



Harnessing Plant Growth-Promoting Rhizobacteria for the Biocontrol of Phytopathogens in Sustainable Agriculture: A Review

P. Saranraj¹, Riyaz Sayyed^{2,*}, K. Kesavardhini¹, B. Lokeshwari¹ and K. Gayathri¹

¹Department of Microbiology, Sacred Heart College (Autonomous), Tirupattur 635 601, India

²Department of Biological Sciences and Chemistry, College of Arts and Sciences, University of Nizwa, Nizwa, 616, Oman

Received: September 16, 2025 Accepted: October 17, 2025



OPEN ACCESS

Editor-in-Chief
Praveen Kumar

Editors (India)

Anita Pandey
Hema Yadav
Neena Singla
Ritu Mawar
Sanjana Reddy
Surendra Poonia
R.K. Solanki
P.S. Khapte

Editors (International)

M. Faci, Algeria
M. Janmohammadi, Iran

***Correspondence**

Riyaz Sayyed
sayyedrz@gmail.com

Citation

Saranraj, P., Sayyed, R., Kesavardhini, K., Lokeshwari, B. and Gayathri, K. 2026. Harnessing plant growth-promoting rhizobacteria for the biocontrol of phytopathogens in sustainable agriculture: A review. *Annals of Arid Zone* 65(3): 31-59
<https://doi.org/10.56093/aaz.v65i3.171763>
<https://epubs.icar.org.in/index.php/AAZ/article/view/171763>

Abstract: Plant diseases significantly reduce worldwide agricultural production, causing yield declines of 21-30% for major crops, while excessive use of pesticides and chemicals poses serious health and environmental risks. Plant growth-promoting rhizobacteria (PGPR) offer an environmentally acceptable, efficient biocontrol approach against phytopathogens. Through direct mechanisms, such as the synthesis of phytohormones and nutrients, and indirect mechanisms, including the synthesis of antibiotics and siderophores and the establishment of induced systemic resistance (ISR), PGPR support plant development and suppress infections. This paper examines the role of PGPR in sustainable agriculture, focusing on their interactions with plant roots, rhizosphere dynamics, and the rhizosphere microbiome, as well as their biocontrol efficacy against fungal, bacterial, and nematode diseases. Key mechanisms include niche exclusion, competition for resources, and the release of antimicrobial compounds. Large-scale PGPR application is hindered by limitations such as inconsistent field performance, environmental acceptability concerns, and regulatory issues. Breakthroughs in microbial ecology, molecular biology, and bioinformatics offer new opportunities to optimize PGPR formulations and enhance crop-specific compatibility. Future studies should focus on developing microbial consortia, enhancing their stress tolerance, and integrating them into organic farming systems to achieve sustainable biocontrol. Within the framework of the green revolution, sustainable agriculture can increase crop yields, enhance soil health, and reduce the use of synthetic agrochemicals by leveraging PGPR-plant associations. This review highlights the promise of PGPR for the biological control of agricultural diseases and discusses the challenges and future directions for its global commercialization.

Key words: Biocontrol, PGPR, Phytopathogens, Rhizosphere

microbiome, sustainable agriculture.

Pests and plant diseases can significantly affect agricultural output. Plant infections pose a severe threat to global food security, with reported yield losses averaging 21-30% for major crops. However, these losses are highly contextual and can be far more devastating for specific crops and pathogens; for instance, aggressive soil-borne fungi like *Fusarium oxysporum* can cause total crop loss (up to 100%) in bananas, while root-knot nematodes (*Meloidogyne* spp.) routinely cause yield reductions of 20-50% in tomatoes and soybeans. Several plant diseases have become resistant to chemical control over time (Singh *et al.*, 2025). There are many instances where some important plant diseases have become prevalent. The most alarming challenges faced by people across the world in terms of public health and environmental sustainability are the reliance on chemical pesticides (Fones *et al.*, 2020). Many insecticides may remain in the soil due to their toxicity, as these substances are resistant to decomposition into less dangerous chemicals (Abdusamatov *et al.*, 2025). Given the environmental sustainability concerns associated with agrochemicals, it is increasingly important to seek alternative products. PGPR are naturally occurring organisms that are non-toxic, useful, and eco-friendly and can serve as an alternative to agrochemicals. PGPR can be a good alternative to chemical pesticides. There are many justifications for taking serious measures to manage plant diseases to improve human health and cope with environmental stresses (Chaloner *et al.*, 2021).

Plant diseases and the widespread use of synthetic pesticides, especially those used to combat them, have threatened crop yields in recent decades. Many plant diseases have developed resistance to conventional chemical control methods. Consequently, the lack of effective chemicals has made it more difficult to control some economically significant plant diseases. Numerous chemical pesticides found in soil persist as hazardous residues, frequently associated with health issues for humans, due to their resistance to degradation into less dangerous and simpler compounds. Increased public awareness of the harmful effects of synthetic chemicals on ecosystems and human health has led to a rise in the popularity of more environmentally sustainable agricultural

management practices that involve reduced use of synthetic chemicals (Fones *et al.*, 2020).

The widespread use of synthetic agrochemicals is referred to as an unsustainable practice (Fig. 1) and emphasizes the evolution of alternative and sustainable farming practices (Nakkeran *et al.*, 2025). From the perspectives of environmental protection and public health, PGPR represent a promising alternative to chemical pesticides. Climatic conditions have always influenced crop production, and climate change is intensifying this effect, thereby posing additional challenges for plant disease management (Chaloner *et al.*, 2021). These challenges include coping with the shifting geographical distribution of pathogens, managing emerging infections, and preventing pathogen establishment in new areas. The widespread application of synthetic agrochemicals is considered unsustainable (Fig. 1), and this section illustrates the mechanisms and modes of action of microbial biocontrol agents as alternatives to chemical pesticides. This figure highlights the importance of developing alternative and sustainable agricultural practices. From an environmental and public health perspective, PGPR is a viable alternative to chemical pesticides. Figure 1 highlights the importance of developing alternative and sustainable farming methods. In terms of safeguarding the environment and public health, PGPR represents an up-and-coming alternative to synthetic pesticides. Agricultural output has consistently been affected by climatic circumstances, and that influence is intensifying due to climate change.

Plant pathogen control will also face additional challenges due to climate change. These challenges include addressing the shifting geographical distributions of infections, treating existing diseases, and preventing the establishment of pathogens (Alsalamah *et al.*, 2024). Figure 1 illustrates the multiple strategies through which beneficial microorganisms suppress plant pathogens and promote crop health. These agents employ direct mechanisms, such as competition for nutrients and ecological niches; antibiosis through the secretion of antibiotics, lytic enzymes, volatile compounds, and siderophores; and parasitism and predation, which degrade pathogen cell walls (Wani *et al.*, 2016). Concurrently, they employ indirect strategies by eliciting

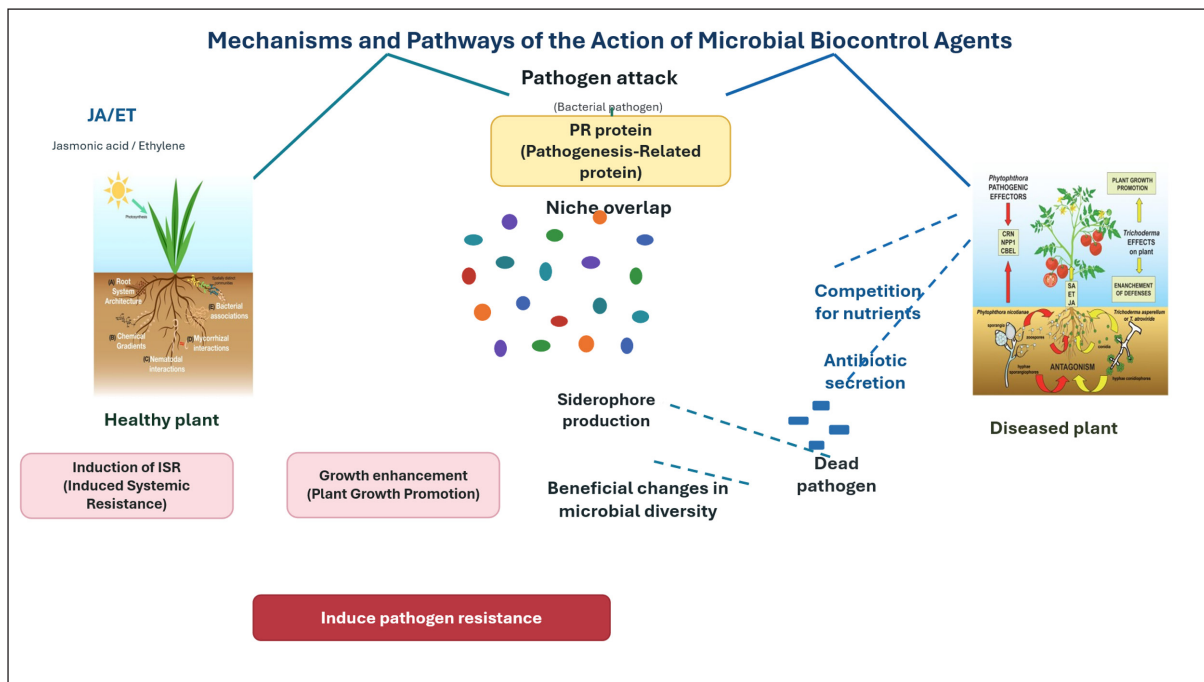


Fig.1. Mechanisms and Pathways of the Action of Microbial Biocontrol Agents (Backer *et al.*, 2018).

immune responses in the host, such as induced systemic resistance (ISR) via jasmonic acid and ethylene signaling pathways and systemic acquired resistance (SAR) via salicylic acid signaling pathways, resulting in the buildup of pathogenesis-related proteins and defense-related compounds (Reshma *et al.*, 2018). Furthermore, the microbial agents stimulate plant growth through the synthesis of plant hormones, enhanced nutrient mobilization, and root biofilm development that not only prevents pathogen colonization but also increases resistance to abiotic stresses. In summary, these multiple strategies provide a protective barrier against diseases and support sustainable agricultural practices.

The effectiveness of promising biological disease control techniques can be hindered by environmental factors that significantly affect their performance (Fones *et al.*, 2020). The plant microbiome is now recognized as a primary factor influencing plant health and productivity (Shanthappa *et al.*, 2025). The key functions of plant-associated microbes include preventing root infections by soil-borne pathogens, regulating rhizosphere processes, and establishing interactions between bacteria and their host plants. There are distinct microbiomes across plant tissues and species, despite overlapping features

among members of the plant microbiota (Bai *et al.*, 2015). Moreover, the functioning of the microflora of roots, soils, and seeds depends on nutrients including amino acids, carbohydrates, and secondary metabolites. As Bulgarelli *et al.* (2013) note, there is a lack of information, especially regarding plants growing under natural conditions and the relationship between their microbiome and plant health.

Nevertheless, the transition from broad-spectrum chemicals in plant protection to the use of specific live microorganisms represents a significant scientific challenge (Jabborova *et al.*, 2025a). The primary problem is the transfer of the high efficiency of PGPR from laboratory and greenhouse conditions to the field. Many factors regulate this problem (Budamagunta *et al.*, 2022). Therefore, this review seeks to address this critical challenge by systematically examining the mechanisms, efficacy, and, most importantly, the existing barriers to the widespread commercialization of PGPR as a cornerstone of sustainable agricultural disease management.

The Current Situation of Plant Diseases

In recent decades, plant diseases and the widespread reliance on synthetic pesticides to manage them have threatened crop yields. Many plant diseases have developed

resistance to conventional chemical control methods. Consequently, the lack of effective chemicals has made it difficult to control some economically significant plant diseases. The globalization of the food market and the use of intensive agricultural production techniques have exacerbated this situation. Many chemical pesticides persist in soil as toxic residues, often linked to human health problems, due to their resistance to degradation into simpler, less harmful chemicals (Fones *et al.*, 2020).

The widespread application of synthetic agricultural chemicals is increasingly regarded as an unsustainable approach, prompting contemporary agricultural research to concentrate on the development of alternative and even sustainable farming practices. The increasing demand for pesticide alternatives has facilitated the implementation of biological control (Suriani *et al.*, 2025). Agricultural output has consistently been affected by climatic circumstances, and that influence is intensifying as climate change progresses. Climate change would intensify difficulties in managing plant diseases due to the altered geographical distribution of pathogens. Biological disease control techniques can significantly affect the effectiveness of sustainable crop disease management (Chaloner *et al.*, 2021).

Plant pathogens and PGPR-mediated biocontrol

Plant growth-promoting rhizobacteria (PGPR) are crucial in sustainable agriculture because they enhance plant growth and protect crops against phytopathogens. PGPR microbes inhabit the rhizosphere and promote growth by solubilizing nutrients, producing phytohormones, and inducing systemic resistance. PGPR-based biocontrol agents are more environmentally friendly than chemical pesticides and do not cause environmental pollution. PGPR can effectively inhibit soil-borne pathogens, including *Fusarium*, *Trichoderma*, and *Pseudomonas*. Their dual function renders them a potential substitute for synthetic agrochemicals. The incorporation of PGPR into crop care can increase productivity while preserving ecological balance. Hence, PGPR are essential partners in sustainable crop protection (Bhattacharyya and Jha, 2012).

Fusarium: *Fusarium* species are pathogenic soil-borne fungi producing vascular wilts, root

rots, and seedling blights in numerous crops. They colonize the plant xylem, obstructing water transport and causing severe wilting. Toxins such as fumonisins and trichothecenes increase disease severity and pose food safety risks. *Fusarium oxysporum* is one of the most notorious species, comprising several host-specific forms (*formae speciales*). Its persistence in soil and formation of resistant chlamydospores render management difficult. Conventional fungicides are not very effective and pose environmental concerns. PGPR, such as *Pseudomonas fluorescens* and *Bacillus subtilis*, have demonstrated suppression of *Fusarium* wilt through antibiotic production and induced resistance. Crop rotation and resistant varieties are also used in integrated management. Information on PGPR-*Fusarium* interactions is crucial for sustainable control methods (Dean *et al.*, 2012).

Nematodes: Nematodes are destructive soil-borne pathogens that parasitize plant roots and cause significant yield losses in a wide range of crops. Among them, root-knot nematodes (*Meloidogyne* spp.) are the most widespread and economically damaging, inducing the formation of root galls that impair nutrient and water uptake, leading to stunted growth, wilting, and poor yield quality. These soil-dwelling parasites release effector molecules that hijack plant cellular machinery, dampen host resistance, and create specialized feeding structures called giant cells. Their broad host range and longevity in soil make management most challenging. Conventional nematicides, though effective, pose environmental and health risks, and their use is becoming increasingly regulated. As alternatives, PGPR, including *Pseudomonas fluorescens* and *Bacillus firmus*, exhibit encouraging nematocidal activity through toxin production, lytic enzymes, and the induction of systemic resistance in plants. In addition, crop rotation with non-host crops, soil amendments, and the use of resistant cultivars remain core components of integrated nematode management. Progressing the knowledge of PGPR-nematode interactions is vital for developing eco-friendly and long-lasting control measures (Jones *et al.*, 2013).

Viral pathogens: Plant viruses pose a significant problem for sustainable crop production because they can spread rapidly, cause systemic infection, and lead to high

yield losses. Insect vectors such as aphids, whiteflies, and leafhoppers, enabling rapid dispersal through cropping systems, primarily transmit these pathogens. Infections tend to cause symptoms such as chlorosis, mosaicism, stunted plant growth, and poor fruit or seed quality, significantly reducing market value. Conventional management, which relies on chemical vector control, has proven only temporarily effective due to vector resistance and environmental issues. Furthermore, the high mutation rates of RNA viruses enable them to evade host resistance genes, complicating breeding programs. Climate change also exacerbates the issue by increasing vector populations and altering virus-host relationships, thereby increasing the likelihood of viral epidemics (Jones, 2016).

Sustainable strategies are gaining prominence for plant viral disease management. Resistant cultivars remain a central strategy, but integrated tactics involving vector management, phytosanitary protocols, and crop diversification are also becoming important. Biological methods, particularly the use of PGPR, are promising because they can induce systemic resistance in plants. This resistance is a state of enhanced defense capacity, activated by the PGPR that primes the plant to respond more rapidly and robustly to viral attack. Thereby, this process lowers the severity of viral infections without compromising the environment (Kloepper and Ryu, 2020). For instance, *Bacillus subtilis* and *Pseudomonas fluorescens* were found to increase plant immunity against viruses while also enhancing growth (Murphy *et al.*, 2018). These approaches are consistent with the philosophy of sustainable agriculture, minimizing reliance on chemical pesticides and providing resistance against climate-induced viral outbreaks. Introducing PGPR-based biocontrol into current management systems thus has great potential to mitigate the growing problem of viral pathogens in crops. PGPR can effectively inhibit soil-borne pathogens, including *Fusarium oxysporum*, *Rhizoctonia solani*, *Pythium ultimum*, and *Macrophomina phaseolina*.

Beneficial Pseudomonas Strains as PGPR

Pseudomonas strains, particularly *Pseudomonas fluorescens* and *Pseudomonas putida*, are among the best-studied and most effective PGPR for biocontrol applications. It is important to note

that while some *Pseudomonas* species are plant pathogens (e.g., *Pseudomonas syringae*), the strains used in PGPR formulations are specifically selected, non-pathogenic, and beneficial. These beneficial *Pseudomonas* strains suppress phytopathogens through multiple mechanisms, including the production of antibiotics such as 2,4-diacetylphloroglucinol (DAPG), pyoluteorin, and phenazines. These metabolites suppress fungal pathogens like *Fusarium*, *Rhizoctonia*, and *Pythium*. Siderophores produced by *Pseudomonas* chelate iron, starving pathogens of this essential nutrient. They also induce Systemic Resistance (ISR) in plants, enhancing defense against a wide range of pathogens. Their effective ability to colonize the rhizosphere makes them persistent and competitive. Apart from pathogen suppression, they stimulate plant growth by solubilizing phosphates and synthesizing phytohormones such as Indole Acetic Acid (IAA) (Pandya *et al.*, 2018; Pradhan *et al.*, 2025; Jabborova *et al.*, 2021). *Pseudomonas*-based bioformulations are already practiced in Integrated Pest Management (IPM) schemes. They are eco-friendly substitutes for fungicides, in accordance with the objectives of sustainable agriculture. Future research aims to develop multi-strain consortia for enhanced biocontrol efficacy (Haas and Defago, 2005).

Plant pathogens are a diverse group of microorganisms that cause plant diseases, including fungi, oomycetes, bacteria, viruses, viroids, phytoplasmas, nematodes, and parasitic higher plants. Among these, fungi and bacteria constitute the primary groups of plant pathogens. Traditional definitions of plant pathogens assume that pathogenic microorganisms must possess specific pathogenicity/virulence factors to satisfy Koch's postulates (Minhans *et al.*, 2025). Many leaf diseases, including those caused by rust and powdery mildew fungi, exhibit race-specific interactions. In contrast, various soil-borne pathogens have been shown to exhibit race-non-specific interactions (Naseem *et al.*, 2025). Fungi can infiltrate plants through direct penetration of plant tissues, wounds, or natural openings like stomata. Some pathogens reside within plant tissues, while others are located on plant surfaces (Kılınç *et al.*, 2025). Molecular markers and cultivation-independent methods are crucial for identifying pathogens, particularly obligate pathogens that cannot be cultured.

Table 1. Bacterial PGPR strains and pathogen control in plants

Host	Pathogen	Disease	PGP strains (Bacteria)	References
Soybean	<i>Macrophomina phaseolina</i>	Root rot	<i>Bradyrhizobium</i> sp.	(Parveen <i>et al.</i> , 2019)
Pigeon pea	<i>Fusarium udum</i>	<i>Fusarium</i> wilt	<i>Rhizobacteria</i> spp.	(Dukare and Paul, 2021)
Apple	<i>Erwinia tracheiphila</i>	Bacterial wilt	<i>Gluconacetobacter</i> sp.	(Fu <i>et al.</i> , 2021)
Strawberry	<i>Macrophomina phaseolina</i>	Charcoal rot disease	<i>Azospirillum brasilense</i>	(Viejobueno <i>et al.</i> , 2021)
Cotton	<i>Macrophomina phaseolina</i>	Charcoal rot disease	<i>Pseudomonas fluorescens</i>	(Rahman <i>et al.</i> , 2017)
Citrus fruit	<i>Penicillium digitatum</i>	Blue mold	<i>Bacillus megaterium</i>	(Mohammadi <i>et al.</i> , 2017)
Brassica <i>campestris</i> L.	<i>Sclerotinia sclerotiorum</i>	Sclerotiniosis	<i>Bacillus thuringiensis</i>	(Wang <i>et al.</i> , 2022)

Table 2. Fungal PGPR strains and pathogen control in plants

Host	Pathogen	Disease	PGP strains (Fungi)	References
Rice	<i>Helminthosporium oryzae</i> , <i>Bipolaris oryzae</i>	Leaf brown spot	<i>Trichoderma viride</i> , <i>T. harzianum</i> , <i>T. hamatum</i>	(Jabborova <i>et al.</i> , 2025)
Scorzonera	<i>Alternaria scorzonerae</i> , <i>Fusarium culmorum</i>	Root and stem rot	<i>Trichoderma harzianum</i>	(Patkowska, 2021)
Okra	<i>Meloidogyne incognita</i>	Root-knot disease	<i>Trichoderma harzianum</i>	(Tariq <i>et al.</i> , 2018)
Beans	<i>Botrytis cinerea</i>	Chocolate spot	<i>Trichoderma virens</i>	(Yones and Kayim, 2021)
Onion	<i>Colletotrichum gloeosporioides</i>	Crop loss	<i>Trichoderma longibrachiatum</i>	(De la Cruz-Quiroz <i>et al.</i> , 2018)
Tomato	<i>Fusarium oxysporum</i>	<i>Fusarium</i> wilt	<i>Trichoderma</i> sp.	(Khafagi <i>et al.</i> , 2020)
Cabbage	<i>Sclerotinia sclerotiorum</i>	Cabbage wilt	<i>Trichoderma hamatum</i>	(Jones <i>et al.</i> , 2014)
Cocoa	<i>Phytophthora palmivora</i>	Black pod	<i>Aspergillus fumigatus</i>	(Sethi <i>et al.</i> , 2025)

Table 1 illustrates the biocontrol potential of diverse PGPR strains against a range of phytopathogens in essential crops such as soybean, pigeon pea, apple, and rice. Molecular markers and cultivation-independent methodologies are crucial for identifying pathogens and summarizing key plant growth-promoting strains and their efficacy against phytopathogens across various crops. For example, *Bradyrhizobium* sp. suppresses root rot in soybeans caused by *Fusarium solani*. Table 2 illustrates the biocontrol potential of diverse fungal PGPR strains against various phytopathogens in different crops, highlighting genera such as *Trichoderma* and *Aspergillus* that demonstrate broad-spectrum activity against fungal diseases like leaf brown spot in rice, root-knot nematode disease in okra, and *Fusarium* wilt in tomato (Jabborova *et al.*, 2025; Patkowska, 2021; Tariq *et al.*, 2018; Khafagi *et al.*, 2020). Table 2 summarizes the functional roles of beneficial phyto-microbiomes, including rhizosphere, endosphere, and phyllosphere microorganisms, in enhancing plant growth, stress tolerance, and pathogen suppression across various host plants. It highlights specific microbial genera and their mechanisms, including siderophore

production, nutrient solubilization, and the induction of systemic resistance.

Diversity of Microorganisms and Epidemic Incidents

Praveen *et al.* (2025) found that endophytic isolates of the *Burkholderia cepacia* complex suppressed *Fusarium moniliforme* on sugarcane. Microorganisms can also prevent the induction of dangerous genes in plants by pathogens that compete for plant resources (Bostan *et al.*, 2024). Furthermore, microorganisms can directly affect plant defense responses by synthesizing antagonistic chemicals within plant tissues or on plant surfaces. These organisms often belong to the Enterobacteriaceae family, renowned for their capacity to decompose plant tissues. In the development of plant protection techniques, both keystone microbial populations and their associated functional groups are intriguing targets for biocontrol strategies (Park *et al.*, 2024).

PGPR as a Promising Biocontrol Agent

The soil's complex ecology comprises a diverse array of microorganisms, including bacteria, fungi, protists, and other organisms.

They play important roles in plant growth, nutrient regulation, and biological regulation. These bacteria live in the plant endo-rhizosphere and rhizosphere and promote plant growth in many direct and indirect ways. Plant microbial communities or phytomicrobiome can have neutral, exploitative, or competitive interactions with plants that can influence crop yield (Lyu *et al.*, 2020). Scientists have recently conducted extensive research on the use of plant growth-promoting rhizobacteria (PGPR) to inhibit phytopathogens and promote plant growth (Alwahshi *et al.*, 2022). Muthukumaran *et al.* (2024) and Pourakbar *et al.* (2021) indicated that the rhizosphere microbiome comprises Bacteria, Archaea, Algae and Fungi, along with their genomic material that inhabit the rhizosphere. Microorganisms, through their extensive co-evolution with plants, can indirectly influence crop health and phenotypic flexibility by regulating plant development and defense mechanisms. Many bacteria present in the rhizosphere make steady supplies of PGPR. The collection of bacteria residing in the rhizosphere, on the root surface, and in the spaces between root cortex cells is referred to as the phytomicrobiome. PGPR co-evolved with their related host plants, establishing a synergistic relationship.

Numerous research efforts have investigated the effects, approaches, and potential for the successful application of PGPR in controlled agricultural plant production environments (Gouda *et al.*, 2018). They have been confirmed as effective in greenhouse research because a significant number of potential Biological Control Agents (BCAs) have been identified and could be deployed under controlled conditions (Dave *et al.*, 2024). *Pseudomonas stutzeri*, *Bacillus subtilis*, and *Bacillus amyloliquefaciens* have been shown to effectively colonize roots and inhibit the disease *Phytophthora capsici* in cucumbers. Vinothini *et al.* (2024) assert that *Bacillus subtilis* can protect tomato fruits from infections caused by *Rhizopus stolonifer* and *Penicillium* sp. during the post-harvest phase. *Bacillus amyloliquefaciens* isolates mitigate *Fusarium oxysporum*, the pathogen responsible for *Fusarium* wilt, in greenhouse environments. PGPR, as biocontrol agents, exhibit efficacy under controlled conditions, highlighting their applications in commercial horticulture and their roles in greenhouse production systems.

The indirect methods of PGPR in mitigating pathogen infections and enhancing plant growth under abiotic stress do not require separate discussion.

Additionally, PGPR that possess biocontrol activities also promote plant growth. PGPR can confer improved resistance to phytopathogens and tolerance to abiotic stresses on plants (Tasnim *et al.*, 2024). PGPR, as biocontrol agents, are effective under controlled conditions, indicating their potential use in commercial horticulture and greenhouse production systems. The indirect PGPR mechanisms for alleviating pathogen infections and promoting plant growth under abiotic stress do not involve differentiation. Additionally, PGPR with biocontrol potential also encourages plant growth (Yao *et al.*, 2021). PGPR have the potential to boost a plant's resistance to phytopathogens that cause plant diseases and its tolerance to abiotic stresses (Ayshasiddeka *et al.*, 2025). Figure 2 demonstrates the function of fungal and bacterial biocontrol agents to suppress phytopathogens and promote plant health through mechanisms like antibiosis, competition, and ISR. It highlights specific examples of PGPR and fungal antagonists that effectively control the disease across various crops.

The use of rhizobacteria to promote the development and maturation of crops in seeds, grains, root systems, and soils has gained significant popularity in recent decades. Rhizobacteria promote nitrogen fixation, enhance plant growth, and offer biological control against phytopathogenic microbes. *Azospirillum*, *Azotobacter*, *Bacillus*, *Rhizobium*, *Serratia*, *Stenotrophomonas*, *Streptomyces*, *Acinetobacter*, *Agrobacterium*, *Alcaligenes*, *Arthrobacter*, *Bradyrhizobium*, *Frankia*, *Pantoea*, *Pseudomonas*, and *Thiobacillus* are among the many microbial species used in bacterization (Barasarathi *et al.*, 2025). Numerous plant diseases caused by nematodes, bacteria, and fungi are reported to be managed by PGPR. Due to their potential adverse effects on the host plant along with other soil microorganisms, BCAs are employed to reduce nematode populations. Crop Rotation, Nematicides, Microbiological Management, or Organic Amendments to the soil have been utilized to mitigate plant-parasitic nematode infestations. Filtrates from *in vitro* cultures of

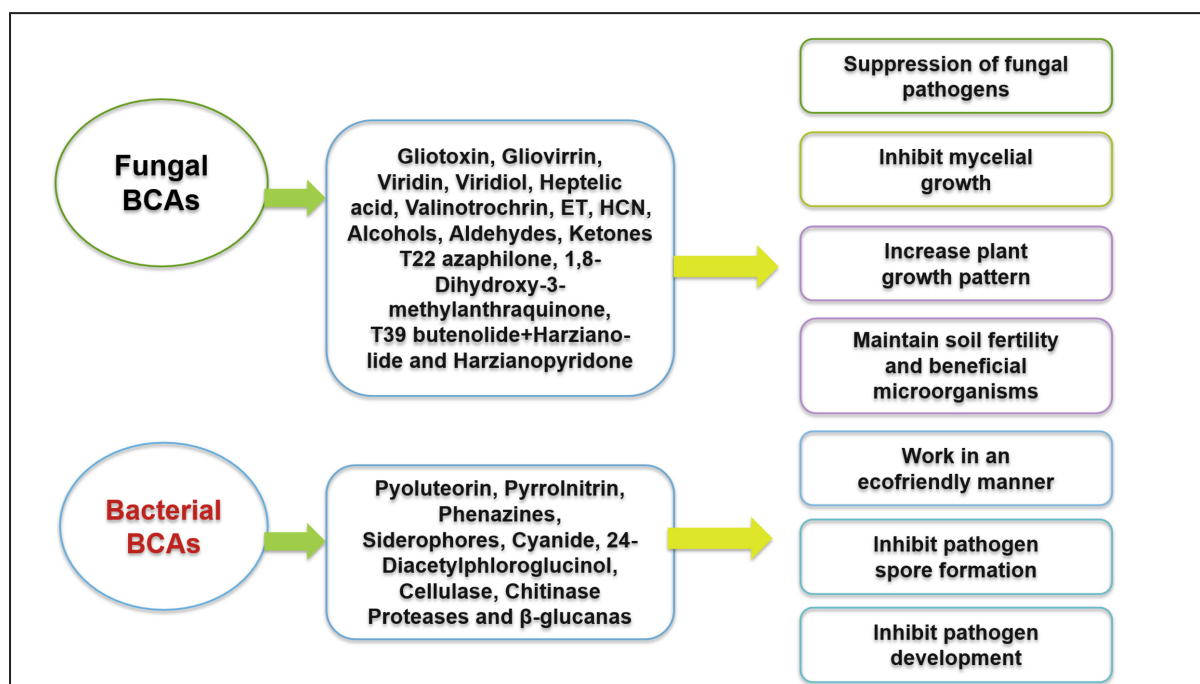


Fig. 2. Fungal and bacterial biocontrol agents and their impact on plants.

a *Pseudomonas* sp. strain significantly reduce the mortality of *Meloidogyne javanica* juveniles, thereby reducing nematode populations and root galls, and concurrently enhancing plant development and yield. Moreover, the behavior and feeding patterns of nematodes are influenced by inoculations of the *Bacillus* species. Additionally, strains of *Bacillus subtilis*, *Pseudomonas striata*, and *Pseudomonas fluorescens* disrupt the nematode population (Hamed *et al.*, 2024).

Bacillus strains have been effectively utilized for the biological control of root-knot nematode (RKN) infestation. Limited research suggests that endophytic *Pseudomonas fluorescens* and even *Bacillus* spp. enhance systemic resistance in crops against nematodes by elevating the activity of defense-related enzymes, including phenylalanine ammonia-lyase, polyphenol oxidase, and peroxidase, which produce antagonistic compounds and modify certain root exudates, such as amino acids and polysaccharides. In tomatoes resistant to RKN, *Pseudomonas fluorescens* isolates enhanced the expression of defense enzymes. Treatment with *Pseudomonas fluorescens* and *Paecilomyces lilacinus* resulted in a lower nematode community in roots, tubers, and soils than in the control (Podder *et al.*, 2025). In India, losses from post-harvest handling of fresh fruits and vegetables

ranged from 4.6% to 15.9% (Showkat *et al.*, 2024). BCAs are used to control post-harvest fungal infections, and this method is the most environmentally friendly. BCAs are currently a practical solution for controlling post-harvest diseases caused by plant pathogens and can generally shield plants from fungal diseases (Alshaikh *et al.*, 2024). The reduction in the use of causative agents in agricultural conservation decreased labor, soil and water contamination from plants, and agricultural waste management (Hamed *et al.*, 2024).

Green vegetables are at risk of mycotoxin contamination from mycotoxin-producing fungi such as *Alternaria* sp., *Aspergillus* sp., *Penicillium* sp., and *Fusarium* sp., which can cause post-harvest diseases. Fruits and vegetables infected with pathogens such as *Alternaria* sp., *Aspergillus* sp., and *Fusarium* sp. produce toxins including aflatoxins, ochratoxins, and *Fusarium* toxins. *Serratia plymuthica* biopriming and pelletizing methods, in conjunction with *Verticillium dahliae*, in canola plants demonstrated notable biocontrol, indicating that BCAs are as effective as chemical fungicides in managing diseases (Vafa *et al.*, 2024). Cucumber, chickpeas, rice, tomatoes, wheat, peanuts, brinjal, and potatoes are among the plants in which several chemicals generated by *Bacillus* species facilitate the biocontrol of plant pathogens. According to

Alkilayh *et al.* (2024), *Pectobacterium carotovorum* can control soft rot disease in tobacco plants when combined with the fungicides BTH and *Bacillus subtilis* strain B4. *Pseudomonas* species, as biological control agents, often mitigate root-knot and root-rot illnesses.

Fungal Biocontrol Agents

Trichoderma - *Trichoderma* is a genus of fungi that is highly valuable as a biocontrol agent against plant pathogens. Unlike pathogenic fungi, beneficial *Trichoderma* species (e.g., *T. harzianum*, *T. viride*, *T. asperellum*) are commercially used for their antagonistic properties against phytopathogens. They inhibit pathogenic fungi through mechanisms including mycoparasitism, competition, and secretion of hydrolytic enzymes (chitinases, glucanases) (Panicker and Sayyed, 2022). *Trichoderma harzianum* and *Trichoderma viride* are commercially used in biocontrol products. *Trichoderma* increases plant resistance by inducing Systemic Resistance (ISR) and promoting the biosynthesis of phytoalexins and antioxidants. In addition to inhibiting pathogens, *Trichoderma* promotes plant growth by solubilizing nutrients and synthesizing growth-promoting substances. Its high growth rate and adaptability enable it to colonize the rhizosphere and suppress pathogens. *Trichoderma* is also responsible for enhancing soil health and the degradation of organic matter. As a non-chemical biocontrol agent, it reduces reliance on chemical fungicides. Future directions include the genetic enhancement of *Trichoderma* strains to broaden their activity (Hermosa *et al.*, 2012).

According to Ahmad *et al.* (2024), PGPR isolates exhibited antifungal properties against *Rhizoctonia solani*, *Macrophomina phaseolina*, *Fusarium solani*, and *Fusarium oxysporum* in mung bean plants. Additionally, root rot caused by fungal infections can be avoided using these isolates. Chili pepper anthracnose can be controlled by applying the bacterial biocontrol agent *Pseudomonas aeruginosa* to combat the causative pathogen, *Colletotrichum capsici*. According to Jisha *et al.* (2018), *Pseudomonas aeruginosa* can also cause Chili Peppers to develop systemic resistance to anthracnose. The primary purpose of synthetic chemical pesticides is to control post-harvest diseases. Plant disease resistance, soil degradation, and toxicological

risks to humans and the environment could result from this. As a result, there is now a general movement to identify alternatives to agrochemicals for managing phytopathological conditions. The use of microbial antagonists, or BCAs, has gained popularity as an alternative to synthetic chemical fungicides due to their many benefits, including being non-hazardous, environmentally friendly, cost-effective, and practical for controlling post-harvest pathogen infections (Fotoohiyan *et al.*, 2024).

Biocontrol Mechanisms of PGPR

PGPR can produce the phytohormones Indole-3-Acetic Acid (IAA), Ethylene (ET), Jasmonic Acid (JA), Gibberellic Acid (GA), and Cytokinins (CKs) or increase the solubilization of specific nutrients (Shahzad *et al.*, 2019). PGPR residing within a host plant can promote plant growth through direct and indirect mechanisms (Fig. 3). Direct approaches encompass the synthesis of plant hormones, phosphorus solubilization, and improved iron assimilation. Antibiotic production, nutritional competition, parasitism, inhibition of pathogen toxins, and induced resistance are some examples of indirect effects (Elnahal *et al.*, 2022) (Fig. 3). Abbas *et al.* (2019) assert that PGPR also restructure root morphology, enhance surface area, and improve function. In addition, PGPR outcompetes other bacteria and inhibits their growth (Wani *et al.*, 2024). Antimicrobial peptides comprise Enzymes, Bacteriocins, and Antibacterial Proteins (Yatoo *et al.*, 2024). Antibiotics, tiny antibacterial agents, are produced by PGPR and may inhibit the growth or metabolic functions of microbial infections. These strain-specific antibiotics can disrupt the cell walls of bacterial pathogens, alter their membrane structure, and interfere with ribosomal RNA (rRNA) (Nazari and Smith, 2020). Most types of bacteria produce bacteriocins and exhibit more varied inhibitory activity. Figure 3 illustrates the Dual mechanisms - Direct (e.g., nutrient solubilization, phytohormone production) and Indirect (e.g., antibiotic synthesis, induced systemic resistance) by which PGPR enhance plant growth and suppress phytopathogens.

Siderophores are specific ferric iron chelating compounds that block the access of phytopathogens to iron, maintaining the vitality of plants, particularly in conditions of limited iron. PGPR can reduce the incidence of

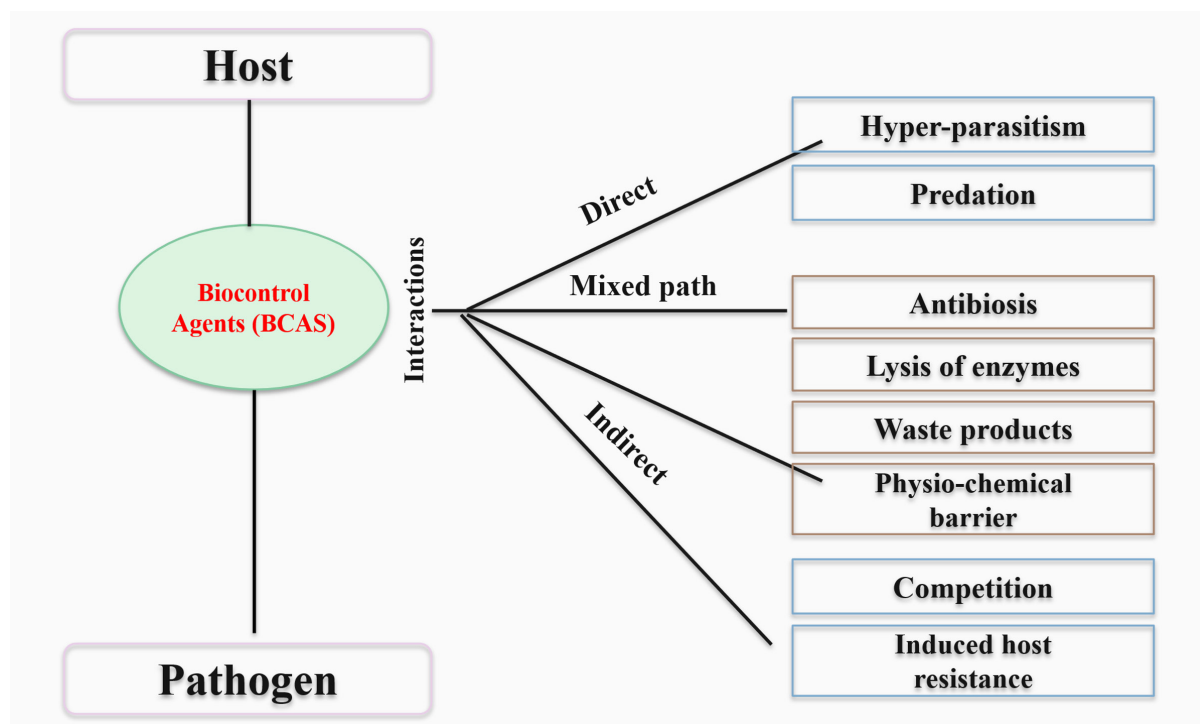


Fig. 3. Mechanism of microbial biocontrol agents.

many plant diseases and excrete extracellular siderophores. Bacteriocins, siderophores, and antibiotics were identified as the three principal strategies for prospective biocontrol before their *in vivo* use. Some studies have investigated PGPR as tools for managing plant diseases and producing plant-beneficial metabolites, such as siderophores (Ferioun *et al.*, 2024). PGPR indirectly enhances crop resistance to stress. Resistance-inducing and antagonistic PGPR can be used as new inoculants with combinations of distinct mechanisms of action, enabling efficient biocontrol and plant growth promotion (Lyu *et al.*, 2020). PGPR can produce Volatile organic compounds (VOCs), which stimulate plant growth and induce Induced Systemic Resistance (ISR) against infection. Fatimah *et al.* (2024) found that PGPR could induce ISR, thereby improving the plant's resistance to disease. Colonization of roots by Arbuscular Mycorrhizal Fungi (AMF) and certain non-pathogenic microorganisms can enhance plant resistance to biotic stresses. Systemic Acquired Resistance (SAR) may be triggered by a pathogen infection (Mathys *et al.*, 2012).

Molecular pathways

Induced systemic resistance (ISR): a plant defense mechanism triggered by rhizosphere

colonization by beneficial microorganisms, particularly PGPR such as *Pseudomonas fluorescens* and *Bacillus subtilis*. Unlike SAR, which utilizes Salicylic Acid (SA) signaling, ISR primarily exploits the Jasmonic Acid (JA) and Ethylene (ET) pathways. When PGPR colonize roots, they secrete molecular cues such as flagellin, lipopolysaccharides, and microbial volatile organic compounds (e.g., 2,3-butanediol) that act as ISR elicitors. Pattern-Recognition Receptors (PRRs) sense the cues on the plant surface, triggering intracellular cascades that activate JA/ET-regulated defense genes. For example, LOX (lipoxygenase) is involved in JA biosynthesis, ERF1 (Ethylene Response Factor) transduces ET signaling, and PDF1.2 (plant defensin) encodes an antimicrobial protein (Sharma *et al.*, 2025). All these genes reinforce cell walls, induce antimicrobial metabolite production, and enhance resistance to necrotrophic pathogens and insect herbivores. One of the most critical aspects of ISR is that it “primes” the plant, which means the defense is not continuously active but responds more rapidly and intensely upon pathogen attack. It decreases metabolic cost while ensuring broad-spectrum protection. Therefore, ISR is a sustainable, microbe-mediated mechanism that

promotes plant resistance without chemical pesticides (Pieterse *et al.*, 2014).

Siderophore gene clusters: Siderophores are low-molecular-weight iron-sequestering compounds excreted by numerous rhizosphere bacteria like *Pseudomonas*, *Enterobacter*, and *Bacillus*. Because Fe^{3+} is sparingly soluble in aerobic soils, siderophore production enables microbes to scavenge this critical micronutrient, thus competing with pathogens for iron sources. For instance, *Pseudomonas fluorescens* produces fluorescent siderophore pyoverdine whose biosynthesis is controlled by the *pvd* gene cluster (Budamagunta *et al.*, 2022). After secretion, pyoverdine forms high-affinity complexes with Fe^{3+} and returns this metal to bacterial cells via specific receptors, thereby aiding microbial growth and the establishment of rhizosphere colonization. Meanwhile, iron limitation, caused by siderophore-mediated iron withdrawal, constrains the growth of pathogens such as *Fusarium* and *Rhizoctonia*, which cannot effectively compete in iron-restricted environments. Besides competitively inhibiting nutrient uptake, siderophores also serve as signals that trigger plant defense. For example, siderophores can induce ISR-like processes, leading to the expression of

JA/ET-dependent defense genes in plants. Therefore, siderophore-producing bacteria act directly by starving pathogens and indirectly by priming the host immune system. This dual activity emphasizes that siderophores are key determinants of microbial biocontrol and plant health within the rhizosphere (Ahmed and Holmström, 2014).

Rhizosphere and microbiome alliance

Rhizosphere interactions: The microbial populations interact with their host plants in the rhizosphere. Both harmful and beneficial microbial populations inhabit the rhizosphere. Figure 4 illustrates the microbe-mediated signaling mechanisms in plants, highlighting both Systemic Acquired Resistance (SAR) and Induced Systemic Resistance (ISR). These pathways enhance plant defense against pathogens through hormone-driven signaling cascades initiated by beneficial microbes. Furthermore, their modifications are contingent on the chemical composition and the characteristics of the soil itself (Suriani *et al.*, 2024). Rhizobacterial partners elicit several responses within the rhizosphere, including the augmentation of soil nutrients, stabilization of soil conditions, promotion of root growth, and further improvement of remediation processes.

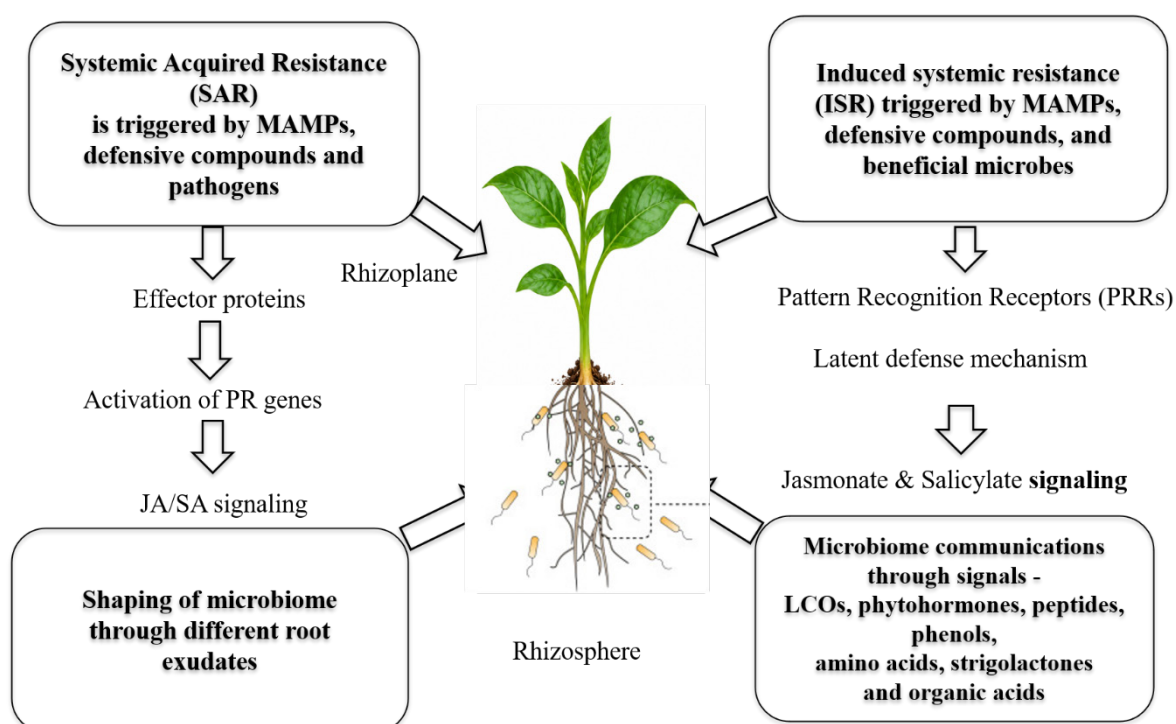


Fig. 4. Mechanisms of microbiome-mediated induction of systemic resistance in plants.

Table 3. Phyto-microbiomes are connected with the plant rhizosphere, endosphere, as well as phyllosphere

Nature	Host	Microorganism	Functional Role(s)	Reference
Rhizosphere	<i>Secale cereale</i> L.	<i>Pseudomonas fluorescens</i>	Produces siderophores for iron acquisition, secretes antibiotics (e.g., phenazines), promotes plant growth, and suppresses pathogens.	(Galindo <i>et al.</i> , 2019)
Rhizosphere	<i>Sorghum bicolor</i> L.	<i>Pseudomonas chlororaphis</i>	Biocontrol agent against fungal pathogens via production of phenazine and pyrrolnitrin; enhances nutrient uptake and root colonization.	(Wipf <i>et al.</i> , 2021)
Rhizosphere	<i>Glycine max</i> L.	<i>Bacillus firmus</i>	Induces systemic resistance, produces extracellular enzymes against nematodes, and promotes growth by solubilizing nutrients.	(Zeffa <i>et al.</i> , 2020)
Rhizosphere	<i>Oryza sativa</i> L.	<i>Halobacillus dabanensis</i>	Halotolerant bacterium aiding salt stress tolerance, enhances osmolyte production, and supports plant growth under saline soils.	(Babarabi <i>et al.</i> , 2024)
Endosphere	<i>Oryza sativa</i> L.	<i>Epichloe festucae</i>	A symbiotic fungus that enhances drought tolerance produces alkaloids that protect plants from herbivores and pathogens.	(Germon <i>et al.</i> , 2018)
Endosphere	<i>Lolium perenne</i> L., <i>Panicum rigidulum</i> L.	<i>Neotyphodium lolii</i> , <i>Balansia henningsiana</i>	Endophytic fungi improve stress resistance, enhancing nutrient assimilation and producing bioactive compounds with defense roles.	(Adeleke and Babalola, 2022)
Endosphere	<i>Syngonium podophyllum</i> L.	<i>Phanerochaetaceae</i> spp., <i>Bjerkandera fumosa</i> , and <i>Phlebiopsis favidoalba</i>	Ligninolytic fungi are involved in secondary metabolite production, plant defense enhancement, and the degradation of complex organic matter.	(Adeleke and Babalola, 2022)
Phyllosphe	<i>Oryza sativa</i> L.	<i>Methylobacterium radiotolerans</i>	Fixes nitrogen, produces cytokinins that enhance leaf growth, and tolerates radiation/oxidative stress—supporting foliar health.	(Feroun <i>et al.</i> , 2025)
Phyllosphe	<i>Glycine max</i> L.	<i>Methylobacterium extorquens</i>	Uses methanol from leaf metabolism, produces phytohormones, and improves plant stress tolerance.	(Pang <i>et al.</i> , 2021)
Phyllosphe	<i>Medicago truncatula</i> L.	<i>Phymatotrichopsis omnivore</i>	Pathogenic fungus causing root rot, but also crucial in microbial competition, shaping the balance of the leaf microbial community.	(Gupta <i>et al.</i> , 2021)
Phyllosphe	<i>Zea mays</i> L.	<i>Bacillus</i> sp., <i>Pseudomonas</i> sp., <i>Microbacterium</i> sp., <i>Stenotrophomonas</i> sp., <i>Enterobacter</i> sp., <i>Pseudarthrobacter</i> sp., and <i>Kocuria</i> sp.	Diverse microbial consortia promote plant growth, suppress diseases, produce phytohormones, and enhance stress tolerance.	(Abadi <i>et al.</i> , 2020)

The rhizobacteria and roots interact in the rhizosphere to enhance nutrient uptake by the shoots and stimulate plant root system growth. Microbial populations in the field are used as alternatives to chemical fertilizers since they have been proven to enhance crop production (Sagar *et al.*, 2024).

Root exudation

Microbial communities in the rhizosphere depend on root exudates as their primary carbon source, and the composition of these

exudates is dynamically shaped by complex rhizobacterial-rhizosphere interactions (Table 3). However, root exudation is not a static process; it is highly modulated by the plant's physiological status and environmental conditions. Key factors such as the plant's nutritional status (e.g., phosphorus or iron deficiency), abiotic stresses (e.g., drought, salinity, and soil pH), and soil type (e.g., texture and structure) directly influence the quantity and quality of secreted compounds (Raklami *et al.*, 2019). This dynamic exudation profile,

in turn, influences root development and microbial colonization, serving as a nuanced mediator in plant-microbe interactions. These root exudates comprise a diverse array of chemical compounds, including peptides, sugars, vitamins, amino acids, enzymes, and various primary and secondary metabolites (Korenblum *et al.*, 2020). The resulting microbial populations are thus linked to specific exudate compounds that promote the development of beneficial communities, thereby enhancing biomass and yield across diverse crop species. Furthermore, certain root exudates have a direct defensive purpose by selectively inhibiting the growth of pathogenic microbes. For instance, Salehi-Sardoei *et al.* (2024) demonstrated that inoculation with *Bacillus* species altered the rhizosphere environment, leading to the suppression of root-borne diseases, an effect likely mediated by changes in the exudate profile.

Bona *et al.* (2019) conducted a study to validate the behaviors of several bacteria within the rhizosphere. The bacterial genera from various groups, such as *Pseudomonas*, *Streptomyces*, *Bradyrhizobium*, *Bacillus*, and *Burkholderia*, have been reported to exhibit high protein expression and therefore trigger several regulatory processes within the rhizosphere, as supported by proteomic studies of the *Vitis vinifera* rhizosphere (Daneshmand *et al.*, 2024). Strigolactone, a root exudate and new phytohormone, is recognized for its ability to promote primary root elongation and even root hair development in the rhizosphere. Various monocot and dicot plants release them as root exudates into the rhizosphere, where they facilitate mutualistic association between the root system and Arbuscular Mycorrhizal fungi (Moghaddam *et al.*, 2024). According to Hamid *et al.* (2024), organic acids are among the root secretions that contain high-energy molecules for microbial symbionts, and they modulate the regulation of various biogeochemical cycle secretions in the rhizosphere.

Tryptophan-containing exudates serve as a precursor for Indole-3-Acetic Acid (IAA) synthesis; however, the production of phytohormones associated with rhizobacteria is impeded by insufficient carbon molecules in root exudates. The microbial partners further utilize ACC, an ethylene precursor, as a carbon and nitrogen source (Xiang *et al.*,

2019). Rhizobacterial symbionts regulate stress-responsive genes, including heat shock proteins, ascorbate peroxidase, and S-adenosylmethionine synthetase, and these rhizosphere interactions influence defense-related processes in plants under diverse environmental stresses (Nithyapriya *et al.*, 2024). In the rhizosphere, they also offer protection from infections and root herbivores. These alliances or partnerships between microbes and plants benefit hosts by enhancing yields, stimulating growth, and facilitating the acquisition of essential nutrients (Pandya *et al.*, 2018; Manasa *et al.*, 2021). These complicated relationships, according to Etesami and Adl (2020), are necessary for plant health and soil health.

Microbiome and Root Architecture

Through both direct and indirect means, microbes can efficiently colonize roots to promote growth. Indirect methods can be used to accomplish this. The phytohormonal ensemble influenced by root-knot bacteria within the roots consists of auxins, cytokinins, and Ethylene, which are signaling chemicals that promote lateral root branching and root hair development. As plants progress through distinct developmental stages, the root exudation mechanism is modulated, leading to variations in the alignment of the rhizo-microbiome. The specific enzymes, antibiotics, siderophores, and essential nutrients that enhance root growth also exhibit antagonistic qualities in many pathogenic organisms (Al-Kahtani *et al.*, 2020).

Secondary metabolites-mediated interaction

Plants encounter a variety of stressors that impair their physiological and metabolic processes; as a result, they must be controlled to ensure their development and survival. These pressures are directly linked to microorganisms, which enable them to modify specific systems. Bacteria that help regulate the plant's metabolic network and activate stress-related genes and metabolites (De la Fuente Cantó *et al.*, 2020) mediate various stress-resistance mechanisms. Microorganisms that produce stress-related metabolites are widely studied. They also change the transcriptional machinery that plants use to withstand stress. Under stress, the expression of WRKY and MYB is also modulated by the activation of the ABA-signalling cascade. When microbes alter plants' metabolic pools, a variety of genetic changes have been seen in response

(Kousar *et al.*, 2020). It has been discovered that the rhizosphere, which serves as the foundation for microbial-mediated interactions, releases a wide variety of secondary metabolites, specifically volatile chemicals and suitable solutes. Different bacteria have characteristics related to ionic homeostasis, stress tolerance, cellular osmoregulation, and the reduction of harmful ions. They also release a variety of volatile chemicals or anti-pathogenic metabolites, including Sugars, Polyols, Betaines, Amino Acids, etc. (Kumar and Verma, 2018).

Microbial secondary metabolites determine the outcome of plant-microbe interactions by modulating stress resistance and downregulating pathogens via selective biochemical pathways (Hidayah *et al.*, 2022). For example, *Pseudomonas fluorescens* produces phenazines, redox-active metabolites that inhibit fungal respiration, controlled by the *phz* gene cluster. In the same way, 2,4-Diacetylphloroglucinol (DAPG), controlled by the *phlACBD* genes, suppresses root-infecting fungi such as *Fusarium* and *Rhizoctonia*. *Bacillus subtilis* is a producer of various lipopeptides, such as Surfactin, Fengycin, and Iturin; these are amphiphilic compounds that insert into pathogen membranes and also induce ISR. Microbial production of Volatile Organic Compounds (VOCs), such as acetoin and 2,3-butanediol, also promotes plant growth and induces JA/ET defense pathways.

In addition to suppressing pathogen populations, microbes emit osmoprotective metabolites such as exopolysaccharides, polyols, and betaines, which stabilize membranes and regulate ion homeostasis under drought or salinity stress (Sayyed *et al.*, 2011; 2015). These metabolites interact with plant regulatory networks by modulating transcription factors such as WRKY and MYB and activating the ABA signaling pathway. This molecular reprogramming enhances drought tolerance, increases photosynthetic efficiency, and primes systemic defenses, leading directly to improved crop biomass, higher yield, and greater field resilience. Together, these microbial secondary metabolites form a biochemical arsenal that promotes plant growth and tolerance by direct antimicrobial action and indirect genetic reprogramming of host metabolism (Ongena and Jacques, 2008).

Plant-microbe interaction

The utilization of mycorrhizal fungi, as well as microorganisms that enhance plant growth, markedly accelerates plant development. Microbes use a variety of biochemical and molecular pathways to sustain development through nutrient uptake and hormone regulation, thereby strengthening plant growth regulators' tolerance to unfavorable conditions (Spence and Bais, 2015). Bacteria also release a variety of metabolites to support specific metabolic processes, including the formation of exopolysaccharides (Sayyed *et al.*, 2011; 2015), nitrogen fixation (Vyas *et al.*, 2026), phosphate and zinc solubilization (Sethi *et al.*, 2025; Pradhan *et al.*, 2025), and hormone signaling, thereby preventing undesirable conditions. To combat adverse circumstances, they can also produce essential enzymes, such as glucanases, ACC-deaminases, lytic enzymes, and chitinases. These qualities may enable them to function as both powerful fertilizers and insecticides in agricultural techniques. Subsequently, this could enhance the overall nutritional quality and yield, benefiting farmers by increasing their revenue and promoting organic and sustainable farming practices (Eswaran *et al.*, 2024).

Plant development, health, and the dynamics of the ecosystem as a whole are all impacted by interactions between microbes and plants. Complex molecular signaling pathways allow bacteria and plants to communicate with one another. Plant immune responses are elicited when plants detect Microbe-Associated Molecular Patterns (MAMPs), enabling them to protect themselves from potential infections. To become successful colonizers, microbes then find mechanisms to evade or suppress these defenses (Wang *et al.*, 2022). At the ecological level, plant-microbe interactions facilitate the establishment of soil structure, nutrient cycling, and the stability of entire ecosystems. They shape biodiversity patterns by determining succession and plant community composition.

Ecosystems may experience structural and functional alterations due to changes in interactions driven by factors such as climate change. The root diameter and length can be constrained by reduced availability of soil photosynthetic material due to global warming (Qiu *et al.*, 2021). Certain constituents of the plant microbiome can alleviate abiotic stress (Sayyed

et al., 2026). They synthesize phytohormones, extracellular polymeric substances (biofilms), 1-aminocyclopropane-1-carboxylate (ACC), and ACC deaminase, and detoxify reactive oxygen species, thus alleviating the effects of abiotic stress on plants (Bright *et al.*, 2025; Nasab *et al.*, 2022; Sheikh *et al.*, 2022). The symbiotic interaction between microbes and plants is central to ecosystem functioning and plays a crucial role in sustainable agriculture (Sayyed *et al.*, 2026). Future research on the intricacies of these interactions will shed light on fundamental biological processes and highlight key environmental and agronomic concerns (Singh *et al.*, 2024).

Microbe-microbe interaction

Competition, parasitism, or cooperation can account for microbial interactions. Recent research suggests that microbial communities harbor keystone taxa that are strongly correlated with other taxa (Banerjee *et al.*, 2020). Irrespective of their geographic and temporal differences, these taxa have a considerable impact on the composition and functionality of the microbiome. They play a unique and significant role in microbiomes, and so does their absence, which is likely to have a substantial effect on the composition and, subsequently, the activity of the microbiota. They have impacted the host microbiota *via* several pathways. They may alter the effector group or serve as intermediaries that modulate microbiome populations and their activity. It has been demonstrated that certain strains of *Pseudomonas fluorescens* generate 2,4-diacetyl phloroglucinol. This secondary metabolite prevents the growth of *Gaeumannomyces graminis* var. *tritici*, the bacterium that causes wheat take-all (Afzal *et al.*, 2019).

Likewise, certain beneficial bacteria (such as *Bacillus*) and fungi (such as *Trichoderma*) produce secondary metabolites that inhibit microbial proliferation (Enshasy *et al.*, 2020). Symbiotic associations between Arbuscular mycorrhizae and various *Burkholderia* species, which may alter abundance and diversity (Vafa *et al.*, 2021), may affect the productivity, variation, and richness of plant communities. Using a systems biology approach, Agler *et al.* (2016) investigated the function of bacteria, fungi, and oomycetes in the formation of the phyllosphere microbiota of *Arabidopsis thaliana*.

The researchers identified a complex network of interkingdom interactions that profoundly influenced community organization, along with many closely related species known as “Microbial Hubs”, which significantly impacted population dynamics (Akter *et al.*, 2024).

Effector proteins, which can block, activate, or alter the host’s defense mechanisms, are produced by pathogens and other symbiotic bacteria (Roberts and Lindow, 2014). These invade hosts with compromised defenses and are primary colonizers that practice hyperparasitism. These underscore the significance of such interactions in shaping the microbiome’s constitution and structure, which can influence microorganism growth in the host (Etminani *et al.*, 2024). No or minimal changes were observed in the rhizosphere, as per a study using 454 amplicon sequencing to examine the impact of *Bacillus amyloliquefaciens* on the lettuce microbiome (Qayoom *et al.*, 2024). Approximately 55% of the introduced bacterial DNA was detected in their environment after one month. Like *Bacillus amyloliquefaciens*, there was a minimal impact on composition (Gowtham *et al.*, 2024).

The Function of Plant-Associated PGPR within Agriculture

Modern-day agriculture depends on the plant-associated microbiome. Symbiotic associations, such as those between plants and Plant Growth Promoting Rhizobacteria, promote plant growth, enhance nutrient acquisition, and increase stress tolerance, leading to higher agricultural productivity and quality. The microbiome’s potential aligns with sustainable agriculture principles that promote environmental conservation and resource efficiency. Sustainable farming systems depend on their ability to increase plant tolerance to ecological shocks (Mahmud *et al.*, 2021). Endophytic and resident epiphytic bacteria associated with plant tissue may be liberated during seed germination, thereby affecting the composition of soil microbes (Tariq *et al.*, 2025). Beneficial seed microbes influence the initial growth of plants, impacting germination and seedling viability (Santos *et al.*, 2019). Microbes use a phosphotransferase system and a periplasmic binding protein to indirectly detect chemicals in root exudates, leading to receptor attachment. *Azospirillum*

brasiliense chemotaxis is linked to the galactose-binding periplasmic protein ChvE and its interacting chemoreceptors. Specific microbes in the soil can absorb certain compounds from root exudates at the plant's growing site, while releasing others (Bodhankar, 2022). Plants can synthesize substances derived from microbes owing to the capacity of soil microbes to produce molecules that modulate plant signaling and metabolism. A variety of microbiome assemblies are produced by certain microbes, including *Penicillium* and *Paenibacillus polymyxa*, which create antibiotics such as Penicillin and polymyxin that alter cell permeability, increase leakage, and increase the exudation of organic molecules (Dastogeer *et al.*, 2020).

Plant's Immunity

Plants may actively recruit beneficial bacteria that have evolved to confront problems over millions of years of co-evolution, rather than merely responding to changes in the microbiome. The majority of plant-microbe interactions transpire in the rhizosphere (Akkurak *et al.*, 2024). Diverse root exudates serve as cues that recruit beneficial bacteria during periods of stress. Leguminous plants, for example, synthesize more flavonoids to attract nitrogen-fixing bacteria whenever Nitrogen (N) is deficient. Similarly, beetroot roots attract beneficial bacteria into the endosphere upon contact with the pathogen *Rhizoctonia solani*, thereby reducing fungal infection (Wolfgang *et al.*, 2023). Rhizospheric bacteria boosted nitrogen availability through nitrification, delayed blooming, and accelerated plant growth by converting tryptophan to indole-3-acetic acid, thereby suppressing genes linked to flowering (Kılınç *et al.*, 2025). Similar to mutualistic connections, flexible associations are present when inorganic phosphate levels are low (Sharma *et al.*, 2025).

Arabidopsis thaliana plants with altered jasmonate signaling pathways exhibit distinct bacterial and archaeal communities compared to the wild type. A greater diversity of *Streptomyces*, *Bacillus*, *Lysinibacillus*, and *Enterobacter* species was identified within the rhizosphere of the mutant plants (Omar *et al.*, 2022). Some studies claim that pathogen infections in plant tissues alter defense-related signaling, which could affect Root Exudate Secretion and,

consequently, the mutant. Microbiome changes in the defensive mechanisms of Salicylic Acid and Jasmonic Acid significantly affect the natural microbiome of *Arabidopsis* (Blouin and Jacquiod, 2020). Furthermore, studies have shown that exogenous glucosinolate synthesis significantly alters the microbial community in the root zone of transgenic *Arabidopsis* (Shahzad *et al.*, 2019).

The microbiome is profoundly influenced by exudates from plant roots, particularly those originating in the rhizosphere, which comprise sugars, organic and phenolic substances, amino acids, and numerous minor secondary metabolites (Tariq *et al.*, 2020). Plant species and genotypes demonstrate considerable variation in root exudates. These variations in exudates could include substrates, chemotactic factors, or Signaling Chemicals that affect the dynamics and structure of microbial communities (Hilton *et al.*, 2021). Roots exude an array of natural chemicals that amalgamate to attract microbial communities. The integrated evolutionary process, governed by host-associated microbiome interactions, is crucial for the dynamic shifts in the plant microbiome. Therefore, it is imperative to develop sensitive and accurate profiling methods (Pang *et al.*, 2021).

Over millions of years of co-evolution, plants have evolved to actively reconfigure their root microbiome through internal signaling pathways to confront specific stresses, rather than merely responding to microbial changes. The jasmonic acid (JA) and salicylic acid (SA) Defense pathways, along with specialized metabolic pathways such as those for glucosinolates, act as central regulators of this process by dynamically altering the composition of root exudates. For instance, leguminous plants under nitrogen deficiency increase flavonoid secretion to recruit nitrogen-fixing rhizobia. At the same time, pathogen attack triggers JA/SA signaling, leading to the exudation of compounds that attract protective endophytes, as seen in beetroot. This causal link is further evidenced by the fact that *Arabidopsis* mutants with altered JA signaling host distinct microbial communities, and transgenic plants producing exogenous glucosinolates profoundly shift their root microbiota. Thus, these signaling cascades translate internal stress perception into a precise chemical dialogue with the soil,

selectively enriching for a beneficial microbiome that enhances agronomic traits like nutrient acquisition and disease resistance (Sridhar *et al.*, 2025).

Challenges Related to the Application of PGPR as a Potential Effective Biocontrol Agent

A biocontrol agent (BCA) should ideally have as many advantageous characteristics as possible, such as the ability to grow for commercial production, high rhizosphere competence, improved plant growth capabilities, a wide range of bioactive metabolites, environmental safety, aggressive compatibility with other rhizobacteria, and abiotic stress tolerance (Lyu *et al.*, 2020). Efficient strains can only combat pathogens when they colonize the rhizosphere or even root tissues; thus, successful root colonization is essential for efficient biocontrol by PGPR. The extensive use of BCA stems from its variable performance, which can be attributed to several environmental conditions, including inadequate soil survival, crop compatibility, and interactions with natural microbial species. According to Murali *et al.* (2023), researchers should see colonization and survival as crucial traits when identifying valuable isolates. This is followed by greenhouse and field research experimentation. Crop species are included owing to the close connections between rhizobacteria and their host plants. The subsequent survival of BCA and its interactions with host plants is further aided by tracking its development in the soil.

According to Khalili *et al.* (2023), a greenhouse is helpful for both providing theoretical support for field applications and offering practical advice on the use of BCAs for controlled-environment crop production. A range of media for culture and development conditions has been examined and optimized during the manufacturing process to yield the appropriate microbial species. The most widely used formulations are liquid ones, and numerous researchers have attempted to extend the shelf life of PGPR by reducing storage temperatures and/or altering additive combinations (Shahdadi *et al.*, 2023). BCAs might endanger local biodiversity and limit the introduction of species or populations into natural systems to combat infections,

also raising ethical and legal issues (Sudha *et al.*, 2023). The substantial regulatory costs associated with importing BCAs into Australia are a primary factor. Governmental organizations, academia, and industry must collaborate closely to register BCAs, enabling the critical assessment and promotion of these novel products (Alsulami *et al.*, 2023). In both local and global markets, commercialization should comply with international laws and regulations. The International Organization for Biological Control (IOBC) has brought together researchers and practitioners from a wide range of disciplines to identify and address restrictions on the widespread use of biocontrol products, thereby reducing these limitations (Bonaterra *et al.*, 2012).

Future Perspectives

One of the most exciting areas of sustainable agriculture is biological control management (Fig. 5). This method of agricultural pest control is environmentally friendly. The technique systematically and consistently reduces insect populations in a manner suited to the environment by using living microorganisms. In industrial countries, biological control is a sensible tool for pest control that is safe, affordable, and long-term, which benefits both producers and consumers, as opposed to artificial (Chemical) Methods. The MBCA antagonistic mechanisms are perceived as suitable substitutes for chemical-based fungicides, encouraging plant growth and development for post-harvest purposes, thereby facilitating the development of new biocontrol technologies and applications. In addition, the interactions between MBCA-pathogen-plants have been elucidated by bioinformatics, molecular biology, analytical chemistry, and biostatistics (Shahbaz *et al.*, 2023).

Bioinformatics

Bioinformatics can revolutionize PGPR research by enabling the identification of bacterial genomes for Biosynthetic Gene Clusters (BGCs) that yield antimicrobial metabolites. Pangenome analysis and comparative genomics can identify strain-specific genes that contribute to biocontrol effectiveness (Sangwan *et al.*, 2022). Metagenomic sequencing of rhizosphere microbiota can unveil new PGPR strains and their eco-physiological interactions with disease-causing pathogens. Machine learning

models can predict plant-microbe interactions and enable the design of synthetic microbial consortia. Network-based bioinformatics tools also predict regulatory associations between microbial metabolites and plant defense genes. These strategies allow the prioritization of the most promising strains for agricultural use. For instance, the identification of new siderophore or lipopeptide genes can guide the development of specific strains for crop biocontrol. Bioinformatics, in general, offers cost- and high-throughput-efficient information for PGPR-initiated sustainable agriculture (Medina-Cordoba *et al.*, 2021).

Molecular Biology Strategies

Molecular biology provides tools to disentangle the mechanisms by which PGPR regulate plant immunity and biocontrol processes at the gene and protein levels (Anbalagan *et al.*, 2024). Functional genomics tools, such as CRISPR-Cas9-Mediated gene deletion in PGPR, can identify genes required for antifungal metabolite biosynthesis. Transcriptomic profiling of PGPR-inoculated plants can reveal upregulation of ISR-associated defense genes, including LOX, ERF1, and PDF1.2. Proteomics and metabolomics can identify new secreted proteins and signaling molecules that

contribute to pathogen suppression. Molecular cloning of biosynthetic genes of interest (e.g., lipopeptide) into high-performance bacterial hosts can enhance metabolite yield. Host-microbe interactions using reporter gene fusions (e.g., GFP-tagged bacteria) allow for visualization of colonization patterns in planta. These strategies can enhance strain selection and engineer PGPR with optimized traits for biocontrol. Such solutions are at the crossroads of basic science and their use in sustainable agriculture (Backer *et al.*, 2018).

Biostatistics Strategies

Biostatistics is essential for validating PGPR research by ensuring a robust experimental design, accurate data analysis, and predictive modeling. Statistical models, such as mixed-effects regression, can analyze the impact of PGPR on crop yield under varied field conditions. A meta-analysis of published trials will provide estimates of the overall efficacy of PGPR-based biocontrol across various crops and environments. Bayesian modeling will incorporate uncertainty in ecological data for forecasting the performance of PGPR under climate change. Multivariate techniques, such as PCA and clustering, can be employed to classify PGPR strains based on metabolite production

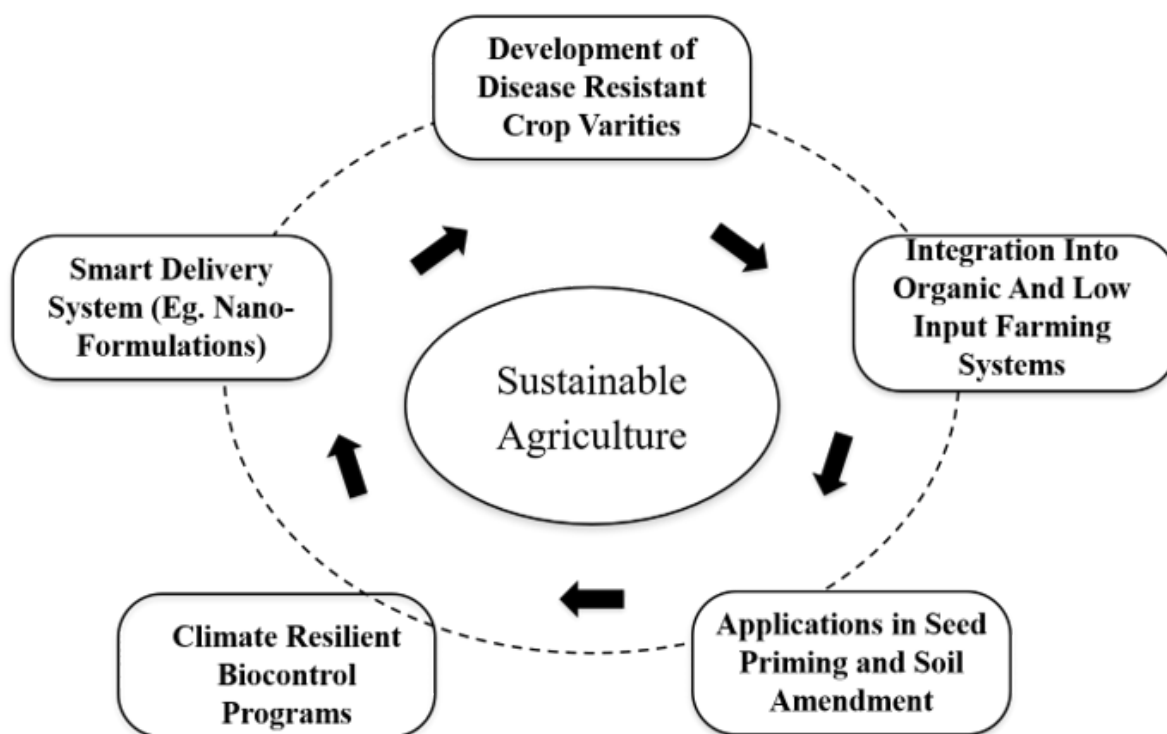


Fig. 5. Future applications of PGPR-associated plants in biocontrol for sustainable agriculture.

and stress tolerance traits. Biostatistical pipelines are also necessary to incorporate multi-omics data (genomics, proteomics, metabolomics) into holistic PGPR-plant-pathogen interaction models. By employing rigorous statistical approaches, scientists can minimize biases, enhance reproducibility, and provide valuable recommendations to farmers. Statistical precision enables the upscaling of PGPR from laboratory experiments to field applications (Köhl *et al.*, 2019).

Conclusions

The significant threats posed by phytopathogens to global food security, coupled with the environmental and health hazards associated with chemical pesticides, necessitate the development of sustainable alternatives for agricultural disease management. Plant growth-promoting rhizobacteria (PGPR) are a biocontrol strategy that can yield advantageous outcomes in disease suppression, plant growth promotion, and increased stress resilience. PGPR species such as *Pseudomonas fluorescens*, *Bacillus subtilis*, and *Azospirillum brasilense* have been shown to effectively inhibit pathogens such as *Fusarium oxysporum*, *Rhizoctonia solani*, and *Phytophthora capsici* while also enhancing nutrient acquisition (Nitrogen Fixation, Solubilization of Phosphorus) and root structure by modulating phytohormones (IAA, Cytokinins, Ethylene). The rhizosphere microbiome, influenced by root exudates and microbial associations, is fundamental to disease suppressiveness, with PGPR as keystone taxa promoting soil health and plant resilience. Issues such as variable field performance, adaptability to environmental conditions, and regulatory constraints hinder the implementation of large-scale PGPR. Soil heterogeneity can reduce biocontrol effectiveness due to host specificity and competition with indigenous microbiota; therefore, tailored formulations and microbial consortia are required across various agroecosystems. The integration of PGPR into sustainable agricultural systems offers a promising approach to reduce chemical inputs while maintaining crop productivity. However, successful implementation requires addressing challenges related to field performance variability, formulation stability, and regulatory compliance. Future research should prioritize the development of region-specific microbial consortia, improved delivery

systems, and integration with precision agriculture technologies. PGPR with organic farming methods, including crop rotation and intercropping, may maximize their utility, whereas nanotechnology and encapsulation methods can optimize delivery and shelf life.

Additionally, international cooperation is necessary to harmonize regulatory mechanisms and ensure the safe and effective commercialization of PGPR-based bio-formulations. PGPR is an innovative instrument for agricultural sustainability that bridges the productivity-viability gap. PGPR, in conjunction with agro-ecological strategies, possesses biocontrol potential to reduce reliance on chemical inputs, mitigate the impacts of climate change, and ensure food availability for future generations.

References

- Abadi, V.A.J.M., Sepehri, M. and Rahmani, H.A. 2020. Role of dominant phyllosphere bacteria with plant growth-promoting characteristics on growth and nutrition of maize (*Zea mays* L.). *Journal of Soil Science and Plant Nutrition* 20(4): 2348–2363.
doi:10.1007/s42729-020-00271-7
- Abbas, R., Rasul, S., Aslam, K., Baber, M., Shahid, M. and Mubeen, F. 2019. Halotolerant PGPR: a hope for the cultivation of saline soils. *Journal of King Saud University – Science* 31(4): 1195–1201.
doi:10.1016/j.jksus.2019.02.019
- Abdusamatov, S., Jabborova, D., Azimova, N., Alimov, J.E., Djalolova, B., Alhewairini, S.S., Sayyed, R., Chaudhary, M., Sultanov, N.N. and Davranov, K. 2025. Eco-Friendly biodegradation of plant biomass using multienzyme-producing *Trichoderma harzianum* for sustainable feed improvement. *Waste and Biomass Valorization*.
doi:10.1007/s12649-025-03132-3
- Adeleke, B.S. and Babalola, O.O. 2022. Roles of plant endosphere microbes in agriculture - A review. *Journal of Plant Growth Regulation* 41(4): 1411–1428.
doi:10.1007/s00344-021-10347-9
- Afzal, I., Shinwari, Z.K., Sikandar, S. and Shahzad, S. 2019. Plant beneficial endophytic bacteria: Mechanisms, diversity, host range and genetic determinants. *Microbiological Research* 221: 36–49.
doi:10.1016/j.micres.2019.02.001
- Agler, M.T., Ruhe, J., Kroll, S., Morhenn, C., Kim, S.-T., Weigel, D. and Kemen, E.M. 2016. Microbial hub taxa link host and abiotic factors to variation in the plant microbiome. *PLoS Biology* 14(1): e1002352.

- doi:10.1371/journal.pbio.1002352
- Ahmad, R., Hassan, A., Sheik, T., Mir, S., Nisa, R., Alkilayh, O.A., Hamid, B., Baba, Z. and Sayyed, R.Z. 2024. Assessment of the sustainability of land use systems through sensitive indicators of soil quality and biophysical properties in a temperate ecosystem. *Egyptian Journal of Soil Science* 64(4): 1115-1127.
doi:10.21608/ejss.2024.294037.1780
- Ahmed, E. and Holmström, S.J.M. 2014. Siderophores in environmental research: roles and applications. *Frontiers in Plant Science* 5: 555.
doi:10.3389/fpls.2014.00555
- Akkurak, H., Güldür, M., Dikilitas, M., Karakas, M., Alfaifi, M.Y., Shati, A.A. and Sayyed, R.Z. 2024. Molecular characterization of *Candidatus* phytoplasma phoenicium infecting almond (*Prunus dulcis*) and evaluation of biochemical defenses produced in the plant. *Journal of Phytopathology*, e13260.
doi:10.1111/jph.13260
- Akter, S., Ali, H., Shati, A.A., Alfaifi, M.Y., Elbehairi, S.E.I., Sayyed, R.Z. and Yeasmin, T. 2024. Antidiabetic activity of methanolic extract of *Hibiscus sabdariffa* Linn. fruit in alloxan-induced Swiss albino diabetic mice. *Open Agriculture* 9: 20220243.
doi:10.1515/opag-2022-024,3
- Al-kahtani, M.D., Fouda, A., Attia, K.A., Al-Otaibi, F., Eid, A.M. and Ewais, E.E.D. 2020. Isolation and characterization of plant growth-promoting endophytic bacteria from desert plants and their application as bioinoculants for sustainable agriculture. *Agronomy* 10(9): 1325.
doi:10.3390/agronomy10091325
- Alkilayh, O.A., Hamed, K.E., Sayyed, R.Z. and Omar, A.F. 2024. Molecular characterization and biodiversity analysis of *Botrytis cinerea*, a grey mould of tomato, and its antagonism using local *Bacillus subtilis*. *Physiological and Molecular Plant Pathology* 133: 102376.
doi:10.1016/j.pmpp.2024.102376
- Alsalamah, M.A., Hamed, K.E., Sayyed, R.Z. and Omar, A.F. 2024. Molecular characterization, etiology of *Sclerotinia sclerotiorum*, an emerging fungal pathogen of white mold disease in eggplant, and its biocontrol using soil bioagents. *Egyptian Journal of Soil Science* 64(3).
doi:10.21608/ejss.2024.221538.1746
- Alshaikh, N.A., Perveen, K., Debnath, S., Paul, A., Hock, O.G. and Sayyed, R.Z. 2024. In silico analysis of LPMO inhibition by ethylene precursor ACCA to combat potato late blight. *Journal of King Saud University – Science* 36: 103436.
doi:10.1016/j.jksus.2024.103436
- Alsulami, J.A., Perveen, K., Alothman, M.R., Al-Humaid, L.A., Munshi, F.M., Adawiyah Ahmad, R. and Sayyed, R. 2023. Microwave-assisted green synthesis of silver nanoparticles by extracts of fig fruits and myrrh oleogum resin and their role in antibacterial activity. *Journal of King Saud University – Science* 35(10): 102959.
doi:10.1016/j.jksus.2023.102959
- Alwahshi, K.J., Purayil, G.P., Saeed, E.E., Abufarajallah, H.A., Aldhaheeri, S.J., AbuQamar, S.F. and Aouada, M. 2022. The ACC deaminase-producing *Streptomyces violaceoruber* UAE1 can provide further protection against sudden decline syndrome in date palm. *Frontiers in Plant Science* 13: 904166.
doi:10.3389/fpls.2022.904166
- Anbalagan, S.A., Appusamy, S., Kumeresan, P.V., Chellappan, G.C., Narayan, S., Rangasamy, A., Perveen, K., Bukhari, N.A. and Sayyed, R. 2024. Deciphering the biocontrol potential of *Trichoderma asperellum* (Tv1) against *Fusarium-nematode* wilt complex in tomato. *Journal of Basic Microbiology* 00, e2400595.
doi:10.1002/jobm.202400595
- Ayshasiddeka, M., Islam, M.M., Akter, S., Ali, H., Haque, M.R., Perveen, K., Alfagham, A.T., Sayyed, R.Z. and Yeasmin, T. 2025. Biodiversity analysis of arbuscular mycorrhizal fungal association with the Euphorbiaceae family. *Sydowia* 77: 111–118.
doi:10.12905/0380.sydowia77-2025-0111
- Babarabi, M., Sardoei, A.S., Dhanalakshmi, K., Malathi, G., Sayyed, R.Z., Sunita, K., Ghasemi, H. and Fazeli-Nasab, B. 2024. Triacantanol: The role player in *Polianthes tuberosavar.* Pearl responds under natural conditions. *Biocatalysis and Agricultural Biotechnology* 58: 103228.
doi:10.1016/j.bcab.2024.103228
- Backer, R., Rokem, J. S., Ilangumaran, G., Lamont, J., Praslickova, D., Ricci, E., Subramanian, S., Smith, D.L. 2018. Plant growth-promoting rhizobacteria: context, mechanisms of action, and roadmap to commercialization of biostimulants for sustainable agriculture. *Frontiers in Plant Science* 9: 1473.
doi:10.3389/fpls.2018.01473
- Bai, Y., Müller, D.B., Srinivas, G., Garrido-Oter, R., Potthoff, E. and Rott, M. 2015. Functional overlap of the *Arabidopsis* leaf and root microbiota. *Nature* 528(7582): 364–369.
doi:10.1038/nature16192
- Banerjee, S., Singh, S., Pandey, S., Bhandari, M.S., Pandey, A. and Giri, K. 2020. Biocontrol potential of *Pseudomonas azotoformans*, *Serratia marcescens*, and *Trichoderma virens* against *Fusarium* wilt of *Dalbergia sissoo*. *Forest Pathology* 50(3): e12581.
doi:10.1111/efp.12581

- Barasarathi, J., Perveen, K., Khan, F., Muthukumaran, M., Debnath, A., Behra, M., Ponggen, M., Sayyed, R. and Mastinu, A. 2025. *Targeting Agrobacterium tumefaciens*: A computational study on quorum-sensing inhibition. *Journal of Basic Microbiology* 00: e70041.
doi:10.1002/jobm.70041
- Bhattacharyya, P.N., Jha, D.K. 2012. Plant growth-promoting rhizobacteria (PGPR): emergence in agriculture. *World Journal of Microbiology and Biotechnology* 28(4): 1327-1350.
- Blouin, M. and Jacquiod, S. 2020. Sampling the control bulk soil for rhizosphere and drillosphere microbial studies. *Geoderma* 380: 114674.
doi:10.1016/j.geoderma.2020.114674
- Bodhankar, G. 2022. Cytoplasmic sensing by *Bacillus subtilis* chemoreceptors. *Doctoral Dissertation* 14: 158-166.
- Bona, E., Massa, N., Novello, G., Boatti, L., Cesaro, P., Todeschini, V., Magnelli, V., Manfredi, M., Marengo, E., Mignone, F., Berta, G., Lingua, G., & Gamalero, E. (2019). Metaproteomic characterization of the *Vitis vinifera* rhizosphere. *FEMS Microbiology Ecology* 95(1), fiy204.
doi:10.1093/femsec/fiy204
- Bonaterrea, A., Badosa, E., Cabrefiga, J., Frances, J. and Montesinos, E. 2012. Prospects and limitations of microbial pesticides for control of bacterial and fungal pomefruit tree diseases. *Trees* 26(1): 215-226.
doi:10.1007/s00468-011-0626-y
- Bostan, N., Ilyas, N., Saeed, M., Debnath, A., Akhtar, N., Tanveer, S., Akhtar, N., Umer, M., Sayyed, R., Perveen, K. and Bukhari, N.A. 2025. *An in vitro* phytotoxicity assessment of UV-enhanced biodegradation of plastics for spinach cultivation. *Frontiers of Environmental Science and Engineering* 19(2): 17.
doi:10.1007/s11783-025-1937-3
- Bright, J.P., Maheshwari, H.S., Thangappan, S., Perveen, K., Bukhari, N.A., Mitra, D., Sayyed, R.Z. and Mantinu, A. 2025. Biofilmed-PGPR: A next-generation bioinoculant for plant growth promotion in rice (*Oryza sativa* L.) under a changing climate *Rice Science*. 32(1): 94-106
doi:10.1016/j.rsci.2024.08.008
- Budamagunta, V., Shameem, N., Irusappan, S., Paray, J.A., Thomas, M., Marimuthu, S., Kirubakaran, R., Jothi, K.N.A., Sayyed, R.Z. and Lim, H.R. 2022. Microbial nanovesicles and extracellular polymeric substances mediate nickel tolerance and remediate heavy metal ions from soil. *Environmental Research* 219, 15, 2023, 114997,
doi:10.1016/j.envres.2022.114997
- Bulgarelli, D., Schlaeppi, K., Spaepen, S., Themaat, E.V.L.V. and Schulze-Lefert, P. 2013. Structure and functions of the bacterial microbiota of plants. *Annual Review of Plant Biology* 64: 807-838.
doi:10.1146/annurev-arplant-050312-120106
- Chaloner, T.M., Gurr, S.J. and Bebbler, D.P. 2021. The risk of plant pathogen infection tracks global crop yields under climate change. *Nature Climate Change* 11(8): 710-715.
doi:10.1038/s41558-021-01104-8
- Daneshmand, S., Niazi, M., Fazeli-Nasab, B., Asili, J. and Shiva.2024. Solid lipid nanoparticles of *Platyclusus orientalis* L. possessing 5-alpha-reductase inhibiting activity for treating hair loss and hirsutism. *Journal of Medicinal Plants and By-products* 1: 233-246.
doi:10.22034/jmpb.2023.364389.1634
- Dastogeer, K.M.G., Tumpa, F.H., Sultana, A., Akter, M.A. and Chakraborty, A. 2020. Plant microbiome – an account of the factors that shape community composition and diversity. *Current Plant Biology* 23: 100161.
doi:10.1016/j.cpb.2020.100161
- Dave, A., Ingle, S., Perveen, K., Bukhari, N.A., Sayyed, R. and Mastinu, A. 2024. Harnessing plant growth-promoting and wilt-controlling biopotential of a consortium of actinomycetes and mycorrhizae in pigeon pea. *Journal of Phytopathology* 172: e13399.
doi:10.1111/jph.13399
- De la Cruz-Quiroz, R., Roussos, S., Rodríguez-Herrera, R., Hernández-Castillo, D. and Aguilar, C.N. 2018. Growth inhibition of *Colletotrichum gloeosporioides* and *Phytophthora capsici* by native Mexican *Trichoderma* strains. *Karbala International Journal of Modern Science* 4(2): 237-243.
doi:10.1016/j.kijoms.2018.03.002
- de la Fuente Cantó, C., Simonin, M., King, E., Moulin, L., Bennett, M.J. and Castrillo, G. 2020. An extended root phenotype: the rhizosphere, its formation and impacts on plant fitness. *The Plant Journal* 103(3): 951-964
doi:10.1111/tpj.14781
- Dean, R., Van Kan, J.A.L., Pretorius, Z.A., Hammond-Kosack, K.E., Di Pietro, A., Spanu, P.D., Rudd, J.J., Dickman, M., Kahmann, R., Ellis, J. and Foster, G.D. 2012. The Top 10 fungal pathogens in molecular plant pathology. *Molecular Plant Pathology* 13(4): 414-430.
doi:10.1111/j.1364-3703.2011.00783
- Dukare, A. and Paul, S. 2021. Biological control of Fusarium wilt and growth promotion in pigeon pea (*Cajanus cajan*) by antagonistic rhizobacteria, displaying multiple modes of pathogen inhibition. *Rhizosphere* 17: 100278.
doi:10.1016/j.rhisph.2020.100278
- Elnahal, A.S., El-Saadony, M.T., Saad, A.M., Desoky, E.S.M., El-Tahan, A.M. and Rady, M.M. 2022.

- The use of microbial inoculants for biological control, plant growth promotion, and sustainable agriculture: A review. *European Journal of Plant Pathology* 162(4): 759-792.
doi:10.1007/s10658-021-02393-7
- Enshasy, H.E.A., Ambehati, K.K., Ashraf, F., Ramchuran, S., Sayyed, R.Z., Amalin, D., Dailin, D.J., Hanapi, S.Z. 2020. *Trichoderma*: Biocontrol agents for promoting plant growth and soil health. In: *Agriculturally Important Fungi for Sustainable Agriculture* (Eds. A. Yadav, S. Mishra, D. Kour, N. Yadav and A. Kumar), *Fungal Biology* Vol 2, pp. 239-259. Functional annotation for crop protection, (Springer-Cham),
doi:10.1007/978-3-030-48474-3_8
- Eswaran, S.U.D., Sundaram, L., Perveen, K., Bukhari, N.A. and Sayyed, R.Z. 2024. Osmolyte-producing microbial biostimulants regulate the growth of *Arachis hypogaea* L. under drought stress. *BMC Microbiology* 4: 165.
doi:10.1186/s12866-024-03320-6
- Etesami, H. and Adl, S.M. 2020. Plant growth-promoting rhizobacteria (PGPR) and their action mechanisms in the availability of nutrients to plants. In: *Phyto-Microbiome Stress Regulation* (Singapore: Springer Nature).
doi:10.1007/978-981-15-2576-6_9
- Etminani, E., Fazeli-Nasab, B., Gowtham, H.G., Mirzaei, A.R., Barasarathi, J. and Sayyed, R.Z. 2024. Bioinformatic investigation of the effect of volatile and non-volatile compounds of rhizobacteria in inhibiting late embryogenesis abundant (LEA) protein that induces drought tolerance. *Open Agriculture* 9: 20220252.
doi:10.1515/opag-2022-0252
- Fatimah, N., Ashraf, S., Nayana, R.U., Anju, P.B., Showkat, M., Perveen, K., Bukhari, N.A., Sayyed, R.Z. and Mastinu, A. 2024. Evaluation of the suitability and biodegradability of the organophosphate insecticides to mitigate insecticide pollution in onion farming. *Heliyon* 10: e32580.
doi:10.1016/j.heliyon.2024.e32580
- Ferioun, M., Bouhraoua, S., Srhiouar, N., Boussakouran, A., Belahcen, D., Ghachtouli, N.E., Sayyed, R.Z. and Louahlia, S.A. 2024. Advanced multivariate approaches for selecting Moroccan drought-tolerant barley (*Hordeum vulgare* L.) cultivars. *Ecological Frontiers* 44(4): 820-828.
doi:10.1016/j.ecofro.2024.02.010
- Ferioun, M., Zouitane, I., Bouhraoua, S., Elouattassi, Y., Belahcen, D., Errabbani, A., Louahlia, S., Sayyed, R. and El-Ghachtouli, N. 2025. Applying microbial biostimulants and drought-tolerant genotypes to enhance barley growth and yield under drought stress. *Frontiers in Plant Science* 15: 1494987.
doi:10.3389/fpls.2024.1494987
- Fones, H.N., Bebbber, D.P., Chaloner, T.M., Kay, W.T., Steinberg, G. and Gurr, S.J. 2020. Threats to global food security from emerging fungal and oomycete crop pathogens. *Nature Food* 1(6): 332-342.
doi:10.1038/s43016-020-0075-0
- Fotoohiyan, A., Shahdadi, F., Sayyed, R.Z., Sardoei, A.S., and Fazeli-Nasab, B. 2024. Tripartite combinational effects of *Alhagimaurosum* plant extract, essential oil, and carbendazim against *Alternaria* and *Penicillium* sp. in post-harvest of citrus fruit. *Sydowia* 76: 137-147.
doi:10.12905/0380.sydowia76-2024-0135
- Fu, B., Olawole, O. and Beattie, G.A. 2021. Biological control and microbial ecology draft genome sequence data of *Glutamicibacter* sp. FBE-19, a bacterium antagonistic to the plant pathogen *Erwinia tracheiphila*. *Phytopathology* 111(5): 765-768.
doi:10.1094/PHYTO-09-20-0380-A
- Galindo, F.S., Rodrigues, W.L., Biagini, A.L.C., Fernandes, G.C., Baratella, E.B., da Silva Junior, C.A., Buzetti, S. and Teixeira Filho, M.C.M. 2019. Assessing forms of application of *Azospirillum brasilense* associated with silicon use on wheat. *Agronomy* 9(11): 678.
doi:10.3390/agronomy9110678
- Germon, A., Guerrini, I.A., Bordron, B., Bouillet, J.-P., Nouvellon, Y., de Moraes Gonçalves, J.L., Jourdan, C., Paula, R.R. and Laclau, J.-P. 2018. Consequences of mixing *Acacia mangium* and *Eucalyptus grandis* trees on soil exploration by fine roots down to a depth of 17 m. *Plant and Soil* 424(1-2): 203-220.
doi:10.1007/s11104-017-3428-1
- Gouda, S., Kerry, R.G., Das, G., Paramithiotis, S., Shin, H.-S. and Patra, J.K. 2018. Revitalization of plant growth-promoting rhizobacteria for sustainable development in agriculture. *Microbiological Research* 206: 131-140.
doi:10.1016/j.micres.2017.08.016
- Gowtham, H.G., Murali, M., Shilpa, N., Amruthesh, K.N., Gafur, A., Antonius, S. and Sayyed, R.Z. 2024. Harnessing abiotic elicitors to bolster plants' resistance against bacterial pathogens. *Plant Stress* 11: 100371.
doi:10.1016/j.stress.2024.100371
- Gupta, R., Anand, G., Gaur, R. and Yadav, D. 2021. Plant-microbiome interactions for sustainable agriculture: A review. *Physiology and Molecular Biology of Plants* 27(2): 165-179.
doi:10.1007/s12298-021-00927-1
- Haas, D. and Défago, G. 2005. Biological control of soil-borne pathogens by fluorescent *Pseudomonas*. *Nature Reviews Microbiology* 3(4): 307-319.
doi:10.1038/nrmicro1129

- Hamed, K.E., Alsaif, A.N., Alhewairini, S.S. and Sayyed, R.Z. 2024. Comprehensive analysis of microbiome biodiversity in popular date palm (*Phoenix dactylifera* L.) fruit varieties. *Scientific Reports* 13: 7378.
doi:10.1038/s41598-023-34359-6
- Hamed, K.E., Alsohim, A.S., Baschien, C. and Sayyed, R.Z. 2024. *Neoscytalidium dimidiatum* associated with *Albizialebbeck* disease in Saudi Arabia: Symptomatology, pathogenicity, and molecular identification. *Forest Pathology* 54: e12884.
doi:10.1111/efp.12884
- Hamid, B., Baba, Z.A., Sheik, T.A., Perveen, K. and Sayyed, R.Z. 2024. Investigating potential protease activity of psychrotrophic bacteria from a municipal landfill for solid waste management. *Biomass Conversion and Biorefinery*.
doi:10.1007/s13399-024-05621-2
- Hermosa, R., Viterbo, A., Chet, I., Monte, E. 2012. Plant-beneficial effects of *Trichoderma* and of its genes. *Microbiology* 158(1): 17-25.
doi:10.1099/mic.0.052274-0
- Hidayah, B.N., Khangura, R. and Dell, B. 2022. Biological control potential of *Trichoderma* species and bacterial antagonists against *Sclerotinia sclerotiorum* on canola in Western Australia. *International Journal of Agriculture and Biology* 27(1): 215-227.
doi:10.17957/ijab/15.1919
- Hilton, S., Picot, E., Schreiter, S., Bass, D., Norman, K., Oliver, A.E., Moore, J.D., Mauchline, T.H., Mills, P.R., Teakle, G.R., Clark, I.M., Hirsch, P.R., van der Gast, C.J. and Bending, G.D. 2021. Identification of microbial signatures linked to oilseed rape yield decline at the landscape scale. *Microbiome* 9(1): 19.
doi:10.1186/s40168-020-00
- Jabborova, D., Sulaymanov, K., Sayyed, R.Z., Alotaibi, S.H., Enakiev, Y., Azimov, A., Jabbarov, Z., Ansari, M.J., Shah, F., Danish, S. and Datta, R. 2021. Effect of different mineral fertilizers on turmeric rhizome mineral nutrients and soil properties under field conditions. *Sustainability* 13: 9437. <https://www.mdpi.com/2071-1050/13/16/9437/htm>
- Jabborova, D., Jabbarov, Z., Abdrakhmanov, T., Fayzullaev, O., Saharan, B.S., Perveen, K., Zaka, S.M., Mastinu, A. and Sayyed, R. 2025a. Assessing the synergistic effects of biochar, hydrogel, and biofertilizer on growth and physiological traits of wheat in saline environments. *Functional Plant Biology* 52: FP24277.
doi:10.1071/FP24277
- Jabborova, D., Zhang, Y., Alhewairini, S.S., Jabbarov, Z., Barasaathi, J., Abdrakhmanov, T., Imomov, O., Abdusamatov, S., Saharan, S.B. and Sayyed, R. 2025. Enhancing growth and physiological traits in alfalfa by alleviating salt stress through biochar, hydrogel, and biofertilizer application. *Frontiers in Microbiology* 16: 1560762.
doi:10.3389/fmicb.2025.1560762
- Jisha, M.S., Linu, M.S. and Sreekumar, J. 2018. Induction of systemic resistance in chili (*Capsicum annum* L.) by *Pseudomonas aeruginosa* against anthracnose pathogen *Colletotrichum capsici*. *Journal of Tropical Agriculture* 56(2): 153-166.
doi:10.33866/phytopathol.030.01.0593
- Jones, E.E., Rabeendran, N. and Stewart, A. 2014. Biocontrol of *Sclerotinia sclerotiorum* infection of cabbage by *Coniothyrium minitans* and *Trichoderma* spp. *Biocontrol Science and Technology* 24(12): 1363-1382.
doi:10.1080/09583157.2014.940847
- Jones, J.T., Haegeman, A., Danchin, E.G.J., Gaur, H.S., Helder, J., Jones, M.G.K., Kikuchi, T., Manzanilla-López, R., Palomares-Rius, J.E., Wesemael, W. and Perry, R.N. 2013. Top 10 plant-parasitic nematodes in molecular plant pathology. *Molecular Plant Pathology* 14: 946-961.
doi:10.1111/mpp.12057
- Jones, R.A.C. 2016. Future scenarios for plant virus pathogens as climate change progresses. *Advances in Virus Research* 95: 87-147.
doi:10.1016/bs.aivir.2016.02.004
- Khafagi, E.Y., El-Syed, A. and Elwan, S.E. 2020. Controlling cabbage Fusarium wilt (yellows) using Topsin M and some commercial biofertilizer products. *Zagazig Journal of Agricultural Research* 47(3): 519-530.
doi:10.21608/zjar.2020.94492
- Khalili, L., Bright, J.B. and Sayyed, R.Z. 2023. Genetically modified, functional, and organic foods and consumers' approach: A critical review. *Journal of Consumer Protection and Food Safety*.
doi:10.1007/s00003-023-01466-5
- Kılınç, B., Güldür, M.E., Türkölmez, S., Alhewairini, S.S., Barasarathi, J., Dikilitas, M. and Sayyed, R. 2025. *Sordaria macrospora*: A new fungal pathogen causing leaf tip and shoot blight on olive (*Olea europaea* L.). *Journal of Phytopathology* 73(3): e70076.
doi:10.1111/jph.70076
- Kloepper, J.W. and Ryu, C.M. 2020. Bacterial endophytes as elicitors of induced systemic resistance. *Plant Disease* 104(9): 2411-2421.
doi:10.1094/PDIS-03-20-0464-FE
- Köhl, J., Kolnaar, R. and Ravensberg, W.J. 2019. Mode of action of microbial biological control agents against plant diseases: relevance beyond efficacy. *Biological Control* 131: 65-75.
doi:10.1016/j.biocontrol.2018.09.003

- Korenblum, E., Dong, Y., Szymanski, J., Panda, S., Jozwiak, A., Massalha, H., Meir, S., Rogachev, I., Aharoni, A. and Sharon, A. 2020. The rhizosphere microbiome mediates systemic exudation of root metabolites via root-to-root signaling. *Proceedings of the National Academy of Sciences USA* 117(7): 3874-3883.
doi:10.1073/pnas.1912130117
- Kousar, B., Bano, A. and Khan, N. 2020. PGPR modulation of secondary metabolites in tomato infested with *Spodoptera litura*. *Agronomy* 10(6): 778.
doi:10.3390/agronomy10060778
- Kumar, A. and Verma, J.P. 2018. Does plant-microbe interaction confer stress tolerance in plants: a review? *Microbiological Research* 207: 41-52.
doi:10.1016/j.micres.2017.11.004
- Lyu, D., Backer, R., Subramanian, S. and Smith, D. 2020. Phytomicrobiome coordination signals hold potential for climate change-resilient agriculture. *Frontiers in Plant Science* 11: 634.
doi:10.3389/fpls.2020.00634
- Mahmud, K., Missaoui, A., Lee, K., Ghimire, B., Presley, H.W. and Makaju, S. 2021. Rhizosphere microbiome manipulation for sustainable crop production. *Current Plant Biology* 27: 100210.
doi:10.1016/j.cpb.2021.100210
- Manasa, M., Ravinder, P., Gopalakrishnan, S., Srinivas, V., Sayyed, R.Z., Enshasy, H.E., Khan, M.Y., ATK Ali, Kassem, H.M. and Hameeda, B. 2021. Co-inoculation of *Bacillus* spp. for growth promotion and iron fortification in sorghum. *Sustainability* 13(21): 12091.
doi:10.3390/su132112091
- Mathys, J., De Cremer, K., Timmermans, P., Van Kerckhove, S., Lievens, B., Vanhaecke, M., Bosmans, L., Van Hulle, M., De Vos, P., Cammue, B.P.A. and Audenaert, K. 2012. Genome-wide characterization of ISR induced in *Arabidopsis thaliana* by *Trichoderma hamatum*T382 against *Botrytis cinerea* infection. *Frontiers in Plant Science* 3: 108.
doi:10.3389/fpls.2012.00108
- Medina-Córdoba, L.K., Mariño-Ramírez, L., Rodríguez-Hernández, N., Restrepo-Montoya, D. 2021. Computational approaches for understanding plant growth-promoting rhizobacteria and their interaction with plants. *Frontiers in Plant Science* 12: 708013.
doi:10.3389/fpls.2021.708013
- Minhans, K., Sharma, S., Sheik, I., Alhewairini, S.S. and Sayyed, R. 2025. Artificial intelligence and plant disease management: An agro-innovative approach. *Journal of Phytopathology* 173: e70084.
doi:10.1111/jph.70084
- Moghaddam, M.H., Moradi, A., Piri, R., Glick, B.R., Fazeli-Nasab, B. and Sayyed, R.Z. 2024. Seed coating with minerals and plant growth-promoting bacteria enhances drought tolerance in fennel (*Foeniculum vulgare* L.). *Biocatalysis and Agricultural Biotechnology* 58: 103202.
doi:10.1016/j.bcab.2024.103202
- Mohammadi, P., Tozlu, E., Kotan, R. and Kotan, M.S. 2017. Potential of some bacteria for biological control of postharvest citrus green mold caused by *Penicillium digitatum*. *Plant Protection Science* 53(3): 134-143.
doi:10.17221/55/2016-PPS
- Murali, M., Gowtham, H.G., Shilpa, N., Singh, B.S., Mohammed, A., Sayyed, R.Z., Shivamallu, C., Achar, R.R., Silina, E., Victor, S., Natalia, M., Shati, A.A., Alfaifi, M.Y., Elbehairi, S.E.I. and Kollur, S.P. 2023. Zinc oxide nanoparticles prepared through microbial-mediated synthesis for therapeutic applications: A possible alternative for plants. *Frontiers in Microbiology* 14: 1227951.
doi:10.3389/fmicb.2023.1227951
- Murphy, B.R., Doohan, F.M., and Hodkinson, T.R. 2018. Yield increase induced by PGPR strains in spring barley under field conditions. *Frontiers in Microbiology* 9: 969.
doi:10.3389/fmicb.2018.00969
- Muthukumar, M., Rawindran, H., Noorjahan, A., Parveen, M., Barasarathi, J., Blessie, J.P.J., Ali, S.S., Sayyed, R.Z., Awasthi, M.K., Hassan, S., Ravindran, B., Vatanpour, V. and Balakumar, V.S. 2024. Microalgae-based solutions for palm oil mill effluent management: Integrating phycoremediation, biomass, and biodiesel production for a greener future. *Biomass and Bioenergy* 191: 107445.
doi:10.1016/j.biombioe.2024.107445
- Nakkeran, S., Vinothini, K., Renukadevi, V., Thinryengadam, V., Saranya, N., Jothi, G., Mohammed, O.B., Al-Zahrani, F.A., Ashraf, S. and Sayyed, R. 2025. MAMP-triggered immunity and *in silico* analysis elucidate the nematocidal properties of *Bacillus velezensis*VB7 against root-knot nematode *Meloidogyne incognita* infecting tomato. *Microbial Pathogenesis* 207: 107862.
doi:10.1016/j.micpath.2025.107862
- Nasab, B.F. and Sayyed, R.Z. 2019. Plant Growth Promoting Rhizobacteria and Salinity Stress: A Journey into the Soil. In: Plant Growth Promoting Rhizobacteria for sustainable stress Management Vol 1 Abiotic Stress Management, Sayyed R, Arora N & Reddy MS (eds), Springer, Singapore, 2019, pp 21-34.
doi.org/10.1007/978-981-13-6536-2_2
- Nasab, B.F., Sayyed, R.Z., Mojahed, L.S., Rahmani, A.F., Ghafari, M., Antonius, S. and Sukamto 2022. Biofilm production: A strategic mechanism for survival of microbes under stress conditions. *Biocatalysis and Agricultural Biotechnology* 42: 102337.

- doi:10.1016/j.bcab.2022.102337
- Naseem, A., Alneghery, L.M., Al-Zaharani, M., Nasr, F.A., Jawad, S.S., Umer, M., Sayyed, R. and Ilyas, N. 2025. An insight into the impacts of pharmaceutical pollutants on the ecosystem, and the potential role of bioremediation in mitigating pharmaceutical pollutants. *International Journal of Pharmaceutics* 680: 125791.
doi:10.1016/j.ijpharm.2025.125791
- Nazari, M. and Smith, D.L. 2020. A PGPR-produced bacteriocin for sustainable agriculture: a review of thuricin 17 characteristics and applications. *Frontiers in Plant Science* 11: 916.
doi:10.3389/fpls.2020.00916
- Nithyapriya, S., Lalitha, S., Devi, S.U., Perveen, K., Alshaikh, N.A., Sayyed, R.Z. and Mastinu, A. 2024. Purification and characterization of desferrioxamine B of *Pseudomonas fluorescens* and its application to improve oil content, nutrient uptake, and plant growth in peanuts. *Microbial Ecology* 87: 60.
doi:10.1007/s00248-024-02377-0
- Omar, A.F., Abdelmageed, A.H.A., Al-Turki A., Abdelhameid, N.M., Sayyed, R.Z., and Rehan, M. 2022. Exploring the plant growth-promotion of four *Streptomyces* strains from rhizosphere soil to enhance cucumber growth and yield. *Plants* 11(23): 3316.
doi.org/10.3390/plants11233316
- Ongena, M. and Jacques, P. 2008. Bacillus lipopeptides: versatile weapons for plant disease biocontrol. *Environmental Microbiology* 10(7): 1573-1585.
doi:10.1111/j.1462-2920.2008.01613.x
- Pandya, N.D., Desai, P.V., Jadhav, H.P. and Sayyed, R.Z. 2018. Plant growth-promoting potential of *Aspergillus* sp. NPF7, isolated from the wheat rhizosphere in South Gujarat. *Environmental Sustainability* 1(3): 245-252.
doi:10.1007/s42398-018-0025-z
- 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. *Frontiers in Plant Science* 12: 621276.
doi:10.3389/fpls.2021.621276
- Panicker, S. and Sayyed, R.Z. 2022. Hydrolytic Enzymes from PGPR against plant fungal pathogens. In: *Antifungal Metabolites of Rhizobacteria for Sustainable Agriculture. Fungal Biology*. (Eds. R. Sayyed, A. Singh, and N. Ilyas), pp. 211-38. Springer, Cham.
doi:10.1007/978-3-031-04805-0_10
- Park, H., Choudhury, R.A., Walitang, D.I., Sayyed, R. and Sa, T.M. 2024. Changes in soil chemical properties and bacterial community composition of the jujube orchard due to oil cake fertilization. *Journal of Microbiology and Biotechnology* 34(12): 2542-2549.
doi:10.4014/jmb.2406.06037
- Parveen, G., Noreen, R., Shafique, H.A., Sultana, V., Ehteshamul-Haque, S. and Athar, M. 2019. Role of rhizobia in suppressing the root diseases of soybean under soil amendment. *Planta Daninha* 37: e019172336.
doi:10.1590/s0100-83582019370100038
- Patkowska, E. 2021. Biostimulants managed fungal phytopathogens and enhanced the activity of beneficial microorganisms in the rhizosphere of *Scorzonera* (*Scorzonera hispanica* L.). *Agriculture* 11(4): 347.
doi:10.3390/agriculture11040347
- Pieterse, M.J., Zamioudis, C., Berendsen, R.L., Weller, D.M., Van, Wees, S.C.M., Bakker, P. A.H.M. 2014. Induced systemic resistance by beneficial microbes. *Annual Review of Phytopathology* 52(1): 347-375.
doi:10.1146/annurev-phyto-082712-102340
- Podder, S., Shaha, R.K., Haque, A., Perveen, K., Alsayed, M.F., Murali, M., Shilpa, N., Yeasmin, T. and Sayyed, R. 2025. Entrapment of cellulase of snail gut *Bacillus amyloliquefaciens* for converting sugarcane bagasse to bioethanol using *Saccharomyces cerevisiae*. *Waste and Biomass Valorization*.
doi:10.1007/s12649-025-02964-3
- Pourakbar, L., Moghaddama, S.S., Enshasy, H.E. and Sayyed, R.Z. 2021. Antifungal activity of the extract of a macroalgae, *Gracilariopsis persica*, against four plant pathogenic fungi in-vitro. *Plants* 10(9): 1781.
doi.org/10.3390/plants10091781
- Pradhan, N., Singh, S., Saxena, G., Pradhan, N., Koul, M., Kharkwal, A.C. and Sayyed, R. 2025. A Review on Microbe-mineral transformations and their impact on plant growth. *Frontiers in Microbiology* 16: 1549022.
doi:10.3389/fmicb.2025.1549022
- Praveen, V., Sudha, A., Amala, S.A., Ramjegathesh, R., Kavitha, S., Perveen, K., Bukhari, N.A. and Sayyed, R.Z. 2025. *Harnessing Trichoderma asperellum*: Tri-trophic interactions for enhanced black gram growth and root rot resilience. *Journal of Basic Microbiology* 65(3): e2400569.
doi:10.1002/jobm.202400569
- Qayoom, I., Balkhi, M., Mukhtar, M., Abubakr, A., Siddiqui, U., Khan, S., Sherwani, A., Jan, I., Sayyed, R.Z. and Mastinu, A. 2024. Assessing organophosphate insecticide retention in muscle tissues of juvenile common carp fish under acute toxicity tests. *Toxicology Reports* 12: 253-259.
doi:10.1016/j.toxrep.2024.02.002
- Qiu, Y., Guo, L., Xu, X., Zhang, L., Zhang, K., Chen, M., Zhao, Y., Burkey, K.O., Shew,

- H.D., Zobel, R.W., Zhang, Y. and Hu, S.2021. Warming and elevated ozone induce tradeoffs between fine roots and mycorrhizal fungi and stimulate organic carbon decomposition. *Science Advances* 7(20): eabe9256. doi:10.1126/sciadv.abe9256
- Rahman, A., Korejo, F., Sultana, V., Ara, J. and Ehteshamul-Haque, S.2017. Induction of systemic resistance in cotton by the plant growth-promoting rhizobacterium and seaweed against charcoal rot disease. *Pakistan Journal of Botany* 49(1): 347-353. doi:10.30848/PJB2017-1(42)
- Raklami, A., Bechtaoui, N., Tahiri, A.I., Anli, M., Meddich, A. and Oufdou, K.2019. Use of rhizobacteria and mycorrhizae consortium in the open field as a strategy for improving crop nutrition, productivity, and soil fertility. *Frontiers in Microbiology* 10: 1106. doi:10.3389/fmicb.2019.01106
- Reshma, P., Naik, M.K., Aiyaz, M., Niranjana, S.R., Chennappa, G., Shaikh, S.S. and Sayyed, R.Z. 2018. Induced systemic resistance by 2, 4-diacetylphloroglucinol-positive fluorescent *Pseudomonas* strains against rice sheath blight. *Indian Journal of Experimental Biology* 56(3): 207-12. <http://nopr.niscpr.res.in/handle/123456789/43660>
- Roberts, E. and Lindow, S. 2014. Loline alkaloid production by fungal endophytes of Fescue species selects for particular epiphytic bacterial microflora. *The ISME Journal* 8(2): 359-368. <https://doi.org/10.1038/ismej.2>
- Sagar, A., Rai, S., Sharma, S., Perveen, K., Bukhari, N.A., Sayyed, R.Z. and Mastinu, A.2024. Molecular characterization reveals the biodiversity and biopotential of *Bacillus* spp. rhizobacterial isolates. *Microbial Ecology* 87: 83. doi:10.1007/s00248-024-02397-w
- Salehi-Sardoei, A., Sayyed, R.Z., Bright, J.P., Almuji, S.S., Almalki, W.H. and Fazeli-Nasab, B. 2024. Hybrid method of gibberellic acid applications: A sustainable and reliable way for improving Jerusalem cherry. *Biocatalysis and Agricultural Biotechnology* 59: 103253. doi:10.1016/j.bcab.2024.103253
- Sangwan, S., Shameem, N., Yashveer, S., Tanwar, H., Parray, J.A., Jatav, H.S., Sharma, S., Punia, H., Sayyed, R.Z., Almalki, W.H., Pocai, P. 2022. Role of Salicylic Acid in Combating Heat Stress in Plants: Insights into Modulation of Vital Processes. *Frontiers in Bioscience (Landmark Ed)*. 27(11): 310 doi:10.31083/j.fbl2711310
- Santos, M.S., Nogueira, M.A. and Hungria, M. 2019. Microbial inoculants: reviewing the past, discussing the present, and previewing an outstanding future for the use of beneficial bacteria in agriculture. *AMB Express* 9(1): 205. doi:10.1186/s13568-019-0932-0
- Sayyed, R., Al-zharani, M., Mubarak, M., Şuğan, N.A., Egamberdieva, D., Sharma, A., Rebouh, N.Y. and Barasarathi, J. 2026. Integrating Epigenetic memory and plant growth-promoting rhizobacteria-mediated signaling for climate-resilient agriculture. *Journal of Applied Microbiology* 137(7): lxag149. doi:10.1093/jambio/lxag149
- Sayyed, R.Z., Jamadar, D.D. and Patel, P.R. 2011. Production of exopolysaccharide by *Rhizobium* sp. *Indian Journal of Microbiology* 51(3): 294-00. doi:10.1007/s12088-011-0115-4
- Sayyed, R.Z., Patel, P.R. and Shaikh, S.S. 2015. Plant growth promotion and root colonization by EPS producing *Enterobacter* sp. RZS5 under heavy metal-contaminated soil. *Indian Journal of Experimental Biology* 53: 116-123. <http://nopr.niscpr.res.in/handle/123456789/30443>
- Sethi, G., Behera, K.K., Sayyed, R., Adarsh, V., Sipra, B.S., Singh, L., Alamro, A.A. and Behera, M. 2025. Enhancing soil health and crop productivity: The role of zinc-solubilizing bacteria in sustainable agriculture. *Plant Growth Regulation*. doi:10.1007/s10725-025-01294-7
- Shahbaz, M., Akram, A., Mehak, A., Haq, E., Fatima, N., Wareen, G., Aamir, S., Hassan, H., Pocai, P., Sayyed, R.Z. and Ilyas, N. 2023. Evaluation of selenium nanoparticles in inducing disease resistance against spot blotch disease and promoting growth in wheat under biotic stress. *Plants* 12(4): 761. doi:10.3390/plants12040761
- Shahdadi, F., Sepideh, K., Sardoei, A.S., Fallahnajmabadi, F., Fazeli-Nasab, B., Almalki, W.H., Almuji, S.S. and Sayyed, R.Z. 2023. GC-MS profiling of *Pistacia vera* L. cv. Ahmad-Aghaei hull essential oil revealed the presence of potent antioxidant and antimicrobial compounds compared to their chemical counterparts. *Scientific Reports* 13: 21694. doi:10.1038/s41598-023-48844-5
- Shahzad, B., Rehman, S., Bajwa, A., Hussain, S., Rehman, A., Alam, S., Abbas, T., Ali, A., Shah, L., Adkins, S. and Li, P.2019. Utilizing the allelopathic potential of Brassica species for sustainable crop production: a review. *Journal of Plant Growth Regulation* 38(1): 343-356. doi:10.1007/s00344-018-9798-7
- Shanthappa, P.M., Gowtham, H.G., Setty, P.B.S., Alhewairini, S., Barasarathi, J., Singh, P., Murali, M., Sayyed, R. and Prasad, S.P. 2025. Deciphering highly potent natural abscisic acid agonists for binding to pyrabactin resistance 1 receptor through computational approaches. *Scientific Reports* 15: 20999.

- doi:10.1038/s41598-025-07113-3
- Sharma, S., Kumari, P., Shandilya, M., Thakur, S., Perveen, K., Sheik, I., Ahmed, Z., Sayyed, R. and Mastinu, A. 2025. The combination of α -Fe₂O₃NP and *Trichoderma* sp. improves antifungal activity against Fusarium wilt. *Journal of Basic Microbiology* e2400613.
doi:10.1002/jobm.202400613
- Sheikh, T., Hamid, B., Baba, Z., Iqbal, S., Yattoo, A., Fatima, S., Nabi, A., Kanth, R., Dar, K., Hussain, N., Alturki, A.-I., Sunita, K., & Sayyed, R. Z. (2022). Extracellular polymeric substances in psychrophilic cyanobacteria: A potential bioflocculant and carbon sink to mitigate cold stress. *Biocatalysis and Agricultural Biotechnology*, 42, 102375.
doi:10.1016/j.bcab.2022.102375
- Showkat, M., Nagesha, N., Umashankar, N., Benherlal, P.S., Shobha, D., Ashraf, S., Gani, S., Fatimah, N., Nabi, A., Perveen, K., Bukhari, N.A., Barasarathi, J. and Sayyed, R.Z. 2024. Optimization of fermentation conditions of *Cordyceps militaris* and in silico analysis of antifungal property of cordycepin against plant pathogens. *Journal of Basic Microbiology* e2400409: 1-18.
doi:10.1002/jobm.202400409
- Singh, A.K., Kumar, P., Mishra, S.K., Tiwari, K.N., Singh, A.K., Pandey, A.K., Shati, A.A., Alfaifi, M.Y., Elbehairi, S.E.I. and Sayyed, R.Z. 2024. A network pharmacology approach with experimental validation to discover the protective mechanism of polyherbal extract on diabetes mellitus. *Journal of King Saud University – Science* 36(4): 103138.
doi:10.1016/j.jksus.2024.103138
- Singh, L., Nayak, A., Behera, M., Sethi, G., Alheswairini, S.S., Barasarathi, J., Sayyed, R., Behera, D.K. and Adarsh, V. 2025. Antifungal potential of cyanobacterium *Desertifilum dzianense* against collar rot pathogen in chickpea. *Scientific Reports* 15: 23740.
doi:10.1038/s41598-025-08395-3
- Spence, C. and Bais, H. 2015. Role of plant growth regulators as chemical signals in plant-microbe interactions: a double-edged sword. *Current Opinion in Plant Biology* 27: 52-58.
doi:10.1016/j.pbi.2015.05.028
- Sridhar, D., Alheswairini, S.S., Barasarathi, J., Enshasy, H.A.E., Lalitha, S., Mir, S.H., Nithyapriya, S. and Sayyed, R. 2025. Halophilic rhizobacteria promote growth, physiology and salinity tolerance in *Sesamum indicum* L. grown under salt stress. *Frontiers in Microbiology* 16: 1590854.
doi:10.3389/fmicb.2025.1590854
- Sudha, A., Durgadevi, D., Rajesh, M., Ramalakshmi, A., Kavitha, S., Perveen, K., Alshaikh, N.A. and Sayyed, R.Z. 2023. Volatilome profiling and evaluation of plant growth stimulation and anti-ergot activity of VOCs produced by *Trichoderma asperelloides*. *Sydowia* 76: 93-109.
doi:10.12905/0380.sydowia76-2024-0093
- Suriani, N.L., Al-zharani, M., Nasr, F.A., Alneghery, L.M., Suprpta, D.N., Suarsana, I.N., Resiani, N.M.D., Enshasy, H.A.E., Sayyed, R., Barasarathi, J., Ho, T.S. and Yanti, Y. 2025. Rhizobacterial consortium improves growth, yield, and phytochemicals in robusta coffee (*Coffea canephora* L.). *Frontiers in Microbiology* 6.
doi:10.3389/fmicb.2025.1602940
- Suriani, N.L., Suprpta, D.N., Suarsana, I.N., Resiani, N.M.D., Perveen, K., Bukhari, N.A., Enshasy, H.A.E., Ho, T.S. and Sayyed, R.Z. 2024. Biopotential of rhizobacteria to improve growth and phytochemical content in Javanese ginseng (*Talinum paniculatum*) herbal plant. *Frontiers in Sustainable Food Systems* 8: 1384700.
doi:10.3389/fsufs.2024.1384700
- Tariq, M., Khan, A., Asif, M. and Siddiqui, M.A. 2018. Interactive effect of *Trichoderma virens* and *Meloidogyne incognita* and their influence on plant growth character and nematode multiplication on *Abelmoschus esculentus* (L.) Moench. *Current Nematology* 29(1): 1-9.
doi:10.17485/ijst/2018/v11i45/137989
- Tariq, M., Khan, A., Asif, M., Khan, F., Ansari, T., Shariq, M., Imran, M. and Sohail, M. 2020. Biological control: A sustainable and practical approach for plant disease management. *Acta Agriculturae Scandinavica, Section B – Soil & Plant Science* 70(6): 507-524.
doi:10.1080/09064710.2020.1784262
- Tariq, A., Tanvir, A., Barasarathi, J., Alsohim, A.S., Mastinu, A., Sayyed, R. and Nazir, A. 2025. Endophytes: key role players for sustainable agriculture: Mechanisms, omics insights and future prospects. *Plant Growth Regulation* 105: 1969-90.
doi:10.1007/s10725-025-01370-y
- Tasnim, A., Roy, A., Akash, S.R., Ali, H., Habib, M.R., Barasarathi, J., Muthukumaran, M., Sayyed, R.Z. and Yeasmin, T. 2024. *Hibiscus sabdariffa* L. petal biomass: A green source of nanoparticles of multifarious potential. *Open Agriculture* 9: 20220332.
doi:10.1515/opag-2022-0332
- Vafa, Z.N., Sohrabi, Y., Sayyed, R.Z., Suriani, N.L. and Datta, R. 2021. Effects of combinations of Rhizobacteria, mycorrhizae, and seaweeds on growth and yields in wheat cultivars under the influence of supplementary irrigation. *Plants* 10(4): 811.
doi:10.3390/plants10040811
- Vafa, Z.N., Sohrabi, Y., Heidari, G., Rizwan, M. and Sayyed, R.Z. 2024. Wheat growth and

- yield response are regulated by mycorrhizae application and supplemental irrigation. *Chemosphere* 364:143068.
doi:10.1016/j.chemosphere.2024.143068
- Viejobueno, J., Albornoz, P.L., Camacho, M., de los Santos, B., Martínez-Zamora, M.G. and Salazar, S.M. 2021. Protection of strawberry plants against charcoal rot disease (*Macrophomina phaseolina*) induced by *Azospirillum brasilense*. *Agronomy* 11(2): 195.
doi:10.3390/agronomy11020195
- Vinothini, K., Nakkeeran, S., Saranya, N., Jothi, P., Richard, J.I., Perveen, K., Bukhari, N.A., Glick, B.R., Sayyed, R.Z. and Mastinu, A. 2024. Rhizosphere engineering of biocontrol agents enriches soil microbial diversity and effectively controls root-knot nematode. *Microbial Ecology* 87: 120.
doi:10.1007/s00248-024-02435-7
- Vyas, V., Alneghery, L.M., Al-zharani, M., Nasr, F.A., Majhi, P.K., Choudhary, S., Singh, S., Barasarathi, J. and Sayyed, R. 2026. Legume-symbiosome signal exchange driving nodulation and nitrogen fixation. *Symbiosis* 99: 99-120.
doi:10.1007/s13199-026-01140-y
- Wang, L., Xi, N., Lang, D., Zhou, L., Zhang, Y. and Zhang, X. 2022. Potential biocontrol and plant growth promotion of an endophytic bacterium isolated from *Glycyrrhiza uralensis* seeds. *Egyptian Journal of Biological Pest Control* 32(1): 1-16.
doi:10.1186/s41938-022-00476-4
- Wani, P.A., Omobolanle, L.A., Hamid, H., Fayokemi, R.A., Perveen, K., Bukhari, N.A., Sayyed, R.Z. and Mastinu, A. 2024. Evaluation of destruction of bacterial membrane structure associated with anti-quorum-sensing and anti-diabetic activity of *Cyperus esculentus* extracts. *Heliyon* 10: e34128.
doi:10.1016/j.heliyon.2024.e34128
- Wani, S.J., Shaikh, S.S. and Sayyed, R.Z. 2016. Statistical-based optimization and scale-up of siderophore production process on laboratory bioreactor. 3 *Biotech.* 6: 69.
doi.org/10.1007/s13205-016-0365-2
- Wipf, H.M.-L., Xu, L., Gao, C., Spinner, H.B., Taylor, J., Lemaux, P., Mitchell, J. and Coleman-Derr, D. 2021. Agricultural soil management practices differentially shape the bacterial and fungal microbiomes of *Sorghum bicolor*. *Applied and Environmental Microbiology* 87(10): e02345-20.
doi:10.1128/AEM.02345-20
- Wolfgang, A., Temme, N., Tilcher, R. and Berg, G. 2023. Understanding the sugar beet holobiont. *Microbiome* 11(1): 25.
doi:10.1186/s40168-023-01468-3
- Xiang, G., Ma, W., Gao, S., Jin, Z., Yue, Q. and Yao, Y. 2019. Transcriptomic and phosphoproteomic profiling and metabolite analyses reveal the mechanism of NaHCO₃-induced organic acid secretion in grapevine roots. *BMC Plant Biology* 19(1): 383.
doi:10.1186/s12870-019-1990-9
- Yao, X., Huang, K., Zhao, S., Cheng, Q., Zhang, S., Yang, L. and Wang, H. 2021. Identification and verification of rhizosphere indicator microorganisms in tobacco root rot. *Agronomy Journal* 113(2): 1480-1491.
doi:10.1002/agj2.20547
- Yattoo, A.M., Ali, M.N., Baba, Z.A., Alsohim, A.S., Muthukumaran, M. and Sayyed, R.Z. 2024. Effect of macrophyte biomass-based vermicompost and vermicompost tea on plant growth, productivity, and biocontrol of Fusarium wilt disease in tomato. *Biocatalysis and Agricultural Biotechnology* 60: 103320.
doi:10.1016/j.bcab.2024.103320
- Yones, A.M. and Kayim, M. 2021. Molecular characterization of *Trichoderma* spp. with biocontrol ability against faba bean chocolate spot (*Botrytis cinerea* Pers. ex Fr.). *Plant Cell Biotechnology and Molecular Biology* 22(5-6): 52-63.
doi:10.56557/pcbmb/2021/v22i5-68243
- Zeffa, D.M., Fantin, L.H., Koltun, A., Oliveira, A.L.M. de, Nunes, M.P.B.A., Canteri, M.G. and Gonçalves, L.S.A. 2020. Effects of plant growth-promoting rhizobacteria on co-inoculation with *Bradyrhizobium* in soybean crop: a meta-analysis of studies from 1987 to 2018. *PeerJ* 8: e7905.
doi:10.7717/peerj.7905

About the Authors

Dr. P. Saranraj: P. Saranraj holds a Ph.D. in Microbiology from Annamalai University and is NET (ASRB-ICAR) qualified, with over 15 years of research and 11 years of teaching experience. His expertise spans environmental, agricultural, and industrial microbiology, nanotechnology, and sustainable ecosystem management. He has published 250+ international research articles, 100+ books, and 120 book chapters, and is an inventor/co-inventor of 11 international patents. He actively contributes as an editor, reviewer, author, and invited academic speaker, demonstrating strong leadership in microbiology and sustainable biotechnology.

Riyaz Sayyed: Prof. Riyaz Sayyed is a globally recognized microbiologist with 22 years of academic and research experience in plant-microbe interactions, rhizosphere engineering, and sustainable agriculture. Author of 300+ research papers, 91 book chapters, and 36 edited books, and 55 textbooks, with a cumulative impact factor of 953.205 and an H-index of 74. Recognized among Clarivate's Top 1% Highly Cited Researchers and Elsevier's Top 2% Scientists. Holds 4 patents. Mentored 200+ graduate students and supervised 8 Ph.D. dissertations (5 ongoing). Serves as Associate, Academic, and Guest Editor for journals published by Springer, Elsevier, Wiley, MDPI, and Frontiers, and has reviewed for 60+ international journals—fellow of the Royal Society of Biology (London) and the Indian Phytopathological Society.

K. Kesavardhini: K. Kesavardhini is an enthusiastic microbiologist with expertise in Microbiology, Microbial Biotechnology, and Agricultural Microbiology. She has contributed to 19 Scopus-indexed publications and actively engages in scientific communication through lecture videos, blogs, and presentations. She has received seven Best Presentation Awards in recognition of her outstanding research presentations and scientific contributions. and completed 11 online courses through agMOOCs, NOUNMOOC, and BHUMMOOC. Her academic journey reflects strong commitment to research, innovation, continuous learning, and scientific communication.

B. Lokeshwari: B. Lokeshwari is a dedicated researcher in Microbiology, Biotechnology, and Nanotechnology, with interests in agricultural and environmental microbiology, microbial pigments, nanobiotechnology, Spirulina research, effluent treatment, and plant-microbe interactions. She is a co-inventor of a UK design patent on Heavy Metal Identification Gloves Using Nanotechnology, granted in 2024. She has published 23 research and review papers and contributed to 49 book chapters with reputed international publishers. She has received multiple Best Presentation Awards in recognition of her research excellence and effective scientific communication. demonstrating her active contribution to interdisciplinary and sustainable research.

K. Gayathri: K. Gayathri is an accomplished microbiologist with expertise in environmental and agricultural microbiology, nanotechnology, medical microbiology, herbal research, Spirulina, and effluent treatment. She has published 31 research papers and contributed to books and book chapters with reputed publishers. She is a co-inventor of a UK patent for a microbiology incubator and portable laboratory and has received several awards for her academic and research contributions. Her work reflects strong contributions to microbiology, biotechnology, nanotechnology, and sustainable research.

