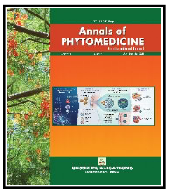
Annals of Phytomedicine 14(2): 297-307, 2025

DOI: http://dx.doi.org/10.54085/ap.2025.14.2.29

Annals of Phytomedicine: An International Journal
http://www.ukaazpublications.com/publications/index.php

Print ISSN : 2278-9839 Online ISSN : 2393-9885



Review Article : Open Access

Microbial enhancement of nutrient dynamics and nutrient use efficiency in sustainable agroecosystems

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Article Info

Article history
Received 15 September 2025
Revised 17 October 2025
Accepted 18 October 2025
Published Online 30 December 2025

Keywords
Bioinoculants
Plant growth-promoting microorganisms (PGPMs)
Nutrient use efficiency (NUE)
Nitrogen fixation
Phosphate solubilization
Potassium mobilization
Sustainable agriculture

Abstract

Sustainable agriculture requires strategies that improve nutrient use efficiency (NUE) while reducing dependence on chemical fertilizers and mitigating their environmental impacts. Plant growth-promoting microorganisms (PGPMs), particularly bioinoculants such as nitrogen-fixing, phosphate-solubilizing, and potassium-solubilizing microbes, play a pivotal role in enhancing nutrient availability, assimilation, and recycling in agroecosystems. These beneficial microbes improve soil fertility through various mechanisms, including biological nitrogen fixation, organic acid production, enzyme secretion, ion exchange, and biofilm formation, thereby converting unavailable nutrients into available forms. In addition to nutrient solubilization and mobilization, they also contribute to plant growth promotion, stress tolerance, and disease suppression.

Nitrogen-fixing diazotrophs replenish soil nitrogen and regulate plant nitrogen metabolism via key enzymes such as nitrate reductase, nitrite reductase, glutamine synthetase, and GOGAT. Phosphate and potassium-solubilizing microorganisms (PSMs and KSMs) mobilize mineral-bound nutrients through acidolysis, chelation, exopolysaccharide secretion, and synergistic interactions with arbuscular mycorrhizal fungi, significantly enhancing nutrient uptake and crop yield. Integrated nutrient management (INM) combines bioinoculants with mineral fertilizers, which have demonstrated improvements in agronomic efficiency, nutrient recovery, and yield, often allowing reductions in chemical fertilizer use without affecting yield. Overall, by integrating bioinoculants into the nutrient management system, agriculture can move towards reduced reliance on chemical fertilizers, healthier soils, and more resilient cropping systems that address the food demands of the future.

1. Introduction

The global population is projected to approach 10 billion by 2050, increasing food demand by nearly 62% (Van Dijk, 2021). Fertilizers play a pivotal role in meeting this demand by enhancing crop productivity and farmers' income. Global fertilizer consumption has steadily increased from 177.2 million metric tons in 2011-2012 to an estimated 195.4 million metric tons in 2023-2024 (Statista Research Department). India, ranking second worldwide and first among south asian association for regional cooperation (SAARC) countries in fertilizer use, reflects the growing dependency on synthetic fertilizers. While fertilizers significantly boost yield and quality, their excessive use often leads to nutrient leaching, soil degradation, and environmental pollution, with diminishing returns on productivity. Most agricultural soils are deficient in one or more essential nutrients, and the shrinking availability of arable land further aggravates nutrient depletion (Shukla *et al.,* 2022). Nitrogen, phosphorus, and potassium are the most critical macronutrients: nitrogen drives protein synthesis and photosynthesis, phosphorus supports energy transfer and root development, and potassium regulates physiological processes, disease resistance, and crop quality. Their role in sustaining agricultural productivity and food security remains indispensable. However, over-reliance on chemical fertilizers poses serious environmental, economic, and health challenges. Optimizing nutrient use efficiency (NUE) is therefore a pressing need for sustainable agriculture (Cordones *et al.,* 2020). Factors influencing NUE include agronomic practices, soil health, fertilizer balance, environmental conditions, and plant biomass. Among the emerging solutions, microbial interventions provide an eco-friendly approach to improving nutrient availability and utilization. Phosphate and potash-solubilizing bacteria, for instance, enhance nutrient dynamics, improving soil fertility, and reduce dependence on synthetic inputs (Prakhyath *et al.,* 2025).

This review examines the roles of nitrogen, phosphorus, and potassium in sustainable agroecosystems, highlights the challenges of nutrient use, and explores microbial strategies to enhance nutrient efficiency. By integrating microbial resources into nutrient management, agriculture can achieve higher productivity while maintaining environmental health and long-term soil fertility.

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2. Bioinoculants to improve nutrient acquisition

Bioinoculants are formulations containing living or dormant cells of beneficial microorganisms that promote plant health under favourable conditions. These microbes enhance soil microbial activity, thereby increasing the availability of nutrients in forms readily absorbed by plants (Cordones *et al.,* 2020; Gulshan *et al.,* 2022). Their multifunctional roles include nutrient supplementation, plant growth promotion, improvement of soil health, and suppression of plant diseases, making them particularly valuable under stressful environmental conditions. Integrating organic fertilizers and biofertilizers with soil test-based fertilizer recommendations have been reported to significantly improve nutrient recovery, with nitrogen (N) increasing from 18% to 66%, phosphorus (P) from 9% to 36%, potassium (K) from 33% to 88%, and sulfur (S) from 17% to 34% (Gulshan *et al.,* 2022).

Beneficial soil microorganisms, including bacteria and fungi, play a vital role in sustainable or "green" agriculture by improving nutrient uptake in the rhizosphere and enhancing plant resistance to both abiotic and biotic stresses. Various plant growth-promoting microorganisms (PGPMs) colonize soil and plant surfaces in large numbers, contributing to improved nutrient cycling, soil quality, and carbon sequestration in organic matter. Interactions within the rhizosphere strongly influence microbial activity, nutrient mobilization, and uptake, thereby determining plant health, nutrient efficiency, and ultimately crop productivity and sustainability (Sarkar *et al.,* 2020). But, they are influenced by agronomic, soil, and environmental factors, as well as fertilizer balance and plant biomass, which can be further enhanced through microbial interventions that provide an eco-friendly means of improving nutrient availability and utilization (Figure 1).

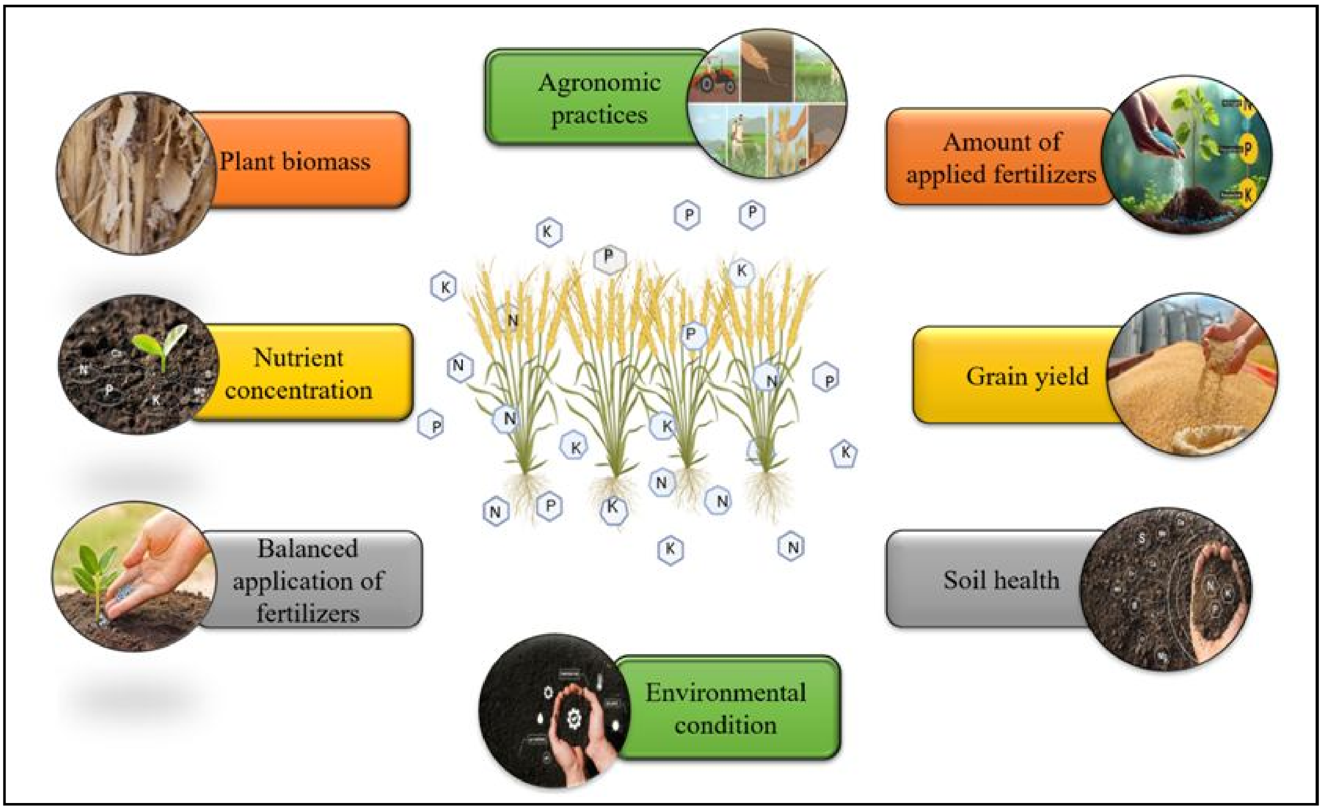


Figure 1: **Nutrient dynamics regulated by agronomic, soil, and environmental factors, together with fertilizer balance and plant biomass, can be enhanced by microbial interventions.**

Biofertilizers are broadly classified into nitrogen fixers and nutrient (or mineral) solubilizers and mobilizers. These microbial formulations promote plant growth and enhance nutrient availability through mechanisms such as nitrogen fixation, solubilization of inorganic nutrients, mineralization of organic matter, mobilization of nutrients, and redox transformations. By employing such strategies, microorganisms improve the availability of both macro- and micronutrients, thereby supporting crop growth and yield (Sairam *et al.,* 2020).

Plant-associated microbes with plant growth-promoting traits hold tremendous potential to address agricultural challenges by enhancing plant biomass and crop yields under both greenhouse and field conditions. Their beneficial effects are attributed to multiple mechanisms, including improved availability of essential nutrients (*e.g.,* N, P, K, Zn, and S), modulation of phytohormones, suppression of plant pathogens, and mitigation of biotic and abiotic stresses. These synergistic plant-microbe interactions serve as ecological engineering tools, enabling sustainable agriculture while reducing dependency on chemical fertilizers. Various microorganisms significantly influenced nutrient use efficiency (NUE) across different crops (Table 1).

For example, the combined application of 100% of the recommended dose of fertilizers (RDF) with phosphate-solubilizing bacteria (PSB) and potassium solubilizing bacteria (KSB) resulted in the highest agronomic use efficiency (AUE) of 132.70% and a maximum microbial response of 35.25%, leading to a yield increase of 135.25% compared to other treatments. Interestingly, even the integration of 75% RDF with PSB and KSB proved highly effective in enhancing davana (*Artemisia pallens*) crop performance, increasing bacterial population, promoting nutrient mineralization, and reducing reliance on chemical fertilizers, thereby minimizing environmental risks (Prakhyath *et al.,* 2025).

Table 1: Impact of various microorganisms on nutrient use efficiency (NUE) across different crops

Name of the crop	Microorganism involved	Changes in the plant system to improve NUE	References
Wheat	Co-inoculation of *A. brasilense* + *B. subtilis*	Improved N usage efficiency (80 kg ha^{-1}), N use efficiency by 31.4%	Gaspareto *et al.* (2023)
Maize	*Azospirillum brasilense*	Improved N assimilation compared with twelve maize genotypes and 1.9% improved nitrogen use efficiency	Zeffa *et al.* (2019)
Cowpea-wheat crop sequence	*Bradyrhizobium* sp. and *Azospirillum brasilense*	Notable improvements were observed in the yield increase (an average increase of 8%) and N uptake (10 to 14%)	Galindo *et al.* (2022)
Tomato	*Azotobacter* sp.	Higher seed germination rates, root development, nutrient uptake, and root and shoot biomass, as well as leaf number, leaf area and improved yield.	Lihiang (2022)
Cotton	*Azovit* with beneficial microorganisms	Total N uptake under N application rates of 135 kg ha^{-1} and 270 kg ha^{-1}.	Chen *et al.* (2010)
Barley	Application of AMF	N uptake 69.09 and 71.70 kg N ha^{-1} in the first and the second growing period	Beslemes *et al.* (2023)
Wheat	AMF with PGPR	Improved the efficiency of N and P fertilization, agronomic efficiency (AE), recovery efficiency (RE), and enhanced the microbiological properties of the soil	Berumen *et al.* (2024)
Maize	*Bacillus subtilis* and *Azospirillum brasilense*, along with varying rates of P, O… application	Development of productive components, improving phosphorus use efficiency (12%)	Pereira *et al.* (2020)
Aerobic rice	AMF genera, *Funneliformis*, *Rhizophagus*, *Glomus*, and *Acaulospora*	Higher correlation coefficients with soil enzymes such as fluorescein diacetate, microbial biomass carbon, and plant phosphorus uptake	Buzo *et al.* (2023)
Maize and wheat	*Pantoea ananatis* and *Bacillus thuringiensis*	Improved PUE and nutrient uptake	Singh *et al.* (2010)
Paddy	*Pantoea agglomerans*, *Raoultella aquatilis*, and *Pseudomonas orientalis*	Dry matter accumulation and K uptake	Khanghahi *et al.* (2018)
Red cabbage	75% of recommended NPK fertilizer with dual inoculation of *T. harzianum* and *P. fluorescens*	Increased macronutrient uptake (N, P, and K)	Sarkar *et al.* (2021)

Inoculation of crops with beneficial microbes has thus emerged as a promising, eco-friendly technology to meet global food demands while conserving natural resources.

3. Nitrogen nutrition and biological nitrogen fixation (BNF)

3.1 Role of bioinoculants in nitrogen (N) nutrition

Nitrogen (N) is a key macronutrient required for proteins, nucleic acids, chlorophyll, and enzymes that drive plant growth and metabolism (Wang *et al.,* 2024). Modern agriculture, however, relies heavily on synthetic fertilizers. In India, nitrogen fertilizer consumption reached 17 million tons in 2020 and is projected to rise to 24 million tons by 2030, largely due to subsidized urea production (Ramkumar, 2024). Excessive application has led to nutrient losses, groundwater contamination, and greenhouse gas emissions, particularly nitrous oxide (N_2O), a potent climate pollutant (Abeydeera *et al.,* 2019). Bioinoculants containing diazotrophic microorganisms offer a sustainable alternative by enhancing natural nitrogen supply and improving nutrient use efficiency.

3.2 Biological nitrogen fixation (BNF)

BNF is the microbial process that converts atmospheric nitrogen (N_2) into (NH_3) *via* the nitrogenase enzyme complex. Globally, BNF contributes an estimated 1.3 × 10^{11} kg of nitrogen annually (Barnard *et al.,* 2022). Bioinoculants based on nitrogen-fixing microbes include *Rhizobium* (symbiotic), *Azotobacter* (free-living), *Azospirillum* (associative), and *Gluconacetobacter diazotrophicus* (endophytic), and also the beneficial symbiotic fungi (AMF). These inoculants not only supplement nitrogen but also modulate plant metabolic pathways, improving nitrogen use efficiency and crop productivity (Thiebaut *et al.,* 2022). Biological nitrogen fixation is a fundamental microbial process that reduces atmospheric nitrogen (N_2) to ammonia (NH_3) or ammonium (NH_4^+), making it available for plant assimilation. This process is carried out by symbiotic, free-living, and endophytic diazotrophs, which play a crucial role in sustaining soil fertility and crop productivity. The fixed ammonia is assimilated into organic forms primarily *via* the glutamine synthetase-glutamate synthase (GS-GOGAT) pathway, with supplementary involvement of glutamate dehydrogenase (GDH). Through these pathways, ammonia is incorporated into amino acids and other nitrogenous compounds essential for plant growth and metabolism (Figure 2).

3.3 Microbial mediation of nitrogen assimilation

In soils, nitrate (NO_3^-) is the main nitrogen source for plants. Once absorbed, it is reduced to nitrite by nitrate reductase (NR) and then to ammonia by nitrite reductase (NiR) in plastids. Ammonia is incorporated into amino acids through the GS/GOGAT cycle (Krapp *et al.,* 2005). In flooded or ammonium-rich soils, NH_2^+ uptake is favoured *via* root transporters (Ludewig *et al.,* 2007), while photorespiration also generates ammonia that must be reassimilated (Keys *et al.,* 2006). Microbial inoculants enhance these processes by stimulating nitrogen-assimilating enzymes and maintaining nitrogen homeostasis under variable soil conditions (Valentine *et al.,* 2011).

3.4 Enzyme regulation by microbial inoculants

Nitrogen assimilation is tightly regulated by enzymes such as NR, NiR, glutamine synthetase (GS), glutamine oxoglutarate amino-transferase (GOGAT), glutamate dehydrogenase (GDH), and alanine aminotransferase (AlaAT) (Kishorekumar *et al.,* 2020). Isoforms of GS and GOGAT have distinct functions:

- **Fd-GOGAT** in chloroplasts assimilates photorespiratory ammonium and supports nitrate reduction (Kumagai *et al.,* 2011).
- **NADH-GOGAT**, expressed in root nodules, assimilates ammonium fixed by symbiotic microbes, and GDH links nitrogen and carbon metabolism under stress (Miyashita *et al.,* 2008).

Bioinoculants influence these enzymatic pathways by supplying ammonium *via* BNF and inducing gene expression linked to nitrogen metabolism, thereby improving assimilation efficiency (Santos *et al.,* 2020).

3.5 Symbiotic nitrogen fixers

Symbiotic nitrogen fixation involves *Rhizobium*-legume and *Frankia*-non-legume associations, where bacteria form root nodules that convert atmospheric N_2 into plant-available forms. This process, regulated by *nod, nif,* and fix genes, relies on plant-microbe signaling *via Nod* factors and flavonoids. Nitrogen fixation contributes 200-300 kg N ha^{-1} $year^{-1}$ in legumes, equivalent to replacing large amounts of synthetic fertilizers (Mahmud *et al.,* 2020; Li *et al.,* 2023). However, excessive external nitrogen suppresses nodulation and reduces fixation efficiency. Co-inoculation of *Rhizobium* with PGPR enhances nitrogen recovery, crop yields, and soil fertility, while reducing dependence on chemical inputs (Galindo *et al.,* 2022). Thus, optimizing host-microbe compatibility and managing nitrogen inputs are key to sustaining symbiotic efficiency and achieving higher nitrogen use efficiency (NUE).

3.6 Free-living nitrogen fixers

Free-living diazotrophs, particularly *Azotobacter*, supply nitrogen in non-leguminous systems through biological nitrogen fixation while also solubilizing phosphorus and enhancing root growth. Inoculation improves seed germination, nutrient uptake, biomass accumulation, and NUE under both field and greenhouse conditions (Aasfar *et al.,* 2021). In saline soils, *Azotobacter chroococcum* (Azovit) applied with reduced fertilizer increased cotton yield and NUE by 90%, enabling a 70 kg reduction in nitrogen fertilizer (Chen *et al.,* 2010). When integrated with other beneficial microbes, *Azotobacter* further enhances plant performance, highlighting its role as a natural biofertilizer for sustainable agriculture.

3.7 Associative symbiotic nitrogen fixers

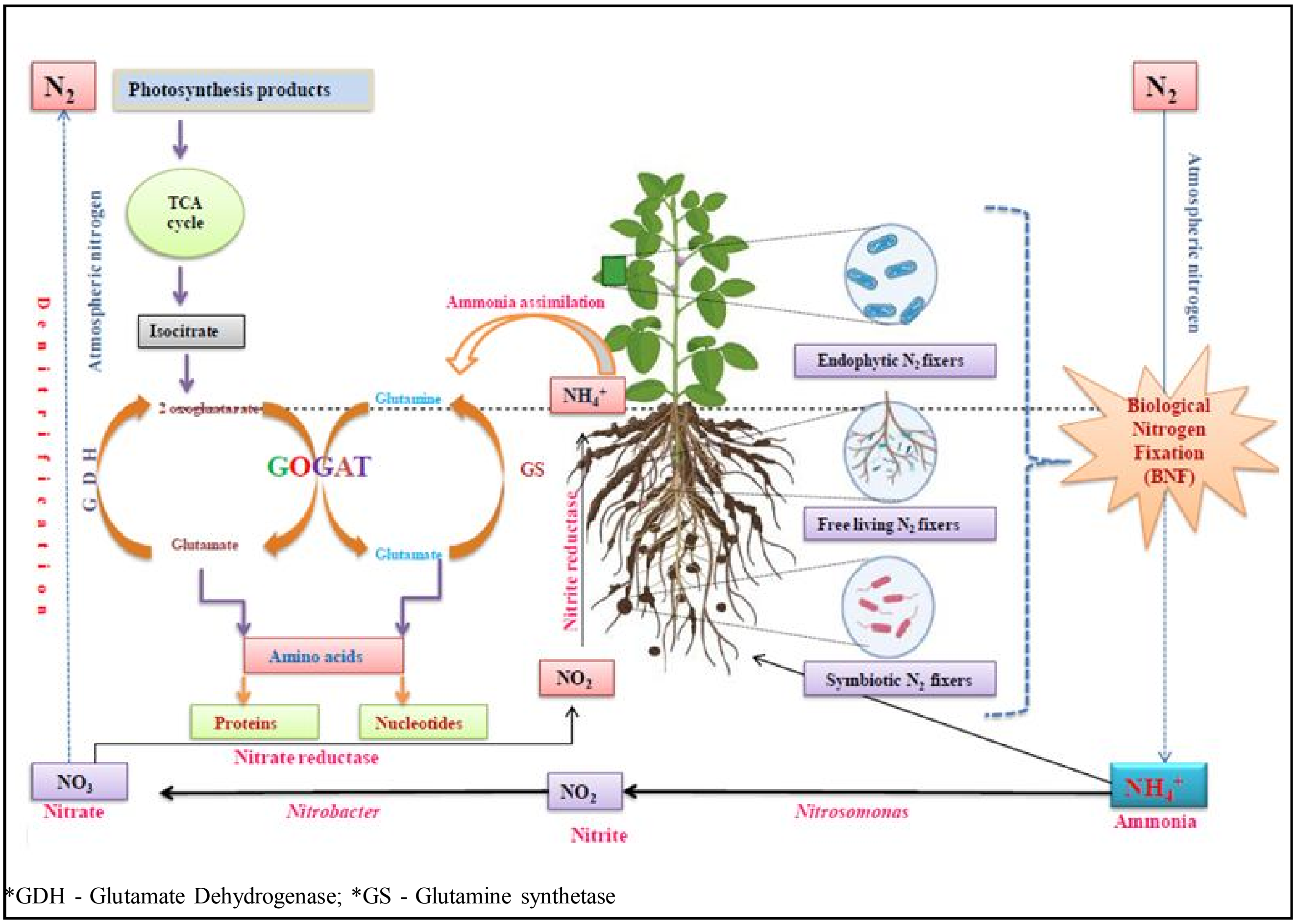
Associative diazotrophs such as *Azospirillum* colonize the rhizosphere of cereals and non-legumes, fixing 20-40 kg N ha^{-1} $year^{-1}$ while promoting root growth and nutrient uptake. Inoculation with *Azospirillum brasilense* and *Bacillus subtilis* enhances nitrogen fixation, phytohormone production, and nutrient recovery, improving yield and NUE in wheat and maize (Okon *et al.,* 1982; Galindo *et al.,* 2021; Marinho *et al.,* 2024; Galindo *et al.,* 2024). Co-inoculation significantly increases nitrogen accumulation and grain yield compared to single inoculation. These diazotrophs not only fix atmospheric nitrogen but also stimulate physiological changes that enhance nutrient and water absorption, supporting cereal production with reduced fertilizer inputs.

3.8 Endophytic nitrogen fixers

Endophytic nitrogen-fixing bacteria reside within plant tissues and contribute to nutrient uptake and NUE without harming the host. *Gluconacetobacter diazotrophicus*, first isolated from sugarcane, is notable for fixing nitrogen under aerobic and nitrate-rich conditions, owing to its lack of nitrate reductase (Cavalcante and Dobereiner, 1988). This bacterium enhances sugarcane biomass, yield, and nutrient uptake, reducing fertilizer demand. Its resilience under high-nutrient conditions and strong plant-growth-promoting properties make it a valuable inoculant for crops with high nutrient requirements. In a pot experiment with paddy soil, rice seedlings were inoculated at the seedling stage with the nitrogen-fixing bacterium R3 (*Herbaspirillum*) in the rhizosphere. The study reported that inoculation influenced the abundance of soil nitrogen-fixing bacterial taxa, which was closely associated with variations in soil available potassium, ammonium nitrogen (NO_4^+ -N), and nitrate nitrogen (NO_3^- -N) contents. Furthermore, the shifts in soil bacterial community structure were correlated with changes in soil nutrient dynamics (Li *et al.,* 2024).

3.9 Arbuscular mycorrhizal fungi (AMF)

Arbuscular mycorrhizal fungi (AMF) form symbioses with >80% of plants, enhancing nutrient uptake, stress tolerance, and soil health. Their hyphal networks extend root absorptive capacity, facilitating NO_3^- and NO_4^+ uptake, while also influencing rhizosphere microbial communities involved in nitrogen cycling (Tang *et al.,* 2022; Ebbisa, 2022). AMF inoculation increases fertilizer recovery, nitrogen utilization efficiency, and biomass in cereals, though excessive inorganic fertilizers suppress colonization (Xue *et al.,* 2024). Preference for NH_4^+ uptake and improved phosphorus availability further strengthen nitrogen assimilation. Integrating AMF with reduced fertilizer inputs offers a sustainable strategy to enhance crop productivity.



*GDH - Glutamate Dehydrogenase; *GS - Glutamine synthetase

Figure 2: Process of biological nitrogen fixation (BNF) in plants.

Biological nitrogen fixation is a natural process by which nitrogen gas (N_2) from the atmosphere is converted into ammonia (NH_2) or ammonium ions (NH_4^+), which plants can use to synthesize proteins, nucleic acids, and other essential molecules. This process is primarily carried out by certain symbiotic (associated with leguminous plants), free, and endophytic nitrogen-fixing bacteria. In ammonia assimilation, plants or other organisms fix ammonia through enzymes such as glutamine synthetase and glutamate dehydrogenase, which incorporate the ammonia into amino acids and other nitrogen-containing compounds.

3.10 Towards sustainable nitrogen management

Heavy dependence on synthetic nitrogen fertilizers is unsustainable both economically and environmentally. Bioinoculants containing nitrogen-fixing microorganisms present a *via*ble solution by enhancing BNF, nitrogen uptake, and assimilation while reducing greenhouse gas emissions. Future efforts should focus on developing robust microbial consortia, understanding plant-microbe interactions, and validating bioinoculant performance across cropping systems. Harnessing the ecological services of beneficial microbes will improve nitrogen use efficiency, maintain soil fertility, and contribute to climate-smart, sustainable agriculture (Vidal *et al.,* 2022).

4. Phosphorus nutrition and phosphate-solubilizing microorganisms (PSMs)

Phosphorus (P) is an essential nutrient for plant growth, involved in numerous metabolic processes. However, its availability in soils is often limited due to its tendency to form insoluble complexes, restricting plant uptake. The finite nature of phosphate rock reserves and the excessive use of chemical fertilizers not only challenge the sustainability of agricultural production but also contribute to environmental problems such as eutrophication of aquatic ecosystems. With the rising global demand for food, improving phosphorus use efficiency (PUE) has become critical. In this context, microorganisms involved in the phosphorus cycle have emerged as promising biotechnological solutions, attracting increasing attention in recent years (Berumen *et al.,* 2024).

Phosphate-solubilizing microorganisms (PSMs) enhance phosphorus availability and uptake in plants through multiple mechanisms. These include the secretion of enzymes and organic acids, the expression of genes involved in phosphorus solubilization, the production of extracellular polysaccharides (EPS), and the activity of arbuscular mycorrhizal fungi (AMF), which facilitate phosphorus mobilization *via* root exudates and extensive mycelial networks (Berumen *et al.,* 2024) (Figure 3).

Microbial solubilization of phosphate rock (PR) offers an environmentally friendly alternative to chemical processing for fertilizer production. Phosphate-solubilizing microorganisms (PSMs), including bacteria, fungi, actinomycetes, and cyanobacteria, employ enzymatic and biochemical processes to transform insoluble forms of phosphorus into plant-available orthophosphates. Their application not only enhances soil fertility but also reduces dependence on synthetic fertilizers, thereby supporting more sustainable farming systems. Mycorrhizal symbiosis further contributes to phosphorus mobilization by facilitating carbon exchange between plants and fungi. The solubilization capacity of PSMs is largely regulated by genes encoding organic acid production, phosphatase enzymes, and other metabolic pathways (Pang *et al.,* 2024). Genes such as *phoD*, *phoA*, *phoX*, and *phoC* encode enzymes like phosphatases and phytases, which play a crucial role in the hydrolysis of organic phosphorus compounds and the release of soluble phosphate. In addition, genes including *gcd*, *pgg*, *mbs*, and *gabY* are associated with the biosynthesis of organic acids such as gluconic, acetic, and oxalic acids, which enhance phosphorus solubilization through acidification and chelation mechanisms, thereby improving nutrient availability and uptake by plants (Garaycochea *et al.,* 2023; Sashidhar and Podile, 2010) (Figure 3).

4.1 Microbial mechanisms of phosphorus solubilization

4.1.1 Secretion of organic acids

The primary mechanism of biological phosphate solubilization is the secretion of organic acids, which chelate cations such as Ca^2 bound to phosphate. Oxalic acid is the most effective, followed by citric, malic, itaconic, and gluconic acids. For instance, the solubilization of apatite $[Ca\ldots (PO_2\,) \pm (OH_2\, F_2\, Cl)]$ using *Aspergillus niger* resulted in oxalic acid production, which precipitated as calcium oxalate, thereby releasing phosphate ions (Mendes *et al.,* 2020). Similarly, glucose dehydrogenase (GDH) and its cofactor, pyrroloquinoline quinone (PQQ), enabled *Pseudomonas* sp. to produce gluconic acid, significantly enhancing phosphate dissolution (Zuluaga *et al.,* 2023). Other strains, such as *Pantoea ananatis* and *Bacillus thuringiensis*, secrete gluconic acid, citric acid, and α-ketoglutarate, improving P availability and crop yields in cereals such as maize and wheat (Jaiswal *et al.,* 2021).

4.1.2 Enzymatic hydrolysis

Enzymatic mineralization of organic phosphorus represents another crucial mechanism. PSMs produce phosphatases and phytases that hydrolyse organic phosphorus compounds into plant-available inorganic orthophosphates. Acid phosphatases (ACP) function predominantly in acidic soils, while alkaline phosphatases (ALP) are active in neutral to alkaline soils, with ACP showing greater resilience under high phosphate concentrations (Liu *et al.,* 2022). Phytases play a key role in breaking down phytate, one of the major forms of organic P, thereby enhancing P bioavailability (Arias and Okoye, 2023). These enzymatic processes account for up to 90% of organic phosphorus mineralization and are central to sustainable nutrient cycling (Rocabruna *et al.,* 2024). In addition to enzymatic and organic acid-mediated mechanisms, several other strategies contribute to phosphorus mobilization and uptake. The excretion of extracellular polysaccharides (EPS) by microorganisms facilitates biofilm formation on root surfaces and soil particles, creating a favorable microenvironment for mineral dissolution and enhancing nutrient diffusion. Proton extrusion, mediated primarily through H -ATPases or organic acid dissociation, leads to localized acidification of the rhizosphere, thereby increasing the solubility of otherwise sparingly available phosphate compounds. Moreover, phosphate starvation-induced genes such as *PstOL* and related components of the phosphate-specific transport (Pst) system are activated under low-phosphorus conditions, enabling high-affinity uptake of phosphate. Similarly, phosphate transporter genes, particularly those belonging to the *Pht* and *Pst* families, play a crucial role in maintaining phosphate homeostasis by facilitating its acquisition, translocation, and distribution within plants. Collectively, these mechanisms complement enzymatic hydrolysis and organic acid production, significantly improving phosphorus availability and utilization efficiency.

4.1.3 Role of arbuscular mycorrhizal fungi (AMF)

Arbuscular mycorrhizal fungi (AMF) form symbiotic relationships with the roots of more than 80% of terrestrial plant species and are vital for phosphorus acquisition under P-limited conditions (Borges *et al.,* 2022). AMF extend the root system through extensive mycelial networks, improving access to immobile soil phosphorus. They mobilize phosphorus and enhance plant tolerance to drought, salinity, and pathogens in exchange for photosynthates.

Field and controlled studies confirm their significance. For example, *Glomus intraradices* increased phosphorus acquisition and above-ground biomass in *Solidago canadensis* under low-P conditions (Dong *et al.,* 2021). In rice, inoculation with AMF genera such as *Funneliformis*, *Rhizophagus*, and *Glomus* improved soil enzyme activities, microbial biomass, and P uptake compared with uninoculated controls (Buzo *et al.,* 2023).

4.1.4. Towards sustainable P management

PSMs, including bacteria (*Bacillus, Pseudomonas, Rhizobium, Escherichia*), fungi (*Aspergillus, Penicillium*), actinomycetes (*Streptomyces, Micromonospora*), and cyanobacteria, play indispensable roles in phosphorus cycling and acquisition (Maharana *et al.,* 2021; Mitra *et al.,* 2024). Their integration with organic amendments and rational fertilizer use enhances crop productivity while mitigating the environmental consequences of excessive fertilizer application. Thus, PSM-based strategies represent a cornerstone for improving phosphorus nutrition, soil fertility, and overall sustainability in modern agriculture.

5. Potassium nutrition and K-solubilizing microorganisms

Potassium (K) is one of the most abundant elements in the soil, yet most of it remains unavailable to plants. Fixed and mineral forms of K dominate, while feldspar and mica serve as the main mineral sources, containing up to 90-98% of the total K (Kumar *et al.,* 2020). In soil, K occurs in four forms: soil solution K (0.1-0.2%), exchangeable K (1-2%), non-exchangeable K (1-10%), and lattice K (95-96%). Only the water-soluble and exchangeable fractions are directly available for plant uptake (Lang *et al.,* 2024; Soumare *et al.,* 2023).

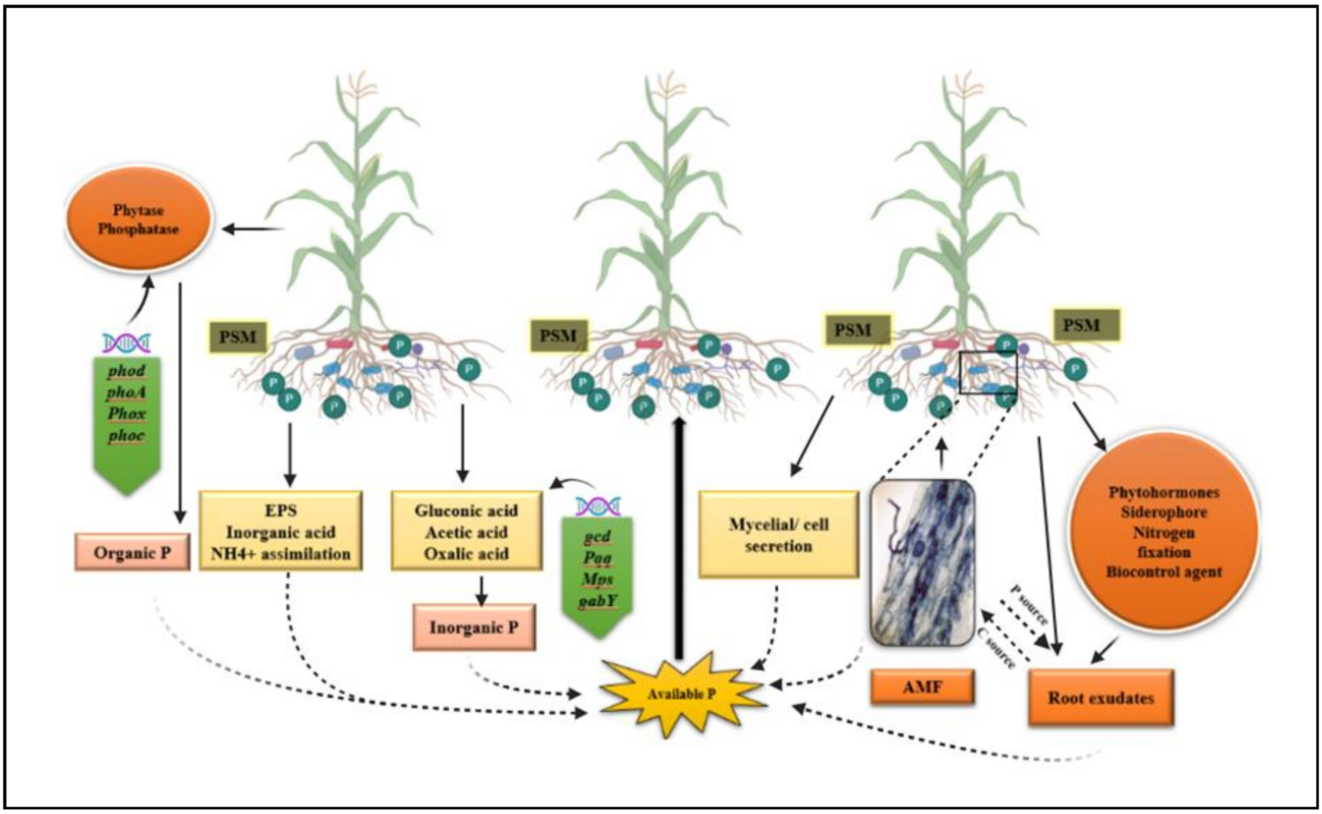


Figure 3: **Phosphate-solubilizing microorganisms (PSMs) improve phosphorus availability through enzyme secretion, organic acid production, extracellular polysaccharides, and symbiosis with arbuscular mycorrhizal fungi (AMF). They solubilize insoluble phosphates, including phosphate rock, into plant-available forms, reducing dependence on chemical fertilizers. Key genes such as *phoD, phoA, phoX,* and *phoC* encode phosphatases and phytases, while *gcd*, *pgg*, *mps*, and *gabY* regulate organic acid biosynthesis (gluconic, acetic, oxalic acids), thereby enhancing phosphorus mobilization and uptake.**

The reliance on chemical K fertilizers has alleviated deficiencies but at the cost of low use efficiency, soil fertility depletion, and environmental pollution. Since K is vital for plant physiology, metabolism, and stress tolerance, sustainable alternatives are required. Potassium-solubilizing microorganisms (KSMs), including bacteria and fungi, offer an eco-friendly approach to mobilize mineral K into bioavailable forms. They release organic acids such as tartaric, citric, and oxalic acids that dissolve K minerals, thereby enhancing plant uptake (Olaniyan *et al.,* 2022; Babar *et al.,* 2024). Beyond solubilization, these microbes improve soil health, stimulate root development, and act as biocontrol agents through antibiotic production.

Several bacterial genera such as, *Bacillus*, *Pseudomonas*, *Enterobacter*, and *Acidithiobacillus* are recognized for their K-solubilizing activity. Their mechanisms include acidolysis, ion exchange, chelation, complexolysis, and secretion of organic acids such as oxalic, gluconic, acetic, citric, and tartaric acids, which disintegrate silicate minerals and release K^+ into the soil solution (Babar *et al.,* 2024). Similarly, arbuscular mycorrhizal fungi (AMF) enhance nutrient absorption and K transport, particularly under low-K stress (Han *et al.,* 2025).

Studies have demonstrated that KSMs not only enhance K uptake but also improve overall nutrient use efficiency (NUE). For instance, AMF inoculation in wheat increased biomass, antioxidant levels, and nutrient uptake, while reducing oxidative damage under low-K stress (Han and Lee, 2005). In rice and chickpea, integrating KSMs with *Rhizobium* or phosphate solubilizers improved nutrient translocation, nitrogen fixation, and fertilizer use efficiency, allowing a 25-50% reduction in chemical K application without yield loss (Verma *et al.,* 2019; Khanghahi *et al.,* 2018).

5.1 Mechanisms of increasing K uptake by potassium-solubilizing microorganisms (KSM)

5.1.1 Acidolysis

KSB weather K-bearing minerals primarily through acidification, which disrupts potassium aluminosilicate complexes and releases soluble K forms (Nawaz *et al.,* 2023). These microbes secrete diverse organic acids-oxalic, citric, malic, gluconic, lactic, and tartaric acids that reduce soil pH and promote K solubilization. Additional mechanisms include ion exchange, chelation with mineral cations, and carbonic acid-driven weathering. These processes collectively mobilize K from minerals, increase exchangeable K, and also enhance the solubilization of Fe and Mg. By improving nutrient availability and root development, acidolytic KSMs contribute to better stress tolerance and plant productivity (Babar *et al.,* 2024; Yadav *et al.,* 2022).

5.1.2 Secretion of polysaccharides

Another important mechanism is the production of exopolysaccharides (EPS) and extracellular polymers. These compounds form biofilms on mineral surfaces, altering their structure and accelerating

K release. EPS also bind K^+ and SiO_2, maintaining mineral-solution equilibrium and improving bioavailability (Jain *et al.,* 2022). Fungi further contribute by secreting organic acids (oxalic, citric, gluconic) and releasing H^+ and CO_2, which degrade feldspar, mica, and clay silicates. Genera such as *Aspergillus, Penicillium,* and *Fusarium* are especially efficient in these processes (Vassileva *et al.,* 2000).

6. Conclusion

Meeting the food demands of a rapidly growing population requires the use of mineral fertilizers with improved eco-efficiency. However, long-term sustainability depends on harnessing the functions of beneficial microbes in the rhizosphere, including nitrogen fixation, phosphate and potassium solubilization, and integrated nutrient cycling. Plant growth-promoting microorganisms (PGPMs) play a vital role in enhancing nutrient availability, mobility, and utilization, while simultaneously improving soil health and crop productivity. Their interactions with plants and soil contribute to the restoration of soil fertility and resilience in nutrient-deficient environments.

Integrated nutrient management (INM), combining microbial inoculants such as N_2-fixers, phosphate-solubilizing microbes (PSM), and potassium-solubilizing microbes (KSM) with reduced chemical fertilizers, has emerged as a promising approach to improve nutrient use efficiency (NUE). While effective, the main challenge lies in the selection of suitable microbial strains. Screening should focus not only on functional traits but also on molecular markers. For instance, the nif KDH gene provides a more reliable indicator of nitrogen-fixing potential than the conventional acetylene reduction assay, while the *gcd* gene is essential for identifying gluconic acid-producing mineral solubilizers. Likewise, the *pho D* gene, which encodes alkaline phosphatase, is critical for efficient phosphorus mineralization. These genetic markers, along with functional parameters, can guide the development of more effective bioinoculants.

7. Future directions

Future research should integrate omics-based tools to unravel the molecular mechanisms underlying microbial nutrient cycling and nutrient dynamics. This will support the development of biofortified crops with improved nutrient-use traits and resilient farming systems that promote biodiversity and ecosystem services. A persistent challenge, however, is the inconsistent performance of microbial inoculants across different environments, often due to poor adaptability and competition in the soil microbiome. Similarly, the compatibility of microorganisms with mineral sources must be carefully evaluated, considering both nutrient concentration and dissolution rate. Field trials across diverse soils and cropping systems will be essential to optimize inoculant-mineral-fertilizer combinations that reduce chemical fertilizer dependence while sustaining yields.

Finally, bridging the gap between research and practical application is critical. Outreach initiatives that demonstrate the benefits of microbial inoculants and integrated nutrient strategies can build farmers awareness and adoption. Educating farming communities on the economic and environmental advantages of microbial technologies will accelerate the transition towards greener agriculture. By integrating multidisciplinary research, innovative technologies, and farmer participation, bioinoculants or microbial-based nutrient management can play a transformative role in achieving sustainable agricultural intensification.

Acknowledgements

The authors are thankful and acknowledge the researchers of the original research works whose publications are cited in the present review. This review article was supported by the Board of Research in Nuclear Sciences (BRNS), Government of India. We acknowledge the use of BioRender.com in the preparation of certain figures, which contributed significantly to the effective visualization of our data and conceptual framework.

Conflict of interest

The authors declare no conflicts of interest relevant to this article.

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Citation **Jayapratha Chokkalingam, Poulomi Mukherjee, K. Kumutha and P. Vijaya Priya (2025). Microbial enhancement of nutrient dynamics and nutrient use efficiency in sustainable agroecosystems. Ann. Phytomed., 14(2):297-307. http://dx.doi.org/10.54085/ap.2025.14.2.29.**