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REVIEW PAPER

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Characteristics of symbiotic relationships between plants and bacteria and the influence of stress factors on them

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ABSTRACT

Symbiotic relationships between plants and bacteria play a fundamental role in ecosystem functioning and sustainable agriculture. Based on extensive literature analysis, this review examines the formation, development, and functioning of plant–bacterial symbioses, with particular emphasis on nitrogen-fixing interactions between legumes and rhizobia. The symbiotic process is described as a complex, multi-stage system regulated by coordinated molecular, physiological, and genetic mechanisms of both partners. Special attention is given to the influence of abiotic and biotic stress factors—such as temperature extremes, drought, heavy metals, and nutrient imbalance—on the establishment and efficiency of symbiosis. While higher plants are generally more sensitive to stress conditions, beneficial microorganisms can mitigate negative effects by enhancing nutrient uptake, physiological stability, and stress tolerance. The review highlights that stress factors often reduce symbiotic efficiency, but targeted use of plant-associated microorganisms offers promising strategies to improve crop productivity and ecological sustainability. Understanding these interactions is essential for developing environmentally friendly agricultural practices and reducing dependence on chemical fertilizers.

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INTRODUCTION

Plant-microorganism symbiosis is one of the fundamental biological interactions governing ecosystem functioning and plant adaptation. Such associations occur between higher plants and diverse microorganisms, including bacteria, and range from neutral coexistence to highly specialized mutualistic relationships (Hassani *et al.*, 2018; Ho *et al.*, 2017). The establishment of plant–bacterial symbiosis is a complex, multi-stage process regulated by coordinated molecular, physiological, and genetic mechanisms of both partners, involving mutual recognition, signal exchange, infection, and functional integration (Tikhonovich and Provorov, 2009; Lindström and Mousavi, 2020).

Among these interactions, the symbiosis between legumes and nitrogen-fixing bacteria of the genus *Rhizobium* is of particular importance. In this association, molecular nitrogen (N_2) is biologically fixed and converted into plant-available forms, allowing plants to satisfy their nitrogen requirements without dependence on synthetic fertilizers (Kebede, 2021; Lindström and Mousavi, 2020). This symbiotic system represents an advanced evolutionary adaptation that enhances survival and productivity within natural and agricultural ecosystems.

Ecological and agricultural importance of plant–bacterial interactions

Plant–bacterial symbioses contribute significantly to soil fertility, nutrient cycling, and sustainable agricultural productivity. Beneficial bacteria associated with plant roots participate in biological nitrogen fixation, synthesis of biologically active compounds, activation of nutrient uptake, induction of systemic resistance, and biological control of phytopathogens (Hassani *et al.*, 2018; Santoyo, 2025). These processes collectively enhance plant growth while reducing the need for chemical inputs. Excessive application of nitrogen fertilizers has resulted in nitrate accumulation in soils, water bodies, and agricultural products, leading to ecological imbalance and risks to human and environmental health (Elumalai *et al.*, 2025). Symbiotic nitrogen fixation offers an environmentally safe alternative, as it supplies nitrogen to plants without disrupting the natural nitrogen cycle (Ladha *et al.*, 2022). It has been estimated that legume–rhizobium symbiosis can fix substantial amounts of nitrogen annually, thereby reducing fertilizer costs and environmental pressure in agricultural systems (Yeremko *et al.*, 2025). Consequently, understanding plant–bacterial interactions is essential for the development of sustainable and eco-friendly agricultural practices.

Rationale for focusing on stress factors

Despite their importance, plant–bacterial symbiotic systems are highly sensitive to environmental stress factors. Abiotic stresses such as drought, temperature extremes, salinity, and heavy metal contamination, as well as biotic stresses including pathogens and competing microorganisms, can disrupt symbiotic establishment and efficiency (Pandey *et al.*, 2017; Mohamed *et al.*, 2025). Higher plants are generally more susceptible to stress conditions, exhibiting altered physiological and biochemical responses that negatively affect growth and symbiotic functioning (Ali *et al.*, 2025).

Stress factors can impair key stages of symbiosis, including bacterial colonization, infection thread development, nodule formation, and nitrogen fixation activity (Nuc and Olejnik, 2025; Yeremko *et al.*, 2025). Heavy metals, for example, interfere with nutrient uptake, water balance, hormonal regulation, and photosynthesis in plants, while also reducing microbial abundance and diversity in the rhizosphere (Pishik *et al.*, 2016; Mohamed *et al.*, 2025). Although microorganisms often show greater tolerance to stress than plants, adverse environmental conditions ultimately weaken the symbiotic system as a whole (Hnini *et al.*, 2025). These observations justify a focused examination of plant–bacterial symbiosis under stress conditions.

Objectives and scope of the review

The objective of this review is to synthesize current knowledge on plant-bacterial symbiotic relationships, with particular emphasis on their formation, regulation, and functioning under abiotic and biotic stress conditions. The review aims to analyze the molecular, physiological, and genetic mechanisms underlying symbiosis, evaluate the effects of stress factors on both symbiotic partners, and assess the potential of beneficial microorganisms to mitigate stress-induced damage in plants (Santoyo, 2025; Yeremko *et al.*, 2025).

By integrating findings from recent studies, this review seeks to identify knowledge gaps and highlight future research directions for improving symbiotic efficiency under unfavorable environmental conditions. A comprehensive understanding of these processes is essential for enhancing crop productivity, promoting sustainable agriculture, and reducing dependence on chemical fertilizers, particularly in regions where agriculture plays a central role in economic development (Ladha *et al.*, 2022; Kebede, 2021).

Overview of plant–bacterial symbiotic relationships

Definition and types of symbiosis

Symbiosis refers to the close and long-term interaction between two different biological organisms living in physical association with one another. In plant–microorganism systems, these relationships can be classified into mutualism, commensalism, and parasitism, depending on the nature and outcome of the interaction for each partner (Ho *et al.*, 2017; Hassani *et al.*, 2018). Mutualistic interactions are characterized by reciprocal benefits, where both the plant and the microorganism gain advantages that enhance survival, growth, or reproduction. In contrast, commensal relationships involve one partner benefiting without significantly affecting the other, while parasitic interactions result in benefit to one organism at the expense of the other.

Among plant–bacterial interactions, mutualism is the most extensively studied due to its ecological relevance and agricultural applications. Mutualistic symbioses include associations that facilitate molecular nitrogen fixation, synthesis of biologically active compounds, activation of nutrient uptake by plant roots, induction of systemic resistance, and biological control of plant pathogens (Kebede, 2021; Santoyo, 2025). These interactions are not static but dynamically regulated by environmental conditions, host specificity, and molecular signaling between partners, highlighting the complexity of plant–bacterial symbiotic systems (Tikhonovich and Provorov, 2009).

Evolutionary significance of plant–bacteria interactions

Plant–bacterial symbioses are the result of long-term co-evolutionary processes that have enabled both partners to adapt to diverse and often unfavorable environmental conditions. Over evolutionary time, plants and bacteria have developed highly specific recognition mechanisms, allowing compatible partners to establish stable and efficient symbiotic relationships (Lindström and Mousavi, 2020). These adaptations are genetically fixed and transmitted across generations, contributing to the emergence of host specificity and cross-infection groups observed in many symbiotic systems (Tsyganova *et al.*, 2021).

The evolutionary success of legume–rhizobium symbiosis illustrates how cooperative interactions can enhance resource acquisition and ecological fitness. The ability of bacteria to fix atmospheric nitrogen and supply it to plants has provided legumes with a selective advantage in nitrogen-poor soils, while bacteria benefit from carbon sources and a protected niche within root nodules (Kebede, 2021; Lindström and Mousavi, 2020). Such co-evolutionary interactions have shaped plant physiology, microbial metabolism, and the structure of terrestrial ecosystems, reinforcing the central role of symbiosis in plant adaptation and biodiversity.

Major groups of symbiotic bacteria associated with plants

A wide range of bacterial taxa are involved in symbiotic and beneficial associations with plants.

Among them, bacteria belonging to the genus *Rhizobium* and related genera within the order Rhizobiales are the most prominent due to their capacity for symbiotic nitrogen fixation in legumes (Lindström and Mousavi, 2020). These bacteria form specialized root nodules in which molecular nitrogen is reduced to ammonia through the activity of nitrogenase enzymes, supporting plant growth and soil fertility.

In addition to rhizobia, various plant growth-promoting bacteria contribute to plant health and stress tolerance. Bacterial genera such as *Klebsiella*, *Agrobacterium*, and *Arthrobacter* have been reported to enhance plant growth by improving nutrient uptake, modulating hormonal balance, and alleviating the negative effects of abiotic stress factors (Santoyo, 2025; Mohamed *et al.*, 2025). These bacteria often colonize the rhizosphere or internal plant tissues and interact with plants through multiple direct and indirect mechanisms (Hnini *et al.*, 2025).

Collectively, these diverse groups of plant-associated bacteria form complex microbial communities that influence plant development, productivity, and resilience. Understanding the diversity and functional roles of symbiotic bacteria is essential for harnessing their potential in sustainable agriculture and environmental management (Hassani *et al.*, 2018; Santoyo, 2025).

Molecular and physiological basis of symbiosis

Signal exchange and recognition mechanisms

Root exudates and bacterial chemotaxis: The establishment of plant–bacterial symbiosis begins with an active exchange of chemical signals between plant roots and soil microorganisms. Plant roots secrete a diverse array of low-molecular-weight compounds, collectively known as root exudates, which include organic acids, amino acids, sugars, phenolics, and secondary metabolites. These compounds play a critical role in shaping the rhizosphere microbiome and serve as chemoattractants for symbiotic bacteria (Chen and Liu, 2024; Ho *et al.*, 2017). Symbiotic bacteria respond to these exudates through chemotactic movement toward the root surface, increasing the likelihood of successful colonization and infection.

In legume–rhizobium symbiosis, bacterial chemotaxis toward specific root exudates represents an early determinant of host specificity. Organic acids released by legume roots are particularly effective in attracting rhizobia, while amino acids and sugars further enhance bacterial accumulation in defined root zones (Nuc and Olejnik, 2025). This selective attraction ensures that compatible bacterial populations dominate the rhizosphere, enabling efficient initiation of symbiotic interactions (Tikhonovich and Provorov, 2009).

Role of flavonoids, Nod factors, and receptors: Among root exudates, flavonoids play a central signaling role in symbiotic recognition. These compounds are secreted by plant roots and act as molecular signals that activate nodulation (nod) genes in compatible rhizobial strains (Liu and Murray, 2016; Kidaj *et al.*, 2024). Flavonoids bind to the bacterial regulatory protein NodD, triggering transcription of nod genes responsible for the synthesis of Nod factors.

Nod factors are lipochitooligosaccharide signaling molecules that determine host specificity and initiate morphological and physiological responses in plant root cells. Upon perception of Nod factors by plant receptors, a cascade of cellular events is induced, including root hair deformation, calcium spiking, infection thread formation, and cortical cell division leading to nodule organogenesis (Wais *et al.*, 2002; Nuc and Olejnik, 2025). Recent studies indicate that receptor-like kinases located on the plant plasma membrane function as Nod factor receptors, translating bacterial signals into intracellular responses essential for symbiosis establishment (Bovin *et al.*, 2024).

Genetic regulation of symbiotic interactions

Nod, nif, and fix genes: The genetic regulation of symbiosis is coordinated by a set of bacterial genes that control nodulation, nitrogen fixation, and symbiotic efficiency. The nod genes are primarily involved in the synthesis and modification of Nod factors and are essential for host recognition and nodule formation. These genes include conserved nod genes (nodA, nodB, nodC) and host-specific nod genes that determine symbiotic compatibility at the strain level (Wais *et al.*, 2002; Lindström and Mousavi, 2020).

Following nodule formation, nitrogen fixation is governed by nif (nitrogen fixation) genes, which encode the nitrogenase enzyme complex responsible for the reduction of atmospheric nitrogen (N_2) to ammonia (NH_3). This process is energetically demanding and tightly regulated, requiring low oxygen conditions within root nodules (Threatt and Rees, 2023). In addition, fix genes participate in regulating electron transport, oxygen control, and energy metabolism necessary for effective nitrogen fixation (Lindström and Mousavi, 2020). Together, nod, nif, and fix genes form an integrated regulatory network ensuring the successful establishment and functioning of symbiotic nitrogen fixation.

Plant genes involved in nodulation and infection control: Symbiosis is not solely regulated by bacterial genes; plant genetic control is equally critical. Host plants possess specific genes, commonly referred to as Nod genes, that regulate root hair deformation, infection thread progression, cortical cell division, and nodule development (Tsyganova *et al.*, 2021). These genes also control the spatial localization and number of nodules, preventing excessive nodulation that could impose metabolic costs on the plant.

Plants further regulate symbiotic interactions through immune-like mechanisms that distinguish beneficial symbionts from pathogens. Early symbiotic signaling suppresses defense responses, while later stages involve strict control of bacterial proliferation within nodules (Hassani *et al.*, 2018). This genetic regulation ensures that symbiosis remains beneficial under varying environmental conditions and contributes to the long-term stability of the plant–bacterial association (Lepetit and Brouquisse, 2023).

Stages of symbiotic development

The development of plant–bacterial symbiosis is a highly coordinated, multi-stage process that requires precise spatial, molecular, and physiological regulation by both partners. In legume–rhizobium associations, symbiosis proceeds through sequential stages that include pre-infection signaling, bacterial infection and nodule formation, and the functioning of mature nodules capable of nitrogen fixation (Tikhonovich and Provorov, 2009; Nuc and Olejnik, 2025).

Pre-infection stage

Root exudation, bacterial attraction, and attachment: The pre-infection stage represents the initial phase of symbiotic interaction and is characterized by intensive chemical communication between plant roots and soil bacteria. Legume roots secrete a diverse mixture of organic acids, amino acids, sugars, and flavonoid compounds into the rhizosphere, which act as chemoattractants and signaling molecules for compatible rhizobial populations (Chen and Liu, 2024; Ho *et al.*, 2017). These root exudates induce bacterial chemotaxis, leading to the accumulation of rhizobia in specific regions of the root surface, particularly near emerging root hairs (Nuc and Olejnik, 2025).

Following attraction, bacterial attachment to the root surface occurs through physical and biochemical interactions involving surface polysaccharides, lectins, and glycoconjugates. Lectins produced by plant cells bind selectively to carbohydrate components on the bacterial cell surface, facilitating partner recognition and stable attachment (Yang *et al.*, 2025). This early recognition step is essential for distinguishing symbiotic bacteria from pathogenic microorganisms and determines whether the interaction proceeds toward symbiosis or defense activation (Hassani *et al.*, 2018).

Infection and nodule formation

Infection thread development: Successful attachment is followed by bacterial penetration into root tissues through the formation of infection threads. Infection threads are tubular, plant-derived structures composed mainly of cellulose and other cell wall components that guide bacteria from the root hair into the cortical cells (Tsyganova *et al.*, 2021). Their formation is triggered by Nod factor signaling, which induces root hair curling, localized cell wall loosening, and cytoskeletal rearrangements in host cells (Wais *et al.*, 2002; Nuc and Olejnik, 2025).

As infection threads elongate and branch, bacteria multiply within them while remaining enclosed by the plant-derived matrix. The progression of infection threads is strictly regulated by the host plant, and many infection events are aborted at early stages as part of nodulation control mechanisms, ensuring optimal bacterial numbers and preventing excessive metabolic costs (Tsyganova *et al.*, 2021; Yeremko *et al.*, 2025).

Nodule organogenesis: Nodule organogenesis begins concurrently with infection thread development and involves the reactivation of cell division in the root cortex. Nod factor signaling induces cortical cell dedifferentiation and division, leading to the formation of nodule primordia (Lepetit and Brouquisse, 2023). These developing nodules differentiate into specialized organs that provide a protected microenvironment for bacterial colonization and nitrogen fixation.

During nodule maturation, bacteria are released from infection threads into plant cells, where they differentiate into bacteroids. The plant supplies carbon sources and regulatory signals, while the bacteria undergo physiological and morphological changes required for nitrogen fixation (Lindström and Mousavi, 2020). The highly organized structure of nodules, including vascular tissues and oxygen diffusion barriers, is essential for maintaining symbiotic efficiency.

Functioning of mature nodules

Nitrogen fixation process: The primary function of mature nodules is the biological fixation of atmospheric nitrogen. This process is catalyzed by the nitrogenase enzyme complex encoded by bacterial nif and fix genes and results in the reduction of N_2 to ammonia (NH_3), which is subsequently assimilated into amino acids and transported to the aerial parts of the plant (Threatt and Rees, 2023; Lindström and Mousavi, 2020). Nitrogen fixation is an energy-intensive process, requiring large amounts of ATP and reducing equivalents supplied through plant-derived photosynthates.

Within nodules, specialized metabolic pathways operate to support nitrogen fixation, including enhanced respiration and the tricarboxylic acid cycle in bacteroids. These processes provide the energy and carbon skeletons necessary for ammonia assimilation and amino acid synthesis (Grzyb *et al.*, 2021).

Role of leghemoglobin and energy metabolism: A critical challenge in nitrogen fixation is the oxygen sensitivity of nitrogenase. Although rhizobia are aerobic organisms, nitrogenase is irreversibly inactivated by oxygen. This paradox is resolved through the presence of leghemoglobin, a hemoprotein synthesized jointly by the plant and bacterial partners (Lindström and Mousavi, 2020). Leghemoglobin binds oxygen with high affinity, maintaining low free oxygen concentrations within nodules while ensuring sufficient oxygen supply for bacterial respiration.

By regulating oxygen availability, leghemoglobin enables efficient oxidative phosphorylation and ATP production without compromising nitrogenase activity. This fine-tuned balance between oxygen transport and protection of nitrogenase is essential for sustained nitrogen fixation and overall symbiotic efficiency (Threatt and Rees, 2023; Warmack and Rees, 2023).

Role of symbiotic bacteria in nitrogen fixation

Biological nitrogen fixation mechanisms

Biological nitrogen fixation (BNF) is a microbially mediated process through which atmospheric nitrogen (N_2) is reduced to ammonia (NH_3), a form that can be assimilated by plants. In plant–bacterial symbioses, this process is primarily carried out by symbiotic bacteria belonging to the genus *Rhizobium* and related taxa within the order Rhizobiales, which form specialized root nodules in leguminous plants (Lindström and Mousavi, 2020; Kebede, 2021). The reduction of N_2 is catalyzed by the nitrogenase enzyme complex encoded by nif and fix genes and requires a strictly regulated, low-oxygen environment within the nodule (Threatt and Rees, 2023).

Nitrogen fixation is an energy-intensive process, requiring at least 16 molecules of ATP for the reduction of one molecule of nitrogen. This energy demand is met through plant-derived photosynthates that fuel bacterial respiration and ATP synthesis within bacteroids (Udvardi and Poole, 2013). The symbiotic system is therefore metabolically integrated, with plants providing carbon and bacteria supplying fixed nitrogen, ensuring mutual benefit and sustained symbiotic efficiency (Lepetit and Brouquisse, 2023).

Contribution to soil fertility and crop productivity

Symbiotic nitrogen fixation plays a critical role in maintaining soil fertility and enhancing crop productivity, particularly in low-input and sustainable agricultural systems. Fixed nitrogen released from nodules contributes directly to plant growth and indirectly enriches soil nitrogen pools through root turnover, residue decomposition, and rhizodeposition (Grzyb *et al.*, 2021; Ladha *et al.*, 2022). As a result, legume cultivation improves soil structure and fertility, benefiting subsequent non-legume crops in crop rotation systems.

Estimates suggest that legume–rhizobium symbiosis can contribute between 100 and 300 kg N ha^{-1} $year^{-1}$, significantly reducing the need for external nitrogen inputs (Kebede, 2021; Yeremko *et al.*, 2025). Beyond nitrogen supply, symbiotic bacteria enhance nutrient uptake, stimulate root development, and improve plant tolerance to abiotic stress, leading to increased biomass accumulation and yield stability under diverse environmental conditions (Santoyo, 2025; Mohamed *et al.*, 2025). These multifunctional benefits position symbiotic bacteria as key drivers of agroecosystem productivity.

Comparison with chemical nitrogen fertilizers

Chemical nitrogen fertilizers have been widely used to increase crop yields; however, their excessive application has led to significant environmental and economic challenges. Nitrate leaching, groundwater contamination, greenhouse gas emissions, and disruption of soil microbial communities are among the major drawbacks associated with synthetic nitrogen fertilizers (Elumalai *et al.*, 2025; Pandey *et al.*, 2017). In addition, fertilizer production and application impose substantial economic costs on farmers and contribute to environmental degradation.

In contrast, symbiotic nitrogen fixation represents an ecologically sustainable alternative that supplies nitrogen in synchrony with plant demand, minimizing losses and environmental pollution (Ladha *et al.*, 2022). Unlike chemical fertilizers, biologically fixed nitrogen is delivered directly to plant tissues through tightly regulated metabolic pathways, resulting in higher nitrogen use efficiency. The integration of symbiotic nitrogen-fixing bacteria into agricultural systems therefore offers a viable strategy to reduce fertilizer dependence, lower production costs, and promote long-term soil health (Kebede, 2021; Yeremko *et al.*, 2025).

Impact of abiotic stress factors on symbiosis

Abiotic stress factors significantly influence the establishment, functioning, and efficiency of plant–bacterial symbiosis. Environmental stresses affect both symbiotic partners individually and disrupt the finely regulated physiological and molecular interactions required for successful symbiosis. In most cases, higher plants exhibit greater sensitivity to stress than microorganisms; however, stress conditions ultimately reduce the stability and effectiveness of the symbiotic system as a whole (Pandey *et al.*, 2017; Yeremko *et al.*, 2025).

Temperature stress

Temperature extremes, both low and high, are major limiting factors for plant growth and symbiotic performance. Elevated temperatures can inhibit root growth, alter membrane stability, and reduce photosynthetic efficiency in plants, thereby limiting carbon supply to symbiotic bacteria (Ali *et al.*, 2025). At the microbial level, temperature stress affects bacterial survival, motility, and nod gene expression, leading to reduced infection efficiency and impaired nodule development (Lindström and Mousavi, 2020).

Low temperatures delay root hair formation, suppress infection thread progression, and slow nodule organogenesis, while high temperatures can destabilize nitrogenase activity and disrupt leghemoglobin function within nodules (Threatt and Rees, 2023). Consequently, temperature stress often results in decreased nodule number, reduced nitrogen fixation rates, and lower overall symbiotic efficiency (Yeremko *et al.*, 2025).

Drought and water stress

Drought and water deficit are among the most detrimental abiotic stresses affecting plant–bacterial symbiosis. Water stress leads to reduced root elongation, altered root exudation patterns, and decreased availability of carbohydrates required for bacterial metabolism (Ali *et al.*, 2025). These changes negatively affect rhizobial colonization and infection processes in the rhizosphere.

In symbiotic systems, drought stress reduces nodule formation, accelerates nodule senescence, and suppresses nitrogenase activity due to limited energy supply and impaired oxygen regulation (Lepetit and Brouquisse, 2023). Although some microorganisms exhibit adaptive responses to drought, such as osmolyte production, the combined effects of water stress on plants and bacteria lead to a marked decline in nitrogen fixation and plant productivity (Pandey *et al.*, 2017; Yeremko *et al.*, 2025).

Salinity stress

Salinity stress exerts both osmotic and ionic effects on plants and symbiotic bacteria. High salt concentrations disrupt water uptake, cause ion toxicity, and induce oxidative stress in plant tissues, resulting in reduced root growth and impaired nodulation (Mohamed *et al.*, 2025). Salinity also alters root exudate composition, which can negatively affect bacterial chemotaxis and attachment.

For rhizobia, elevated salinity reduces cell viability, inhibits nod gene expression, and decreases the synthesis of Nod factors, leading to reduced infection efficiency (Nuc and Olejnik, 2025). As a result, salinity stress significantly lowers nodule number, nitrogen fixation capacity, and symbiotic effectiveness. While some salt-tolerant bacterial strains can partially alleviate these effects, salinity remains a major constraint on symbiotic nitrogen fixation in saline soils (Santoyo, 2025).

Heavy metal stress

Heavy metal contamination represents one of the most severe abiotic stresses affecting plant–bacterial symbiosis. Metals such as cadmium, lead, and mercury interfere with nutrient uptake, hormonal regulation, photosynthesis, and cellular metabolism in plants, leading to growth inhibition and reduced stress tolerance (Mohamed *et al.*, 2025). In the rhizosphere, heavy metals reduce microbial diversity and population density, directly impacting symbiotic bacteria (Pishik *et al.*, 2016).

Although rhizobia are generally more resistant to heavy metals than plants, elevated metal concentrations disrupt infection processes, nodule development, and nitrogenase activity (Pishik *et al.*, 2016; Hnini *et al.*, 2025). Heavy metals can induce both specific and non-specific stress responses in symbiotic systems, weakening symbiotic efficiency and reducing nitrogen fixation. Co-inoculation with metal-tolerant plant growth-promoting bacteria has been shown to mitigate some of these negative effects, but overall symbiotic performance remains compromised under high metal stress conditions (Santoyo, 2025).

Overall effects on symbiotic efficiency

Across all abiotic stress types, a common outcome is the disruption of coordinated plant–bacterial interactions required for effective symbiosis. Stress factors impair early signaling, infection processes, nodule development, and nitrogen fixation, resulting in reduced plant growth and productivity. While microorganisms may contribute to partial stress mitigation, the combined stress effects generally lead to decreased symbiotic efficiency and stability (Pandey *et al.*, 2017; Yeremko *et al.*, 2025). Understanding these stress-induced limitations is essential for improving symbiotic resilience and developing stress-adapted agricultural systems.

Impact of biotic stress factors on symbiosis

Biotic stress factors, including pathogenic organisms and competition from non-symbiotic microorganisms, strongly influence the establishment and efficiency of plant–bacterial symbiosis. Unlike abiotic stresses, biotic stresses involve dynamic biological interactions that can alter host recognition, infection processes, and resource allocation within the symbiotic system. These stresses affect both the plant host and the microbial partner, often leading to reduced nodulation and impaired nitrogen fixation (Hassani *et al.*, 2018; Hnini *et al.*, 2025).

Pathogens and competing microorganisms

Plant roots are continuously exposed to a wide range of soil microorganisms, including pathogens and non-beneficial competitors. Pathogenic fungi and bacteria can interfere with symbiotic signaling by triggering plant defense responses that suppress rhizobial infection and nodule formation (Pandey *et al.*, 2017). Activation of plant immune pathways during pathogen attack often results in reduced root hair curling, inhibition of infection thread development, and premature abortion of nodules (Tsyganova *et al.*, 2021).

In addition to pathogens, competition from other rhizosphere microorganisms can limit the availability of infection sites and nutrients required for symbiotic bacteria. Non-symbiotic or weakly compatible bacterial strains may outcompete effective rhizobia for root colonization without contributing to nitrogen fixation, thereby reducing overall symbiotic efficiency (Santoyo, 2025). Such competitive interactions can be intensified under stress conditions, when plant resources are limited and microbial community composition is altered (Hnini *et al.*, 2025).

Host specificity and cross-infection groups

Plant–bacterial symbiosis is characterized by a high degree of host specificity, resulting from long-term co-evolution between plants and their microbial partners. Only specific combinations of host plants and bacterial strains are capable of establishing effective nitrogen-fixing symbiosis, a phenomenon that has led to the classification of rhizobia into cross-infection groups (Lindström and Mousavi, 2020; Tsyganova *et al.*, 2021). This specificity is determined largely by molecular compatibility between plant receptors and bacterial signaling molecules, such as Nod factors.

Biotic stress factors can disrupt host specificity by altering signaling pathways or modifying the rhizosphere environment. Under pathogen pressure or microbial competition, plants may restrict symbiotic infection to prevent colonization by potentially harmful microorganisms, even if this limits nitrogen fixation (Hassani *et al.*, 2018). Similarly, stress-induced changes in bacterial gene expression can reduce compatibility with host plants, leading to ineffective or aborted symbiotic interactions (Nuc and Olejnik, 2025). These responses underscore the delicate balance between symbiosis and defense in plant–microbe interactions.

Regulation of nodule number under stress

Plants possess sophisticated regulatory mechanisms to control the number and distribution of nodules formed on their roots. This regulation is essential to balance the metabolic costs of symbiosis with its nutritional benefits. Under optimal conditions, only a fraction of initial infection events leads to successful nodule formation, as plants actively suppress excessive nodulation (Tsyganova *et al.*, 2021).

Biotic stress factors intensify this regulatory control. Pathogen infection or microbial competition often results in early termination of infection threads, accumulation of defense-related compounds, and localized cell death resembling hypersensitive responses (Pandey *et al.*, 2017). These responses limit bacterial entry and reduce nodule numbers, particularly in root zones exposed to stress. Such self-regulation mechanisms prevent excessive carbon expenditure on symbiosis under unfavorable conditions but also lead to reduced nitrogen fixation and plant growth (Yeremko *et al.*, 2025).

Overall, biotic stress factors reshape plant–bacterial symbiosis by influencing microbial community dynamics, host specificity, and nodulation control. Understanding these interactions is critical for improving symbiotic resilience and designing effective microbial inoculants for sustainable agriculture.

Microbial mitigation of stress effects in plants

Microorganisms associated with plant roots play a crucial role in mitigating the negative effects of environmental stress on plant growth and productivity. Beyond classical nitrogen-fixing symbionts, a broad range of beneficial bacteria collectively referred to as plant growth-promoting rhizobacteria (PGPR) enhance plant resilience by modulating physiological, biochemical, and molecular responses under stress conditions. These microorganisms act either independently or in combination with symbiotic bacteria, contributing to improved plant performance in adverse environments (Santoyo, 2025; Hnini *et al.*, 2025).

Plant growth-promoting rhizobacteria (PGPR)

Plant growth-promoting rhizobacteria are a diverse group of soil and root-associated bacteria that stimulate plant growth through direct and indirect mechanisms. Common PGPR genera include *Klebsiella*, *Agrobacterium*, *Arthrobacter*, *Pseudomonas*, and *Bacillus*, many of which have been shown to alleviate the adverse effects of abiotic stresses such as drought, salinity, and heavy metal contamination (Santoyo, 2025; Mohamed *et al.*, 2025).

PGPR enhance plant growth by improving nutrient availability, synthesizing phytohormones such as auxins and cytokinins, solubilizing phosphate, and producing siderophores that facilitate iron uptake. Under stress conditions, these activities contribute to improved root development, enhanced photosynthetic capacity, and stabilization of plant water relations (Hnini *et al.*, 2025). In addition, PGPR can modulate plant defense signaling pathways, allowing plants to better tolerate stress while maintaining growth and symbiotic functionality (Pandey *et al.*, 2017).

Co-inoculation strategies

Co-inoculation refers to the simultaneous application of symbiotic nitrogen-fixing bacteria and other beneficial microorganisms to plants. This strategy has gained increasing attention as a means of enhancing symbiotic efficiency and plant stress tolerance. Co-inoculation of legumes with *Rhizobium* species and PGPR has been shown to improve nodulation, nitrogen fixation, and plant biomass under both optimal and stress conditions (Santoyo, 2025; Yeremko *et al.*, 2025).

The benefits of co-inoculation arise from complementary functional roles of different microbial partners. While rhizobia primarily contribute to nitrogen fixation, PGPR support root growth, nutrient acquisition, and stress mitigation, thereby creating a more favorable environment for symbiosis (Lepetit and Brouquisse, 2023). Under abiotic stress, co-inoculated plants often exhibit higher chlorophyll content, improved water-use efficiency, and reduced oxidative damage compared to plants inoculated with a single microbial strain (Mohamed *et al.*, 2025). These findings highlight co-inoculation as a promising approach for sustaining symbiotic performance in stress-prone agricultural systems.

Mechanisms of stress tolerance enhancement

Microbial mitigation of stress effects in plants is mediated through multiple physiological and molecular mechanisms. One of the key mechanisms involves modulation of plant hormonal balance, particularly through the production of auxins, gibberellins, and stress-related signaling molecules that regulate root architecture and stress responses (Santoyo, 2025). PGPR also produce ACC deaminase, an enzyme that lowers ethylene levels in plants, thereby preventing stress-induced growth inhibition (Glick, 2014).

Another important mechanism is the enhancement of antioxidant defense systems. Beneficial microorganisms stimulate the activity of antioxidant enzymes such as superoxide dismutase, catalase, and peroxidases, which reduce oxidative damage caused by stress-induced reactive oxygen species (Ali *et al.*, 2025). In addition, some PGPR sequester or immobilize toxic ions, including heavy metals, reducing their bioavailability and toxicity to plants (Pishik *et al.*, 2016).

Collectively, these microbial-mediated mechanisms improve plant physiological stability, maintain symbiotic interactions, and enhance stress tolerance. By integrating microbial functions with plant stress responses, plant–microbe partnerships offer effective and environmentally sustainable solutions for improving crop performance under adverse conditions (Hnini *et al.*, 2025; Yeremko *et al.*, 2025).

Agricultural and environmental implications

Sustainable agriculture and eco-friendly fertilization

Plant–bacterial symbiosis, particularly symbiotic nitrogen fixation, represents a cornerstone of sustainable and eco-friendly agricultural systems. By supplying biologically fixed nitrogen directly to plants, symbiotic bacteria reduce dependence on synthetic nitrogen fertilizers, which are energy-intensive to produce and environmentally costly to apply (Ladha *et al.*, 2022; Kebede, 2021). The integration of legumes and beneficial microorganisms into cropping systems promotes nutrient recycling, improves soil structure, and enhances long-term soil fertility, all of which are essential components of sustainable agriculture.

Microbial-based fertilization strategies, including the use of rhizobial inoculants and plant growth-promoting rhizobacteria, align with ecological intensification approaches that seek to increase productivity while minimizing environmental impact (Santoyo, 2025). Such biologically driven systems support plant nutrition through natural processes, preserve soil microbial diversity, and contribute to the resilience of agroecosystems under changing climatic conditions (Yeremko *et al.*, 2025).

Reduction of nitrate pollution

One of the most significant environmental benefits of plant–bacterial symbiosis is the reduction of nitrate pollution associated with excessive use of chemical nitrogen fertilizers. Nitrate accumulation in soils and water bodies disrupts natural nitrogen cycles and poses serious risks to human health, aquatic ecosystems, and biodiversity (Elumalai *et al.*, 2025). Leaching of nitrates into groundwater and surface waters is a major contributor to eutrophication and degradation of water quality.

In contrast, nitrogen supplied through symbiotic fixation is tightly regulated by plant demand and microbial metabolism, resulting in higher nitrogen use efficiency and reduced losses to the environment (Ladha *et al.*, 2022). By partially or fully replacing mineral fertilizers with biologically fixed nitrogen, agricultural systems can significantly lower nitrate runoff and leaching, thereby mitigating environmental pollution and supporting ecosystem health (Kebede, 2021; Yeremko *et al.*, 2025).

Relevance to crop production systems

The application of plant–bacterial symbiosis has broad relevance across diverse crop production systems, particularly in legume-based and mixed cropping systems. Incorporation of legumes into crop rotations enhances nitrogen availability for subsequent crops, reduces fertilizer requirements, and improves overall system productivity (Grzyb *et al.*, 2021; Ladha *et al.*, 2022). These benefits are especially valuable in low-input and resource-limited agricultural systems, where access to synthetic fertilizers may be constrained.

Furthermore, the use of microbial inoculants and co-inoculation strategies enhances crop performance under stress conditions, contributing to yield stability and resilience (Santoyo, 2025; Mohamed *et al.*, 2025). As global agriculture faces increasing challenges related to climate change, soil degradation, and environmental pollution, harnessing plant–bacterial symbiosis offers practical solutions for improving crop productivity while safeguarding environmental sustainability (Pandey *et al.*, 2017; Yeremko *et al.*, 2025).

Knowledge gaps and future research directions

Unresolved molecular mechanisms

Despite significant progress in understanding plant–bacterial symbiosis, many molecular mechanisms governing the initiation, regulation, and maintenance of symbiotic interactions remain unresolved. While the roles of Nod factors, receptor-like kinases, and nodulation genes have been well established, the downstream signaling networks that integrate symbiotic cues with plant developmental and defense pathways are still incompletely understood (Oldroyd, 2013; Gourion *et al.*, 2015). In particular, the molecular basis by which plants discriminate between beneficial symbionts and pathogens under fluctuating environmental conditions requires further clarification.

Another major gap lies in understanding how stress signals are integrated with symbiotic signaling pathways at the cellular and transcriptional levels. Abiotic and biotic stresses often suppress nodulation and nitrogen fixation, yet the precise regulatory nodes where stress-response pathways intersect with symbiotic gene networks remain largely unknown (Pandey *et al.*, 2017; Yeremko *et al.*, 2025). Elucidating these interactions is essential for improving symbiotic efficiency under adverse conditions.

Need for multi-omics approaches

Traditional genetic and physiological studies have provided valuable insights into plant–bacterial symbiosis; however, they are insufficient to capture the complexity of these interactions. Integrated multi-omics approaches—including genomics, transcriptomics, proteomics, metabolomics, and microbiome profiling—are increasingly recognized as essential tools for advancing symbiosis research (Hassani *et al.*, 2018; Santoyo, 2025). These approaches enable comprehensive analysis of host–microbe interactions at multiple biological levels and under diverse environmental conditions.

Multi-omics studies can reveal regulatory networks controlling nodulation, nitrogen fixation, and stress adaptation, as well as identify novel microbial traits associated with symbiotic efficiency. Moreover, microbiome-level analyses are crucial for understanding how complex microbial communities influence symbiotic performance and plant resilience (Hnini *et al.*, 2025). Future research integrating omics data with functional validation will be critical for translating fundamental knowledge into practical agricultural applications.

Climate change and symbiosis research priorities

Climate change poses significant challenges to plant–bacterial symbiosis through increased temperature extremes, altered precipitation patterns, soil salinization, and the accumulation of pollutants. These changes are expected to intensify stress conditions that negatively affect nodulation, nitrogen fixation, and overall plant productivity (Ali *et al.*, 2025; Mohamed *et al.*, 2025). However, current knowledge of how climate-driven stresses influence symbiotic systems across different agroecological zones remains limited.

Future research should prioritize the identification of stress-tolerant plant genotypes and microbial strains capable of maintaining symbiotic efficiency under climate change scenarios. Long-term field studies, combined with molecular and ecological analyses, are needed to assess the stability of symbiotic interactions under variable environmental conditions (Ladha *et al.*, 2022; Yeremko *et al.*, 2025). Addressing these research priorities will be essential for harnessing plant–bacterial symbiosis as a sustainable solution for food security and environmental resilience in a changing climate.

CONCLUSION

This review demonstrates that plant–bacterial symbiosis is a highly coordinated biological system regulated through intricate molecular, physiological, and genetic interactions between plants and microorganisms. Symbiotic relationships, particularly those involving nitrogen-fixing bacteria, play a fundamental role in plant nutrition, soil fertility, and ecosystem stability, with effective symbiosis depending on precise signal exchange, host recognition, controlled infection processes, and the functional integration of mature nodules capable of sustaining biological nitrogen fixation. The analysis further reveals that both abiotic and biotic stress factors significantly influence the formation and efficiency of plant–bacterial symbiotic systems, as environmental stresses such as temperature extremes, water scarcity, salinity, heavy metal contamination, pathogen pressure, and microbial competition disrupt early signaling events, nodulation, and nitrogen fixation processes. Although microorganisms often exhibit greater tolerance to stress than plants, stress conditions ultimately weaken the symbiotic system and reduce plant productivity; however, beneficial microorganisms can partially alleviate stress-induced damage by supporting plant physiological stability and maintaining symbiotic functionality. Overall, plant–bacterial symbiosis offers a strong foundation for developing sustainable and environmentally friendly agricultural practices, as the use of symbiotic bacteria, plant growth-promoting rhizobacteria, and co-inoculation strategies has the potential to reduce dependence on chemical nitrogen fertilizers, mitigate environmental pollution, and enhance crop resilience under adverse conditions. Future progress will rely on advancing mechanistic understanding of symbiosis under stress, improving microbial inoculant technologies, and integrating these biological solutions into diverse crop production systems, making strengthened plant–microbe partnerships a promising pathway toward sustainable crop productivity, improved soil health, and long-term agricultural sustainability.

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