid both kinds of stress: directly by activation of the plants own tolerance or defense mechanisms, and indirectly when the biotic stress is mitigated without the plant becoming involved by the microorganisms' own production of toxins or antimicrobial compounds (Fig. 1), (Francis et al. 2020).

PGPRs produce defense hormones (MeJA, ET, and SA), antimicrobial compounds, and toxins that mitigate the effects of pathogens and pests (Pandey et al., 2023). The diversity of PGPRs and their wide range of functions mean that we often understand only part of their potential. However, PGPR-mediated stress mitigation is generally positively correlated with growth enhancement, yield improvement, hormonal signaling, production of specialized metabolites, tolerance, and ion transport (Pattnaik et al., 2021; Voccianti et al., 2022; Table 1).

Stress-mitigating effects of PGP-rhizobia extend beyond growth promotion through direct activation of the plant's own defense systems. When receptors on the plant cell membrane recognize biological elicitors, they may trigger either systemic acquired resistance (SAR) or induced systemic resistance (ISR) (Arora et al., 2016; Kamle et al., 2020; Fig. 2). SAR and ISR are complementary defense mechanisms. SAR provides long-term, systemic protection against biotrophs via salicylic acid signaling, while ISR primes plants for rapid defense against necrotrophs and herbivores through jasmonic acid and ethylene pathways. Both are critical for enhancing plant resilience in natural and agricultural systems, and while ISR has mostly been associated with responses to pathogen infestations, the most potential ISR responses may be those activated by beneficial microbes in the rhizosphere (Pieterse et al., 2014).

Stress memory is the special case of ISR, when induced changes become evident only after a secondary pathogen inoculation in systemic tissues, the phenomenon is also referred to as defense priming - a stress memory that enables a stronger and faster induced response (Martinez-Medina et al., 2016; Westman et al., 2019). The plant memory is considered to be ruled by epigenetic changes (Pikaard and Scheid, 2014; Verhoeven and Preite, 2014), and although the evidence is

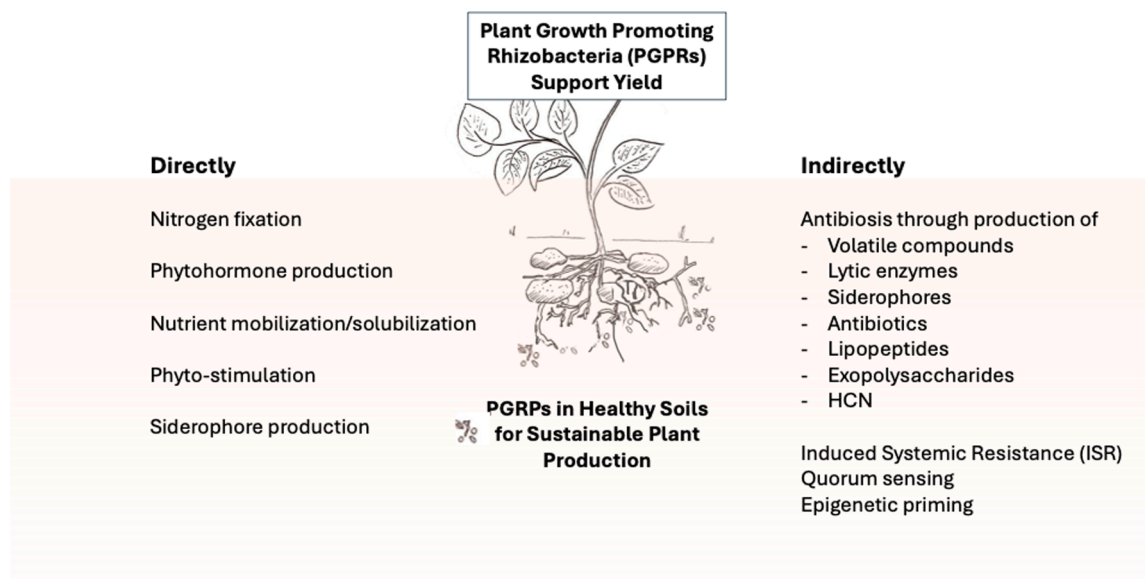


Fig. 1. Examples of direct and indirect plant growth promotion mechanisms mediated by plant growth-promoting rhizobacteria (PGPR). These mechanisms collectively enhance soil health, a critical prerequisite for sustainable plant production.

Table 1
A selection of experimental studies on major crops using Plant growth-promoting microorganisms to investigate mechanisms underlying the mitigation of abiotic or biotic stress. The reported traits from each study are listed, with empty cells indicating missing data. The traits represent the plant promoting effects on growth (G), hormonal signaling (H), induction of specialized products (P), tolerance (T), antioxidant activity (A), yield (Y), oxidative stress (S), ion transport (I). An upward arrow (↑) indicates an increase in a trait, while a downward arrow (↓) indicates a decrease.

	Stress	Type	Crop	PGPR Taxon	G	H	P	T	A	Y	S	I	References
Abiotic Stresses	Drought		<i>O. sativa</i>	<i>Bacillus altitudinis</i> + <i>Bacillus methylotrophicus</i>	↑		↑			↑			Narayanasamy and Uthandi, 2020
			<i>Z. mays</i>	<i>Bacillus subtilis</i> + <i>Acaulospora laevis</i>	↑			↑		↑			
	Heavy metal	Cadmium	<i>T. aestivum</i>	<i>Bacillus subtilis</i> + <i>Aspergillus niger</i>	↑			↑					Bashir et al., 2022
			<i>S. bicolor</i>	<i>Bacillus cereus</i> + <i>Myroides odoratimimus</i> + <i>Providencia rettgeri</i>	↑		↓		↑				
			<i>S. melongena</i>	<i>Bacillus subtilis</i>	↑		↑		↑				
	Salinity	Lead	<i>Z. mays</i>	<i>Bacillus anthracis</i>	↑			↑	↑				Shah et al., 2021
				<i>Bacillus mycoides</i>	↑				↑		↓		
				<i>Bacillus safensis</i>	↑		↑↓	↑	↑			↑	
				<i>Bacillus thuringiensis</i>	↑			↑	↑			↓	
				<i>Bacillus velezensis</i>	↑	↑				↑			
Biotic Stresses	Pathogen	<i>Alternaria solani</i>	<i>S. tuberosum</i>	<i>Bacillus megaterium</i> + <i>Pseudomonas fluorescens</i> + <i>A. chroococcum</i>	↑	↓			↓				(Rizvi et al., 2024)
		<i>Burkholderia</i>	<i>S. bicolor</i>	<i>Bacillus pumilus</i> + <i>Pseudomonas pseudoalcaligenes</i>	↑			↑			↓		
		<i>Fusarium oxysporum</i>	<i>G. max</i>	<i>Bacillus aryabhattai</i>	↑						↓		Jha and Mohammad, 2023
		<i>Fusarium oxysporum</i>	<i>S. lycopersicum</i>		↑						↓		
		<i>Fusarium solani</i>	<i>S. tuberosum</i>	<i>Bacillus sp.</i>	↑						↓		Mehmood et al., 2021
		<i>Phytophthora infestans</i>	<i>S. tuberosum</i>	<i>Bacillus subtilis</i> , <i>Pseudomonas putida</i> , and <i>fungi Trichoderma erinaceum</i> , <i>T. paraviridescens</i>	↑			↑					
		<i>Phytophthora infestans</i>	<i>S. tuberosum</i>	<i>Bacillus simplex</i> , <i>Azotobacter sp.</i> , <i>Trichoderma sp</i>	↑			↑		↑			Contreras-Liza et al., 2022
		<i>Rhizoctonia solani</i>	<i>G. max</i>	<i>Pseudomonas fluorescence</i>	↑					↑	↓		
		<i>Rhizoctonia solani</i>	<i>S. lycopersicum</i>	<i>Pseudomonas sp.</i>	↑		↑		↑		↓		Pandey and Gupta, 2020
		<i>Rhizoctonia solani</i>	<i>S. tuberosum</i>	<i>Bacillus subtilis</i>	↑						↓		

inconsistent, more than 130 genes in the model plant *Arabidopsis* are epigenetically controlled. Methylation, histone modifications including acetylation, ubiquitination, and methylation of histone N-tails, and short non-coding RNAs-mediated post-transcriptional silencing are the main mechanisms proposed as involved in epigenetic regulations of gene expression (Pikaard and Scheid, 2014).

While biological priming is likely a ubiquitous phenomenon in nature, chemical priming has been instrumental in elucidating the mechanisms behind plant defense priming, revealing a diversity of memory-triggering and priming-response mechanisms (Hönig et al. 2023). Studies in *Arabidopsis thaliana* support the role of histone modifications and chromatin remodeling following SA priming (Yi et al. 2014, 2015), as well as the accumulation of amino acids, IAA, and SA after β-aminobutyric acid (BABA) priming (Pastor et al. 2014). Similarly, diverse priming effects have been observed in tomato, including increased JA, SA, and polyphenol levels following MeJA priming (Koley et al. 2022) and transcriptional changes after hexanoic acid (Hx) priming (Finiti et al. 2014). The transcriptional coactivator NONEXPRESSOR OF PR1 (NPR1) is a central regulator of plant immunity, salicylic acid signaling, and induced resistance, particularly after chemical priming (Hönig et al., 2023). PGPR are suggested to contribute to defense priming by activating the jasmonic acid and ethylene pathways and ISR, and by modulating salicylic acid - responses that converge on NPR1, enhance systemic plant immunity (SAR) (Backer et al., 2019; also see Fig. 2).

2.3. *Pseudomonas* and *bacillus* as complementary PGPRs for sustainable agriculture

The role of plant growth-promoting rhizobacteria (PGPR) as key mediators of ISR (Zhu et al. 2022). Table 1 highlights the shared plant health-promoting mechanisms of two essential PGPR genera, *Pseudomonas* and *Bacillus*, both of which play significant roles in enhancing

crop health and productivity (Buyer et al. 1986). These complementary traits make *Pseudomonas* and *Bacillus* valuable tools in sustainable agriculture.

The genus *Pseudomonas* comprises a highly diverse group of bacteria found in soil, water, and on plant surfaces (Sah et al. 2021). With over 200 species, it includes well-known PGPRs, as well as opportunistic pathogens like *P. aeruginosa* and obligate phytopathogens such as *P. syringae* (Nakagami et al. 2024). The *Pseudomonas* genera is known for its rapid colonization ability and for its ability to take part in a wide spectrum of interactions with plants, ranging from beneficial to pathogenic. Known for their metabolic versatility, *Pseudomonas* species produce phytohormones such as auxins, cytokinins, and gibberellins, which directly promote plant growth (Timofeeva et al. 2024). Additionally, they solubilize phosphorus, produce siderophores to enhance iron availability, and contribute to nitrogen cycling in the soil by facilitating co-colonization with AMF (Goyal et al. 2024).

Pseudomonas species also indirectly enhance plant growth by suppressing pathogens through antibiotics (e.g., DAPG, phenazines, pyoluteorin), volatile compounds like hydrogen cyanide (HCN), and lytic enzymes that degrade fungal cell walls (Maurya et al. 2024). Furthermore, they trigger plant immune responses and use quorum sensing to regulate bioactive compound production, facilitating effective plant-microbe interactions. Prominent strains include *P. fluorescens* for its biocontrol properties, *P. putida* for strong root colonization and phosphate solubilization, and *P. chlororaphis* for suppressing soilborne pathogens like *Fusarium* and *Pythium* (Sarma et al. 2011; Bello et al., 2024).

Bacillus species, from the Firmicutes phylum, are widely used PGPRs due to their ability to survive extreme conditions (Akinsemolu et al. 2024). Like *Pseudomonas*, they produce phytohormones and solubilize nutrients such as phosphorus, potassium, and zinc (Buyer et al. 1986). Although not classical nitrogen-fixers, *Bacillus* species enhance nitrogen

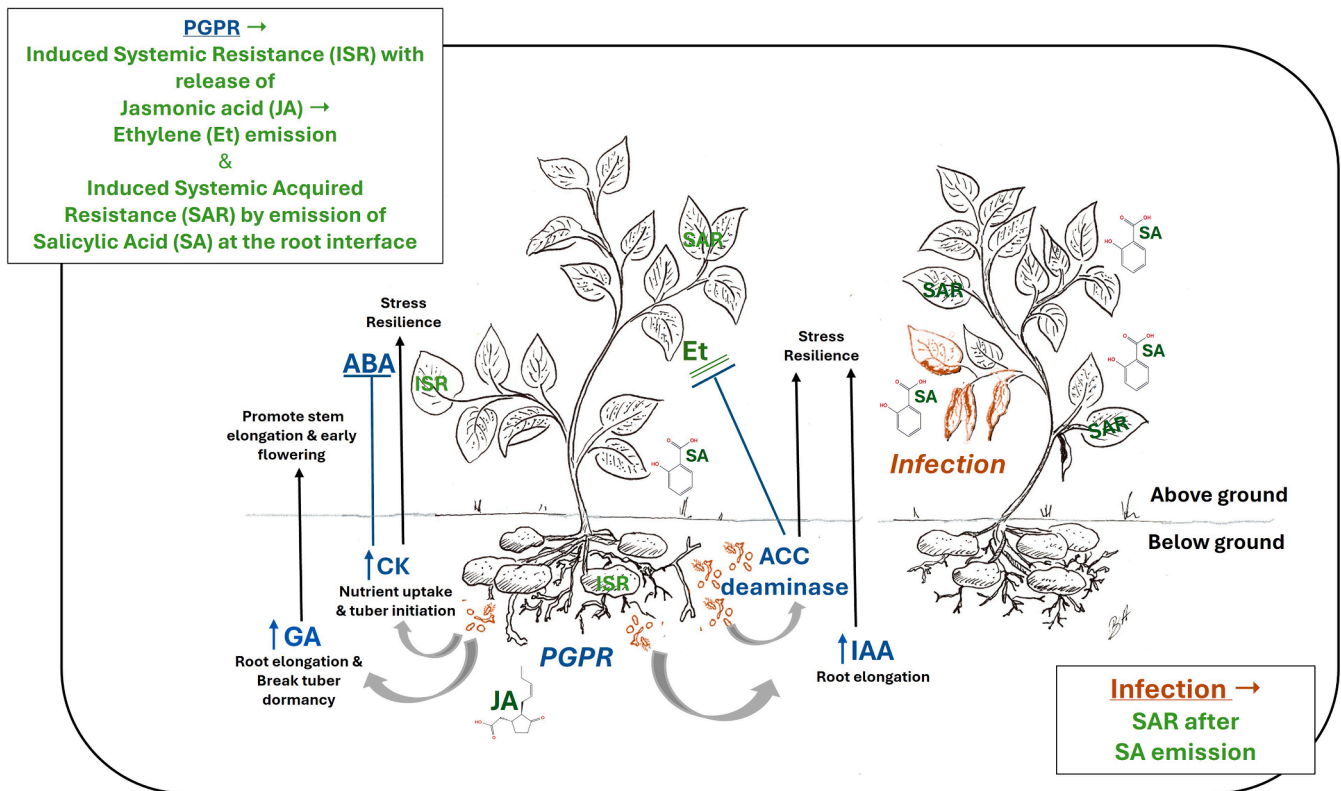


Fig. 2. Stress-mitigating effects of plant growth-promoting rhizobacteria (PGPR) extend beyond growth promotion and include activation of the plant's innate defense systems. Recognition of microbial elicitors by plant cell surface receptors can trigger systemic acquired resistance (SAR) or induced systemic resistance (ISR). SAR provides long-lasting protection against biotrophic pathogens via salicylic acid signaling, while ISR primes defenses against necrotrophic pathogens and herbivores through jasmonic acid and ethylene pathways. Although ISR is often associated with pathogen responses, it may be most effectively activated by beneficial microbes in the rhizosphere. In addition, PGPR contribute to plant stress tolerance and development through the secretion of key phytohormones such as indole-3-acetic acid (IAA), gibberellic acid (GA), and the enzyme ACC (1-aminocyclopropane-1-carboxylate) deaminase, which modulates ethylene levels under stress conditions—mechanisms that have also been experimentally demonstrated.

availability by cycling organic matter (Jain et al., 2021).

As biocontrol agents, *Bacillus* produces lipopeptides (e.g., surfactin, fengycin, iturin), antibiotics (e.g., bacilysin), and hydrolytic enzymes (e.g., chitinases) that disrupt fungal and bacterial pathogens (Ajuna et al., 2024). They also trigger ISR in plants by activating jasmonic acid and ethylene signalling pathways. Additionally, *Bacillus* species emit volatile organic compounds (e.g., acetoin, 2,3-butanediol) that promote plant growth and suppress pathogens (Etmnani et al., 2024). Notable strains include *B. subtilis* and *B. amyloliquefaciens* for their biocontrol and plant growth-promotion abilities, *B. thuringiensis* for its insecticidal Cry proteins, and *B. pumilus* for controlling fungal pathogens (Vasanth Srinivasan et al., 2025). *Bacillus* is distinguished by its ability to form durable endospores, making it particularly effective for bioformulations that remain stable during storage and field applications (Hubballi et al. 2023; Bhutani et al., 2024).

The interaction between *Bacillus* and *Pseudomonas* in the rhizosphere is complex and often context dependent. While both genera are known for their plant growth-promoting traits their co-inoculation can lead to either synergistic or antagonistic outcomes. Consortia consisting of *Bacillus halotolerans*, *Pseudomonas sihuiensis*, and *Bacillus atrophaeus* for example enhanced wheat growth under drought stress by improving nutrient uptake and antioxidant activity (Tanveer et al., 2024). Conversely, choice of *Pseudomonas* strain significantly influenced the interaction with *Bacillus subtilis*, *P. protegens*, and *P. entomophila* at times inhibiting the *Bacillus* biofilm formation through metabolite excretion of 2,4-diacytylphloroglucinol (Lyng et al., 2024).

Both *Pseudomonas* and *Bacillus* play central roles in agricultural biotechnology as biofertilizers, biopesticides, and tolerance enhancers

(Pattnaik et al., 2021; Ogunsola et al. 2024). The inherent resilience of *Bacillus* spores often provides an advantage in commercial formulations, enabling longer shelf life and environmental stability. Meanwhile, advances in genetic engineering are opening new opportunities to explore and enhance the versatility and synergistic potential of rhizobacteria in supporting plant production (Akinsemolu et al., 2024; Ogunsola et al., 2024).

2.4. Microbial consortia: beyond the sum of their parts

Microbial consortia offer significant advantages over single-strain inoculants in agriculture due to enhanced functional diversity, ecological resilience, and synergistic interactions (Christel et al., 2021). A global meta-analysis of 51 studies found that while single-species inoculants increased plant growth by 29 %, microbial consortia achieved a 48 % increase, and similarly improved pollution remediation by 80 % compared to 48 % (at the most) for single strains (Liu et al., 2023). These benefits stem from the ability of consortia to combine complementary microbial functions such as nitrogen fixation, phosphate solubilization, and pathogen suppression, while also promoting mutual growth through metabolite exchange and signaling. Additionally, microbial consortia appear to adapt more effectively to diverse and fluctuating soil environments, across crop and field conditions compared to single strains applications that often underperform (Hashmi et al., 2019; Bradáčová et al., 2019), suggesting that microbial consortia provide a generally more robust and sustainable inoculate compared to single species solutions.

Several studies further underscore the positive functional effects of

microbial soil consortia as reported for *Arabidopsis thaliana* (Kudjordjie et al., 2022); tomato, *Solanum lycopersicum* L. (Sarma et al. 2011); mung bean and green gram, *Vigna mungo*, (Saikia et al., 2018) and *V. radiata*, (Kumar et al., 2011); corn, *Zea mays* L. (Saleem et al., 2025); and eggplant, *Solanum melangona* L. (Khatoon et al., 2024). These findings support that synergies or additive effects within the microbial consortia can significantly increase yields, potentially surpassing the benefits provided by individual organisms alone (Zhu et al., 2024).

Similar robustness is reported for consortia enhancing stress resistance and tolerance with relevance of agriculture (Chauhan and Upadhyay, 2024) and conservation purposes (Zhang et al., 2019). In potato, the combination of *Trichoderma viride*, *Bacillus subtilis*, and *Pseudomonas fluorescens*, was more effective against *Alternaria solani* infestation, compared to individual treatments, as the consortia added enhancement of systemic resistance by modulating antioxidants and phenylpropanoid pathways (Kumar et al., 2023; Ogunsola et al., 2024). Similarly, the combined inoculation of *Azospirillum brasilense* and *Ochrobactrum cytisi* increased auxin and cytokinin levels while reducing ABA, resulting in an improved drought tolerance in potato microplants (Arkhipova et al., 2020).

3. Tools and techniques in studying plant-microbe interactions

The natural microbiome is diverse and hidden from the naked eye. Modern techniques have revolutionized our ability to observe and study the microbiome and its members, opening up for new avenues both regarding basal knowledge and application potentials (Saadh et al., 2024). We here exemplify this process in Table 2, that provides an overview of PGPR with emphasis on studies of *Pseudomonas* and *Bacillus* species in the service of potato production over the last 40 years. Potato (*Solanum tuberosum*) is the third most important food crop worldwide and is uniquely relevant to both small-scale sustainable farming and large-scale commercial agriculture (Buyer et al., 1986; Arkhipova et al., 2020). As a highly nutritious yet disease-prone crop, potato production benefits greatly from alternative farming strategies, including PGPR-based approaches, to enhance resilience and yield (Priya et al., 2023). The growing interest in PGPR applications over time is highlighted with a shift in research focus, from nutrient uptake towards stress mitigation, biotechnology-based formulations, and predictive approaches for optimizing PGPR use (Kadiri et al., 2023; Adamo et al., 2024; Table 2).

This trend further reflects advancements in novel techniques and biotechnological solutions that leverage PGPR for improved agricultural sustainability, extending beyond potato to other crops. To aid the interpretation of the huge data amounts that these modern techniques generate, the field of bioinformatics is exploding providing a potential to better understand the mechanisms that drive plant microbial symbiotic associations (Khanna et al., 2022).

3.1. Omics approaches to plant-microbe interactions

Advances in omics (e.g. genomics, metabolomics, transcriptomics, proteomics) technologies have transformed our understanding of plant-microbe interactions by enabling comprehensive, system-level analyses. Genomic sequencing of both plants and microbes reveals key genes involved in colonization, signaling, and stress responses (White et al., 2017). In particular, comparative genomics help identify conserved and strain-specific features in beneficial microbes like *Pseudomonas* and *Bacillus*, offering insights into their plant growth-promoting capabilities (Wang et al. 2023).

Transcriptomic approaches, such as RNA sequencing, allow researchers to monitor gene expression changes during plant-microbe interactions, including both host and microbial responses (Nobori et al. 2022). These studies can uncover regulatory pathways involved in defense, hormone signaling, and nutrient exchange. Metagenomics and amplicon sequencing (e.g., 16S rRNA) are widely used to characterize

microbial community composition in the rhizosphere and its shifts in response to environmental factors or inoculation strategies (Nwachukwu and Babalola, 2022). Together omics tools leverage a huge potential to unravel functional relationships within microbiomes and between microbiomes and their hosts, and such insights at the molecular level may very well be our ticket to the next Green Revolution (Singh and Ramakrishna, 2021).

In addition to omics tools, synthetic biological approaches such as CRISPR-based genome editing offer powerful strategies to unravel and enhance plant-microbe interactions. For example, a CRISPR/Cas system combined with single-stranded DNA (ssDNA) has been successfully developed to enable precise gene deletion, insertion, replacement, and transcriptional repression in *Pseudomonas putida* KT2440 (Bisht et al., 2019). Such targeted manipulation of microbial traits indeed open avenues for designing next-generation bioinoculants (Mmotla et al., 2025). However, challenges such as data integration, environmental variability, and the scalability of lab-based findings to field conditions persist.

3.2. Imaging tools for spatial and cellular insights

Imaging technologies for visualisation of the ways microbes interact with plants across spatial and cellular contexts are also fastly developing, combining microscopy with labeling techniques that allow studies of localization and dynamics between the microbe and its plant host.

Fluorescence microscopy often combined with GFP-tagged microbes or fluorescent dyes, is widely used to monitor microbial colonization on root surfaces or within plant tissues (Pieterse et al., 2021). Confocal laser scanning microscopy (CLSM) in combination with fluorescent in situ hybridization (FISH), allow for precise localization of microbial taxa within plant compartments (Bulgari et al., 2011; Posada et al., 2018). Rhizotron platforms and transparent soil systems further enable non-destructive 3D imaging of root colonization in near-natural conditions (Handakumbura et al., 2021).

Together, these imaging tools offer critical spatial and temporal insights that complement molecular and omics-based approaches in plant-microbe interaction research.

4. Harnessing microbiomes for sustainable agriculture

Despite the growing recognition of the role soil microbiomes play in plant health and productivity, critical gaps remain in research and application (Ray et al., 2020). They include the lack of baseline data on soil microflora, a limited understanding of microbial interactions, and the current reliance on external agricultural inputs (Jeger et al., 2024). Addressing these issues is essential for unlocking the full potential of PGPRs towards more sustainable farming practices.

4.1. Lack of baseline soil microflora data

Conventional industrial farming disrupts soil microbiomes, which may take years to stabilize and restore. Without baseline data, predicting soil recovery is challenging. Expanding sequencing efforts for many habitats and origins is therefore crucial in order to characterize unknown native and local taxa, and thus advance metagenomic tools including the creation of comprehensive databases and updated bioinformatic processes. High-throughput screening of native microbial species will help fill knowledge gaps by adding relevant information at the species and subspecies levels to the reference databases. Optimization of taxonomic markers and primers are continuously updated to refine high-throughput sequencing platform (e.g. Illumina, Pacbio and Oxford Nanopore) and minimize the co-amplification of non-targeted organisms, such as host plant DNA through advanced techniques such as peptide nucleic acid (PNA) clamps may enhance the accuracy of soil microbiota profiling (Ihrmark et al., 2012; Nilsson et al., 2019; Viotti

Table 2

Examples of plant growth-promoting (PGP) *Pseudomonas* (P.) and *Bacillus* (B.) species and strains, used individually or in consortia, and their reported effects on potato crops. The table highlights observed benefits, reflecting the growing body of research on PGP rhizobacteria and the advancement of techniques used to study their potential in sustainable agriculture. (*) indicates the effects of consortium included in the study.

Organisms	Composition	Plant rel.	Growth rel.	Other focus	Techniques	Reference
<i>P. spp</i>	Consortium*	Nutrient uptake	Siderophore production, Fe3	Anti-pathogen effects	HPLC	Buyer and Leong, 1986
<i>P. spp</i>	Consortium*	Nutrient uptake	Siderophore production, Fe3	HCN production	A gas trapping and chemical analysis approach	Bakker and Schippers, 1987
<i>P. fluorescens/putida</i>	Consortium*	Nutrient uptake	Siderophore production, Potato rotation praxis		Bioassay, growth response	Bakker et al., 1987
<i>P. putida</i>	Consortium*	Production	Colonization, coexistence	<i>Glomus fistulosum</i> (AMF)	Chemical analyses, microscopy	Vosátka and Gryndler, 1999
<i>P. mosselii</i>	Single strain	Stress mitigation	POX and PAL enzyme activity	<i>Streptomyces</i> spp. (path)	Spectrophotometry	Singhai et al., 2011
<i>B. subtilis</i> MB73/2	Single strain	Production	Localization		Confocal laser scanning microscopy	Krzyzanowska et al., 2012
<i>P. sp. P482</i>	Single strain	Stress mitigation		<i>Streptomyces</i> spp. (path)	Bioassay, growth responses	Meng et al., 2013
<i>B. amyloliquefaciens</i> BAC03	Single strain	Production	Colonization, coexistence	<i>Rhizophagus irregularis</i> (AMF)	RT-qPCR	Velivelli et al., 2015
<i>P. rhizophila</i>	Consortium*	Stress mitigation		<i>Rhizoctonia solani</i> (path)	RT-qPCR, microscopy	Khedher et al., 2015
<i>B. subtilis</i> V26	Single strain	Production	Plant hormonal production		GC/MS	Meng et al., 2016
<i>B. velezensis</i>	Single strain	Stress mitigation	Defense gene activity	<i>Phytophthora infestans</i> (path)	RT-qPCR	Morrison et al., 2017
<i>P. fluorescens</i>	Consortium*	Stress mitigation		<i>Rhizoctonia</i> diseases (path)	Bioassay, growth responses	Ali et al., 2017
<i>B. subtilis</i>	Consortium*	Stress mitigation		<i>Phytophthora infestans</i> (path)	Bioassays, growth responses	De Vrieze et al., 2018
<i>P. spp</i>	Single strain	Stress mitigation	Development of nanocomposite beads	<i>Fusarium solani</i> (path)	Bioassays, scanning electron microscope, IFT_IT, XRD	Pour et al., 2019
<i>P. fluorescens</i>	Consortium	Stress mitigation	Field application	<i>Phytophthora infestans</i> (path)	16 s sequencing; phylogenetic analysis	Kumbar et al., 2019
<i>B. subtilis</i>	Single strain	Stress mitigation	Antioxidant prod; plant health	Salt tolerance	Ion concentration, spectrophotometry	Tahir et al., 2019
<i>B. strains</i>	Consortium*	Stress mitigation	Bacterial abundances; disease; yield	<i>Streptomyces</i> spp. (path)	Metabarcoding; Diversity indices	Wang et al., 2019
<i>B. subtilis</i>	Single strain	Production	Phyto beneficial Rhizosphere colonization	"Biolog", RT-qPCR		Zboralski et al., 2020
<i>B. licheniformis</i> strain POT1	Single strain	Stress mitigation	SAR, phenolic accumulation	Alfalfa mosaic virus (path)	GC/MS, HPLC, RT-qPCR	Abdelkhalek et al., 2020
<i>B. strain</i> CIK-515	Single strain	Production	Increased biomass		Metrics: height, weight, N and P content	Ahmad et al., 2020
<i>B. spp and P spp.</i>	Consortium	Stress mitigation		<i>Streptomyces</i> spp. (path), <i>Rhizoctonia</i> spp. (path)	Field study, microscopy	Papp et al., 2021
<i>B. simplex</i>	Consortium*	Production		<i>Tricoderma</i> sp, <i>Azotobacter</i> sp (symb)	Metrics: height, weight	Contreras-Liza et al., 2022
<i>B. licheniformis</i>	Single strain	Stress mitigation	Water use efficiency		LI-Cor, Dualex, ΨI, Kjeldahl analyses	Liu et al., 2022
<i>P. fluorescens</i> SLU99, <i>Serratia plymuthica</i> S412, <i>S. rubidaea</i> AV10, and <i>S. rubidaea</i> EV23	Single strain	Production	Plant hormonal production prediction	(symbionts)	Transcriptomics comparisons	Hanifah et al., 2023
<i>B. velezensis</i>	Single strain	Stress mitigation	ISR, plant hormonal production	<i>Alternaria solani</i> (path)	RT-qPCR, LC/MS, bioassay	Bai et al., 2023
<i>B. consortium</i>	Consortium*	Nutrient uptake	Colonization, coexistence	(symbionts)	Bioassays	Boussageon et al., 2023
<i>B. velezensis</i>	Single strain	Stress mitigation	Fungicide replacement	<i>Phytophthora infestans</i> (path)	Bioassays, molecular docking, comparative genome analyses	Kadiri et al., 2023
<i>B. subtilis</i>	Consortium*	Stress mitigation	Fungicide replacement	<i>Rhizoctonia solani</i> (path)	Metabarcoding	Maslennikova et al., 2023
<i>B. sp. PM31</i>	Single strain	Stress mitigation	Plant hormonal production	<i>Fusarium solani</i> (path)	Morpho-, physio-, biochemical, antioxidative analyses	Mehmood et al., 2023
<i>P. rhizophila</i>	Single strain	Nutrient uptake	Phosphate solubilization	Heavy metal and salt tolerance	Biochemical analyses	Sghaier et al., 2024
<i>B. amyloliquefaciens</i>	Single strain	Nutrient uptake	Biotech formulation	greenhouse and field test	Metabarcoding, physiochemical properties	Adamo et al., 2024
<i>B. spp.</i>	Consortium*	Stress mitigation	Biotech formulation (spore based)	<i>Rhizoctonia solani</i> (path)	Sanger sequencing of endophytic fungi;	Debez et al., 2024

et al. 2024). These advancements have the potential to facilitate detection of cryptic taxa, monitor of microbial interaction networks, and identify emerging pests, all of which cannot be obtained through culturing techniques.

4.2. Rethinking agricultural practices

Modern agriculture faces mounting challenges, including adaptation to weather fluctuations and soil degradation. A shift toward soil-based strategies that support soil health may reduce the dependency of chemical additives, while enhancing crop resilience (Bhattacharjya et al., 2021; Varjani et al., 2024).

However, a big challenge is the actual scaling from the lab to the field environment, as field studies on sustainable farming methods using microbial aids are still scarce (Kumar et al., 2023). Organic amendments are being investigated for their potential role in soil conservation and restoration, particularly for their ability to enrich microbial diversity, modify enzyme activities, and enhance carbon sequestration. Rice straw biochar in combination with humic acid for example improved maize performance under salinity (Varjani et al., 2024; Irin et al., 2024).

Co-application of *B. subtilis* and biochar both enhanced the yield and productivity of canola, *Brassica napus* L. (Muhammad et al., 2025), and improved nutrient contents, soil properties, and growth in einkorn wheat, *Triticum monococcum* L. (Çiğ et al., 2021). The combination of biochar with the ACC deaminase producing PGPRs *Achromobacter xylosoxidans*, *Pseudomonas aeruginosa*, *Leclercia adecarboxylata*, and *Enterobacter cloacae*, reduced ethylene production and enhanced nutrient uptake more efficiently in maize, *Zea mays*, under drought stress compared to any individual treatment (Danish et al., 2020). In tomatoes, the joint application of biochar and PGPR strains (*Bacillus amyloliquefaciens* and *Paenibacillus polymyxa*) resulted in an 87 % increase in soil nitrate content and nitrogen utilization efficiency compared to any individual treatment (Wang et al., 2021). Likewise, co-application of biochar and *Bacillus megaterium*, a nitrogen-fixing rhizobacteria, improved soil water retention by 18 % and 24 % compared to biochar or PGPR treatments alone (Ren et al., 2020). These combinations may further foster native microbial proliferation, reinforcing soil function and sustainability (Malik et al., 2022).

4.3. Complementarity and stability in microbial consortia

Beneficial synergistic effects are increasingly documented across various crops. The plant microbiome represents several distinct but sometimes overlapping mechanisms and effects. Nutrient acquisition, for example, include organic acid secretion, enzymatic activity, and the production of siderophores, all of which enhance nutrient availability in the rhizosphere (Wei et al., 2024), and members of the microbial community may both depend on other community members and environmental contexts.

Although, most studies of PGPR have focused on specific crops and a narrow set of microbes, it is increasingly recognized that microbial consortia (comprising multiple interacting microbial species) outperform single-strain inoculants in promoting plant growth and resilience, making consortia particularly attractive as plant growth-promoters (Teiba et al., 2023; Christel et al., 2021). Formulations are developed with use of screening techniques and functional prediction tools, revealing consortia with demonstrable field efficacy. For example, a rhizosphere-derived microbial bioproduct consisting of *Bacillus subtilis* and *Trichoderma harzianum* significantly increased potato tuber yield and suppressed common scab (Wang et al., 2019). Similarly, a combination of *Pseudomonas* strains S19 and S49 effectively controlled *Phytophthora infestans* development in potato (Vrieze et al., 2018).

While exhaustive empirical testing of microbial combinations for individual crops is both time- and resource-intensive, a more strategic path lies in understanding microbial interactions and the synergistic effects that underpin functional outcomes. Such knowledge enables the

rational design of microbial consortia with predictable and reproducible performance. Recent advances in metagenomics, high-throughput sequencing, and computational approaches - including machine learning and deep learning - now offer powerful tools for predicting microbial traits, community dynamics, and functional compatibility (Nam et al., 2023; Kumar et al., 2023). Such integrative frameworks pave the way for more efficient, targeted development of next-generation microbial formulations for sustainable agriculture.

4.4. Application strategies

To improve the survival, effectiveness, stability, and synergy of microbial inoculants, systems-based approaches that integrate microbial ecology, formulation science, and precision agriculture are in demand. This may be achieved through several integrated strategies.

4.4.1. Selection of strains

Robust microbial strains for enhanced stress-tolerance such as *Pseudomonas*, *Bacillus*, and *Trichoderma* are pivotal in enhancing plant resilience to abiotic stress while simultaneously promoting growth. The capacity to compose synthetic microbial communities (SynComs) grows, with consortia that enhance plant nutrient uptake and stress resilience (Alzate Zuluaga et al., 2024; Mehlferber et al., 2024; Tariq et al., 2025). Recent advances in SynCom engineering (socalled host-mediated microbiome engineering, HMME), for example make use of plant genotypes that favor particular beneficial microbial recruitments.

4.4.2. Formulation of synergistic microbial consortia

Compatible microbial consortia that complement each other's functions while avoiding antagonistic interactions have been described from field-scale studies, that simultaneously modulate the rhizosphere microbiome, enhance iron uptake, and improve drought resilience in crops like maize by influencing plant hormonal balance and root exudation patterns (Francioli et al., 2025).

Recent research further emphasize the importance of constructing multi-functional microbial communities, recognizing that plant growth-promoting rhizobacteria (PGPR) rarely function in isolation within the rhizosphere. The networks they form with other microbes tend to be synergistic rather than additive enhancing the overall functionality (Sarsan et al., 2021). Metabolic cross-feeding, quorum sensing, and co-regulation of gene expression enable dynamic adaptation to environmental changes and plant needs. For example, one microbe may solubilize phosphate, another may produce phytohormones, and a third may suppress pathogens together creating a resilient and efficient system that surpasses the capabilities of any single strain (Alzate Zuluaga et al., 2024), crucial for the ecosystem services of a plant growth supportive microbiome.

4.4.3. Update of delivery technologies

Delivery technologies rely on a controlled application that keep the microbiome intact, protects it from environmental stress, and extend its viability in the soil. They may be divided into seed coating and seed inoculation, soil drenching, root dipping or seedling dipping treatments, foliar sprays, granular and powder formulations, encapsulation (e.g., alginate beads, hydrogels), biochar- or compost-based carriers, and drip irrigation systems (i.e. Jambhulkar et al. 2015)

4.4.4. Refinement of soil and crop management practices

Management practices to conserve and restore soil microbiomes are roughly divided into 1. soil-focused practices such as organic amendments, reduced or no-tillage preparation to conserve the soils, regular soil testing, and irrigation management, 2. crop focused practices that consider crop rotation and diversification, cover cropping, reduced chemical inputs, and integration of indigenous knowledge, and 3. microbe focused practices that include inoculant compatibility testing, microbial delivery techniques, and precision microbiome management

(French et al. 2021)

4.4.5. Use of omics tools

Genomics and metagenomics information may aid identification of beneficial traits, as well as monitoring of microbial dynamics and interactions to enable the fine-tuning of inoculant performance under diverse field conditions (Díaz-Rodríguez et al., 2025). Omics-focused techniques (transcriptomic and metabolomic analyses) also promise to unravel PGPR consortia functions by comparing activities at the gene and metabolite levels (Mmotla et al., 2025). Such insights are crucial for designing stable and effective microbial consortia.

However, translating these findings to field conditions remains a challenge and continued integration of omics data, ecological modeling, and field trials is essential to bridge this gap and develop scalable, climate-resilient bioinoculants for sustainable agriculture. Furthermore, genome-resolved microbiome data, particularly metagenome-assembled genomes (MAGs), are revolutionizing our understanding of microbial ecosystems. MAGs reveal that many dominant microbes in nature are uncultivated and underrepresented in laboratory cultures. This is reshaping our understanding of microbial diversity and providing rationales for the design of synthetic microbial consortia (Olo Ndela, 2025).

4.4.6. Involvement of farmers and stakeholders

Integrated efforts involving farmers, researchers, and other stakeholders are crucial for advancing sustainable PGPR-supported practices. Proper training in the handling and application of microbial inoculants is essential, and both practical and theoretical collaboration are needed to drive forward knowledge and adoption.

Several noteworthy global initiatives exemplify how co-created knowledge and participatory approaches can strengthen soil health and microbiome management. In Europe, projects like the UK Crop Microbiome CryoBank and RECETOX engage stakeholders in soil sampling to monitor microbial composition and soil quality. In Asia, the FAO-supported Farmer Field Schools (FFS) - established in Indonesia in 1989 - have trained over 2 million farmers across countries such as China, India, and Vietnam. These schools promote agroecological learning through collective field observations, experimentation, and local adaptation.

In Africa, initiatives such as the Soil Initiative for Africa (SIA), the African Soil Microbiology Project (AfSM), and the PROLINNOVA Network integrate indigenous knowledge with scientific research to promote sustainable resource management. In Latin America, Farmer Research Committees (CIALs) facilitate on-farm adaptive trials, allowing farmers to test microbial inoculants and other innovations collaboratively with researchers. This bottom-up model has been shown to significantly increase adoption rates - by up to 40 % - when innovations are developed through farmer-led trials (Pires et al., 2024).

5. Conclusion

Plant-associated microbes offer a promising, sustainable solution to mitigate the negative impacts of biotic and abiotic stress on crop productivity. Through mechanisms such as phytohormone modulation, improved nutrient uptake, and immune priming, microbial consortia can enhance plant resilience and yield. However, realizing their full agricultural potential requires a deeper understanding of functional interactions at the molecular level, along with more targeted field applications. This review highlights the value of well-characterized genera like *Pseudomonas* and *Bacillus*, while emphasizing the need to expand research into broader microbial groups. Future efforts should prioritize baseline soil microbiome assessments, mechanistic studies, and practices that restore and conserve soil health to support resilient, microbe-enabled crop systems.

CRedit authorship contribution statement

Neha Sharma: Writing – original draft. **Lovely Mahawar:** Writing – review & editing, Investigation. **Arti Mishra:** Writing – review & editing, Supervision. **Benedicte Riber Albrechtsen:** Writing – review & editing, Project administration, Conceptualization.

Declaration of competing interest

The authors declare that there are no conflicts of interest related to the research, authorship, or publication of this work.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.stress.2025.100966.

Data availability

No data was used for the research described in the article.

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