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# Biochemistry of plant-microbe interactions in biofertilizer applications

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**Abstract**
The biochemical interplay between plants and soil microorganisms forms the cornerstone of sustainable agriculture through the application of biofertilizers. This review presents a comprehensive overview of the key biochemical mechanisms underpinning plant-microbe interactions, focusing on nutrient mobilization, metabolic integration, and stress alleviation. Biological nitrogen fixation, facilitated by nitrogenase enzymes in symbiotic and free-living diazotrophs, exemplifies how microbial processes supply essential nitrogen to plants under strict regulatory and oxygen-protective conditions. Similarly, phosphorus and potassium solubilization by microbial secretion of organic acids and enzymes such as phytases and phosphatases enhances the availability of otherwise inaccessible nutrients. Microbial production of plant growth regulators, including indole-3-acetic acid, gibberellins, and cytokinins, further stimulates root development and nutrient uptake. Iron acquisition via siderophores and modulation of stress responses through antioxidant enzyme stimulation and ACC deaminase activity are additional biochemical strategies that support plant growth under adverse conditions. The review also highlights the role of signaling molecules like flavonoids, Nod factors, and quorum sensing compounds, as well as root exudates, in establishing mutualistic networks that facilitate nutrient exchange and metabolic cooperation. Case studies in cereals, legumes, and vegetables demonstrate the practical applications of these biochemical interactions, confirming improvements in nutrient uptake, yield, and soil health. By synthesizing recent advances in molecular signaling, enzymatic activity, and nutrient cycling, this review underscores the potential of biofertilizers as eco-friendly solutions to enhance crop productivity and soil sustainability.

**Keywords:** Biofertilizers, rhizosphere biochemistry, biological nitrogen fixation, phosphorus solubilization, potassium mobilization and siderophores

## 1. Introduction
Sustainable agriculture relies increasingly on harnessing the natural potential of soil microorganisms to enhance crop productivity while reducing chemical inputs. The rhizosphere, often described as a hotspot of biochemical activity, hosts diverse plant-microbe interactions that govern nutrient cycling, growth promotion, and stress tolerance. Unlike synthetic fertilizers, which provide direct but often inefficient nutrient supplementation, beneficial microbes mobilize nutrients, regulate plant physiology, and improve soil health through tightly coordinated biochemical processes.

Central to these interactions are mechanisms such as biological nitrogen fixation, phosphorus and potassium solubilization, production of phytohormones, and siderophore-mediated iron acquisition. For example, nitrogen-fixing bacteria transform atmospheric $N_2$ into plant-available ammonia through the activity of nitrogenase under highly regulated and oxygen-protected conditions. Phosphate-solubilizing microorganisms secrete organic acids and enzymes that release otherwise inaccessible phosphorus, while potassium-solubilizing microbes employ acidolysis, chelation, and ion exchange to mobilize mineral-bound K and other nutrients. In parallel, microbial synthesis of phytohormones including indole-3-acetic acid, gibberellins, and cytokinins directly influences root and shoot development, enhancing nutrient uptake and plant vigor.

Equally important are microbial roles in stress alleviation and signaling. Siderophore production improves iron availability and suppresses pathogens, whereas ACC deaminase activity reduces

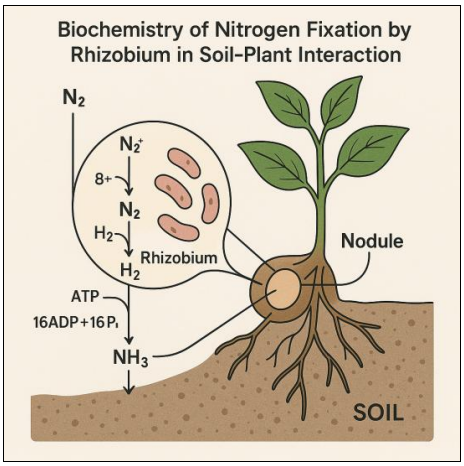
ethylene accumulation, enabling plants to withstand drought, salinity, and other stresses. Furthermore, molecular exchanges involving flavonoids, Nod factors, and quorum-sensing signals shape mutualistic associations that sustain nutrient exchange and metabolic cooperation.

By integrating advances in enzymology, molecular signaling, and field-based applications, this review emphasizes how biochemical mechanisms at the plant-microbe interface underpin biofertilizer efficacy. Understanding these processes not only explains the success of microbial inoculants in cereals, legumes, and vegetables but also provides insights into their role in promoting soil fertility, crop yield, and ecological resilience.

## 2. Biochemical Mechanisms of Plant-Microbe Interactions

### 2.1 Nitrogen Fixation

Biological nitrogen fixation (BNF) in plant-microbe systems is a multi-step biochemical process that couples microbially catalyzed reduction of atmospheric $N_2$ to host-derived signaling, metabolic integration, and tight regulatory control. In legumes the process occurs inside specialised root or stem nodules formed after a multistage signalling and infection programme in non-legumes, associative or endophytic diazotrophs fix $N_2$ in the rhizosphere or inside plant tissues (Xu *et al*., 2023) [68].




**Recognition and nodule organogenesis**

Nodule formation begins with molecular dialog, plant flavonoids released from roots induce bacterial synthesis of lipo-chitooligosaccharide "Nod factors," which trigger root hair curling, calcium spiking, and downstream kinase cascades that reprogramme cortical cells to form the nodule primordium. Key plant regulators (for example NIN) and calcium-dependent kinases coordinate infection thread formation and bacterial entry. This signalling cascade both permits symbiont entry and establishes the developmental program that yields the oxygen-buffered environment required for nitrogenase activity (Oldroyd, 2004) [48].

**Nitrogenase: structure and catalytic mechanism**

Nitrogenase is the two-component metalloprotein complex composed of the Fe (iron) protein and the MoFe (molybdenum-iron) protein (for the canonical Mo-nitrogenase). The active site (FeMo-cofactor) on the MoFe protein carries out $N_2$ reduction. Catalysis proceeds by stepwise delivery of single electrons from an external electron donor to the Fe-protein, ATP-dependent transfer of electrons from Fe-protein to MoFe-protein (Lowe-Thorneley kinetic framework), accumulation of electron/proton equivalents at FeMo-co, and eventual binding/reduction of $N_2$ to $NH_3$. The overall process is strongly ATP-consuming and yields obligatory $H_2$ as a side product under most conditions. Electron donors in vivo include ferredoxin or flavodoxin; dithionite is used in vitro. Electron transfer from Fe-protein to MoFe-protein is MgATP-dependent with a high ATP cost per electron; classical estimates place the energetic cost of biological $N_2$ reduction in the tens of ATP molecules per $N_2$ reduced. (Seefeldt, 2009) [57] Alternative nitrogenases (V- or Fe-only) may be expressed when Mo is limiting, these enzymes are homologous but have different metal cofactors and catalytic efficiencies (Florence *et al*., 2018) [24].

**Oxygen protection and micro aerobic metabolism**

Nitrogenase is irreversibly inactivated by molecular $O_2$, so diazotrophs and nodulated hosts deploy multiple oxygen-management strategies: (i) plant synthesis of leghemoglobin buffers $O_2$ within nodules to permit respiration but protect nitrogenase, (ii) high respiratory rates or specialised bacterial proteins in free-living diazotrophs provide "respiratory protection," and (iii) regulatory switches turn nif gene expression off under high oxygen or fixed-N conditions. These mechanisms together maintain the low-$O_2$, energy-rich environment required for efficient fixation. (Rutten *et al*., 2019).

**Regulation and host control**

Nitrogenase expression and activity are tightly regulated at transcriptional and post-translational levels. In many diazotrophs NifA is the central transcriptional activator of nif genes, and its activity is modulated by oxygen, fixed nitrogen, and other signals. Plants also exert control over bacteroid differentiation and activity via peptide signals and nutrient provisioning, effectively making bacteroids organelle-like nitrogen factories in many legume symbioses.

**Table 1:** Key biochemical features of the nitrogenase enzyme complex in nitrogen fixation

| Feature | Details |
|---|---|
| Reaction | $N_2 + 8H^+ + 8e^- + 16ATP \rightarrow 2NH_3 + H_2 + 16ADP + 16Pi$ |
| Fe-Protein (Reductase) | [4Fe-4S] cluster, ATP hydrolysis, electron delivery |
| MoFe-Protein (Catalyst) | Contains P-cluster and FeMo-co; active reduction site |
| Electron Flow | Ferredoxin → Fe-Protein → P-cluster → FeMo-co |
| Energy Requirement | ~16 ATP per $N_2$ fixed |
| $O_2$ Sensitivity | Protected by leghemoglobin in nodules |
| Biological Role | Provides ammonia for assimilation into biomolecules |

**Metabolic integration and nutrient exchange**

Efficient symbiotic fixation requires close metabolic exchange: the plant supplies carbon (e.g., dicarboxylates) and ATP-generating respiration to support bacterial N fixation, while the bacteria supply ammonia (or assimilated nitrogen forms) to the host. Transporters and membrane interfaces in the symbiosome coordinate this exchange, and phosphate, iron, and molybdenum availability in nodules critically influence nitrogenase assembly and function (White *et al*., 2007) [67].

### 2.2 Phosphorus Solubilisation

#### 2.2.1 Organic Acid Production

Microorganisms improve phosphorus availability by secreting low-molecular-weight organic acids. These acids carry hydroxyl and carboxyl groups that interact with phosphate-bearing minerals such as calcium, magnesium, iron, and aluminium.

Through this interaction, they not only bind with these minerals but also lower the pH of the surrounding soil. This acidification dissolves otherwise insoluble phosphate compounds and releases phosphorus in a form that plants can readily absorb (Kim *et al*., 1997) [35].

Among the various acids released, gluconic acid is the most common, followed by citric and oxalic acids. Gluconic acid is synthesized when bacteria oxidize glucose using the enzyme glucose dehydrogenase, which requires the cofactor pyrroloquinoline quinone (PQQ). Genes such as the *pqq* operon and *gcd* play a central role in regulating this enzyme system. Other acids, including citric and oxalic acids, promote solubilisation by chelating metal cations ($Ca^{2+}$, $Fe^{3+}$, $Al^{3+}$) that bind phosphate, while simultaneously reducing local pH(An and Moe, 2016) [5].

The composition and quantity of acids released vary with microbial species, available carbon sources, and soil or culture conditions (Menezes-Blackburn *et al*., 2016) [42]. Analytical tools like HPLC and LC-MS have consistently detected mixtures of gluconic, oxalic, malic, citric, and lactic acids in culture supernatants. These studies show a clear relationship between acid secretion, pH reduction, and increased soluble phosphorus (Zaidi *et al*., 2009) [71]. In essence, phosphorus solubilisation by microbes largely depends on organic acid release, with gluconic acid being particularly significant. The actual mix and efficiency, however, depend on the microbes genetic capacity and the environmental conditions.

### 2.2.2 Enzymatic Contribution: Phytases and Phosphatases

Phytases are specialized enzymes capable of hydrolysing phytic acid (myo-inositol hexakisphosphate), a major organic phosphorus reserve in plants. By sequentially removing phosphate groups, they release inorganic phosphorus available for plant and microbial uptake. These enzymes occur widely in bacteria, fungi, and plant-associated microbes, playing a crucial role in organic phosphorus turnover (Rizwanuddin *et al*., 2023; Duong *et al*., 2018; Gerke, 2015) [52, 21].

Different microbial phytases vary in their catalytic efficiency, optimal pH and temperature, and their ability to function under field conditions, all of which determine how much phytate-bound phosphorus is released in soils (Yuand Chen, 2013; Caffaro *et al*., 2020) [70, 17].

Phosphatases, including acid and alkaline phosphomonoesterases, hydrolyzes a broad range of organic phosphorus compounds such as glycerophosphates, sugar phosphates, and phospholipids. Both plant roots and soil microbes contribute to phosphatase activity, which is vital for short-term phosphorus mineralization in the rhizosphere (Spohn and Kuzyakov, 2013; Cabugao *et al*., 2017) [63, 16]. Acid phosphatases typically act best in acidic conditions (pH 4-6) and are concentrated in root-associated soils, while alkaline phosphatases function better in neutral to alkaline soils. Together, they expand the range of organic phosphorus substrates that can be mobilized (Ding *et al*., 2011) [19].

### 2.2.3 Biochemical Mobilization of Insoluble Phosphorus

Phosphate-solubilizing microorganisms (PSMs) mobilize phosphorus via two main strategies:

1. **Mineral dissolution:** Organic acids and protons solubilize mineral-bound phosphate by chelating or displacing metal cations.
2. **Organic P mineralization:** Extracellular enzymes like phytases and phosphatases break down organic phosphorus compounds, releasing inorganic phosphate (Pi) (Pan and Cai, 2023) [49].

The effectiveness of microbial phosphorus mobilization depends on soil pH, mineral composition, organic matter, and how strongly phosphorus is bound to iron, aluminium, or organic complexes. Microbial metabolism, oxygen supply, and interactions with plant root exudates also play key roles (Hunter *et al*., 2014) [32].

In many soils, phosphorus availability is governed by a combination of microbial activities, including acid release, siderophore production (for iron binding), and enzymatic degradation of phytate. Since metal-organic complexes can hinder enzyme access, microbes with multiple phosphorus-releasing mechanisms are especially effective (Wang *et al*., 2021) [66].

Experimental studies have shown that inoculating crops with PSMs capable of producing both organic acids (gluconic, oxalic) and enzymes (phytases, phosphatases) enhances phosphorus uptake and plant growth. However, success in the field is variable and influenced by soil type and management (Timofeeva *et al*., 2022) [64]. Recent advances include detailed insights into the *pqq*/*gcd* system, discovery of more stable microbial phytases, and development of microbial strains with multiple phosphorus-mobilizing traits for greater agricultural reliability.

### 2.3 Potassium & Other Nutrient Mobilization

Potassium (K) is a vital macronutrient for plant growth and development, yet a large portion of soil potassium exists in insoluble mineral forms such as feldspar, mica, and illite. Under normal soil conditions, these mineral-bound K sources are largely inaccessible to plants. Microorganisms play a central role in mobilizing this potassium into bioavailable forms through a range of biochemical mechanisms.

One of the primary strategies is acidolysis, where potassium-solubilizing microorganisms secrete organic acids such as citric, oxalic, gluconic, tartaric, and lactic acids. The acidification of the surrounding microenvironment breaks down mineral lattices, releasing $K^+$ ions for plant uptake (Etesami *et al*., 2017) [22].

Chelation represents another key mechanism. Microbial metabolites, including specific organic acids, bind to metal cations such as $Fe^{3+}$, $Al^{3+}$, and $Ca^{2+}$, destabilizing mineral matrices and facilitating potassium liberation (Etesami *et al*., 2017) [22]. Additionally, ion-exchange reactions occur when protons or other cations released during microbial metabolism displace potassium ions adsorbed onto mineral surfaces, further enhancing K availability. Microbial respiration also contributes to nutrient mobilization; $CO_2$ released by microbes dissolves in soil moisture to form carbonic acid, promoting mineral dissolution and nutrient solubilization (Babar *et al*., 2024) [10].

Microbial extracellular products, such as exopolysaccharides (EPS) and biofilms, further improve nutrient mobilization. These compounds create localized microenvironments that concentrate organic acids and enzymes near mineral surfaces, amplifying the solubilization of potassium, magnesium, calcium, and zinc (Yadav, 2022: Figiel *et al*., 2025) [69, 23]. EPS and biofilm structures act as protective and concentrating matrices, enhancing microbial efficiency in nutrient release.

Beyond potassium, these mechanisms are effective in mobilizing other essential nutrients. Magnesium ($Mg^{2+}$) and calcium ($Ca^{2+}$), commonly present in silicate and carbonate minerals, are solubilized through similar microbial acidolysis and chelation processes (Basak and Biswas, 2009) [11]. Zinc, often present in insoluble mineral complexes, becomes bioavailable through microbial-mediated acidification and chelation (Kamran *et al*.,

2017) [33]. Collectively, these microbial strategies exemplify how biochemical interactions between soil microorganisms and minerals orchestrate the release of multiple essential nutrients, supporting plant growth and soil fertility.

## 3. Production of Plant Growth Regulators

Plant-microbe interactions form the biochemical foundation of biofertilizer efficacy, where beneficial microorganisms colonize plant roots and modulate growth through nutrient mobilization and plant growth regulator (PGR) production. Unlike synthetic inputs, these interactions are eco-friendly, improve soil fertility, and enhance crop productivity (Bhattacharyya and Jha, 2012) [13].

### 3.1. Indole-3-Acetic Acid (IAA)

Indole-3-acetic acid (IAA), the most abundant auxin, regulates cell elongation, division, and differentiation in plants. In plant-microbe systems, many plant growth-promoting rhizobacteria **(**PGPR**)** such as *Azospirillum*, *Rhizobium*, and *Pseudomonas* synthesize IAA, primarily through tryptophan-dependent pathways. The indole-3-pyruvate (IPyA) and indole-3-acetamide (IAM) pathways are the most common microbial routes, where tryptophan is converted into IAA via enzymatic intermediates (Spaepen and Vanderleyden, 2011) [62]. Microbial IAA enhances root hair formation, lateral root development, and nutrient uptake, thereby improving host plant growth (Dobbelaere *et al*., 2003) [20].

### 3.2. Gibberellins (GAs)

Gibberellins are diterpenoid hormones that promote stem elongation, seed germination, flowering, and fruit development**.** Several PGPRs, including *Azospirillum brasilense*, *Herbaspirillum seropedicae*, and some *Bacillus* spp., produce gibberellins that mimic or supplement plant biosynthesis (Bottini *et al*., 2004). Microbial GA biosynthesis proceeds through the terpenoid pathway**,** starting from acetyl-CoA → mevalonate → geranylgeranyl diphosphate (GGDP), and leading to GA intermediates and bioactive forms (e.g., $GA_1$, $GA_3$). These microbial gibberellins stimulate cell wall loosening and expansion of stem and root tissues**,** enhancing plant biomass accumulation (Kang *et al*., 2014) [34].

### 3.3. Cytokinins

Cytokinins are adenine derivatives that control cell division, chloroplast development, nutrient mobilization, and delay of senescence**.** Symbiotic and associative bacteria such as *Rhizobium*, *Agrobacterium tumefaciens*, and *Bacillus subtilis* are known cytokinin producers (Arkhipova *et al*., 2007) [7]. Microbial cytokinins are synthesized via the isopentenyl transferase (IPT) pathway**,** where isopentenyl groups are transferred to adenosine monophosphates. These compounds influence shoot initiation, stimulate leaf expansion, and balance root-shoot growth ratios. In legumes, cytokinins produced by rhizobia play a key role in nodule initiation by activating cortical cell division (Miri *et al*., 2016) [44].

## 4. Siderophore Production and Iron Sequestration

### 4.1 Structure of Siderophores

Siderophores are low-molecular-weight compounds (500-1500 Da) secreted by bacteria, fungi, and some plants to capture ferric iron ($Fe^{3+}$), which is otherwise poorly available in aerobic soils (Amsri *et al*., 2022) [4]. The functional groups used for $Fe^{3+}$ binding: catecholates (phenolates), hydroxamates, carboxylates (including α-hydroxycarboxylates), and mixed types (Boda *et al*., 2016; Miethke and Marahiel, 2007) [14, 43].

- **Catecholates** (e.g., enterobactin) bind $Fe^{3+}$ through catechol groups, forming highly stable hexadentate complexes (Liu *et al*., 2023) [39].
- **Hydroxamates** (e.g., ferrichrome, desferrioxamine) use oxygen atoms of hydroxamate groups, usually forming octahedral coordination around $Fe^{3+}$ (Raymond *et al*., 2015) [51].
- **Carboxylates**, common among soil microbes and plants, bind $Fe^{3+}$ via carboxyl and hydroxyl groups and typically form less hydrophobic complexes than catecholates (Hider *et al*., 2024) [30].
- **Phytosiderophores**, such as mugineic acids produced by grasses, are derived from amino acids and contain carboxyl, hydroxyl, and amino groups. These compounds selectively chelate $Fe^{3+}$, enhancing iron uptake in graminaceous plants (Kobayashi, 2025) [36].

### 4.2 Mechanism of Iron Chelation and Uptake

In oxygen-rich environments, $Fe^{3+}$ occurs as insoluble oxides. Siderophores solubilize this iron by tightly binding it into $Fe^{3+}$-siderophore complexes, increasing its bioavailability (Kraemer, 2004). By competing with soil minerals for $Fe^{3+}$, siderophores also facilitate the desorption and mobilization of iron and other metals (Saharan *et al*., 2023) [55].

Plants employ two primary strategies to acquire iron:

- Strategy I (non-graminaceous plants): roots acidify the rhizosphere and enzymatically reduce $Fe^{3+}$ to $Fe^{2+}$ before uptake.
- Strategy II (graminaceous plants): roots release phytosiderophores that chelate $Fe^{3+}$, which are then absorbed as complexes (Grillet *et al*., 2019) [27].

Non-graminaceous plants may indirectly benefit from microbial siderophores. At the root interface, $Fe^{3+}$-siderophore complexes can be reduced to $Fe^{2+}$ and taken up, or in some cases, entire $Fe^{3+}$-siderophore complexes may be transported directly via specific root proteins (Schmidt., 1999; Murata *et al*., 2006) [56, 46].

Certain bacterial siderophores, such as pyoverdines from fluorescent *Pseudomonas*, provide iron to both Strategy I and Strategy II plants under iron limitation. Remarkably, these natural chelators can even surpass synthetic chelates in improving plant iron nutrition (Shirley *et al*., 2011) [60].

Beyond plant nutrition, siderophores also influence metal homeostasis and phytoremediation. By altering the availability of toxic metals, microbial siderophores can alleviate heavy-metal stress in plants and promote their growth in contaminated soils (Rajkumar *et al*., 2010) [50]. The wide structural diversity of siderophores shapes their ecological functions, and plants exploit both microbial and self-produced siderophores to secure iron from otherwise inaccessible soil pools (Aznar and Dellagi, 2015) [9].

## 5. Stress Alleviation Mechanisms

### 5.1 Antioxidant Enzyme Stimulation

Microbial inoculation often leads to an upregulation of enzymatic antioxidants including superoxide dismutase (SOD), catalase (CAT), and peroxidases (POD, APX). These enzymes play a critical role in neutralizing reactive oxygen species (ROS) such as superoxide radicals, hydrogen peroxide, and hydroxyl radicals that accumulate under stress conditions. For instance, inoculation with *Pseudomonas* and *Bacillus* strains enhanced

SOD, CAT, POD, and APX activity in *Pisum sativum* under salinity, significantly reducing oxidative damage (Gupta *et al.*, 2022) [28]. Similarly, rice inoculated with beneficial microbes showed upregulation of antioxidant enzymes and stress-responsive genes, resulting in better drought tolerance. In chickpea, AST-PGPB inoculation promoted transcriptional upregulation of antioxidant genes such as CAT, APX, and SOD under salt stress (Muneer *et al.*, 2021) [45]. Endophytic fungi with ACC deaminase activity also increased POD and CAT activities in *Moringa oleifera*, while boosting phenolic and flavonoid accumulation under drought conditions (Abdelaziz *et al.*, 2022) [1]. Such microbial modulation of the host antioxidant system lowers lipid peroxidation and sustains plant growth under adverse environments.

### 5.2 ACC Deamination

The enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase is widely produced by beneficial soil and endophytic microbes. This enzyme hydrolyzes ACC, the immediate precursor of ethylene, into α-ketobutyrate and ammonia, thereby interrupting the ethylene biosynthesis pathway (Glick, 2014) [26]. The deamination process reduces the pool of ACC available for ethylene formation and ensures that plants under stress maintain hormonal balance rather than accumulating excess ethylene. This biochemical mechanism has been recognized as a critical trait for microbes colonizing stress-prone rhizospheres, allowing them to directly influence plant physiology through metabolic regulation of ethylene precursors (Shahzad *et al*., 2021) [58].

### 5.3 Ethylene Regulation and Stress Alleviation

Abiotic stresses such as drought, salinity, and nutrient deficiency trigger excessive ethylene production in plants, which restricts growth by inhibiting cell elongation, root proliferation, and photosynthetic activity. Microorganisms capable of ACC deaminase production counteract this effect by lowering ethylene levels and promoting stress resilience. For instance, *Pseudomonas fluorescens* carrying ACC deaminase significantly improved barley growth and yield traits under salinity stress (Belimov *et al.*, 2023) [12]. In guinea grass, inoculation with *Bacillus licheniformis* and *B. subtilis* promoted drought tolerance by enhancing biomass, chlorophyll concentration, and osmolyte accumulation (Ali *et al.*, 2021) [3]. Additionally, co-application of biochar with ACC deaminase-producing microbes improved stomatal conductance and reduced ethylene-induced stress in maize grown under drought conditions (Ahmad *et al.*, 2020) [2]. These findings highlight microbial regulation of ethylene as a central strategy for sustaining crop productivity in stressful environments.

## 6. Biochemistry of Soil-Microbe-Plant Interactions: Signal Molecules, Root Exudates, and Symbiotic Networks

The complex biochemical communication systems among plants, soil microorganisms, and the rhizosphere environment form intricate biological networks vital for the functioning of terrestrial ecosystems. These systems involve molecular exchanges facilitated by signal molecules such as flavonoids, Nod factors, and quorum sensing compounds, with root exudates acting as key biochemical mediators. Gaining insight into these interactions is crucial for promoting sustainable agriculture and creating biotechnological solutions to improve plant health (Peck *et al*., 2006; McLaughlin *et al*., 2023; Shrestha *et al*., 2020) [72, 73, 74].

### 6.1 Signal Molecules: The Chemical Language of the Rhizosphere

#### 6.1.1 Flavonoids as Plant-Derived Signals

Flavonoids are well-researched plant-derived signal molecules that play multiple roles in plant-microbe interactions (Peck *et al*., 2006; Begum *et al.*, 2001) [72]. These phenolic compounds are continuously secreted by plant roots, attracting specific microbial partners while repelling harmful organisms. In legume-rhizobial interactions, flavonoids like genistein, daidzein, and apigenin act as molecular keys that trigger bacterial nodulation genes.

Peck *et al*. (2006) [72] showed that various flavonoids stimulate NodD1 binding to nod gene promoters in Rhizobium species. Their research indicated that when Sinorhizobiummeliloti NodD1 was expressed, nod gene transcription was initiated solely in response to luteolin, whereas Rhizobium leguminosarumNodDs responded to a wider range of inducers. Hungria and Phillips (2001) [75] discovered that flavanones such as hesperetin and naringenin, and flavones like apigenin and luteolin, were the most active inducers, with R. Leguminosarum pIJ1477 exhibiting maximum activity with hesperetin (9560 units of β-galactosidase activity) and R. leguminosarum 5280 with apigenin (4369 units).

#### 6.1.2 Nod Factors: Bacterial Response Molecules

Nod factors are bacterial responses to plant flavonoid signals and are among the most biologically potent signaling molecules known (Spaink, 2000; Ritsema *et al*., 2006) [76, 77]. These lipochitooligosaccharides have β-1,4-linked N-acetyl-D-glucosamine backbones with modifications that determine host specificity. Research consistently demonstrates that Nod factors can induce root hair deformation at concentrations as low as 10^-10 M in alfalfa roots.

Ritsema *et al*. (2006) [77] provided insights that challenge the traditional understanding of LCO synthesis. By analyzing in-frame deletion mutants of key nod genes using mass spectrometry, they found that most substituent's could be transferred to short chitin backbones before acylation by NodA, suggesting this is likely one of the final steps in LCO biosynthesis rather than the initial step as previously thought.

#### 6.1.3 Quorum Sensing Molecules

N-acyl homoserine lactones (AHLs) play a crucial role in regulating bacterial activities and plant colonization in the rhizosphere (Shrestha *et al*., 2020; Abisado *et al*., 2018) [74, 78]. These small, diffusible compounds allow bacteria to detect their population density and synchronize actions such as biofilm development and the production of virulence factors.

In their study, Shrestha *et al*. (2020) [74] explored the response of Arabidopsis thaliana to various AHL molecules and their combinations. The findings suggested that the interactions between multiple AHLs and plants could lead to unexpectedly similar results. Combinations of long-chained AHL molecules, whether triple, quadruple, or double, enhanced resistance to Pseudomonas syringaepv. Tomato. Subsequent research showed that plants reacted to AHL mixtures via jasmonate-mediated pathways.

#### 6.1.4 Root Exudates: Primary Biochemical Mediators

Root exudates serve as the main point of communication between plants and the rhizosphere microbiome, comprising complex mixtures of metabolites that can account for up to 40% of the carbon fixed through photosynthesis. This significant allocation underscores the vital role of root-microbe interactions in plant survival.

### 6.1.5 Metabolomic Diversity

In their 2023 study, McLaughlin *et al*., [73] investigated Arabidopsis thaliana, Brachypodiumdistachyon, and Medicagotruncatula, identifying around 150 metabolites in both roots and exudates. Of these, 43% were found in the roots of all species, forming the core metabolome, while 21% were common across all species' exudates, constituting the core exudate metabolome.

Recent technological advancements have facilitated detailed characterization of exudates. Weis *et al*. (2024) [79] performed a meta-analysis showing that plants typically release about 960 metabolites, with numbers ranging from 7 to 33,870 depending on the analytical techniques used. LC-MS analyses identified a broader range of metabolites (15-14,954, median: 200), whereas GC-MS analyses detected fewer (9-1110, median: 56) but with a higher percentage of annotations.

### 6.1.6 Environmental Responsiveness

Environmental conditions play a crucial role in shaping root exudate composition (Lin *et al*.; Williams and de Vries, 2018) [80, 81]. Lin *et al*., [80] studied cotton root exudates under drought stress using Fourier-Transform Ion Cyclotron Resonance Mass Spectrometry, discovering over 700 unique metabolites induced by drought. Under extreme drought conditions, pathways related to flavonoid compounds, plant hormones like abscisic acid and jasmonic acid, and secondary metabolites were significantly activated.

## 6.2 Symbiotic versus Associative Signaling Mechanisms

### 6.2.1 Symbiotic Signaling: Rhizobial and Mycorrhizal Interactions

Symbiotic signaling is characterized by highly specific, co-evolved recognition systems (Maillet *et al*., 2011; Peck *et al*., 2006) [82, 72]. The rhizobial-legume symbiosis demonstrates precise molecular dialogue resulting in nitrogen-fixing nodules. Plant perception involves sophisticated receptor complexes discriminating between compatible and incompatible signals.

Walker *et al*. (2000) [66] demonstrated that live Rhizobium trigger rapid calcium spiking responses that are Nod factor-dependent. Application of NodRm-IV(C16:2,S) at 10^-10 M concentrations causes membrane potential depolarization within 5-30 minutes, leading to root-hair deformation after 1 hour.

Mycorrhizal signaling involves both chitooligosaccharides and lipo-chitooligosaccharides. Maillet *et al*. (2011) [82] showed that S-LCO was approximately 10-fold less active than S. meliloti Nod factor, while NS-LCO was 10,000-fold less active in activating calcium oscillations. Strigolactones function as long-distance chemical attractants, with Akiyama *et al*. (2005) [83] demonstrating stimulation of AM fungus Gigasporarosea at concentrations as low as 10^-13 M.

### 6.2.2 Associative Signaling: PGPR Interactions

Plant growth-promoting rhizobacteria represent diverse microorganisms enhancing plant growth through various mechanisms without intimate cellular associations. These interactions involve complex signaling networks coordinating bacterial colonization and plant growth promotion.

Randive (2017) demonstrated that PGPR isolates produce significant IAA amounts, enhanced by tryptophan supplementation. Pantoeaagglomerans produced 25.0 µg/ml IAA, while Pseudomonas putida produced 46.6 µg/ml and Pseudomonas sp. produced 60.0 µg/ml with tryptophan supplements. López-Bucio *et al*. (2007) [84] identified Bacillus megaterium strain affecting Arabidopsis root systems through cytokinin-mediated mechanisms rather than auxin pathways.

### 6.2.3 Plant Recognition and Signal Transduction

Plants have evolved sophisticated recognition systems distinguishing between beneficial microorganisms and pathogens through pattern recognition receptors (PRRs) detecting conserved microbial features.

### 6.2.4 Immune Recognition Systems

Felix *et al*. (1999) demonstrated that Arabidopsis FLS2 protein plays important roles in pathogen-associated molecular pattern-triggered immunity. Flagellin binding to FLS2's extracellular domain activates signaling cascades resulting in defense gene activation or repression.

Büttner (2016) [85] showed that most Gram-negative plant-pathogenic bacteria depend on type III secretion systems translocating effector proteins into plant cells. These effectors suppress plant innate immunity and interfere with cellular processes including protein degradation, hormone signaling, and gene expression.

### 6.2.5 Signal Transduction Pathways

Calcium signaling represents a central component of plant-microbe signal transduction. Walker *et al*. (2000) [66] demonstrated that symbiotic interactions trigger characteristic calcium oscillations in root hair nuclei, with frequency and amplitude encoding microbial partner identity and compatibility information.

Kosuta *et al*. (2003) [86] found that mycorrhizal-induced calcium oscillations require DMI1 and DMI2, with mathematical analysis revealing significant differences between Nod factor-induced and mycorrhizal-induced calcium responses. Fourier analysis showed Nod factor-induced calcium spiking had major peaks at 90-second intervals, while mycorrhizal-treated cells showed peaks at 30-second intervals.

## 7. Biotechnological Applications and Future Perspectives

Understanding plant-microbe biochemical communication drives innovative biotechnological applications for improved crop productivity and sustainability. Enhanced understanding of PGPR mechanisms enables development of more effective biological solutions through optimized hormone production and environmental manipulation.

Shrestha *et al*. (2020) [74] research on AHL-mediated quorum sensing provides opportunities for developing biological control approaches enhancing natural protective mechanisms. Complex AHL mixtures generally promote plant pathogen resistance, informing microbial consortia development for enhanced plant protection.

Raman *et al*. (2022) [87] demonstrated that engineered Agrobacterium expressing type III secretion systems can deliver bacterial effectors enhancing plant transformation efficiency by 250%-400% in wheat, alfalfa, and switchgrass. This represents novel approaches to engineering plant-microbe interactions for biotechnological applications.

## 8. Case Studies of Biofertilizer Use in Cereals, Legumes, and Vegetables

In cereal crops, numerous field investigations confirm that microbial inoculants enhance both yield and nutrient uptake. For example, inoculation of *Azospirillum* and *Azotobacter* in rice and maize was associated with greater nitrogen fixation, improved root development, and higher grain productivity (Bhattacharyya and Jha, 2012) [13]. Wheat responded positively to co-inoculation with phosphate-solubilizing bacteria (PSB) and arbuscular mycorrhizal fungi (AMF), which collectively

improved phosphorus availability, biomass production, and nutrient efficiency (Singh *et al*., 2011; Celador-Lera *et al*., 2018) [61, 18]. These findings illustrate the effectiveness of microbial consortia in strengthening nutrient acquisition pathways in cereals.

Leguminous crops, which naturally establish symbioses with nitrogen-fixing bacteria, also demonstrate marked benefits from biofertilizer application. In soybean and chickpea, *Rhizobium* inoculation led to enhanced nodulation, increased nitrogen fixation, and higher seed protein levels (Hungria *et al*., 2013) [31]. The dual application of rhizobia with AMF further improved phosphorus uptake and drought resilience in common bean, with superior yields compared to single inoculations (Herridge *et al*., 2008; Celador-Lera *et al*., 2018) [29, 18]. Vegetable crops have shown comparable responses; tomato plants treated with *Azotobacter* exhibited better germination, seedling vigor, and early growth than those given chemical nitrogen (Mahato *et al*., 2009) [41]. In okra, combining *Azospirillum*, AMF, and *Frateuria* with farmyard manure significantly enhanced yield attributes including fruit weight and total production (Anisa *et al*., 2016) [6], while in pea, integration of *Rhizobium*, *Azotobacter*, and PSB with recommended fertilizer rates boosted nodulation, nitrogen fixation efficiency, and seed protein content (Kothyari *et al*., 2017) [37].

## 8. Biochemical Improvements in Nutrient Uptake, Yield, and Soil Health

### 8.1 Nutrient Uptake

Biofertilizers improve nutrient availability through specific microbial biochemical pathways. Nitrogen-fixing organisms like *Rhizobium* and *Azotobacter* convert atmospheric nitrogen into ammonia with the help of the nitrogenase enzyme, directly enriching plant nitrogen supply (Vessey, 2003) [65]. Phosphate-solubilizing microbes release acids such as gluconic and citric acids and secrete enzymes like phytases and phosphatases, which transform unavailable phosphorus into forms that plants can absorb (Sharma *et al*., 2013) [59]. Similarly, potassium-mobilizing bacteria secrete organic acids and chelators that release $K^+$ from soil minerals, improving nutrient uptake efficiency (Journal of Applied Biology, 2016).

### 8.2 Yield Enhancement

The biochemical activity of biofertilizers also boosts crop yields by influencing plant growth and physiology. Plant growth-promoting rhizobacteria (PGPR) synthesize hormones such as IAA, gibberellins, and cytokinins that stimulate root development, thereby enhancing nutrient and water absorption (Vessey, 2003) [65]. In legumes, rhizobial associations significantly increase nitrogen fixation, raising seed protein levels. Co-inoculation with arbuscular mycorrhizal fungi (AMF) has been shown to enhance phosphorus uptake and improve plant tolerance to stress, which translates into higher productivity and seed quality (Hungria *et al*., 2013) [31]. In addition, microbes producing ACC deaminase help reduce ethylene accumulation during stress, maintaining plant growth and yield under adverse conditions (Glick, 2014) [26].

### 8.3 Soil Health

Beyond direct plant benefits, biofertilizers strengthen soil health through biochemical activities that enhance microbial activity and nutrient cycling. Inoculation increases key soil enzyme activities, including urease, dehydrogenase, and phosphatase, which are crucial for maintaining fertility. Siderophores released by microbes aid in iron mobilization, reducing its availability to pathogens and thereby improving rhizosphere microbial balance (Neilands, 1995) [47]. Moreover, long-term application of biofertilizers enriches organic matter turnover, supports microbial diversity, and sustains nutrient reserves, contributing to soil health and ecological resilience (Singh *et al*., 2011) [61].

## 9. Application in Agriculture

The biochemical capacities of soil microorganisms have profound applications in sustainable agriculture by enhancing nutrient availability, promoting growth, and strengthening plant resilience. Nitrogen-fixing microbes such as *Rhizobium*, *Azospirillum*, and *Azotobacter* convert atmospheric nitrogen into plant-usable ammonia, reducing dependence on synthetic fertilizers. In legumes, symbiotic nodulation ensures high nitrogen inputs, while in cereals and vegetables, associative and endophytic diazotrophs contribute to yield improvement through biological nitrogen fixation. Complementing this, phosphate-solubilizing microorganisms release organic acids (gluconic, citric, oxalic) and enzymes (phytases, phosphatases) that mobilize both mineral and organic phosphorus pools, improving phosphorus nutrition across diverse soil types. Similarly, potassium-solubilizing bacteria employ acidolysis, chelation, and ion-exchange mechanisms to unlock mineral-bound K, along with magnesium, calcium, and zinc, thereby improving overall nutrient efficiency.

Beyond nutrient acquisition, plant growth-promoting rhizobacteria (PGPR) synthesize phytohormones such as indole-3-acetic acid, gibberellins, and cytokinins, which stimulate root development, enhance shoot growth, and delay senescence. Siderophore-producing microbes further facilitate iron acquisition under limiting conditions and suppress pathogens through competitive sequestration. Stress mitigation is another crucial agricultural application, with ACC deaminase-producing microbes lowering ethylene accumulation during salinity, drought, or nutrient stress, thereby sustaining growth. Additionally, microbial inoculants enhance soil enzyme activities, organic matter turnover, and microbial diversity, contributing to long-term soil fertility and ecosystem stability.

Collectively, these microbial functions reduce chemical input needs, enhance crop yields, and promote environmentally sustainable farming practices, positioning biofertilizers as vital tools for future agroecosystem management.

## 10. Challenges

Despite the significant potential of plant-microbe interactions for sustainable agriculture, several challenges limit their widespread application. One major constraint is the variability in field performance of microbial inoculants compared with controlled laboratory or greenhouse trials. Soil heterogeneity, competition with native microbiota, and fluctuating environmental factors often reduce the survival and efficiency of biofertilizers. For nitrogen fixation, oxygen sensitivity of nitrogenase, high ATP cost, and micronutrient (Mo, Fe) limitations remain critical bottlenecks. Similarly, microbial phosphorus solubilisation is strongly influenced by soil pH, organic matter, and mineral composition, making consistent outcomes difficult to achieve. Potassium and micronutrient mobilization mechanisms are effective in vitro but often constrained under field conditions due to mineral stability and environmental stress. Moreover, large-scale production, formulation, and storage of microbial inoculants require technologies that maintain viability, adaptability, and long shelf life, which are still under development.

## 11. Future Perspectives

Future perspectives lie in advancing multi-strain and consortia-based formulations that integrate nitrogen fixers, phosphorus solubilizers, potassium mobilizers, and plant growth- promoting microbes for synergistic effects. Omics-driven tools, synthetic biology, and gene editing will enable the development of engineered strains with enhanced stress tolerance, efficient signaling, and multifunctional traits. Integration with precision agriculture tools, such as sensors and soil microbiome monitoring, can further optimize their application. Ultimately, bridging laboratory innovations with field-level adaptability, supported by policy frameworks and farmer awareness, will transform biofertilizers into reliable, eco-friendly alternatives to chemical fertilizers, promoting long-term soil fertility and crop productivity.

## 12. Conclusion

Plant-microbe interactions are governed by complex biochemical mechanisms that regulate nutrient mobilization, stress alleviation, and growth promotion. Processes such as nitrogen fixation, phosphorus solubilisation, potassium release, and siderophore-mediated iron sequestration ensure efficient nutrient supply, while microbial production of phytohormones and ACC deaminase enhances plant development and resilience under stress. Root exudates, signal molecules, and symbiotic networks orchestrate these exchanges, integrating plant and microbial metabolism. Harnessing these mechanisms through biofertilizer technologies offers eco-friendly strategies to enhance crop productivity, soil health, and sustainability in modern agriculture.

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