

Phosphate solubilization and mobilization: bacteria–mycorrhiza interactions

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Abstract

Phosphorus (P) is an essential macronutrient for plant growth and development. However, most of the P in the Earth's crust is insoluble, making it inaccessible to plants. This review examines the ability of phosphate-solubilizing microorganisms (PSMs) to convert these insoluble forms of P into plant-accessible forms, highlighting their potential use as biofertilizers. PSMs mainly consist of phosphate-solubilizing bacteria and fungi, which play crucial roles in the soil P cycle. The mechanisms of P solubilization encompass not only the key components of the soil P cycle but also relate to PSM species and the presence of phosphatase/phosphohydrolysis-related genes. Organic P are mineralized by enzymatic activity, while inorganic P, such as iron-phosphate, aluminium-phosphate, and calcium-phosphate are solubilized through organic acid production, proton extrusion, siderophore secretion, and exopolysaccharide production. Additionally, arbuscular mycorrhizal fungi are among the PSMs that effectively enhance P uptake in plants. Using PSM inoculants as biofertilizers has shown promise in improving soil P availability. However, further research is needed to determine the optimal application conditions, including timing, inoculum forms, and dosages, to maximize their effectiveness.

Impact Statement

Phosphorus is an essential macronutrient for plants, playing a crucial role in key metabolic processes, including cell division, energy production, and photosynthesis. Although phosphorus is generally considered to have low mobility in soil, it can be strongly adsorbed by clay minerals, iron (Fe) and aluminium (Al) and be unavailable to plants. This review provides a comprehensive analysis of the mechanisms of phosphate solubilization and mobilization by soil microorganisms, and the potential use of these microorganisms as biofertilizers for plant nutrition.

Keywords: bioinoculant; fungi–bacteria interactions; phosphate-solubilization; plant–soil–microbe interaction; sustainable agriculture

Introduction

Phosphorus (P) is the second most vital macronutrient after nitrogen, playing a crucial role in plant metabolism and development (Rawat et al. 2021). It is essential for regulating agricultural production (Rodrigues et al. 2016, Du et al. 2020) and is involved in several key plant metabolic processes, including cell division, energy production, macromolecule synthesis, signal transduction, and photosynthesis (Zhong et al. 2023). Although the natural content of total P in soils ranges from 50 to 3000 mg kg⁻¹, only a negligible amount (<1%) is available to plants (Richardson et al. 2009, Zhu et al. 2018). This limited availability of P to plants is due to its strong adsorption by 1:1 clay minerals such as kaolinite, montmorillonite, illite, vermiculite, and beidellite, as well as by iron (Fe) and aluminum (Al) oxides (Fink et al. 2016). Furthermore, high soil acidity increases P complexification, which reduces its bioavailability and significantly limits plant nutrition, thereby affecting, agricultural production. In tropical and subtropical soils, meeting

the P requirements of crops primarily relies on the application of P fertilizers (Mumbach et al. 2021). However, these fertilizers are often applied in an unbalanced (both over-dose and under-dose) manner. This mismanagement adversely affects crop production and poses environmental risks.

The uneven distribution of global P reserves, with over 78% of phosphate rock production concentrated in just four countries (Morocco, the USA, China, and Russia), creates vulnerabilities in the supply chain and leads to price fluctuations. These issues disproportionately affect countries with limited access to these vital resources (Macintosh et al. 2019). For instance, the price of phosphate rock surged by 800% in 2008, resulting in a global shortage of P fertilizers (McGill 2012, Cordell et al. 2015). Most developing countries, which rely heavily on imported P fertilizers, face significant challenges in securing a stable and affordable P fertilizers supply. Furthermore, conflicts among major fertilizer-producing nations and high energy demand hinder the fertilizer supply chain, impact-

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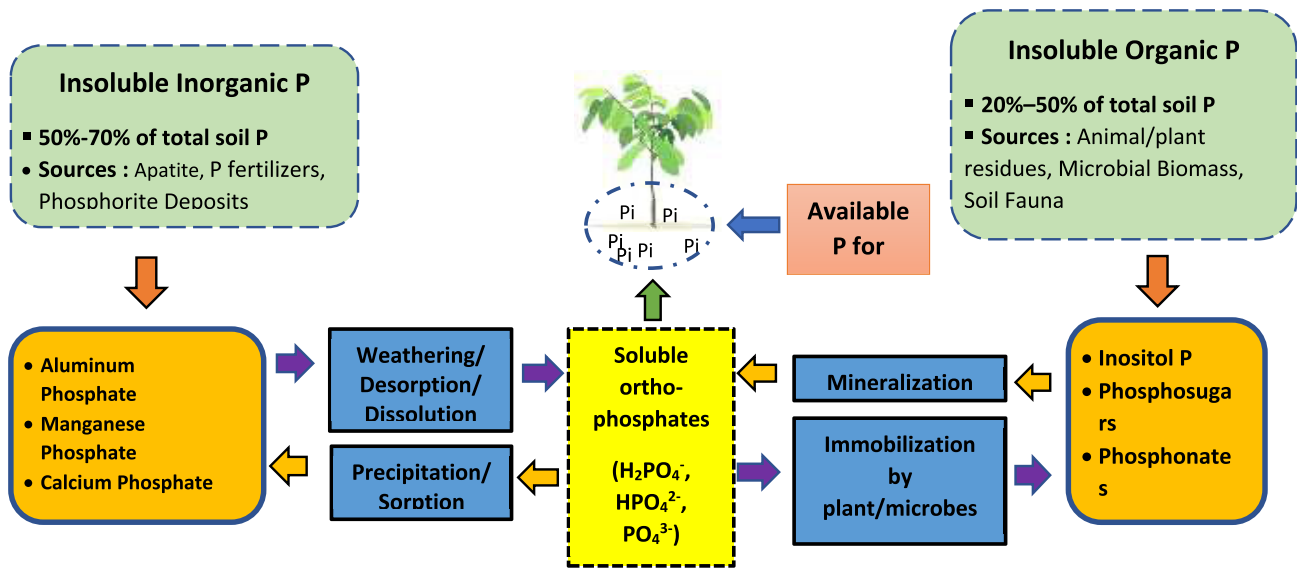


Figure 1. Different forms of P and their dynamics in soil (figure adapted from Rawat et al. 2021). It illustrates the forms, sources, and dynamic of P in soil. Soil P originates from both mineral and organic sources. Po, derived from animal and plant residues or microbial debris, primarily exists as phosphoesters, phosphonates, and phosphoric acid anhydrides. Through mineralization, Po is converted from insoluble to soluble forms. Soluble P may be immobilized in plant and animal tissues and subsequently returned to organic forms. Pi, including Fe-P, Al-P, and Ca-P, accounts for 50%–70% of total soil P. It is sourced from primary minerals such as apatite and is gradually released as these minerals weather. Pi also enters soil through fertilizers or phosphate rocks like phosphorite. In soils with high concentrations of Fe and Al in acidic soils) or Ca in alkaline soils, soluble P can become precipitated or bound.

ing global food supplies, especially in sub-Saharan Africa. This exacerbates soil fertility constraints, limits agricultural productivity, and threatens food security, making these nations highly vulnerable to global market disruptions and current geopolitical tensions (Lang and McKee 2022). In light of these challenges, there is an urgent need for an eco-friendly alternative that can match the effectiveness of synthetic P fertilizers, while reducing harmful environmental and socioeconomic impacts (Rawat et al. 2021). One promising solution lies in leveraging the natural abilities of soil microorganisms to address the challenges of P availability and the environmental impact of synthetic fertilizers (Ramos Cabrera et al. 2024).

Soils harbor specialized microorganisms, known as phosphate-solubilizing microorganisms (PSMs), which can solubilize organic P (Po) in carbon–hydrogen compounds and inorganic P (Pi) bound to metal ions or calcium. PSMs are primarily composed of bacteria and fungi and play a crucial role in enhancing P bioavailability for plants. Various mechanisms are employed by PSMs to increase P bioavailability, including, but not limited to, the secretion of organic and inorganic acids such as gluconic acids and carbonic acids, respectively. Additionally, PSMs produce a diverse range of P-solubilizing enzymes, such as phosphatases and phytases. Alternatively, other mechanisms include acidification through proton excretion or the production of ion chelators, such as siderophores. Regardless of the specific mechanism employed, these processes collectively enhance the bioavailability of P for plants (Tomer et al. 2016, Prabhu et al. 2019).

PSMs are promising bio-inoculants that can effectively reduce the need for heavy applications of chemical P fertilizers (Alori et al. 2017). Although PSMs alone can meet P needs in some cases, they may not fully replace chemical fertilizers in high-demand crops (Othman and Panhwar 2014). Combining PSMs with organic fertilizers or micro doses of chemical fertilizers is often the most effective and sustainable ap-

proach (Zhang et al. 2025). For instance, Sundara et al. (2002) demonstrated that inoculating PSMs along with P fertilizers led to a 25% reduction in the required P fertilizer for sugarcane. They also found that up to 50% of P fertilizers could be substituted with phosphate rock, a cheaper P source, when applied in combination with PSMs. Furthermore, PSMs can synergistically interact with arbuscular mycorrhizal fungi (AMF), nitrogen-fixing bacteria, or other plant growth-promoting microorganisms to enhance the mobilization and uptake of water and nutrients by plants (Jatana et al. 2021).

Given the rising interest in PSMs as alternatives to conventional P fertilizers, this review comprehensively analyses the mechanisms by which soil microorganisms solubilize and mobilize P. Additionally, it also explores the potential of these microorganisms as biofertilizers, highlighting their role in improving plant nutrition and maintaining soil health. Additionally, this review discusses future research prospects and practical applications in sustainable agriculture.

Phosphate in the soil

P in the soil is derived from both mineral and organic sources (Fig. 1). Over 20% of the total P in the soil exists as Po (Rawat et al. 2021). Po, which is part of organic compounds containing carbon–hydrogen bonds, primarily originates from the assimilation of orthophosphates and is released through microbial debris, animal manure or plant residuals (Turner and Newman 2005, Huang et al. 2017). Soil Po can be categorized based on the chemical structure of its bonds into three types: phosphoesters, which have C–O–P bonds; phosphonates (or organophosphonates), which possess C–P bonds; and phosphoric acid anhydrides (Turner et al. 2005, Zhu et al. 2024).

Phosphoesters are further classified by the number of ester groups linked to each P atom into phosphomonoesters ($R-O-PO_3^{2-}$) and phosphodiester [(R_1O) (R_2O) PO_2^-].

Phosphomonoesters, such as sugar phosphates, phosphoproteins, and mononucleotides, are the dominant Po compounds found in soil (Harrison 1987). The most prevalent type of phosphomonoester is inositol phosphate, a six-carbon inositol molecule that can have one to eight P groups linked through ester bonds (Giles et al. 2011). Phosphate diesters, including nucleic acids (DNA and RNA), phospholipids, and teichoic acids make up a smaller proportion (<10%) of the soil Po (Turner et al. 2003). Most phosphate diesters are present in plant residues and microbial debris (Alshareef 2024). Beyond phosphomonoesters and phosphodiester, which have a biological origin, there are also synthetic phosphotriesters introduced into the soil through herbicides, insecticides, flame retardants, and plasticisers (Yadav et al. 2018, Wang et al. 2019). A typical example is S, S, S-tributyl phosphorotrithioate or tribufos, which is mostly used as preharvest defoliant for cotton.

Phosphonates are widely found in both biogenic and synthetic compounds. Among the diverse range of naturally occurring phosphonates in the environment, 2-aminoethylphosphonic acid (2-AEP) is by far the most abundant (Ruffolo et al. 2023). 2-AEP is found in most living organisms, either in an unbound form or as a component of cell membranes phospholipids (Kafarski and Mastalerz 1984), proteins, and polysaccharides (Kononova and Nesmeyanova 2002). Currently, the most widespread synthetic phosphonate is N-phosphonomethylglycine, commonly known as glyphosate, which is an active ingredient in many herbicide formulations (Sviridov et al. 2012). Phosphoric acid anhydrides contain both phosphomonoester and anhydride bonds (Turner et al. 2005). The most important phosphoric acid anhydrides in nature are adenosine triphosphate (ATP) (De Nobili et al. 1996) and adenosine diphosphate (Zhu et al. 2024), which are involved in energy transfer. Scheerer et al. (2019) has reported that ATP is present in the plant rhizosphere, where it serves as a source of both P and N.

While Po accounts for ~20%–50% of total P in soils, Pi is typically the primary source of P for young plants (Boitt et al. 2018). The most common form of Pi found in soil are orthophosphates (HPO_4^{2-} and H_2PO_4^- ions), which can be easily extracted by both plant and microbial cells. Pi is also present in soil in the forms of polyphosphates and pyrophosphates, which are generally derived from biological sources but are generally present in lower concentrations than orthophosphates (Condon et al. 2005). In acidic soils, the Pi can bind to Al, Mn, and Fe, while in alkaline soils, it can bind to Ca (Deng 2021). The primary natural source of Pi in soils is the mineral apatite [$\text{Ca}_5(\text{PO}_4)_3(\text{F}, \text{Cl}, \text{OH})$]. Apatite is found in igneous, metamorphic, and sedimentary rocks, and it gradually releases phosphate ions into the soil as it weathers. Pi is often added to soils through fertilizers such as single superphosphate, triple superphosphate, and diammonium phosphate. These fertilizers dissolve in soil moisture, releasing phosphate ions that are available for plant uptake.

The availability of P is influenced by the parent material and farming management practices (Dhillon et al. 2017). Several major soil orders, including oxisols, ultisols, and spodosols, which are common in regions with substantial precipitation, exhibit significant P deficiencies due to high weathering (Brady and Weil 2008). Consequently, the soil solution may become dominated by Fe and Al in acidic soils, and by Ca in alkaline soils, which enhances the soil capacity to fix P and reduces its availability for plant uptake (Dhillon et al. 2017).

Although P is generally characterized by low mobility in soil (Holford 1997), it can still be lost through leaching, as well as surface and subsurface runoff. This loss is influenced by factors such as soil texture, organic matter content, topography, tillage, and fertilization practices (Akplo et al. 2022).

Phosphate solubilization microorganisms

PSMs convert insoluble forms of P into forms accessible to plant and play a pivotal role in the soil P cycle (Rawat et al. 2021). Recent scientific advancements, particularly in high-throughput sequencing technologies, have enhanced our understanding of PSMs, including their structural characteristics, mechanisms, and diversity. PSMs primarily consist of phosphate-solubilizing bacteria (PSBs), which comprise 1–50% of the bacterial population, and phosphate-solubilizing fungi (PSFs), which account for 0.1%–0.5% of the fungal population (Sharma et al. 2013). PSBs belong to several bacterial phyla, including *Pseudomonadota* (formerly Proteobacteria), which are Gram-negative bacteria; *Bacillota* (formerly Firmicutes), which are Gram-positive bacteria; *Actinomycetota* (formerly Actinobacteria), which are high G + C Gram-positive bacteria; and *Cyanobacteriota* (formerly Cyanobacteria), which are photosynthetic bacteria (Table 1). Some studies have reported P-solubilizing traits among *Pseudomonadota* species, including *Agrobacterium tumefaciens* (Don and Diep 2014), *Stenotrophomonas maltophilia* (Vishwakarma et al. 2024), and *Pantoea agglomerans* (Saadoui et al. 2021). The *Bacillota* phylum is represented by the genera *Bacillus*, where species such as *Bacillus megaterium* var. *phosphaticum* have been found to enhance P solubilization and mineral uptake, leading to improved growth in a variety of crops (Azaroual et al. 2020, Iqbal et al. 2024). Some *Bacillus* also have additional beneficial traits for plant growth, such as the production of siderophore, secretion of phytohormones, and the induction of systemic resistance in plants (Jensen et al. 2024, Sharma et al. 2024).

Actinomycetota are increasingly recognized as a viable biological tool for environmentally friendly farming practices (Abdellatif et al. 2024). Numerous traits related to P solubilization in Actinomycetota have been extensively documented (Gupta and Pandey 2019, Chukwuneme et al. 2020, Umar et al. 2021, Djemouai et al. 2024). Recently, Boukeloul et al. (2024) demonstrated that Actinomycetota isolated from soils in arid Saharan regions exhibit both antifungal and plant growth-promoting activities. They reported that Actinomycetota, such as *Streptomyces enissocae-silis* A1 produce siderophores and bioactive molecules that solubilize P.

Cyanobacteriota, commonly known as Blue-Green Algae, are photosynthetic prokaryotes that are recognized for their ability to fix atmospheric nitrogen (N_2) and serve as biofertilizers (Alvarez et al. 2021). They also have the capacity to solubilize P, which is beneficial for soil health (Yandigeri et al. 2011). Recent study shown that Cyanobacteriota can solubilize various inorganic compounds, including tricalcium phosphate ($\text{Ca}_3(\text{PO}_4)_2$), strengite ($\text{FePO}_4 \cdot 2\text{H}_2\text{O}$), varicite ($\text{AlPO}_4 \cdot 2\text{H}_2\text{O}$), and hydroxyapatite ($\text{Ca}_5(\text{PO}_4)_3\text{OH}$) (Jaiswal et al. 2019, Rai et al. 2019). Additionally, they have been reported to solubilize organic sources of P (Afkairin et al. 2021). Several species of Cyanobacteriota including *Anabaena variabilis*, *Westiellopsis prolifica*, and *Calothrix braunii*, exhibit P-solubilizing abilities (Yandigeri et al. 2010,

Table 1. List of P-solubilizing bacteria along with their taxonomic classes.

Taxonomic classes	Species
Bacillota	<i>Bacillus subtilis</i> A2-9; <i>B. subtilis</i> ANctri3; <i>B. subtilis</i> ZE15; <i>B. subtilis</i> ZR3; <i>B. subtilis</i> FMCH002; <i>Bacillus cereus</i> DZ4; <i>Bacillus aryabhattai</i> PSB59; <i>Bacillus circulans</i> CB7; <i>B. megaterium</i> mj1212; <i>B. megaterium</i> B119; <i>B. subtilis</i> B2084; <i>Bacillus pumilus</i> PJ-3; <i>Paenibacillus edaphicus</i> EA3-10; <i>Paenibacillus polymyxa</i> CE42; <i>P. polymyxa</i> M1; <i>Bacillus thuringiensis</i> AG-82; <i>B. licheniformis</i> QA1; <i>B. licheniformis</i> UBPSB-07; <i>B. licheniformis</i> FMCH001; <i>B. licheniformis</i> CKA1;
Alphaproteobacteria	<i>A. tumefaciens</i> M5; <i>A. tumefaciens</i> AN17; <i>A. tumefaciens</i> B228; <i>A. tumefaciens</i> NGB-SR16; <i>A. tumefaciens</i> B8S; <i>A. tumefaciens</i> T912-2; <i>A. tumefaciens</i> BLN4; <i>Azotobacter tropicalis</i> KBS; <i>A. tropicalis</i> BKK.2; <i>A. tropicalis</i> IARI-THW-22; <i>Azospirillum brasilense</i> ; <i>Hartmannibacter diazotrophicus</i> gen. nov., sp. nov.; <i>Rhizobium tropici</i> CIAT 899; <i>R. tropici</i> CAF439; <i>R. tropici</i> Br859; <i>Rhizobium leguminosarum</i> NGB-FR-137; <i>R. leguminosarum</i> J-7HPT1; <i>R. leguminosarum</i> 37-2; <i>Rhizobium multihospitium</i> CC-13H; <i>R. multihospitium</i> CCBAU 83364;
Betaproteobacteria	<i>Burkholderia cenocepacia</i> CR318; <i>Burkholderia cepacia</i> DA23; <i>Burkholderia vietnamiensis</i> M6; <i>Burkholderia multivorans</i> WS-FJ9; <i>Burkholderia</i> sp. FDN2-1; <i>B. cepacia</i> CC-A174; <i>Achromobacter</i> sp. EMCC1936; <i>Achromobacter aegrifaciens</i> (MH1); <i>Achromobacter</i> sp. 5B1
Gammaproteobacteria	<i>Acinetobacter calcoaceticus</i> LCR59; <i>A. calcoaceticus</i> LCR100; <i>A. calcoaceticus</i> LCR102; <i>A. calcoaceticus</i> EU99; <i>A. calcoaceticus</i> LCR17; <i>Enterobacter ludwigii</i> AFFR02; <i>Enterobacter asburiae</i> QF11; <i>Pseudomonas donghuensis</i> SVBP6; <i>Pseudomonas fragi</i> CS11RH1; <i>Serratia marcescens</i> CTM 50650; <i>Serratia</i> sp. S119; <i>Serratia plymuthica</i> BMA1; <i>Rahnella aquatilis</i> HX2; <i>P. agglomerans</i> V8R67; <i>S. maltophilia</i> BCM; <i>S. maltophilia</i> MTP42; <i>S. maltophilia</i> YC
Actinomycetota	<i>Streptomyces</i> sp. WA-1; <i>Streptomyces djakartensis</i> TB-4; <i>Streptomyces rochei</i> IDWR19; <i>Streptomyces carpinensis</i> IDWR53; <i>Streptomyces thermolilacinus</i> IDWR81; <i>Streptomyces cellulosa</i> mhcr 0816; <i>Streptomyces tricolor</i> mhce 0811; <i>Streptomyces</i> sp. PSA-7; <i>Streptomyces violascens</i> TNC-1; <i>Streptomyces asenionii</i> MNC-1; <i>Streptomyces alboviridis</i> P18; <i>Streptomyces cavourensis</i> sub sp. <i>Washintogensis</i> strain NRRL 8-8030; <i>Candidatus streptomyces philanthi</i> biovar <i>basilaris</i> ; <i>Micromonospora aurantiaca</i> ; <i>Micromonospora flavogrisea</i> ; <i>Micromonospora echinaurantiaca</i>
Cyanobacteriota	<i>A. variabilis</i> , <i>W. prolifica</i> , <i>C. braunii</i> , <i>Nostoc</i> sp., <i>Scytonema</i> sp

Sharma et al. 2013). Furthermore, Cyanobacteriota produce bioactive molecules, including phytohormones, polysaccharides, phenolic compounds, and amino acids, which can act as high-value biostimulants for plants (Agwa et al. 2017, Jaiswal et al. 2019).

PSFs are found in the genera *Penicillium*, *Trichoderma*, *Aspergillus*, *Hymenella*, *Neosartorya*, *Mucor*, *Candida*, and *Entrophospora* (Li et al. 2016, Adhikari and Pandey 2019, Perea Rojas et al. 2019, Mercl et al. 2020). Although PSFs make up <1% of the total fungal population, they produce more acids than PSBs and are able to move through the soil more easily (Venkateswarlu et al. 1984). As a result, they play a significant role in P solubilization within soil environments compared to PSBs (Kucey 1983).

Mechanisms of phosphate solubilization by PSMs

In natural ecosystems, bioavailability of P in soil involves key components of the soil P cycle, which include dissolution–precipitation, mineralization–fixation, and adsorption–desorption. Additionally, it is influenced by the species of PSMs and the presence of phosphatase/phosphohydrolysis-related genes (Rawat et al. 2021, Pan and Cai 2023). The mechanisms of P solubilization are summarized in Fig. 2 and Table 2 presents a brief list of PSMs, their host, P-solubilizing ability, and mechanistic attributes.

Pi solubilization

PSMs solubilize Pi forms, including Fe–P, Al–P, and Ca–P, primarily through the secretion of organic acids, such as citric acid, lactic acid, and gluconic acid into the soil, which lower the pH around the microbial cells and help dissolve insoluble P. Organic acids chelate cations such as Ca, Fe, or Al, releasing P ions for plant absorption. These acids are produced through

microbial metabolism, including oxidative respiration and fermentation of organic carbon sources (e.g. glucose) (Trove et al. 2003). Alternatively, organic acids can directly solubilize Pi through the ion exchange between the acid anion and P with or by chelating Fe, Al, and Ca ions that are bound to P. In acidic soils, the monovalent phosphate anion H_2PO_4^- is the dominant soluble form of Pi. Consequently, the secretion of organic acids by PSMs acidifies the soil, releasing P ions from Pi through substituting H^+ for the cation bound to P (Goldstein 1995). Among the various acids generated by bacterial species, gluconic acid has been identified as crucial for P solubilization (Rashid et al. 2004).

PSMs can also synthesize inorganic acids such as sulfuric, nitric, and carbonic acids, which facilitate P solubilization (Rashid et al. 2004). These inorganic acids originate from the oxidation of nitrogenous or inorganic sulfur compounds by nitrifying and sulfur-oxidizing bacteria. Notably, bacteria from the genera *Nitrosomonas* and *Thiobacillus* are identified as nitric and sulfuric acid-producing microorganisms (Azam and Memon 1996).

Additional mechanisms for Pi solubilization include proton extrusion, siderophores, and EPS production. Several PSMs are capable of extruding protons (H^+ ions) into the surroundings. The extrusion of H^+ ions by PSMs lowers pH, facilitating the dissolution of insoluble P compounds into soluble forms, such as H_2PO_4^- and HPO_4^{2-} , which can be absorbed by plants (Gand 2016). The release of H^+ ions originates from three primary sources: the assimilation of NH_4^+ , the production of respiratory H_2CO_3 , and the extrusion of organic acid anions (Arvieu et al. 2003). The extent of pH reduction depends on the specific inorganic nitrogen source, with pH reduction being more significant when NH_4^+ is the sole nitrogen source compared to NO_3^- .

P solubilization by siderophore production is another intriguing mechanism of microbial activity, particularly in environments where both Fe and P are limiting nutrients. PSMs

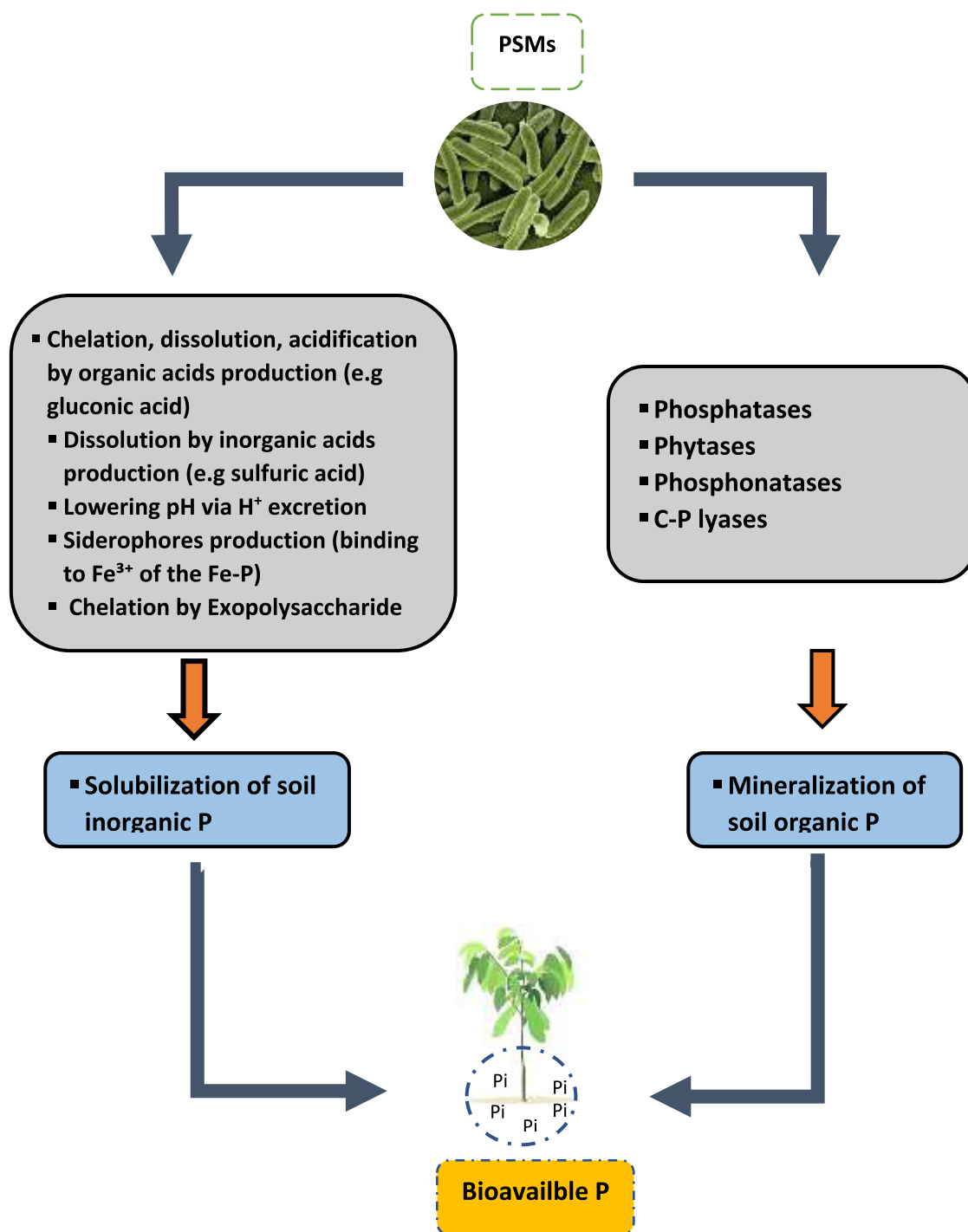


Figure 2. Mechanisms of inorganic and organic phosphate solubilization by microorganisms. It highlights the mechanisms of P solubilization by P solubilizing microorganisms. Po is mineralized by enzymes such as phosphatases, phosphonatases, phytases, and C-P lyases. Pi, such as Fe-P, Al-P, and Ca-P, is solubilized by organic acid production, proton extrusion, siderophore secretion, and exopolysaccharide (EPS) production.

produce siderophores that bind strongly to Fe³⁺ ions in the Fe-P complex. By binding to Fe³⁺, siderophores effectively remove Fe from the Fe-P complexes, thereby disrupting their structure (Collavino et al. 2010). This process releases PO₄³⁻ ions into the soil solution, making them more available for plant uptake. Some bacterial species, such as those from the genera *Pseudomonas*, *Bacillus*, and *Azotobacter*, as well as certain fungi from the genera *Aspergillus* and *Penicillium*, are known to solubilize P through siderophore production.

Microbial EPS have an indirect role in P solubilization. EPS are high-molecular-weight carbohydrate polymers secreted by microorganisms in response to stress or during biofilm formation. They contain a high density of functional groups that can bind to metal ions, such as Ca²⁺, Fe³⁺, and Al³⁺ (Ochoa-Loza et al. 2001). By chelating these metal ions, EPS can disrupt mineral complexes, releasing soluble P into the soil solution (Kishore et al. 2015).

Table 2. List of PSMs, their host, phosphate-solubilizing ability, and P-solubilizing mechanisms attributes.

PSMs	Host plant	Amount of P solubilized (μgml^{-1})	P solubilizing mechanisms	References
Bacteria				
<i>Bacillus siamensis</i> , <i>Rahnella aceris</i> , <i>Pantoea herici</i> , <i>Bacillus paramycooides</i>	<i>Triticum aestivum</i>		Organic acids production (notably glycolic acid), and induced activities of acid phosphatases and pyrophosphatases, Improvement wheat growth and root P acquisition	Khourchi et al. (2022)
<i>S. phymothica</i> (BMA1)	<i>Vicia faba</i> L.	450.00	Improvement P uptake in roots and shoots, plant biomass and plant height increment, enhanced carotenoid, and chlorophyll content in leaves	Borgi et al. (2020)
<i>Burkholderia gladioli</i> (MTCC 10216), <i>Pseudomonas</i> sp. (MTCC 9002) and <i>B. subtilis</i> (MTCC 8528)	<i>Trigonella foenum-graecum</i> L., <i>Lycopersicon esculentum</i>		Increase in seed germination, plant height, and weight, decrease in pH due to production of several organic acids, increment in soil P 40%–60%	Kumar et al. (2020)
<i>P. agglomerans</i>	<i>Capsicum annuum</i>	851.61	IAA and phytaes production increment in above and below ground biomass	Li et al. (2020)
<i>Pseudomonas</i> sp. (P34)	<i>Triticum aestivum</i>	101.60	Siderophore production, enhancement in root traits, and dry matter accumulation of plant	Liu et al. (2019)
<i>E. asburiae</i> , <i>Acinetobacter</i> sp., <i>B. cereus</i>	<i>Mentha arvensis</i> L.	430	Acidification, mineralization of Po by phosphatase	Tomer et al. (2016)
<i>Bacillus</i> sp. (STJP)		610.33	Siderophores, IAA, HCN production, increment in dry matter, and yield	Prakash and Kumar (2019)
<i>Serratia nematodiphila</i> (RJ10)	<i>Vigna mungo</i> , <i>Pisum sativum</i>	86.00	ACC deaminase, siderophores, and IAA production, increase in biomass of crops under drought stress conditions	Salkia et al. (2018)
<i>B. licheniiformis</i> (MF 589720)	<i>Vigna radiata</i>	222.00	Enhancement in seed germination, IAA and ammonia production, Improvement in the host plant's resistance to copper and zinc toxicity	Biswas et al. (2018)
<i>A. brasilense</i> (DSM1690)	<i>Triticum aestivum</i>	18.00	IAA, peroxidase, ascorbate peroxidase production under salt stress conditions	Kadmiri et al. (2018)
Fungi				
<i>Aspergillus niger</i> S-36	<i>Cicer arietinum</i>	366.25	Augmentation of root shoot biomass, chlorophyll content of inoculated plants	Saxena et al. (2015)
<i>Penicillium oxalicum</i>	<i>Triticum aestivum</i> , <i>Zea mays</i> L.	586.00	Increment in Shoot height, yield of <i>Triticum aestivum</i> and increment in root shoot biomass and yield of <i>Zea mays</i>	Singh and Reddy (2011)

ACC, 1-aminocyclopropane-1-carboxylate; HCN, hydrogen cyanide; IAA, indole acetic acid.

Po solubilization

Po solubilization generally occurs through a mineralization process catalyzed by a broad range of enzymes (Kumar and Shastri 2017). These enzymes can be either cell-wall bound or released extracellularly into the environment. While extracellular enzymes are believed to have a more pronounced effect on P concentrations in the soil solution, empirical evidence regarding the activities of exoenzymes and endoenzymes remains poorly understood (Kishore et al. 2015).

The mechanisms employed to solubilize the Po are largely dependent on the chemical bonds they contain. For instance, solubilization of organophosphates (C–O–P) bonds is carried out by nonspecific phosphatases and phytases. These enzymes, however, display no activity toward organophosphonates (C–P) bonds. Instead, cleavage of the C–P bond for the solubilization of organophosphonates require specialized phosphonate specific enzymes, which are not active toward phosphate esters. Mechanisms for organophosphate and organophosphonate solubilization are described below.

Organophosphate solubilization (C–O–P) compounds

For the solubilization of C–O–P esters of organophosphates, a range of mechanisms is employed. For example, nonspecific phosphatases hydrolyze various phosphate monoesters, rather than being substrate-specific. They catalyze the dephosphorylation of phosphoesters and phosphoanhydride bonds. Nonspecific phosphatases include acid phosphatases (pH optima of 4.5–6.5) and alkaline phosphatases (pH optima 8.0–10.5), both exhibiting broad activity (Renella et al. 2006, Cabugao et al. 2017). Acid phosphatases are released by plant roots and microorganisms, while alkaline phosphatases mainly originate from microbial sources (Sharma et al. 2013). For example, *Bacillus licheniformis* MTCC 2312 produces alkaline phosphatases that solubilize Po in the soil. Additionally, Rinu and Pandey (2010) reported that *A. niger* excretes both intracellular and extracellular acid phosphatases. Phytases are a specific group of phosphomonoesters that hydrolyze the phosphomonoester bond of plant phytate. They degrade phytate (myo-inositol hexakisphosphate) into lower-order inositol phosphates and eventually release soluble P (Sharma et al. 2013). Based on their molecular structure and biochemical properties, phytases are classified into histidine acid phosphatases (EC 3.1.3.2), purple acid phosphatases (EC 3.1.3.2), β -propellor phytases, and cysteine phytases (EC 3.1.3.26) (Mullaney and Ullah 2007). Phytases have been isolated from several soil bacteria, such as *B. subtilis* (Kerovuo et al. 1998), *Acetobacter* sp. (Kumar et al. 2013), and *B. acillus laevolacticus* (Gulati et al. 2007).

Organophosphonate solubilization (C–P compounds)

For the solubilization of C–P bonds of organophosphonates, a range of phosphonate-specific C–P cleaving enzyme systems are employed to release the Pi component, which plants can easily assimilate. Among the best-characterized of these are the PhnWX and PhnWYA hydrolytic pathways (Epiktetov et al. 2024). These pathways are substrate specific for the mineralization of the most abundant phosphonate 2-AEP. The 2-AEP specific transaminase, PhnW, converts 2-AEP to phosphonoacetaldehyde. The phosphonoacetaldehyde can then be further degraded, either by phosphonoacetaldehyde hydrolase (PhnX), a reaction that generates acetaldehyde and Pi. Alternatively, the PhnW-generated phosphonoacetaldehyde can be

mineralized by phosphonoacetaldehyde dioxygenase (PhnY) to generate phosphonoacetate before C–P cleavage by phosphonoacetate hydrolase (PhnA), a reaction that generates acetate and Pi. However, phosphonoacetate and phosphonoacetaldehyde present in the environment can also be degraded by the PhnA or PhnX enzymes alone, also releasing the Pi moiety.

An oxidative pathway for 2-AEP catabolism involving a putative 2-oxoglutarate dioxygenase (PhnY*) and a phosphohydrolase (PhnZ) has been reported by Martinez et al. (2010). This PhnY*Z pathway has been reported as an alternative mechanism used by *Escherichia coli* to metabolize 2-AEP (Villarreal-Chiu et al. 2012). However, the biochemical reactions involved in this process have yet to be characterized. Other phosphonate compounds, such as phosphonoalanine, can be degraded in the PalB–PalA pathway (Kim et al. 2002, Freestone et al. 2017). This pathway involves the 2-AEP: pyruvate aminotransferase (EC 2.6.1.37) that catalyzes the conversion of the 2-AEP into phosphonoacetaldehyde by transferring the amino group to pyruvate, forming alanine and the phosphonoacetaldehyde hydrolase (PhnA), which hydrolyzes phosphonoacetaldehyde into acetaldehyde and Pi by cleaving the C–P bond. This pathway has been widely reported in natural environments. Notably, the soil bacterium *B. cepacia* Pal6 was shown to produce phosphonoacetate hydrolase (PhnA) in a study by Ternan and Quinn (1998). While another study on *Pseudomonas fluorescens* 23F by McMullan et al. (1992) demonstrated the activity of phosphonoacetate hydrolase toward phosphonoacetate, resulting in the subsequent release of Pi and acetate.

In contrast to the substrate-specific enzyme systems described above, the C–P lyase system has a broad substrate range and can degrade structurally diverse alkylphosphonate compounds into their corresponding hydrocarbon and Pi (Stosiek et al. 2020). The multisubunit C–P lyase complex comprises upward of 14 genes depending on the organism; however, the key C–P core enzymes responsible for C–P cleavage are denoted PhnGHIJKLM. Notably, the C–P lyase system can also cleave the C–P bond of xenobiotic phosphonates, making it important for environmental detoxification.

Role of microorganisms in phosphate uptake

P solubilized by PSMs may not reach the root surface due to limited diffusion capacity (Kishore et al. 2015). AMFs are widely distributed within the plant kingdom and play a crucial role in enhancing plant nutrition and growth (Smith et al. 2011). These fungi can increase the root zone absorption area by a factor of 10–100, which boosts the capacity of plants to mobilize essential nutrients such as P, Cu, K, Mg, N, and Zn (Etesami et al. 2021). The mycorrhizal species *Rhizophagus* (formerly *Glomus*) *intraradices* and *Funneliformis* (formerly *Glomus*) *mosseae* are among the most extensively studied mycorrhizas and are known to enhance P mobilization and uptake in various crop plants (Krüger et al. 2012). For instance, Cozzolino et al. (2013) reported that maize inoculated with *R. intraradices* showed an increase in available soil P. Arbuscular mycorrhizal plants utilize two mechanisms for absorbing P from the soil. The first mechanism involves the direct uptake of P into the plant through the root epidermis and hairs, which is common to both arbuscular mycorrhizal and nonarbuscular mycorrhizal plants. The second mechanism involves

Table 3. Phosphate-solubilizing biofertilizers available in the market.

Trade names	P-solubilizing microorganism	Formulation	Target crop
Phospho MAX	<i>B. megaterium</i>	Liquid	Vegetables
PHOSPHODEWS	<i>B. megaterium</i>	Liquid/Powder	For all types of nonlegumes crops
Katyayani Soluphos	<i>Bacillus</i> sp. <i>Pseudomonas</i> sp.	Liquid/Powder	NS
Greenedge PhosGreen	<i>B. megaterium</i>	Liquid	NS
BACTOPHOS	<i>B. megaterium</i>	Liquid	Banana, Papaya, Cotton, Sunflower, Jowar, Bajra, Maize Wheat, Onion Sugarcane, Garlic, Ginger, Turmeric, Pomegranate, Watermelon Mosambi, Grapes, Oranges, Mango, Nursery Plants, and Floriculture Plants
PSB Biofertilizers	<i>Bacillus polymyxa</i> , <i>B. megaterium</i> , <i>Pseudomonas fluorescence</i> <i>Aspergillus</i> sp.	Liquid	NS
Phosphoz	<i>Bacillus coagulans</i>	Liquid	NS
Anshul Phosper	<i>B. megaterium</i>	Liquid/Powder	NS
BACTOPHOS	<i>B. megaterium</i>		NS
Bio-Phospho	<i>B. subtilis</i>	Liquid	NS
PHOSPHO	<i>Bacillus</i> sp.	Solid	NS
BACTERIA			
Phos Activator	<i>Penicillium Bilaiae</i>	Powder	NS
Agroright—PSF	<i>Aspergillus</i> sp.	Liquid	Wheat, Rice, Tuff, Barley, Maize, Sweet and baby corn, Sorghum, Pearly, Millets, Black and Green Gram, Cicer, Cowpea, Chickpea, Lettuce, Cabbage, Cauliflower Broccoli, French Bean, Lentils, Cluster bean, Sugarcane, Fruits trees and crops, and ornamental plants.
P Sol B	<i>B. megaterium</i> (MCC 0053)	Carrier and Liquid	Cereals, pulses, oilseeds, cotton, jute, banana, and turmeric
Premium Avatar	<i>B. megaterium</i> var phosphaticum	Carrier and granular	NS

NS nonspecific.

the introduction of P into root cortical cells, where it is transported through fungal hyphae via symbiotic interfaces, such as arbuscules or hyphal coils (Fiorilli et al. 2013).

PSMs as biofertilizers for plant nutrition

The use of PSMs as biofertilizers represents a promising approach that is unlikely to have any adverse environmental or socioeconomic impacts (Ramos Cabrera et al. 2024). This alternative is particularly relevant during recurrent fertilizer crises. In recent years, PSMs have mainly been utilized as biofertilizers. However, they also serve as biological control agents and assist organisms in coping with extreme stress conditions, such as heavy metal toxicity, by producing ACC deaminase (Prabhu et al. 2019, Bashir et al. 2024). The fertilizing capacity of PSMs stems from their ability to solubilize P and make it available to plants (Bai et al. 2024). Unlike chemical P fertilizers, which readily form complexes in the soil upon application, PSM biofertilizers allow microbes to continuously supply available P to plants over an extended period (Alori et al. 2017). Table 3 lists various phosphate-solubilizing biofertilizers currently available on the market.

Commercial inoculants based on PSBs have been developed, including species such as *B. subtilis*, *B. megaterium*, *Bacillus coagulans*, *Pseudomonas putida*, and *Bacillus polymyxa* (Prabhu et al. 2019). Studies have shown that inoculation with PSBs promote growth and yield in a number of plant species, including *Glycine max*, *Solanum lycopersicum*, *Vigna unguiculata*, *Vigna radiata*, *Vigna mungo*, *Zea mays*, *Cajanus cajan*, *Saccharum officinarum*, *Oryza sativa*, *Cicer arietinum*, and *Solanum tuberosum* (Stephen et al. 2015, Ali et al. 2020, El Maaloum et al. 2020, Bhutani et al. 2021, Bilal et al. 2021,

He and Wan 2021, Romero-Perdomo et al. 2021, Pantigoso et al. 2022). PSB inoculants can be applied either as a standalone treatment or in combination with other microbial inoculants, such as N-fixing bacteria (Yandigeri et al. 2010) or AMF (Xing et al. 2024). For example, the co-inoculation of PSBs, such as *Pseudomonas striata*, and nitrogen-fixing bacteria, such as *Bradyrhizobium japonicum*, significantly improved soybean growth, yield, and quality (Shome et al. 2022). Tagore et al. (2013) reported that co-inoculation of *B. japonicum* and PSBs increased chickpea yield by 37% compared to the noninoculated control, and by 9% compared to the inoculation with *B. japonicum* alone. Furthermore, Yasmeen and Bano (2014) revealed that co-inoculation with *B. japonicum* Tal 377 and *Enterobacter* sp A resulted in a maximum increase in IAA and gibberellin content, soybean plant biomass, root nodulation, and soybean yield compared to the control (noninoculated) and single-inoculation plants.

The potential of fungal inoculants to solubilize and mobilize P is well documented, with AMF being among the most studied. In exchange for photosynthates, AMFs provide their host plants with essential nutrients, including P. Commonly used mycorrhizal inoculants include *R. intraradices* and *F. mosseae* (Krüger et al. 2012, Cozzolino et al. 2013). An increasing body of research indicates that AMF can interact synergistically with other soil microorganisms, such as bacteria, which colonize the surface of the extraradical hyphae and perform multiple essential functions (Etesami et al. 2021). Combining PSMs and AMF may help overcome the limitations of PSMs effectiveness in enhancing plant P uptake in soils with high P-fixation capacity (Kishore et al. 2015). PSBs have been demonstrated to facilitate AMF extraradical hyphal growth, enabling hyphae to access solubilized P sources (Ordoñez et al.

2016). Furthermore, PSBs can stimulate the formation, proliferation, and germination of indigenous AMF (Berta et al. 2014).

Future actions for successful integration of PSMs as biofertilizers

Despite significant advancements in understanding the potential of PSMs fertilizers, further research is imperative to elucidate the intricate interactions between soil, plants, and microbes. This is a key step toward fully replacing agrochemical P fertilizers with environmentally beneficial microbial inoculants.

The response of crops to the inoculation of PSMs depends on several factors, including soil conditions (i.e. nutrient content, pH, salinity), the source of insoluble P, the method of inoculation (solid, liquid), the energy sources and the strain of microorganism used (Sharma et al. 2013). Integrating PSMs into sustainable agricultural practices begins with identifying and selecting local strains that exhibit high P solubilization efficiency (Khuong et al. 2024). By focusing on local strains, we can harness naturally occurring microorganisms that are adapted to local soil types, climatic conditions, and agricultural practices, thus enhancing their effectiveness in promoting plant growth.

In addition, research is needed to identify effective and efficient PSMs compatible with various crops and adaptable to diverse soil types (Rawat et al. 2021). These investigations should consider potential interactions between PSMs and other soil microorganisms, as such relationships can significantly enhance nutrient availability and overall soil health (Khan et al. 2023). The synergistic combination of these microorganisms in inoculant formulations has proven beneficial in numerous agricultural contexts; however, further research could improve their efficiency and application. Specific strains of PSMs have demonstrated the ability to solubilize potassium, an essential nutrient for plant growth (Yan et al. 2024, Zhang et al. 2024). Additionally, certain PSMs strains have been identified as effective for bioremediation, providing plants with resistance to various biotic stresses (Tian et al. 2024). This multifaceted functionality supports plant health and productivity, contributing to improved soil health by fostering a diverse microbial community that enhances nutrient cycling and soil structure. Further investigations into strains exhibiting these diverse roles are crucial for optimizing their use in agriculture.

A critical step towards the large-scale application of PSMs is investigating the optimal conditions for their use, including the ideal timing for inoculation, the most suitable formulation (liquid, powder, or granular), and the appropriate quantities to achieve maximum effectiveness. Multilocation and multi-year field trials on various crop species are needed to validate PSM strains and evaluate their efficacy under natural conditions (Ramos Cabrera et al. 2024). The best formulations must be tested for stability and shelf-life to ensure their quality over time (Soumare et al. 2020). Continued extension efforts are essential for the successful adoption of PSM biofertilizers. It is crucial to develop training programs and educational materials that illustrate the use and benefits of PSM biofertilizers, from both economic and environmental perspectives (Ramos Cabrera et al. 2024).

Conclusions

It is clear that PSMs can serve as viable alternatives to the widespread application of P fertilizers. Utilizing biofertilizers based on PSMs offers the dual benefit of promoting sustainable agricultural systems and enhancing soil quality. These microorganisms are naturally present in soil environments and utilize various mechanisms to solubilize phosphate, making it readily available for plant uptake. A substantial body of literature demonstrates that the efficacy of PSMs can be augmented when they are co-inoculated with other microbial species, such as AMF. However, the efficacy of PSMs can vary significantly depending on environmental factors and soil conditions.

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Author contributions

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