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Phosphorus dynamics and sustainable agriculture: The role of microbial solubilization and innovations in nutrient management

José Abraham García-Berumen [a], Juan Armando Flores de la Torre [b], Sergio de los Santos-Villalobos [c], Alejandro Espinoza-Canales [a], Francisco Guadalupe Echavarría-Cháirez [d], Héctor Gutiérrez-Bañuelos [a,*]

[a] *Unidad Académica de Medicina Veterinaria y Zootecnia, Universidad Autónoma de Zacatecas, Zacatecas, Mexico*
[b] *Unidad Académica de Ciencias Químicas, Universidad Autónoma de Zacatecas, Carretera Guadalajara km 6 Ejido la Escondida, 98060, Zacatecas, Zacatecas, Mexico*
[c] *Departamento de Ciencias Agronómicas y Veterinarias, Instituto Tecnológico de Sonora, Ciudad Obregón, Sonora, Mexico*
[d] *Campo Experimental Zacatecas. Instituto Nacional de Investigaciones Forestales, Agricolas y Pecuarias (INIFAP), Km. 24.5 Carretera Zacatecas-Fresnillo, 98500, Calera de Víctor Rosales, Zacatecas, México*

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ABSTRACT

Phosphorus (P) is an essential element for plant growth, playing a crucial role in various metabolic processes. Despite its importance, phosphorus availability in soils is often restricted due to its tendency to form insoluble complexes, limiting plant uptake. The increasing demand for phosphorus in agriculture, combined with limited global reserves of phosphate rock, has created challenges for sustainable plant production. Additionally, the overuse of chemical phosphorus fertilizers has resulted in environmental degradation, such as eutrophication of water bodies. Increasing agronomic phosphorus (P) efficiency is crucial because of population growth and increased food demand. Hence, microorganisms involved in the P cycle are a promising biotechnological strategy that has gained global interest in recent decades. Microorganisms' solubilization of phosphate rock (PR) is an environmentally sustainable alternative to chemical processing for producing phosphate fertilizers. Phosphorus-solubilizing microorganisms (PSMs), including bacteria and fungi, and their enzymatic processes offer an eco-friendly and sustainable alternative to chemical inputs by converting insoluble phosphorus into forms readily available for plant uptake. Integrating PSMs into agricultural systems presents a promising strategy to reduce dependence on chemical fertilizers, enhance soil health, and contribute to the transition toward more sustainable and resilient agricultural practices. It can be an alternative that reduces the loss of phosphorus in the environment, especially the eutrophication of aquatic systems. This paper explores the challenges of phosphorus availability in agriculture and the potential of microbial phosphorus solubilization as a sustainable alternative to conventional practices.

Introduction

Phosphorus (P) is a crucial macronutrient that plants require in high amounts. It plays an essential role in forming DNA, generating ATP and NADPH (in catabolic processes), and influencing photosynthesis, respiration, and protein synthesis rates (Kumar and Mohapatra, 2021). One of the roles of P-solubilizing microorganisms is to break down non-solubilizing tricalcium phosphate or rock phosphate forms so that plants can uptake P (Rawat et al., 2021). In many crop production systems, available P has been the primary factor limiting plant growth rates (P is the most common limiting nutrient in crop production). Soil deficiencies of phosphorus are traditionally solved by using inorganic phosphate fertilizers; however, using large amounts of these fertilizers is uneconomical and poses significant environmental risks (Cordell and White, 2014). Economic efficacy concerns and the apprehension of high levels of P in the aquifers have led ecologists to investigate the links between P bioaccumulation in water ecosystems and P levels in the soil to find long-lasting and effective alternatives to the use of P fertilizers (McMahon and Read, 2013; Alewell et al., 2020).

The alternative of using PSMs to access insoluble forms of P compounds allows plants to uptake more phosphorus and minimizes the side effects on the environment (Silva et al., 2023). PSMs are ubiquitous and

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* Corresponding author.
E-mail address: hgutierrez@uaz.edu.mx (H. Gutiérrez-Bañuelos).

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an essential component of the biogeochemical P cycle because phosphate mobilization occurs in many natural (eutrophic lakes and oceans) and extreme environments (volcanic, marine sediments, and deserts). These microorganisms are mainly bacteria and fungi, known for their ability to solubilize hardly soluble phosphates (Tian et al., 2021). Several PSMs tend to produce alkalinizing organic acids (such as citric, lactic, gluconic, tartaric, formic, acetic, and oxalic acid), which have high affinities for aluminum and calcium, the primary metal ions that form insoluble aluminum and calcium phosphates in the soils (Varga et al., 2020). They also have the extraordinary ability to form chelates of Fe released from insoluble Fe forms to enhance their phosphorus colonization. These arguing capacities are beneficial to the plants, which absorb nourishment through their roots, directed by complex signals released by the microorganisms, such as water, pH, nutrients, chemical signals, root exudates, and plant growth inhibitors (Wang et al., 2021). Another mechanism includes enzyme secretion and complex population dynamics (Rawat et al., 2021).

PSMs are an essential link between the geosphere, hydrosphere, and biosphere. They deliver P to plants by intercepting the dissolved P and mineralizing P carried into the soil by the weather (Liu, 2021). The soil type has a significant effect on the ability of the PSMs. Several researchers (Dissanayaka et al., 2021; Wang et al., 2021) have found that the growth of phosphorus-solubilizing bacteria and fungi tends to be higher in acidic soils (pH 5.0 to 6.5) than in alkaline soils, with bacterial growth also limited in alkaline soils (pH above 7.0). Consequently, the actual populations and variety of PSMs in the soil are influenced by the site's numerous biotic and abiotic features, such as physical, chemical, and ecological factors (Dey et al., 2021). The PSMs exert various plant-promoting effects, making added organic phosphorus more available to plants (Rawat et al., 2021). Their use offers an environmentally friendly and biologically more sustainable alternative for long-term success and sustainable agriculture (Pang et al., 2024; Silva et al., 2023). The growing interest in this group of microbes is not exclusively due to their capability of solubilizing insoluble forms of phosphorus but also to the use of plant growth-promoting *Rhizobacteria* and plant growth-promoting *Rhizophagous* fungi to enhance the health of plants and crop yield (Varga et al., 2020). This review aims to provide an overview of challenges associated with phosphorus availability in agriculture systems, and to investigate the potential of microbial PSMs and their enzymatic processes in enhancing phosphorus bioavailability, while also examining sustainable strategies, such as the development of microbial inoculants, to improve phosphorus use efficiency and reduce environmental impacts in agriculture.

Phosphorus, an essential element for the plant nutrition and food production

Phosphorus (P) is one of the 17 essential elements for plant growth and is crucial for a range of metabolic processes. These include energy generation, nucleic acid synthesis, photosynthesis, glycolysis, respiration, membrane synthesis and stability, enzyme activation/inactivation, redox reactions, signaling, carbohydrate metabolism, and nitrogen fixation (Vance et al., 2003). Moreover, phosphorus is involved primarily in core and important molecules for living organisms, including DNA, RNA, sugar, lipids, proteins, ATP, ADP, and NADPH (Zhang et al., 2014).

Agronomically, after nitrogen, phosphorus is the second limiting nutrient for the development and growth of plants since the concentration of P reaches up to 0.5 % of the dry weight of the plant (Vance et al., 2003). Phosphorus rock minerals are the only phosphorus resources in the world, and these advantages come at a significant cost (Geissler et al., 2018). Mobilizing phosphate rock into the environment faster altered the global phosphorus cycle by mobilizing four times the natural level of phosphorus from phosphate rock into the environment (Alewell et al., 2020). This has not only contaminated many of the world's freshwater bodies and oceans but also created human dependence on a single non-renewable resource and contributed to widespread nutrient pollution of many of the world's lakes, rivers, and oceans. Additionally, the depletion of this finite resource, which took tens of millions of years to form, is a concern (Filippelli, 2008; World Resources Institute, 2008).

Chemist and science writer Isaac Asimov described phosphorus as "the bottleneck of life" and warned 30 years ago: "Perhaps we can replace coal with nuclear energy, wood with plastics, meat with yeast and isolation for friendship, but for phosphorus, there is no substitute or replacement" (Asimov, 1974).

Achieving global food security means ensuring that food is available, accessible, and nutritious for all people at all times (FAO, 2023). However, this is likely one of the most significant challenges of the 21st century. At the same time, food demand is expected to double to feed 9 billion mouths by 2050 (Roser and Richie, 2023). Many of the essential resources that support food production are increasingly scarce. Food can only be produced with access to water, energy, land, and nutrients. However, unlike water scarcity, energy limitation, and nitrogen management, soil loss through erosion and dwindling phosphorus availability represent one of the most significant regional and global challenges to sustaining food production (Alewell et al., 2020).

Phosphorus remains essential in food production. Thanks to phosphate fertilizers, crop yields have increased in the last 50 years and contributed to the world population (Cordell and White, 2011).

The significance of phosphorus in crop growth was established as far back as 1840 by Liebig, who identified phosphorus as the limiting nutrient in plant growth, which led to the collection and grinding of bones for their high phosphate value and the discovery of guano as another phosphate source (Salgado Garcia et al., 2012). Large deposits of phosphate-rich rocks were also found in the United States, which could be easily mined for their fertilizer value (PotashCorp, 2011). Historically, crop production relied on natural soil phosphorus levels, supplemented by organic sources such as manure, crop residues, and human excrement (Timsina, 2018). The post-World War II era, marked by population growth, hunger, and urbanization, spurred the Green Revolution to increase crop productivity through new crop varieties and synthetic fertilizers (John and Babu, 2021). Phosphate rock extraction increased rapidly to keep up with nitrogen production through the Haber-Bosch process (FAO, 2022).

Currently, commercial fertilizers are multiple and could be found as simple fertilizers when only a single nutrient is present, such as superphosphate or triple super phosphate, such as urea or ammonium sulfate for simple nitrogen fertilizers, while ammonium phosphate (MAP), ammonium diphosphate (DAP), nitro phosphate (NP) and NPK, among other fertilizers, those that contain more of an essential nutrient. Improving agricultural productivity to guarantee food security is a cause for concern since it will undoubtedly require adequate raw materials to produce these essential nutrients, including P (Castro and Melgar, 2005).

Fertilizer production primarily comes from nonrenewable sources and is generated through chemical synthesis reactions. These reactions produce intermediate products of broad commercial value for other industries and mineral salts in solid or liquid form (IFDC and UNIDO, 1979). The primary raw material for producing phosphate fertilizers is phosphate rock, a mineral extracted from the ground (Geissler et al., 2018). Phosphate or phosphate rock is treated with sulfuric acid to produce phosphoric acid, which is then concentrated or mixed with ammonia to create a variety of phosphate fertilizers (P_2O_5). It may also be treated with other inorganic acids (nitric or hydrochloric) or organic acids (citric) to generate other phospho-nitrogen compounds, such as MAP and DAP, and potassium salts to form complex NPK mixtures. Potassium fertilizers, conversely, come from treating mineral rocks in the soil and reusing ashes and organic waste. Through several chemical processes, the potash rock and these materials are converted into plant food, obtaining potassium chloride, sulfate, and nitrate salts (Fertilizers Europe, 2023).

Challenges in phosphorus plant availability

Plants absorb phosphorus in the orthophosphate (Pi) forms $H_2PO_4^-$ and HPO_4^{2-}, found in soil solutions at deficient concentrations of 0.1–10 μM (Hinsinger, 2001). An optimal pH for absorption of Pi of 4.5 to 5.0 indicates a preferential uptake of $H_2PO_4^-$ by the plant over HPO_4^{2-} (Raghothama, 1999). The soil solution P concentration gradient for plant cells exceeds 2000 times, with an average inorganic phosphate (Pi) concentration of 1 μM in the soil solution (Bieleski, 1973). This concentration is well below the K_m of plant uptake. Therefore, although bound P is relatively abundant in many soils, it is largely unavailable for uptake. As such, P is frequently the most limiting element for plant growth and development. Crop yields, which are between 30 % and 40 % of the arable land in the world, are limited by the availability of P (Schachtman et al., 1998).

Although the total P content of soil generally ranges from 500 to 2000 ppm, the total bioavailable P, measured by soil extractors, maybe only a few ppm (Sanyal and DeDatta, 1991). Up to half of soil P can be organic, derived from plant residues and soil organisms, where the utilization of organic P by plants and microorganisms requires the mineralization (hydrolysis) of substrates by phosphatase enzymes that can be of plant or microbial origin. This increases phosphatase activity in response to P deficiency as part of P deficiency responses (Horst et al., 2001). In plants, this includes the release from roots of extracellular phosphatases that are considered necessary to capture and recycle organic P lost from roots or to allow greater access to soil organic P (Richardson et al., 2005). In response to P deficiency, increased phosphatase activity in the rhizosphere has been observed in many plant species. It is commonly reported to be higher in P-deficient soils (Richardson and Simpson, 2011).

Although P is an essential nutrient, plants only absorb a small fraction, estimated at 20 to 25 % of the P fertilizer applied to a crop. There has been a long-held view that any P residue is fixed in the soil and is unavailable for use by following crops (Johnston et al., 2014). Additionally, phosphorus is unavailable because it rapidly forms insoluble complexes with cations, particularly aluminum and iron, under acidic conditions. For example, since the 1980s, it has been documented that eroded, acidic soils in the tropics and subtropics are particularly prone to P deficiency (Sanchez and Uehara, 1980). This is where applying fertilizers containing P intervenes as the recommended treatment to improve the availability of P in the soil and stimulate crop yields (Vance et al., 2003).

However, applying phosphate fertilizers presents environmental challenges for both intensive and extensive agriculture in developed and developing countries. Because, in intensive agriculture, to obtain a corn yield of 6 to 9 t ha^{-1}, an absorption of 30 to 50 kg P ha^{-1} is required (Ellington, 1999; Vance, 2001; Johnston, 2002), of which approximately two-thirds are removed in the harvested portion of the harvest. Small grains yielding 3 t ha^{-1} again absorb between 15 and 22 kg P ha^{-1} with a removal rate of 70 %. For example, soybeans absorb 20 to 25 kg of P ha^{-1}, and 80 to 100 % is removed in the harvested portion (Johnston, 2002). However, as already mentioned, even with adequate P fertilization, only 20 % or less of the applied P is removed during the first year's growth due to soil retention (Russell, 1973).

Phosphate rock and apatite minerals as a phosphorus reserve

Reserves of mineral phosphorus in nature are found geologically in sedimentary rocks of apatite, which is the primary source of phosphorus and phosphate and is essential in manufacturing phosphoric acid and mineral fertilizers (Van Kauwenbergh, 2010). Some of them like carbonate apatite and igneous rocks fluoro-chloro-hydroxy-apatite formed by fire (Hughes and Rakovan, 2015). Apatite is part of a substitutional solid solution, in which atoms of approximately the same size replace the original atoms of the crystal lattice. The general composition of apatite is expressed as $A(_5XO_4)_3Zq$, and various elements can be substituted for A, X, and Z (Kono et al., 2022). Hughes and Rakovar (2015) presented the diversity of the variations in the chemical composition of apatite. Pan and Fleet (2002), investigated minerals included in the apatite group and synthetic apatite and summarized their elemental substitutions (Fig. 1), including 53 elements, about half the 109 elements in the periodic table, that can be substituted in the apatite crystal structure. For example, in the apatite series, $Ca_5(PO_4)_3$(F, OH, and Cl), the apices of the compositional triangle can be represented by F, OH, and Cl, respectively, making A = Fluorapatite, B = Hydroxylapatite, and C = Chlorapatite." (Fig. 1). According to Kono et al., 2022, these are a group of mineral phosphates whose approximate chemical composition is $Ca_5(PO_4)_3$ (F, Cl, OH). Depending on the anion that predominates in the second part of the formula, three species are considered: fluorapatite ($Ca_5(PO_4)_3$ F), which is the main mineral of tooth enamel; chlorapatite ($Ca_5(PO_4)_3$ Cl) and hydroxyapatite ($Ca_5(PO_4)_3$ OH) the main mineral of bones. For instance, in the OH–F series, hydroxyapatite includes all combinations in the composition range of $Ca_{10}(PO_4)_6(OH)_2$ to $Ca_{10}(PO_4)_6$ (OH, F)$_2$. The color of the rock is variable, although colorless, white, yellow, and rarely brownish or greenish specimens predominate; they are also frequently found in hexagonal crystals (White and Dong, 2003).

Notably, 90 % of phosphate rock (PR) is used for food production: 82 % for fertilizers, 5 % for feed, and between 2 % and 3 % for food additives (Castro and Melgar, 2005). However, phosphorus resources are unevenly distributed globally: more than 95 % of P rock is found in 10 countries (Morocco and Western Sahara alone control 75 % of global reserves), and 6 % in China (Roy et al., 2022; Kiani, 2023). However, the accelerated flow of phosphate rock from the Earth's crust for fertilizer use has been both a blessing and a curse for food security and the environment, increasing crop yields while also leading to widespread water contamination and creating a precarious dependence of the world's food systems on a single source of phosphorus (Cordell and White, 2014).

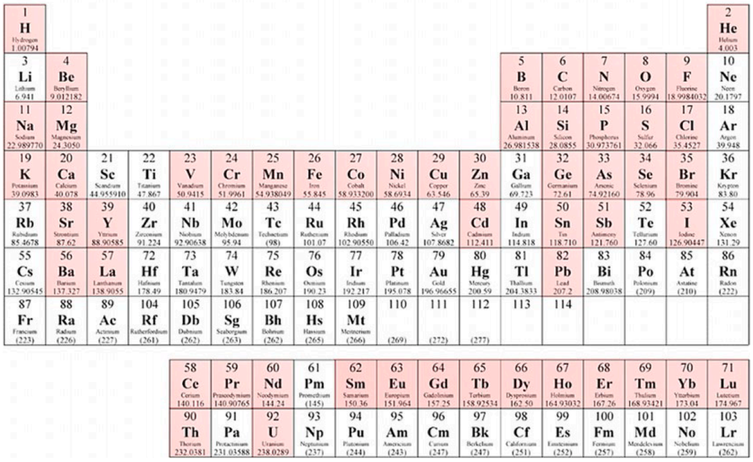
The environmental cost of phosphorus mismanagement

It is worth mentioning that P, like nitrogen, is a pnictogenous element due to its electronic configuration in the outer layer, and this strongly affects its chemodynamic behavior. Unlike N, P^{5+} oxides in the highest oxidation state tend to be highly insoluble with metal ions (especially Mg^{2+} and Ca^{2+}), which are the most abundant in the Earth's crust and when combined with trivalent ions. Such as $Fe^{3+}$and Al^{3+}. The forms of inorganic P include precipitated P-containing minerals, defined as minerals that contain P as a structural element, such as apatites, strange, and variscite, which are very stable, and their solubility depends on the pH of the soil (Jusino- Maldonado et al., 2022).

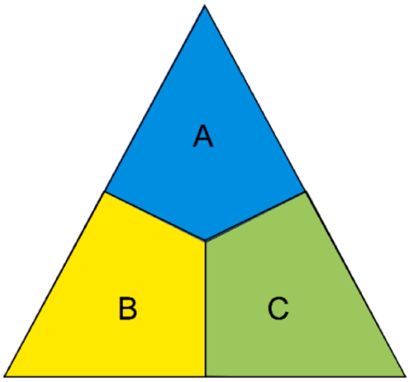
Meanwhile, the secondary forms are adsorbed or bound P, such as minerals that absorb P, mainly Al, Ca, and Fe (El Bamiki et al., 2021). This is the fate of many phosphate fertilizers, including diammonium phosphate, mono ammonium phosphate, triple superphosphate, and single superphosphate (amounting to about 16.5 ± 3 Mt $year^{-1}$ P), which are marketed worldwide and are applied to agricultural fields and pastures around the world (Alewell et al.,2020). However, plant roots absorb only 15–30 % of the annually applied phosphorus in fertilizers (in addition to residual soil phosphorus), which subsequently dissolves into the soil solution (Zhao et al., 2021).

That is why phosphorus in soil exists in different chemical forms, whether organic or inorganic (Pi). In addition to the readily available P fraction that phosphate fertilizers can significantly provide, the activities of both roots and associated microorganisms also contribute to improving P availability in the rhizosphere soil (Richardson and Simpson, 2011). However, these advantages are coupled at a significant cost. Mobilizing phosphate rock into the environment much faster alters the global phosphorus cycle by mobilizing four times the natural phosphorus level from phosphate rock to the environment (Tian et al., 2021).

Phosphorus enters the livestock sector through feed, forage,



a) Periodic table of the elements that occur in apatite minerals.



b) Diagrammatic representation of a complete ternary solid-solution series.

Fig 1. Periodic table of the elements that occur in apatite minerals and Diagrammatic representation of a complete ternary solid-solution series. a) The elements present in apatite supergroup minerals in the range of ppm to several tenths' percent of total weight. The relevant elements are shown in red. This figure was prepared by Hughes and Rakovan (2015) based on the data from Pan and Fleet (2002). b) Diagrammatic representation of a complete ternary solid-solution series. A, B, and C represent the three compositional fields that merit a mineral name. Considering apatite as an example, the three vertices (A, B, and C) representing fluorapatite, hydroxyapatite, and chlorapatite, respectively. Then by the 50 % rule, in the OH-F system, the components of $Ca_{10}(PO_4)_6(OH)_2$ to $Ca_{10}(PO_4)_6(OH, F)$ are called hydroxyapatite (Kono et al. 2022).

supplements, fertilized pastures, or natural grasslands. Once phosphorus is consumed, it leaves the world's feedlots, pastures, and grasslands as animal products, and the rest ends up in manure and eroded soils (Zhao et al., 2021). Manure alone is estimated to contain about 16 ± 1 Mt year^{-1} of P from the world's 63 billion livestock. Half of this is productively reused in agricultural or grassland soils, while the other half is estimated to be lost to non-agricultural soils or water. Approximately 11 Mt of P is absorbed by crops and grasslands each year, while an estimated 12 Mt of P is added to soil reserves yearly. About 5 ± 3 Mt year^{-1} of soil P is exported through wind and water erosion from fields to water bodies and non-agricultural soils (Alewell et al., 2020). Other, more conservative estimates speak of a loss of up to 4–6 Mt P year^{-1} reaching the soil to the oceans (Filippeli, 2008).

Some authors estimate that human intervention in the global phosphorus cycle has mobilized an additional 22 Mt year^{-1} of P to enter the ocean, contributing to 50 % of its loss beyond the natural cycle (Alewell et al., 2020). This intervention leads to excess nutrients in freshwater and oceans, causing eutrophication. This process can lead to excessive growth of toxic algal blooms, with severe consequences for aquatic ecosystems, water quality, and recreation (McMahon and Read, 2013). The adverse effects of eutrophication cannot be overstated, making it a critical issue to address.

Sustainable opportunities for phosphorus management

A deficiency in phosphorus can lead to reduced crop yields, which poses a significant threat to food security. It is estimated that by 2050, more than 5.7 billion people could face phosphorus scarcity (White et al., 2010). Addressing this issue requires efficient cultivation and storage practices, as well as maintaining a consistent supply of organic phosphorus from soil macromolecules. The historical addition of phosphate to soils through mining activities during the 19th and 20th centuries raises environmental concerns, including soil degradation and water pollution (Elrys et al., 2021; Nedelciu et al., 2020). Proper management of phosphorus resources is crucial to minimizing these environmental risks while ensuring sustainable agricultural productivity.

However, organic matter contains about 80 % of total soil P and is the important reservoir of soil P, although it is often primarily unavailable to plants. A similar situation prevails in the rhizosphere, which is the proximity of plant roots (Senesi and Loffredo, 2018). However, one of the many exciting microorganisms living in the rhizosphere is a soil bacterium called *Pseudomonas*. Like many other representatives of this genus, *Pseudomonas fluorescens* are motile and possess a polar flagellum (Yanes and Bajsa, 2016). These organisms contain the enzyme phosphatase, responsible for the microbial solubilization of inorganic P. These bacteria are PSMs, and because of their rhizosphere location in soil, *Pseudomonas* species are candidates for exploitation in sustainable agriculture (Kögel-Knabner and Amelung, 2021; Witzgall et al., 2021).

Microbial phosphorus solubilization

To increase the agronomic efficiency of PR, the use of agriculturally essential microorganisms involved in the P cycle is a promising biotechnological strategy that has gained global interest in recent decades. In early studies, PSMs were defined as microbes that transform insoluble Pi and Po into soluble P forms and regulate the biogeochemical cycle of P in agroecosystems (Halder and Chakrabartty, 1993; Sperber, 1957). Among the heterogeneously distributed soil microflora, a large number of heterotrophic and autotrophic microorganisms are commonly found, including phosphate-solubilizing bacteria (PSB), phosphate-solubilizing fungi (PSF), phosphate-solubilizing actinomycetes (PSA), and cyanobacteria (Turan et al., 2006; Zaidi et al., 2010; Maharana et al., 2021). PSBs, such as *Bacillus sp.*, *Pseudomonas* sp., *Rhizobium sp.*, and *Escherichia sp.*, among many others, form the largest microbial communities with P solubilization capacity in soil (Tian et al., 2021).

Microorganisms solubilize phosphorus through several mechanisms, including organic acids, enzyme production, siderophore synthesis, and microbial respiration. Organic acids help dissolve phosphorus by acidifying the rhizosphere, while enzymes like phosphatases convert organic phosphorus into soluble forms. Siderophores chelate metal cations, aiding phosphorus release and enhancing efficiency (Table 1). Acid phosphatases are more effective in acids soils, while alkaline phosphatases function optimally in basic soil conditions.

The biological solubilization process of PR is significantly influenced by the microbial production of organic acids, which play a crucial role in chelating the cations (mainly calcium) bound to the phosphate (Fig 1).

Table 1
Biotechnological strategies and applications of microbial phosphorus solubilization.

Organism	Mechanism	Application	Reference
Rhizobium sp.	Production of 2-keto gluconic acid	Solubilization of hydroxyapatite	Halder et al. (1993)
Aspergillus niger and Penicillium sp.	Phytases and acid phosphatases.	Rock phosphate solubilization	Saber et al. (2009)
Aspergillus niger	Production of oxalic acid	Rock phosphate solubilization	Schneider et al. (2010)
Bacillus sp.	Gluconic, lactic, acetic, succinic and propionic acid.	Solubilization of ash, bones, fish bones, and phosphate rock.	Saeid et al. (2018)
Aspergillus niger Trichoderma reesei	Phytases and phosphatases	Chemical industry, biofuels, and animal nutrition.	Ribeiro Corrêa and Fernandes de Araújo (2020)
Burkholderia sp., and *Rahnella* sp.	Solubilization by organic acids.	Endophytes of *Populus trichocarpa*	Varga et al. (2020)
Burkholderia sp., and *Paraburkholderia* sp.	Production of organic acids and siderophores.	Plant growth promotion in *Zea mays* L.	Barrera-Galicia et al. (2021)
Pleurotus ostreatus	Tartaric, malic, citric, lactic, and succinic acid.	Rock phosphate solubilization	Maharana et al. (2021)
Penicillium sp.	pH reduction by organic acids.	Phosphate chelation of heavy metals	Eigbike and Salihu (2023)

Several studies have shed light on the efficiency of these compounds, with oxalic acid being the most effective, followed by citric, malic, itaconic, and gluconic acids. For instance, using the phosphate rock called apatite [$Ca_5(PO_4)_3(OH, F, Cl)$], for every mmol of oxalic acid, 21 mg of phosphorus were released, while sulfuric acid solubilized 14 mg of phosphorus (de Oliveira Mendes et al., 2020).

Schneider et al. (2010) reported that after the solubilization of PR by *Aspergillus niger*, all oxalic acid produced precipitated as calcium oxalate crystals. Therefore, the formation of calcium oxalate contributes to the solubilization of apatite by removing Ca^{2+} from the solution and by ligand exchange reactions at the mineral surface (Kaleeswari and Subramanian, 2001; Robinson et al., 1992; Stumm, 1986; Welch et al., 2002).

Microbial respiration and the release of CO_2 can contribute to phosphorus solubilization. The increase in CO_2 concentration in the rhizosphere leads to the formation of carbonic acid, which further contributes to the acidification of the soil and promotes the dissolution of calcium phosphate (Rawat et al., 2021).

Many experimental studies have proved synergies can occur when combining PSB and PR, likely leading to cost-effective P-based microbial inoculants directly applicable to acidic or alkaline soils (Richardson and Simpson, 2011). For example, the dual application of PR and PSB (such as *Azotobacter, Azosporillum, Rhizobium*, and *Klebsiella*) significantly improved the P nutrition of both cereal and legume plants (Tomer et al., 2016). Moreover, the extracellular exudation of enzymes into the rhizosphere, either by roots or associated microorganisms, are additional mechanisms that contribute significantly to improving P availability (Rawat et al., 2021), with acid phosphatases being the most P-hydrolyzing enzymes, abundantly produced under low P conditions (Vance et al., 2003).

This comprehensive set of mechanisms highlights how microbial activity is critical in making phosphorus more available to plants, thus supporting sustainable nutrient management in agriculture.

Microbial enzymes for phosphorus solubilization

Phytase enzymes (myoinositol hexakisphosphate phosphohydrolases) are phosphatases that hydrolyze phytic acid (phytates), preferably to Myo-inositol and six inorganic phosphors. Still, releasing mono, di, tri, tetra, or penta phosphate intermediates is possible when hydrolysis occurs (Ribeiro Corrêa and Fernandes de Araújo, 2020). Phytases can be classified based on the attack on the carbon molecule present in phytic acid, pH optima, or catalysis and structural information (Singh et al., 2020). Based on catalysis and structural information, Mullaney and Ullah, in 2003, classified phytases into histidine, acidic phosphatases, purple acid phosphatases, and β-helix-propeller phytases (BPPs alkaline phytases) according to their catalytic domains. Subsequently, Chu et al. (2004) reported isolating and characterizing a cysteine phytase from a bacteria found in the bovine rumen. The dependence of all living organisms on Pi has led nature to develop many types of catalytic mechanisms to split phytic acid into Pi (Mullaney, 2007). Generally, phytases are grouped into four different groups phytases and three classes, namely histidine acid phosphatases, cysteine phytase, and β-propeller phytase, have been reported as being of microbial origin (Singh et al., 2020). Animals, plants, and microorganisms ubiquitously produce these enzymes and generally exhibit optimal activity at pH and temperature of 4.5 to 6.0 and 45 to 60 °C, respectively, with an acid isoelectric point, the molecular weight of around 40 to 70 kDa and monomeric state (Ribeiro Corrêa and Fernandes de Araújo, 2020).

Phytates are abundantly present in the soil in the form of organic P. However, they are relatively unavailable to plants because plants have no phytase activity in their root systems. Therefore, the ability of plants to uptake phytate-P from soils would be improved by direct supplementation of a phytase enzyme or by inoculation with a microbial strain that can release phytase (Singh et al., 2020).

For example, phytase activity was recently recorded in two bacterial enzymes of the metallo-β-lactamase family, expanding the phosphatase activity to other proteins (Castillo Villamizar et al., 2019). PAHs are recognized as "fungal phytases," such as those present in *Aspergillus niger*. However, they are also present in bacteria, yeasts, and plants (Ribeiro Corrêa and Fernandes de Araújo, 2020). Most research has focused on the application of phytases in animal nutrition. Phytases represent 60 % of the feed enzyme market, equivalent to $350 million annually. Moreover, about 70 % of feeds contain phytase as an additive (Gontia et al., 2012).

While phytase is widely recognized for its ability to break down phytic acid, other enzymes such as phosphatases, carbon-phosphorus lyases, and d-glycerophosphatases also significantly contribute to phosphorus cycling. Phosphatases catalyze the hydrolysis of organic phosphorus compounds. Phosphatases are classified into two main categories based on their optimal pH: acid and alkaline phosphatases. Acid phosphatases are commonly found in fungi and certain bacteria and are produced in the phloem, cortex, epidermis, and roots of plants. In contrast, alkaline phosphatases are prevalent in a variety of microbial species and are active in basic soil with a pH $>$ 7 (Campdelacreu Rocabruna et al., 2024). Carbon-phosphorus lyases cleave the strong carbon-phosphorus bonds in organophosphonates. This enzyme system is especially relevant in agricultural soils with high organophosphonate content, as it enables microorganisms to access phosphorus from these compounds (Silva et al., 2023). d-glycerophosphatase assists in the mineralization of glycerophosphate, which is a low molecular weight form of organic phosphorus (Turner et al., 2005).

These enzymatic activities collectively enhance the availability of phosphorus for plant growth, reduce the reliance on chemical fertilizers, and promote sustainable agricultural practices, highlighting the importance of microbial enzymes in nutrient management and soil fertility.

Development of inoculants for sustainable use of phosphorus

Ecological consideration should be taken as a starting point to create innovative fertilization strategies in which both environmental and biological processes (such as, specific nutrient interactions in the rhizosphere and plants, soil and plant microbiomes, etc.), and technologies can be combined, exploited through concerted research and development efforts to achieve the goal of sustainable agricultural production (Fig. 2). Solubilization of phosphate rock by microorganisms is an environmentally sustainable alternative to chemical processing for the production of phosphate fertilizers (Rawat et al., 2021). In some studies, it has been seen that the interaction of PSMs (*Pseudomonas, Mycobacterium, Bacillus, Pantoea, Rhizobia,* and *Burkholderia*) and phosphate fertilizers improved wheat grain yield (22 %) and phosphorus absorption (26 %) by the time that reduced the fertilizer contribution by 30 % (from 120 to 90 kg P_2O_5 ha^{-1}). Moreover, these microbial inoculants are safe and non-toxic to the environment.

Batch solids addition achieves an effective solubilization activation strategy that is very promising compared to the results reported elsewhere for similar conventional and PR processes (igneous origin). Saber et al. (2009) cultivated *A. niger* under SmC using a similar igneous PR (fluorapatite rock from Giza, Egypt) and obtained 99.7 mg L^{-1} soluble phosphorus after 216 h Under similar conditions, Schneider et al., 2010 obtained 281 mg l^{-1} of soluble phosphorus after 192 h of cultivation using hydroxyapatite rock from Catalão, Brazil. De Oliveira Mendes et al., 2020, also grew *A. niger* under SmC using Araxá rock from Brazil, and obtained 74.4 mg l^{-1} of soluble phosphorus after 144 h In this work, the maximum soluble P concentration obtained was approximately 350 mg L^{-1} after a processing time of only 120 h (Klaic et al., 2021).

In addition to the use of PSMs for nutritional purposes, some of these microorganisms have been described to promote plant growth; some of the most interesting are those belonging to *Burkholderia* sensu lato, which are rhizosphere bacteria of corn, which also have an effect of biocontrol, mediating the suppression of rot caused by *Fusarium* spp., in the roots of corn (Barrera-Galicia et al., 2021). Among the most exciting strains, those of the *Paraburkolderia* genus stand out, such as *P. kisternboschensis, P. graminis,* and *P. rhynchosiae* with phosphorus solubilization activities (399, 415, and 475 mg l^{-1} of P, respectively), these bacteria are capable of growing using an insoluble phosphate source (Fig. 3). Likewise, some other activities have been determined, such as nitrogen fixation through the acetylene reduction test,

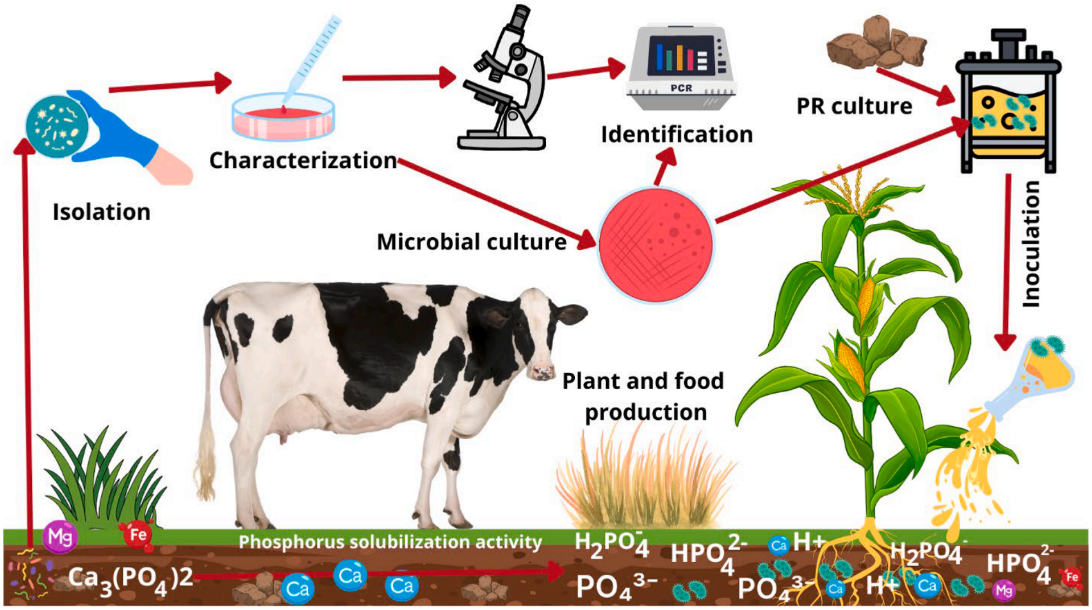


Fig. 2. Development process of microbial inoculants for the use of phosphate rock as a sustainable agricultural production strategy. The red arrows indicate the steps to follow; however, they are only representative since the methodologies used vary depending on the available resources and the advancement of microbiological characterization techniques. The solubility of phosphorus carried out by soil microbes may be mediated by the release of organic acids, production of enzymes, or acidification mechanisms (release of protons) that facilitate the absorption of phosphate available (HPO_4^{2-}, PO_4^{3-}, H_2PO^{4-}) for plants (Raymond et al., 2021). In this work, we also propose evaluating and measuring phosphorus solubility based on microbial activity and considering the biosafety of the inoculant.

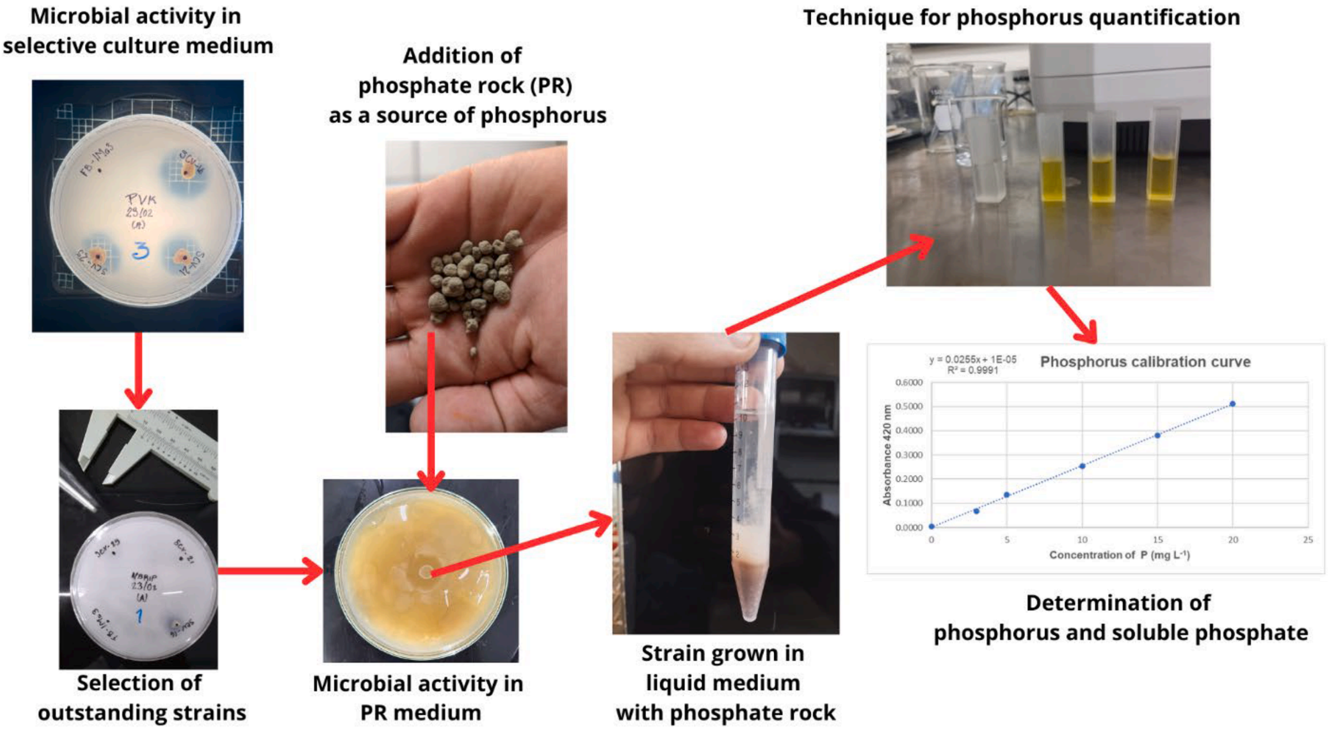


Fig. 3. Technique for the microbial solubilization activity of phosphoric rock. The red arrows describe the research process implemented in our laboratory to develop a methodology for evaluating, characterizing, and measuring microbial solubilization activity. In this example, the phosphorus source used is commercial phosphate rock; however, other sources of phosphorus can be implemented. Phosphorus includes dicalcium, tricalcium phosphate, magnesium phosphate, apatite, and other sources of insoluble phosphorus. Also, organic and inorganic acids are used to quantify the soluble phosphorus of different arrays.

production of siderophores, and generation of exopolysaccharides (Barrera-Galicia, 2023). Plant Growth Promoting Microorganisms (PGPMs) change the pH of the soil to solubilize inorganic phosphates. In alkaline soils, pH is reduced due to the excretion of organic acids, such as gluconate, citrate, lactate, and succinate, solubilizing $Ca_3(PO_4)_2$. Moreover, in acidic soils, MPCV increases the production of protons during the assimilation of ammonium (NH_4^+), solubilizing $AlPO_4$ and $FePO_4$ (Martínez-Viveros et al., 2010).

Carrier materials play a vital role in the effectiveness of the bacterial formulation. The main properties of a suitable carrier are (i) non-toxicity to microbes, (ii) good exchange surface, (iii) ease of both sterilization and processing, (iv) availability in large quantities, renewable and economical, and (v) non-toxic to plants, human health, and the environment (Reddy, 2014).

Liquid bioformulations offer numerous advantages over traditional solid bioformulations, including extended shelf life, higher microbial viability, reduced risk of contamination, and enhanced field performance (Yafetto, 2022). These benefits have driven a surge in interest from companies worldwide, positioning liquid microbial inoculants as the next generation of sustainable agricultural inputs. In countries like Japan and the United States, companies are actively producing and utilizing microbial inoculants with *Rhizobium* spp. as inoculants for a variety of crops, including lentils, soybeans, corn, sorghum, sugar beets, wheat, and canola (Yafetto et al., 2023).

Since the early 2000s, research interest in these microorganisms has significantly grown, reflecting their role in sustainable agriculture and mitigating phosphorus scarcity. Among the leading contributors to research output, India stands out with 542 published papers, followed by China (336), Brazil (225), Pakistan (217), and the United States (158). Collectively, these five countries account for 52.6 % of the total research publications, highlighting their major contributions to this field, likely driven by their vast agricultural sectors and significant demand for phosphorus-based fertilizers (Ramos Cabrera et al., 2024).

Recent advances in microbial engineering for phosphorus solubilization

Microbial engineering has emerged as a promising field to enhance phosphorus solubilization, facilitating a transition to sustainable agricultural practices. Recent advancements have primarily focused on genetic modifications that improve the efficiency of microorganisms in mobilizing phosphorus from insoluble sources. These engineered microorganisms are crucial for increasing nutrient availability and boosting crop productivity. One of the most prominent advances has been engineering microbial strains, particularly those of *Pseudomonas, Bacillus*, and *Rhizobium*, to overproduce organic acids such as citric and gluconic acids. These acids play a critical role in solubilizing calcium-bound phosphates in the soil. Genetic modification has been employed to enhance metabolic pathways responsible for organic acid production, increasing the overall efficiency of phosphorus release. These engineered strains demonstrate a higher capacity for making phosphorus bioavailable to plants under various soil conditions (Ke et al., 2021; Singh et al., 2024; Xu et al., 2020).

The application of CRISPR-Cas9 technology has allowed for precise editing of genes involved in phosphorus solubilization. Researchers have targeted specific genes that regulate phosphate transport systems and organic acid production. By fine-tuning these genes, engineered bacteria can produce more effective enzymes and acids, optimizing phosphorus solubilization without negatively impacting other microbial functions (Fazeli-Nasab and Rahmani, 2021; Malik et al., 2024; Singh et al., 2024). This approach has enabled the creation of microbial strains tailored to different soil types and agricultural needs.

Advances in synthetic biology have facilitated the design of microbial consortia where different strains are engineered to cooperate synergistically, enhancing phosphorus solubilization efficiency. For example, recent studies have successfully engineered a straw-degrading bacterium that solubilizes phosphorus simultaneously. Such microbial consortia leverage complementary mechanisms—including acid production, enzyme secretion, and phosphorus uptake—creating a multifaceted approach to phosphorus bioavailability (Che et al., 2024; El Maaloum et al., 2020; Emami et al., 2020). Beyond improving organic acid production, enzyme engineering has also played a vital role in recent advances. Phosphatases, phytases, and other enzymes key to phosphorus mineralization have been genetically enhanced to be more stable under various environmental conditions, including extreme pH and temperature. When expressed by soil microorganisms, these engineered enzymes significantly increase the phosphorus solubilization rate, thereby improving plant nutrient uptake (Li et al., 2024; Timofeeva et al., 2022). Another recent development involves modifying quorum sensing mechanisms in phosphorus-solubilizing microorganisms (PSMs). Quorum sensing, a process by which bacteria communicate based on population density, is crucial for coordinating enzyme secretion and organic acid production. Researchers have successfully engineered PSMs to either overexpress or inhibit specific quorum sensing pathways, ensuring a more controlled and efficient phosphorus solubilization process (Lucero et al., 2023; Zhang et al., 2023).

Conclusion

Phosphorus is indispensable for plant nutrition and agricultural productivity, yet its availability in the soil presents a significant challenge due to its tendency to bind with other elements and form insoluble compounds. Conventional practices, such as the excessive application of chemical phosphorus fertilizers, have led to severe environmental consequences, including water pollution and soil degradation. The global dependency on finite phosphate rock reserves further exacerbates the need for sustainable alternatives in phosphorus management.

Microbial phosphorus solubilization offers a promising solution to these challenges. PSMs and their enzymes can mobilize phosphorus from insoluble sources through various mechanisms, such as rhizosphere acidification and phosphatase excretion. This approach supports the development of microbial inoculants for in situ application, enhancing phosphorus uptake by plants. Advances in microbial inoculant development can contribute to sustainable and efficient phosphorus use in agriculture, reducing dependence on chemical fertilizers and minimizing environmental impact.

Advanced sequencing techniques, such as metagenomics and metatranscriptomics, can reveal the diversity of microbial communities capable of phosphorus solubilization and their gene expression under different soil and environmental conditions. This approach would provide insights into understanding the specific genes and molecular pathways involved in phosphorus solubilization, paving the way for targeted interventions (Hu et al., 2023). Future research can also focus on genetically engineering PSMs to enhance their efficiency in solubilizing various insoluble forms of phosphorus (Rawat et al., 2021).

The integration of microbial solutions into phosphorus management offers a pathway to more sustainable agricultural systems, promoting nutrient cycling, soil health, and long-term productivity. However, challenges remain in scaling up microbial technologies and ensuring their effectiveness across diverse agroecosystems. Future research should focus on optimizing microbial inoculants, understanding their interactions in different soil environments, and developing strategies to maximize their potential in sustainability agriculture.

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Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author upon reasonable request.

CRediT authorship contribution statement

José Abraham García-Berumen: Conceptualization, Writing – original draft, writing – review & editing. **Juan Armando Flores de la Torre:** Writing – original draft, writing – review & editing. **Sergio de los Santos-Villalobos:** Writing – original draft, writing – review & editing. **Alejandro Espinoza-Canales:** Writing – original draft, writing – review. **Francisco G. Echavarría-Cháirez:** Writing – original draft, writing – review. **Héctor Gutiérrez-Bañuelos:** Conceptualization, Writing – original draft, writing – review & final editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

No data was used for the research described in the article.

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