

Enhancing plant resistance to biotic stresses through rhizobacteria for sustainable agriculture

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Abstract

Plant Growth-Promoting Rhizobacteria (PGPR) play a crucial role in the enhancement of plant growth. These microorganisms inhabit plant roots and positively influence plant growth through various mechanisms. PGPR facilitate nutrient absorption, combat pathogens, and regulate plant hormone levels. Their impact is achieved through direct actions such as hormone production, enhanced iron uptake via siderophores, phosphate solubilization, and emission of volatile compounds that affect plant signaling and metabolism. In addition, PGPR interactions with rhizosphere microorganisms and the soil indirectly improve plant growth. Numerous biotic stressors affect plant PGPR. The interaction between plants and microorganisms boosts the host resistance to biotic stress. This interaction also regulates the rhizosphere soil by converting organic compounds into plant-absorbable forms, increasing molecule mobilization, and supplying amino acids, carbohydrates, lipids, metabolites, and phytohormones to the host plants. In instances where plants do not secrete lipids, amino acids, carbohydrates, or terpenoids during these interactions, microorganisms contribute these compounds to plants. Investigating these mechanisms, along with changes in gene expression and receptor-mediated signaling in plants, is vital. Utilization of microbial sources as alternatives to conventional agricultural methods is a promising approach. Incorporation of these sources can enhance plant production, quality, growth, and yield.

Keywords: biotic stress; enhancing plant resistance; plant growth-promoting rhizobacteria (PGPR); sustainable agriculture

Introduction

Agricultural commodities, which serve as essential sources of sustenance and livelihood for populations, also function as pivotal raw materials for the industrial sector. Given the shifts in climate patterns and emergence of novel diseases and pests, there is a pressing need to enhance agricultural output by 70%. This increase aims to cater to the nutritional demands of approximately 9.8 billion individuals globally by 2050 (FAO, 2017). Within diverse farming landscapes, a significant 31-42% reduction in yield has been documented, attributable to biotic agents such as pathogenic fungi, bacteria, viruses, nematodes, insects, and weeds. Additionally, adverse climatic conditions and soil factors, such as alkalinity, salinity, and acidity, along

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with occurrences of drought, pollution, and flooding, lead to degradation of soil health due to abiotic factors. A central avenue to elevate agricultural productivity is to curtail losses stemming from stressors. Chemical intervention has been a prevalent strategy against plant ailments in farming. However, the prohibition of numerous chemical fungicides by the European Union has spurred the development of sustainable and innovative alternatives for disease management (Koike *et al.*, 2015). Given these detrimental repercussions, the demand for novel substitute approaches to minimize chemical dependency in disease mitigation has increased recently (Koike *et al.*, 2015). Microorganisms play a crucial role in maintaining Earth's ecological equilibrium and supporting life. Advanced molecular techniques, such as metagenomics, have enabled on-site identification of microorganisms, leading to improved comprehension of their ecological roles within microbial communities (Berendsen *et al.*, 2012). Plant microbiota, also known as the plant microbiome, is composed of diverse microorganisms residing within different parts of plants, such as the rhizosphere, phyllosphere, and endosphere. These microorganisms significantly contribute to plant health and growth (Brader *et al.*, 2017). The rhizosphere, housing plant roots, and surrounding soil are particularly dynamic, and mark a zone of intense interactions between plants, soil, and microfauna. It is recognized as the most active area and exhibits a high microbial diversity in the soil. As the root interface approaches, the influence of plants on microbial communities increases (Brader *et al.*, 2017).

Ecological relationships between plants and microbes encompass various scenarios, including competition, exploitation, neutrality, compensation, and mutualism, which occur within the rhizosphere, phyllosphere, and endosphere. While numerous studies have concentrated on mitigating negative impacts, such as infections (Zhang *et al.*, 2013) and stress alleviation, there is a longstanding interest in comprehending the beneficial ecological interactions that bolster plant growth. Understanding the functional aspects of plant-rhizobacteria interactions and the underlying gene expression regulatory mechanisms not only advances our understanding of the plant as a meta-organism but also reveals how plants can harness the benefits of rhizobacterial partnerships, thereby fostering enhanced crop production and product quality (Hacquard, 2016). Most rhizobacteria can break down organic matter in the soil, including cellulose, hemicellulose, polysaccharides, hydrocarbons, and lignin derivatives, thereby converting them into usable forms. Furthermore, they convert soil-bound nitrogen and sulfur and select minerals (such as Fe^{+3} and Fe^{+2}) into accessible forms, thus facilitating the transformation of plant nutrients into utilizable forms. Plant Growth-Promoting Rhizobacteria (PGPR) are autonomous bacteria that positively affect plant development through root colonization. These PGPRs mitigate the severity of various plant diseases and increase crop yield. PGPR have been utilized across different crops to enhance yield, foster seedling growth, and improve food and environmental standards, with some formulations entering commercial markets (Hardoim *et al.*, 2015; Reinhold-Hurek *et al.*, 2015).

Effects of biotic stresses on plants

In Both internal and external factors regulate the growth and development of plants. Optimal environmental conditions are essential for normal growth and development of plants. Variations in environmental factors can affect plant growth and can lead to stress. These stressors not only diminish agricultural productivity but also impede the utilization of new land for farming purposes. Stress triggers diverse morphological, anatomical, and metabolic responses in plants. Consequently, environmental stressors play a pivotal role in shaping plant structure and function. Natural conditions concurrently expose the plants to multiple stressors. Stress is defined as an alteration induced by various environmental and biological factors that are involved in physiological processes. It is also referred to as the "potential to inflict harm," which can manifest as reduced growth, yield, or even plant demise. Stress resilience, or the ability to endure adverse conditions, is the defining trait of an organism. While certain plant parts, such as seeds and dormant buds, are

inherently stress resistant, others, such as meristems and fleshy organs, are susceptible (Larcher, 1995). In addition, the degree of stress resistance in a plant can evolve during its growth and development cycles. The factors influencing a plant's response to stressors include the severity and duration of stress, the specific tissue or organ exposed, and the developmental stage during stress exposure. Moreover, different cultivars or genotypes of the same species may respond differently to identical stressors. Various biotic factors in the natural environment can induce plant stress. Changes in response to biotic stressors are also classified as stress-induced alterations. Stress negatively affects plant growth and development by triggering physiological and metabolic changes. It can lead to diminished product quality and quantity, plant or organ mortality, and disruption of the overall plant function. The extent of damage from stressors depends on the genetic adaptation of the plant to its surroundings, which is a pivotal factor in determining the optimal growth in diverse regions. Biotechnological advancements aim to develop stress-resistant plant varieties and to preclude potential future nutritional issues. Plants exhibit two primary mechanisms of stress resistance, prevention and tolerance. They either counteract stress factors by activating their developed preventive mechanisms, or persevere through tolerance mechanisms (Larcher, 1995). Excessive soil stress reduces transpiration, respiration, root development, and water uptake by plants. These conditions contribute to a decline in photosynthetic rate, impaired nitrate utilization, and reduced protein synthesis (Dölarslan *et al.*, 2012). Biotic stress is caused by animals, insects, microorganisms, pathogens, and weeds. Plants experiencing stress deploy various mechanisms to mitigate the detrimental effects of stress or combat stress through their resistance pathways. The escalation of free radicals due to stress triggers the peroxidation of membrane lipids, resulting in the impairment of macromolecules, such as proteins and nucleic acids. Furthermore, stress disrupts the integrity of cell walls and membrane structures (Sreenivasulu *et al.*, 1999). To counteract these effects, plants possess an array of enzymes known as antioxidants that target the oxygen radicals generated in response to stress. One prominent example is superoxide dismutase (SOD), an enzyme synthesized by plants that counteracts the deleterious effects of the superoxide oxygen radical (O_2^-). SOD activity leads to the formation of hydrogen peroxide (H_2O_2) as a by-product. Subsequently, H_2O_2 , which can be toxic, is converted into harmless components, namely water (H_2O) and oxygen (O_2), catalyzed by specific enzymes such as ascorbate peroxidase (APX), glutathione reductase (GR), and catalase (CAT) (Dionisio-Sese *et al.* 1998, Hernandez *et al.*, 1995). Studies conducted worldwide have shown that biotic stress is the most common stress factor (Figure 1).

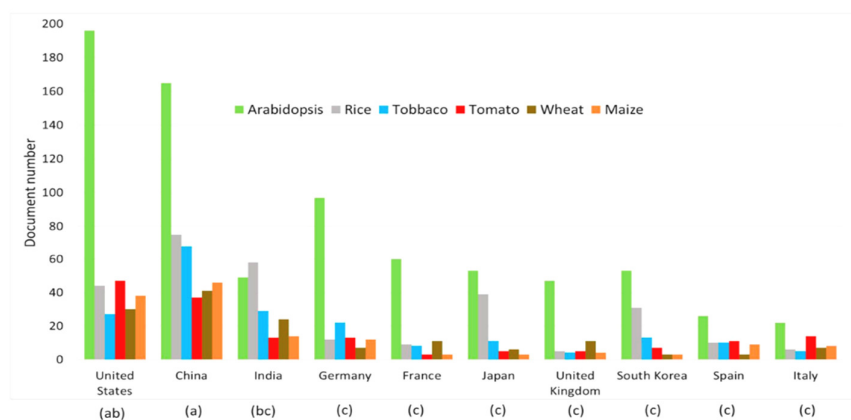


Figure 1. The global research distribution (%) of biotic stress according to the subject area was categorized by Scopus (Gimenez *et al.*, 2018)

Rhizobial inoculants have demonstrated potential to enhance growth, nutrient absorption, seedling vitality, and rice yield (Biswas *et al.*, 2000). Plant Growth-Promoting Rhizobacteria (PGPR) contribute to disease mitigation through diverse mechanisms, including the competitive exclusion of resources and space, as well as the initiation of systemic resistance (ISR). By eliciting systemic resistance, PGPR can indirectly facilitate biological control of several plant diseases. The application of certain PGPR categories to seeds or seedlings has been shown to induce ISR in treated plants. This phenomenon is referred to as induced systemic resistance, and is triggered by various biotic factors. Furthermore, apart from the basal resistance responses enacted at the site of pathogen invasion, plants possess the capacity to develop nonspecific resistance that effectively counters pathogen assault (Udayashankar *et al.*, 2011).

Enhancing growth through plant growth-promoting rhizobacteria

Plant Growth-Promoting Rhizobacteria (PGPR) directly or indirectly enhance plant growth by improving plant physiology and by conferring resistance to various phytopathogens through diverse mechanisms (Zakry *et al.*, 2012). These mechanisms include nutrient fixation, enzymatic disease prevention, mitigation of biotic stress, and the emission of volatile organic compounds. However, the modus operandi of distinct PGPR types vary based on the host plant in which they interact with (García-Fraile *et al.* 2015). Biotic factors encompass a multitude of elements that influence plant genotypes, defence mechanisms, developmental stages, and microbial communities (Vacheron *et al.*, 2013). Several bacterial species produce indole acetic acid (IAA), an auxin derivative. Notable examples include *Sphingomonas*, *Hizobium*, *Mycobacterium*, *Azospirillum*, *Burkholderia* spp., and the Microbacterium Uma Maheshwari. (2013). Numerous studies have highlighted the substantial impact of PGPR application on the hormone levels in cabbage seedlings. PGPR inoculation increased IAA, gibberellic acid, and salicylic acid levels. *P. agglomerans* exhibited the highest levels of IAA, gibberellic acid, and salicylic acid. Conversely, the abscisic acid levels were most pronounced in the control group (Turan *et al.*, 2014). Recognized PGPR species include *Pseudomonas putida*, *Pseudomonas aeruginosa*, *Enterobacter asburiae*, *Paenibacillus polymyxa*, *Azotobacter chroococcum*, *Mesorhizobium ciceri*, *Klebsiella oxytoca*, *Rhizobium leguminosarum*, and *Stenotrophomonas maltophilia*. These bacteria synthesize ethylene, kinetin, auxins, and gibberellins, which are hormones pivotal for fostering root growth (Ahemad *et al.*, 2014). Plants cultivated in challenging environments often exhibit elevated levels of 1-aminocyclopropane-1-carboxylic acid (ACC), a precursor of ethylene, a vital phytohormone that regulates various physiological processes. However, elevated concentrations of this phytohormone impede plant growth and trigger senescence (Figure 2). Plant Growth-Promoting Rhizobacteria (PGPR) have been identified as effective agents in modulating plant ethylene levels. PGPR achieve this by expressing genes encoding ACC deaminase, an enzyme responsible for breaking down ACC into α -ketobutyrate and ammonia, consequently curbing ethylene production. This enzyme has been isolated from a range of rhizobacteria including *Alcaligenes*, *Achromobacter*, *Acidovorax*, *Klebsiella*, *Enterobacter*, *Pseudomonas*, *Methylobacterium*, *Variovorax*, and *Rhizobium* (Chandran *et al.*, 2021). The synthesis of indole acetic acid by PGPR initiates elongation in plant cells, which in turn prompts the transcription of a pivotal enzyme linked to ethylene synthesis. ACC synthase, which is responsible for converting S-adenosyl methionine into ACC, catalyzes the primary step followed by the conversion of ACC to ethylene by ACC. In the event of prolonged stress exposure, plants trigger ACC synthase activity, leading to the release of ACC from roots into the soil. Subsequently, as ACC concentration increases, it activates bacterial ACC deaminase, thereby facilitating its breakdown. The adoption of PGPR has emerged as a vital biotechnological advancement in sustainable agriculture, fostering enhanced plant growth and stress tolerance through ACC deaminase activity.

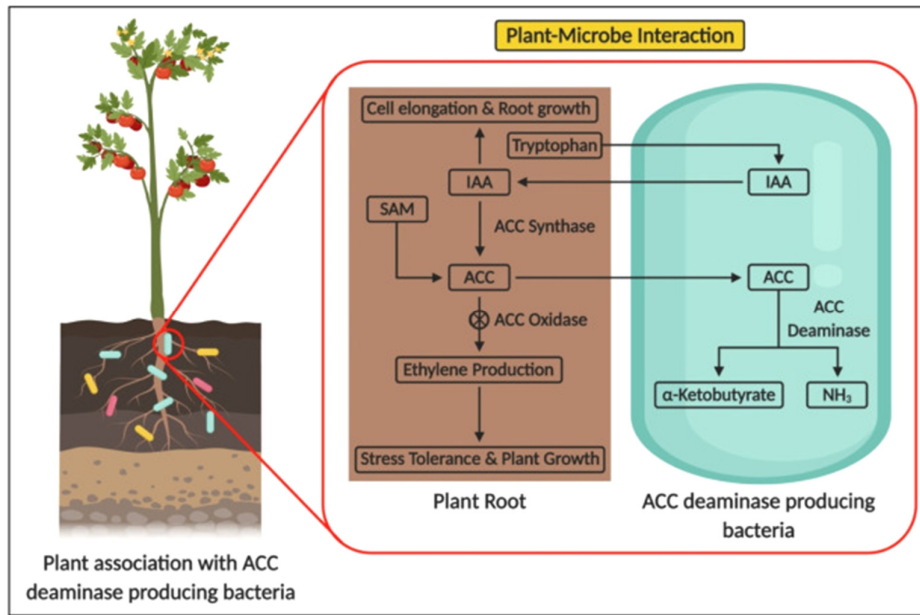


Figure 2. The utilization of ACC deaminase in PGPR facilitates plant growth by breaking down ACC, an ethylene precursor (Murali *et al.*, 2021)

Systemic Impact of PGPRs on Plant Physiology and Functioning

Plant Growth-Promoting Rhizobacteria (PGPR) can influence plant physiology and function by affecting various plant tissues, extending beyond root colonization. One notable effect was the enhancement of nutrient absorption in the root zone. Additionally, certain PGPR strains elicit systemic responses through intricate signaling pathways that remain largely unidentified. Notably, PGPR-induced changes in metabolite accumulation and gene expression are evident, as evidenced by studies involving plant transcriptomics and metabolomics. These findings offer valuable insights into the holistic effects of PGPR. Advancements in microorganism research are directed towards the creation of novel bioprotectants, bioinoculants, and bio-enhancers. These innovative solutions supply essential compounds, such as biosurfactants, osmoprotectants, antioxidant enzymes, phytohormone precursors, and nutrients. In addition to conferring biotic stress resistance, consortia of diverse bacteria contribute to phytopathogen management. Maximizing the potential of these interactions necessitates the increased utilization of rhizobacteria-based inoculants to elucidate their impact on plant systems. Ultimately, this approach holds promise for promoting plant growth and enhancing the tolerance to various biotic stressors. Targeted investigations are crucial for tailoring bioformulations capable of supporting plant growth under stressful conditions. These efforts require meticulous exploration of stress-tolerant rhizobacterial gene expression profiles and the multifunctional properties of PGPR (Woo *et al.*, 2018).

Impact of PGPRs on Plant Nutrition

Plant Growth-Promoting Rhizobacteria (PGPR) play a crucial role in enhancing root growth by stimulating the uptake of nutrients within plant nutrition (Mantelin *et al.*, 2004). These beneficial bacteria orchestrate a range of pathways to enhance nutrient absorption effectively, thereby fostering plant growth. Rhizobacteria can activate ion transport mechanisms within the root zone, consequently increasing the nutrient availability. A notable effect of PGPR on plant nutrition is their ability to enhance phosphate

solubility. This phenomenon leads to the gradual accumulation of substantial phosphorus deposits from applied fertilizers in the soil. However, it is important to note that only a minor proportion of the amassed phosphorus is utilized by plants. Plants primarily absorb monobasic and dibasic phosphate ions. In instances of organic and insoluble phosphate, microbial processes are imperative for mineralization and subsequent dissolution (Ramaekers *et al.*, 2010). Noteworthy examples of phosphate-solubilizing bacteria include *Pseudomonas*, *Bacillus*, and *Rhizobium* spp. (Richardson *et al.*, 2009).

Impact of PGPRs on plant transcriptome

The effect of gene expression on the utilization of plant growth-promoting rhizobacteria (PGPR) in plant applications is a subject of investigation. A study involving the grafting of a *Pseudomonas putida* strain onto Arabidopsis leaves resulted in the upregulation of approximately 520 genes. These genes are implicated in diverse metabolic processes, ABA and calcium signaling, ISR (Induced Systemic Resistance) initiation, and chemical synthesis (Srivastava *et al.*, 2012). Nitrogen (N) was acquired through nitrogen fixation using the bacterial strains *Azospirillum brasilense* Sp245, Cultivar IR42, and IAC 4440 on two contrasting rice cultivars. In this context, elevation in ethylene receptor expression has also been observed (Vargas *et al.*, 2012). A complete ensemble of ethylene receptor transcripts is crucial for establishing a favorable relationship between plants and bacteria (Miche *et al.*, 2006). The introduction of *Herbaspirillum seropedicae* led to the activation of ethylene- and auxin-sensitive genes in rice. Additionally, this process suppresses defense related proteins PBZ1 and thionines (Brusamarello-Santos *et al.*, 2012). The application of biocontrol PGPR to plants notably enhances their resistance to bacterial pathogen infections. Responsiveness to jasmonate and ethylene hormones is essential for Rhizobacteria-mediated ISR in Arabidopsis plants. Significant alterations in the expression of 97 genes in the roots were induced by *Pseudomonas fluorescens* WCS417r (Verhagen *et al.*, 2004). Arabidopsis plant shoots containing bacteria exhibit heightened levels of transcripts related to defence mechanisms (Van de Mortel *et al.*, 2012). ISR facilitated by *Pseudomonas fluorescens* SS101 demonstrated a more pronounced signaling effect of salicylic acid compared to other hormones (Van de Mortel *et al.*, 2012). Moreover, it plays a pivotal role in the modulation of glucosinolates and camalexin via the ISR pathway. Increased expression of defense related transcripts was detected in wheat treated with *Pseudomonas fluorescens*, emphasizing the impact of these interactions on bolstering plant immunity (Maketon *et al.*, 2012). These intricate associations underscore the reciprocal and crucial coordination among PGPR, plants, and beneficial microorganisms, all of which profoundly influence plant immunological responses.

Impact of PGPRs on plant metabolome

Metabolic alterations induced by PGPR manifest as variations in plant metabolite profiles under both stressful and non-stressful conditions. Modulations in the enzymatic activities of PGPRs within plant roots resulting from changes in their metabolite synthesis roles also contribute to the observed transformations (Shaw *et al.*, 2006). Some strains of *Azospirillum* have been found to increase the release of carbon compounds from plant roots into the soil, with approximately one-third of the total carbon compounds released (Heulin *et al.*, 1987). Additionally, microbial compounds, such as DAPG and phenazines, have been shown to enhance amino acid production in diverse plant species (Phillips *et al.*, 2004). For instance, the rhizobacterium *Chryseobacterium balustinum* displays variance in flavonoid exudation from the soybean roots (Dardanelli *et al.*, 2010). The efflux of flavonoids from the roots of Fabaceae plants is influenced by either PGPRs or *Azospirillum* spp. (Dardanelli *et al.*, 2010; Burdman *et al.*, 1996). Application of *Herbaspirillum seropedicae* to

rice plant roots has led to notable elevations in malate and amino acid concentrations in the rice shoots (Curzi *et al.*, 2008). Further studies have highlighted shifts in the levels of secondary metabolites. Several types of PGPR applications have been shown to increase isoflavone content in soybean plants (Ramos-Solano *et al.*, 2010). Moreover, medicinal plants subjected to PGPR treatment exhibit marked increases in terpenoid and alkaloid contents and compounds with significant pharmacological value (Bharti *et al.*, 2013). *Azospirillum* strains have been applied to various maize (Walker *et al.*, 2011), and rice cultivars (Chamam *et al.*, 2013) have triggered adjustments in secondary metabolite profiles, with outcomes contingent upon the specific strain-cultivar combination (Chamam *et al.*, 2013). When *Azospirillum*, *Rhizophagus*, *Pseudomonas* strains, or a combination of all three are applied to maize roots (Walker *et al.*, 2012), discernible differences in the root secondary metabolites were observed. These variations depend on the microbial type and the extent of fertilization. Notably, PGPRs play a pivotal role in mitigating plant stress. The treatment of rice roots with *Pseudomonas pseudoalcaligenes* led to increased levels of glycine betaine (Bharti *et al.*, 2013). The application of *Bacillus subtilis* GB03 to Arabidopsis roots led to an increase in glycine betaine content (Zhang *et al.*, 2010). Moreover, the application of *Burkholderia phytofirmans* PsJN to grapevine roots has been shown to alleviate cold stress, which is accompanied by the activation of cold-responsive genes and an augmented defence response (Barka *et al.*, 2006; Theocharis *et al.*, 2012). Bacterization has been associated with a two-fold increase in soluble sugar and starch content. Additionally, bacteria-treated seedlings exhibit higher levels of sugars associated with cold tolerance (Fernandez *et al.*, 2012).

Influence of plant-rhizobacteria interactions on secondary metabolites

The chemical constituents of herbs can be categorized into primary and secondary metabolites, each with distinct functions and following a specific biosynthetic pathway. Primary metabolites are consistently synthesized in various organisms to fulfill fundamental life processes. Secondary metabolites are intricate organic compounds that facilitate plant adaptation to the environment, contribute to reproduction, and play vital roles in safeguarding plants against biotic and abiotic stressors (Alvarez, 2014). These secondary metabolites are more intricate in structure than primary metabolites (Bartwal *et al.*, 2012). The concept of secondary metabolites was introduced by Kossel in 1891 (Bourgau *et al.*, 2001). Many plants that produce secondary metabolites are exclusive to specific regions, underscoring the need for innovative approaches to sustainably produce these compounds. Secondary metabolites are typically grouped into three categories based on their chemical structure: phenolics, terpene steroids, and alkaloids. These compounds are often present in minute quantities within specialized cells during particular plant developmental stages or in response to stressful conditions (Alvarez, 2014). Researchers are actively investigating the causes and mechanisms of fluctuations in secondary metabolite levels. The interplay of secondary metabolites in plant-microorganism relationships has attracted considerable attention. The interaction between fungi and plants, for instance, has been linked to increased leaf phosphorus content and alterations in leaf metabolomes in plants from the *Plantaginaceae*, *Fabaceae*, and *Poaceae* families, which were inoculated with rhizophagus irregular (Schweiger *et al.*, 2014). An intriguing query pertains to the origin of bioactive phytochemicals, whether they are synthesized autonomously by the plant or arise as a consequence of interactions with beneficial organisms within tissues. This has spurred ongoing research in this field. Researchers have discovered that a combination of stimuli from both plants and fungi contributes to increased accumulation of secondary metabolites in plants and fungi (Engels *et al.*, 2008). Examination of bacteria-plant interactions revealed that introducing *Bacillus subtilis* (GB03) to basil plants (*Ocimum basilicum*), abundant in secondary metabolites, significantly enhanced terpene synthesis derived from α -terpineol and eugenol (Banchio *et al.*, 2009). Similarly, Italian thyme roots exhibit a notable increase in monoterpenes (thymol, carvacrol, sabinen hydrate, and terpinene) after

inoculation with soil bacteria (*A. brasilense* and *P. fluorescens*) (Banchio *et al.*, 2010). *Agrobacterium rhizogenes* facilitates root formation by transferring auxin synthesis genes from bacterial DNA into host tissues (Ream, 2009). Concurrently, the activation of disease-resistant genes triggers the increased expression of secondary metabolites (Flores *et al.*, 1999). The modulation of gene expression in plant-microorganism interactions has prompted researchers to examine changes in secondary metabolite-related gene expression. When moths (*Catharanthus roseus*) were exposed to bacterial strains (*Curvularia* sp., *Choanephora infundibulifera*, *Aspergillus japonik*, and *Pseudomonas* sp.), genes responsible for secondary metabolite production exhibited increased expression (Singh *et al.*, 2020). Although soil is often viewed by plant physiologists as merely a nutrient source, it constitutes a multifaceted ecosystem that houses bacteria, fungi, protists, and animals. Soil microorganisms profoundly impact ecosystems by influencing critical processes, such as nutrient cycling, carbon and nitrogen cycling, and soil formation (Rillig *et al.*, 2006). Interactions between plant roots and the microbiota in the rhizosphere, including bacteria, fungi (AMF), oomycetes, viruses, and similar structures, trigger alterations in plant primary and secondary structures (Schweiger *et al.*, 2014; Singh *et al.*, 2020). Diverse perspectives exist regarding the origin of secondary metabolism in plants (Karuppusamy, 2009). These perspectives suggest that secondary metabolites are produced either by the plants themselves or by endophytic fungi associated with the plants and rhizosphere microbes. Radiolabeled primary amino acid studies have revealed that plants and endophytic fungi exhibit distinct yet somewhat similar metabolic pathways for secondary metabolite production (Zhang *et al.*, 2009). The quality of secondary metabolites in plants is strongly influenced by the biotic and abiotic factors in the rhizosphere. Microbial diversity within the rhizosphere substantially contributes to enhancing the properties of medicinal aromatic plants. However, a comprehensive description of the rhizosphere microbiome is challenging because of variations in microbial diversity compared to bulk soil as well as disparities between various studies. In addition to descriptive analysis of the rhizosphere microbiome, it is imperative to investigate the mechanisms governing the selection of specific microbial populations. Medicinal aromatic plants are associated with various bacterial and fungal species in the host plant rhizosphere and significantly contribute to nutrient uptake and secondary metabolite production. This interplay between plants and microorganisms not only bolsters the host plants' resilience to biotic and abiotic stressors but also facilitates the transformation of organic molecules into forms assimilable by plants. This intricate dual relationship provides essential molecules. Furthermore, exploring the specific amino acids, carbohydrates, lipids, and terpenoids involved in plant-microbial interactions, elucidating the mechanisms behind their exchange, the resulting alteration in plant gene expression, and the receptors involved in signaling reception are paramount (Cetiz *et al.*, 2021).

Influence of PGPR on plant root growth and structure

A comprehensive investigation was conducted to explore the mechanisms of action of Plant Growth-Promoting Rhizobacteria (PGPR) by using a specific host plant and strain. Notably, PGPRs do not operate in isolation and their interactions can yield synergistic or antagonistic effects when different PGPR populations interact with a host plant. Rhizobacterial strains that foster plant growth belong to diverse taxonomic groups that coexist in soil (Almario *et al.*, 2013). The identification of specific bacterial isolates is critical to ascertain their taxonomic classification for their positive impacts on plant growth. Plant Growth-Promoting Rhizobacteria (PGPR) populations with similar functions collectively form functional groups such as those involved in plant growth promotion, Induced Systemic Resistance (ISR), and nitrogen fixation. Relevant genes must be well documented prior to utilizing functional group approaches. The coexistence of various PGPR strains, the effects of which vary based on the genetic interactions between PGPR and plants, has two notable outcomes. First, the populations of synergistic PGPR strains exhibited enhanced effects compared with those of the individual strains. This increased functionality contributes to the increased nutritional requirements of

plants. However, the functional group adapts its performance to prevent the excessive or inadequate production of signaling compounds known as oxinic signals (Spaepen *et al.*, 2007). The implementation of the PGPR function also needs to consider regulatory effects (Prigent-Combaret *et al.*, 2008). In specific rhizospheric regions, significant interactions occur among the different PGPR types. Some functional groups of PGPRs display inhibitory and competitive behaviors (Coullero *et al.*, 2011), whereas others demonstrate positive signaling (Combes-Meynet *et al.*, 2011). These interactions influence spatial colonization patterns in plant roots, thus affecting PGPR efficacy (Coullero *et al.*, 2011). Rhizobial colonization of root tips of plants belonging to the Fabaceae family plays a pivotal role in initiating nodule development (Desbrosses *et al.*, 2011). For PGPRs to exert their beneficial properties, they must possess qualities that facilitate root colonization in plants (Combes-Meynet *et al.*, 2011). Furthermore, PGPR strains are affected by both abiotic and biotic factors. These strains can modify plant root system structure through the effects of PGPRs on plant hormones. PGPRs engage in a range of soil activities that contribute to their sustainable production (Gupta *et al.*, 2015). PGPRs compete for space while colonizing the root zone. Simultaneously, these rhizobacteria participate in diverse mechanisms, such as phosphate solubilization, root growth stimulation, surface area regulation (Ahmad *et al.*, 2012), nitrogen fixation (Glick, 2012), siderophore production (Jahanian *et al.*, 2012), 1-aminocyclopropane-1-carboxylate (ACC) deaminase, and hydrogen cyanide release (Xie *et al.*, 2016), all of which contribute to enhanced plant growth. Therefore, PGPRs can stimulate phytohormone synthesis in plants. Phytohormones are organic compounds that modulate, inhibit, or stimulate plant growth even at low concentrations (Damam *et al.*, 2016). Examples of phytohormones include brassinosteroids, gibberellins, abscisic acid, cytokinins, auxins, and ethylene, which foster root hair and lateral root proliferation, thereby enhancing the overall plant growth (Damam *et al.*, 2016). These plant growth regulators can be administered externally to plant tissues or can be derived from natural or synthetic sources. Phytohormones play a pivotal role in regulating nutrient absorption depending on climatic conditions and soil composition. One common outcome of the effect of phytohormones is an increase in root hair and lateral roots, along with a reduction in primary root growth. Through the synthesis of growth metabolites, PGPRs confers stress resistance during root colonization in host plants. Consequently, a significant boost in crop yield is achievable, along with benefits, such as root repair and stress tolerance.

Promoting activation of the plant rhizobacterial defense response

The various mechanisms employed by Plant Growth-Promoting Bacteria (PGPB) have been subject to prior examination, encompassing scenarios of nonexistence (Khatoon *et al.*, 2020; Phour *et al.*, 2020), and the occurrence of diverse abiotic and biotic stressors (Ullah *et al.*, 2019; Morales-Cedeño *et al.*, 2021). This discussion provided a concise overview of the underlying mechanisms.

Direct mechanisms

The primary mechanisms for promoting plant growth include the direct facilitation of resource and nutrient acquisition, as exemplified by the solubilization and mineralization of phosphates (Glick, 2012). This mechanism, similar to that of mycorrhizal fungi, enhances plant growth and nutrition. Additionally, Plant Growth-Promoting Bacteria (PGPB) can generate siderophores that foster iron solubilization and binding in the rhizosphere. Rhizobia and certain other PGPBs exhibit the ability to fix atmospheric nitrogen (N₂), transforming it into ammonia, and making it accessible to plants. This assimilation of bacterially fixed nitrogen not only fosters plant growth but also augments the nutritional quality of cultivated crops (Peralta *et al.*, 2004). Another mechanism that stimulates plant growth involves hormone synthesis, which is essential for plant

development and growth. These include indoleacetic acid, cytokinin, gibberellin, abscisic acid, salicylic acid, brassinosteroids, and jasmonate (Munne-Bosch *et al.*, 2013). Some PGPB species can produce multiple hormones, the effects of which are contingent on prevailing endogenous hormone concentrations in plants. In addition to hormone production, numerous PGPB harbor ACC deaminase, an enzyme that moderates plant ethylene levels (Glick, 2004). The interplay between hormones generated by PGPB and those synthesized by plants can regulate diverse growth phases, whether confronted with biotic or abiotic stresses, or in their absence (Kumar *et al.*, 2020; Wu *et al.*, 2020).

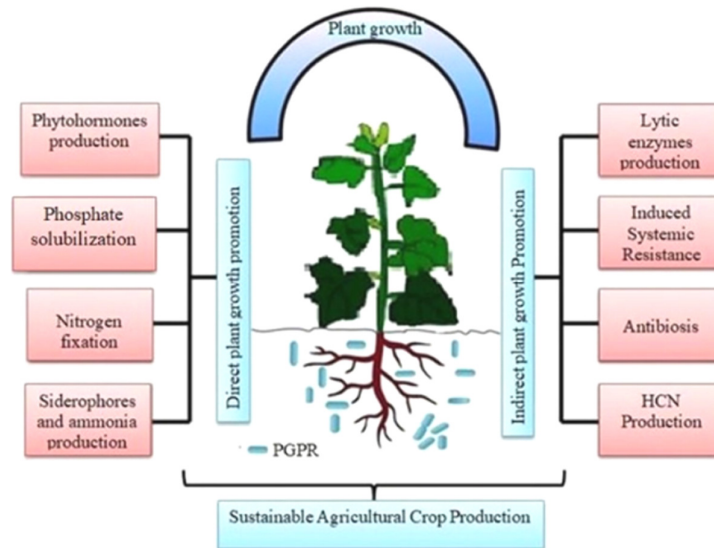


Figure 3. The direct and indirect mechanisms of PGPR (Mhatre *et al.*, 2019)

Indirect mechanisms

Plant Growth-Promoting Rhizobacteria (PGPB) can stimulate plant growth via both direct and indirect mechanisms. These indirect mechanisms are particularly valuable as they involve the inhibition of potential pathogens and enhancement of the plant's immune response, thus avoiding the need for chemical biocides (Khatoon *et al.*, 2020). This dual functionality of PGPBs presents advantages for their application as comprehensive bioinoculants (Hernandez Leon *et al.*, 2015). When PGPBs possess both types of mechanisms and interact favorably with other rhizospheric microorganisms, such as mycorrhizae, their combined effects on plant health can be synergistic. The investigation of the molecular intricacies of microbial interactions is of significant interest. Some PGPBs produce lytic enzymes capable of breaking down the cell walls of pathogenic fungi and oomycetes. These lytic enzymes include glucanase, chitinase, cellulase, protease, and lipase, which target the structural components of the fungal and oomycete cell walls (Bowman *et al.*, 2006). Oomycetes, which are mainly plant pathogens, are particularly susceptible to enzymatic attacks (Inglis *et al.*, 2002). Recognizable examples of such pathogens include *Bremia lactucae*, *Hyaloperonospora parasitica*, and *Phytophthora infestans* (Dodds *et al.*, 2009). By counteracting these pathogens, PGPBs contribute to safeguarding agricultural ecosystems against the substantial losses caused by these diseases (Morales-Cedeno *et al.*, 2021). Furthermore, PGPBs produce diffusible (e.g., 2,4-diacetylphloroglucinol, phenazines) and volatile (e.g., dimethyl disulfide, dimethylhexadecylamine, and hydrogen cyanide) properties (Glick, 2012). This antibiotic activity is complemented by mechanisms such as occupying spaces in the plant that pathogens could otherwise inhabit and generating chelating compounds such as siderophores. Siderophores restrict the availability of iron to harmful microorganisms under iron-limited conditions (Dowling *et al.*, 1994; Kloepper *et al.*, 1980). Certain compounds and enzymes, such as pyoverdine, chitin, and β -glucanase can induce systemic

resistance (ISR) in plants. These compounds have been shown to trigger ISR in various plants during greenhouse and field trials, thereby bolstering their defense against biotic stressors (Sarma *et al.*, 2015). During times of stress due to biotic factors, plants generate excess ethylene, a stress hormone responsible for senescence, chlorosis, and abscission. PGPBs can alleviate this stress by producing 1-aminocyclopropane-1-carboxylate (ACC) deaminase, which reduces the ethylene precursor ACC to α -ketobutyrate and ammonia. By curbing ethylene production, PGPBs alleviate plant stress signals and protect plants from pathogenic attacks, including fungal and oomycete attacks. Moreover, ACC deaminase and other compounds, such as trehalose, can mitigate ethylene levels in plants stressed by abiotic factors such as flooding, salinity, heavy metal contamination, or drought (Orozco-Mosqueda *et al.*, 2020). Plants exposed to multiple stressors generate reactive oxygen species (ROS), leading to oxidative damage. To counteract this, plants employ antioxidant defense systems, including enzymatic (SOD, POD, CAT, APX, and GR) and non-enzymatic (tocopherol, flavonoids, phenols, glutathione, and ascorbic acid) components to neutralize ROS (Chandran *et al.*, 2021). PGPB inoculation enhances these systems, protecting plants from oxidative damage due to various abiotic stresses such as drought, salinity, and heavy metal exposure. This inoculation increases the expression and activity of antioxidant enzymes, further improving the overall antioxidant status of the plants (Chandran *et al.*, 2021).

Table 1. Beneficial Rhizobacteria for Plant Growth and their Mechanisms of Promotion (Kumawat *et al.* 2022)

Plant	PGPR	Plant growth-promoting mechanism(s)	Reference
Soybean	<i>Bacillus firmus</i> SW5 <i>Bradyrhizobium japonicum</i> USDA 110, <i>Pseudomonas putida</i> TSAU1	Antioxidant enzyme production; alternation in root architecture	(El-Esawi <i>et al.</i> , 2018)
Soybean	<i>Pseudomonas putida</i> H-2-3	Production of ABA, salicylic acid, jasmonic acid, and gibberellins	(Kang <i>et al.</i> , 2014)
Soybean	<i>Pseudomonas simiae</i>	IAA and siderophore production; phosphate solubilization	(Vaishnav <i>et al.</i> , 2016)
Soybean	<i>Bradyrhizobium</i> spp. LSBR-3, <i>Pseudomonas aeruginosa</i> LSE-2, <i>Leclercia adecarboxylata</i> LSE-1	IAA, ACC deaminase, and siderophore production; phosphate solubilization; exopolysaccharide and biofilm formation	(Kumawat <i>et al.</i> , 2019a; 2019b)
Cucumber	<i>Rhodopseudomonas palustris</i> G5	N fixation; phosphate and potassium solubilization; IAA and 5-aminolevulinic acid synthesis	(Ge <i>et al.</i> , 2019)
Cucumber	<i>Pseudomonas fluorescens</i> , <i>Bacillus megaterium</i> , <i>Variovorax paradoxus</i>	ACC deaminase, IAA, siderophore, and exopolysaccharide production	(Nadeem <i>et al.</i> , 2016)
Tomato	<i>Pseudomonas fluorescens</i> YsS6, <i>Pseudomonas migulae</i> 8R6	ACC deaminase production	(Ali <i>et al.</i> , 2014)
Tomato	<i>Streptomyces</i> sp. PGPA39	Phosphate solubilization; ACC deaminase and IAA production	(Palaniyandi <i>et al.</i> , 2014)

Rice	<i>Pantoea agglomerans</i> KL	ACC deaminase, exo polysaccharide IAA, and ammonia production; phosphate solubilization	(Bhise <i>et al.</i> , 2019)
Rice	<i>Curtobacterium albidum</i> SRV4	N fixation; ACC deaminase, IAA, exo-polysaccharide, and HCN production	(Vimal <i>et al.</i> , 2019)
Rice	<i>Enterobacter</i> sp. P23 Phosphate	solubilization; ACC deaminase, IAA, siderophore, and HCN production	(Sarkar <i>et al.</i> , 2018)
Wheat	<i>Enterobacter cloacae</i> ZNP-3	Phosphate solubilization; ACC deaminase, IAA, and HCN production	(Singh <i>et al.</i> , 2017)

Plant defense utilizing bio-control agents

Soil plays a dual role, acting as a source of vital nutrients for plant growth and as a complex ecosystem in which a variety of organisms, such as bacteria, fungi, protists, and animals, thrive in diverse and interactive communities. These soil microorganisms are associated with plant roots, collectively known as the phytomicrobiome, and they engage in various relationships with plants that can be competitive, exploitative, or neutral. This interplay between plants and their associated microorganisms gives rise to a holobiont comprising both the plant and its phytomicrobiome. Recent studies have explored the potential of beneficial rhizobacteria in mitigating pathogenic effects and enhancing plant growth. Plant roots host an extensive array of microbes, with the next step being the identification of specific rhizobacteria or combinations thereof that best facilitate host plant growth (Figure 4). A significant aspect of this effort involves the development of strategies to control pathogens that affect target plant species. Microbial strains that have co-evolved with plants over extended periods and promote plant growth are likely to offer dual benefits, including pathogen control. The composition of rhizosphere microbiomes varies among plant species because plants influence the composition of these microbial communities. The prolonged co-evolution of microbes with plants enables them to indirectly affect plant health and phenotypic plasticity by modulating plant development and defense responses. The rhizosphere is home to a wide range of microorganisms and is a valuable reservoir of PGPR. Plant Growth-Promoting Rhizobacteria (PGPR) constitute beneficial members of the phytomicrobiome, colonizing the rhizosphere, root surfaces, spaces between root cortex cells, and even within the root cells themselves. Owing to their long-standing symbiotic relationship with plants, PGPR have developed synergistic interactions with their host plants. Numerous studies have examined the effects, mechanisms, and potential applications of PGPR in controlled environments for the cultivation of crop plants. This holds particular significance for advancing broader biological control strategies, including in field conditions. In the context of vegetable production, where quality control and safety are closely linked to human health, given the often minimal processing, the application of PGPR is important. Deploying PGPR in controlled greenhouse systems is more feasible owing to regulated environmental conditions. Additionally, a wealth of potential Biological Control Agent (BCE) strains have been identified and could be harnessed for deployment. Certain strains such as *Bacillus* spp. and *Pseudomonas fluorescens* have shown promise as biocontrol agents under field conditions. Notably, specific isolates such as *Pseudomonas stutzeri*, *Bacillus subtilis*, and *B. amyloliquefaciens* exhibited successful root colonization and significant suppression of the pathogen *Phytophthora capsici* during cucumber growth. *Bacillus subtilis* has also proven effective in controlling *Penicillium* spp. and *Rhizopus stolonifer*

infections during the post-harvest stages. Furthermore, under greenhouse conditions, isolates of *B. amyloliquefaciens* have demonstrated substantial inhibition of *Fusarium* wilt disease caused by *Fusarium oxysporum*. These examples underscore the effectiveness of PGPR as biological control agents (BCAs) in controlled environments, lending strong support to their application in greenhouse production systems. This ensured the practicality and efficacy of PGPR in commercial horticulture production. It is important to recognize that PGPR mechanisms for preventing pathogen infections and promoting plant growth under abiotic stress are interconnected and should not be viewed in isolation. Moreover, for practical implementation, PGPR with biocontrol effects are even more valuable if they also contribute to plant growth (Singh *et al.*, 2021). A fundamental process in plant-pathogen interactions, induced resistance, and plant defense is protein phosphorylation (Xing *et al.*, 2002). This process can modify the inherent biological activity, subcellular localization, and lifespan of proteins, thereby influencing the scope and duration of the defense responses. Numerous protein kinases and phosphatases have been identified that bridge the gap between signal perception mechanisms and plant defence reactions. The fields of genomics and proteomics have already uncovered novel components and are expected to continue to significantly impact the understanding of phosphorylation in the context of plant-pathogen interactions (Xing *et al.*, 2002).

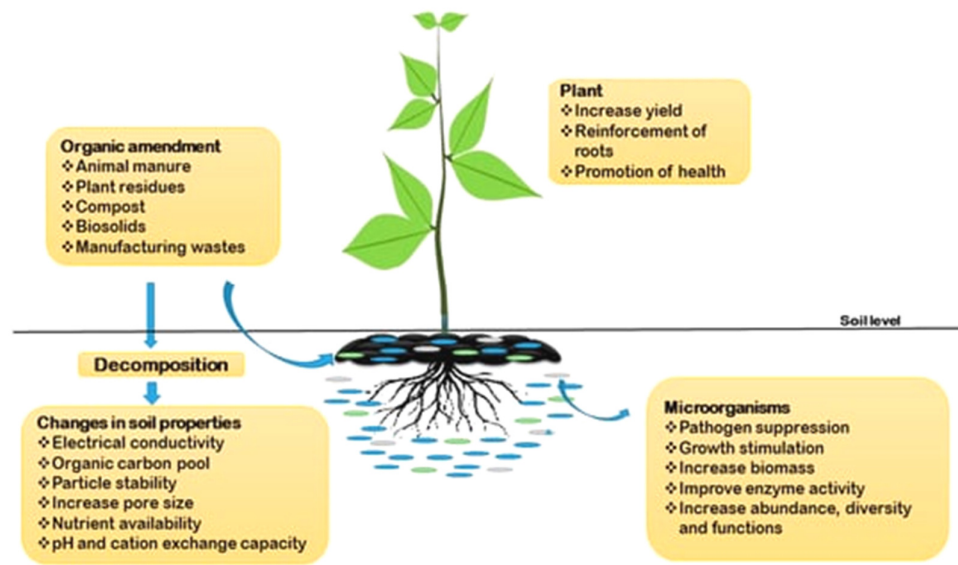


Figure 4. The impact of organic amendments on soil and plant and soil microorganisms

Conclusions

We focus on Plant Growth-Promoting Rhizobacteria (PGPR), which are abundantly present in the rhizosphere and the region surrounding the plant roots. These beneficial bacteria play crucial roles in agriculture and plant well-being. This section elaborates on how certain PGPRs contribute to plant growth and development through both direct and indirect mechanisms. These mechanisms include enhancement of metabolite production, antibiotics, enzymes, bioactive substances, and growth stimulants. In summary, specific PGPRs serve as advantageous rhizobacteria that can function as biofertilizers. These eco-friendly and cost-effective alternatives can be employed to augment agricultural crop yields while reducing reliance on synthetic fertilizers. This will facilitate improved soil health, nutrient availability, and sustainable agricultural practices. The strategic use of PGPR in agriculture is imperative to ensure optimal crop productivity without compromising ecosystems. Undoubtedly, the integration of PGPRs into agriculture is an effective measure,

offering a renewable solution for sustainable farming. The ecological feasibility and versatile applications of PGPRs in the agricultural sector provide a foundation for generating novel bioactive compounds and genetic materials. Factors such as mode of action, colonization capabilities, diversity, formulation, and practical implementation of PGPRs are vital components that can bolster sustainable agricultural management and stimulate future advancements.

Authors' Contributions

Both authors read and approved the final manuscript.

Ethical approval (for researches involving animals or humans)

Not applicable.

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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