agriculture

Review

Phosphorus-Solubilizing Microorganisms: A Key to Sustainable Agriculture

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Abstract: Phosphorus (P) is one of the essential macronutrients for plant growth, being a highly required resource to improve the productive performance of several crops, especially in highly weathered soils. However, a large part of the nutrients applied in the form of fertilizers becomes "inert" in the medium term and cannot be assimilated by plants. Rationalizing the use of phosphorus is a matter of extreme importance for environmental sustainability and socioeconomic development. Therefore, alternatives to the management of this nutrient are needed, and the use of P-solubilizing microorganisms is an option to optimize its use by crops, allowing the exploration of less available fractions of the nutrient in soils and reducing the demand for phosphate fertilizers. The objective of this study is to discuss the importance of phosphorus and how microorganisms can intermediate its sustainable use in agriculture. In this review study, we present several studies about the role of microorganisms as phosphorus mobilizers in the soil. We describe the importance of the nutrient for the plants and the main problems related to the unsustainable exploitation of its natural reserves and the use of chemical fertilizers. Mainly we highlight how microorganisms constitute a fundamental resource for the release of the inert portion of the nutrient, where we describe several mechanisms of solubilization and mineralization. We also discussed the benefits that the inoculation of P-solubilizing microorganisms provides to crops as well as practices of using them as bioinoculants. The use of microorganisms as inoculants is a viable resource for the future of sustainable agriculture, mainly because its application can significantly reduce the application of P and, consequently, reduce the exploitation of phosphorus and its reserves. In addition, new research must be conducted for the development of new technologies, prospecting new biological products, and improvement of management practices that allow for higher efficiency in the use of phosphorus in agriculture.

Keywords: phosphorus mobilization; mineralization; microbial mechanisms; natural resources; sustainable agriculture; plant growth promoting microorganisms

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1. Introduction

Agriculture is fundamental to human beings and the constitution of society [1]. This activity is responsible for the livelihood of about 40% of the global population and one-third of the earth's surface is dedicated to agriculture (excluding frozen areas), which demonstrates the impact and representativeness of this practice globally [2,3].

However, agricultural production depends on resources, one of which is phosphorus (P). This nutrient is essential for plant growth and is a limiting factor for crop yields [4,5]. The use of high-concentration phosphate fertilizers has become a continuous practice that threatens natural resources, especially the natural reserves of high-level phosphate, which are not renewable resources. After the harvest, the phosphorus removed from the soil and retained in agro-industrial residues is unlikely to return to the soil, mainly due to the global aspect of the production chains and the disruption of small local chains, which could facilitate the return and incorporation of this residue to the soil, returning part of the phosphorus applied in the form of mineral fertilizer [6]. In addition, most of the fertilizers applied to the soil become unavailable for assimilation by plants and can even lead to biological imbalances in soil and water [7,8]. In this way, more sustainable alternatives for agriculture should be proposed, considering the problems of modern agricultural systems based on monocultures, the demand for safe food with better socio-environmental quality, and the need to preserve environmental resources for future generations [9].

Many microorganisms have the potential of increasing phosphorus availability in soil. Bacteria, fungi, cyanobacteria, mycorrhizal fungi, and actinobacteria have several mechanisms that allow the mineralization of organic P and the solubilization of part of the inorganic P unavailable to plants [10–12]. Additionally, these microorganisms can promote plant growth by fixing nitrogen, producing phytohormones, supporting nutrient assimilation, and promoting resistance to stress and pathogens. Therefore, they are an interesting alternative to the P supplied in agriculture, as they reduce the demand for phosphate fertilizers while promoting plant growth and productivity [13,14].

This study addresses the importance of phosphorus and its main sources in agriculture, the threats related to phosphorus fertilizers production and application, and the impact of soil microbes on phosphorus availability and related microbial mechanisms. Emphasis is given to how microorganisms can intermediate sustainable alternatives in agriculture, considering the different mechanisms that make possible the bioavailability of the insoluble part of phosphorus, previously not accessible to plants, and their role in promoting the growth of various vegetables. In this way, this study presents a bibliographic review that gathers research about the use of P and the mechanisms and use of phosphate-solubilizing microorganisms.

2. Phosphorus and Phosphate Fertilizers

P is an indispensable nutritional requirement for plants. Although it is not the nutrient most demanded by plants, the amount supplied to crops is high, especially in highly weathered soils, owing to the intensity of the specific adsorption processes of P in abundant soil minerals such as goethite, hematite, and gibbsite. In the plant, P is a constituent of certain sugars, nucleic acids, lipids, and other compounds. In metabolism, it is a mediator of carbohydrate synthesis and acts in the activation and inactivation of enzymes. It also stimulates germination, root growth, flowering, and seed formation [15,16]. It is even involved in energy transfer processes such as photosynthesis and is also a component of molecules such as ATP and GTP [17].

P is described as a limiting factor in plant growth in several studies, where its deprivation triggers cellular and physiological changes [5,18,19]. Meng et al. [20] show that P availability affected the growth of sour pummelo (*Citrus grandis*). Its deficiency limits the accumulation of dry matter in leaves and branches. In addition, the results of this study show that low P also inhibits plant growth, affecting the absorption of other nutrients, decreasing photosynthetic performance, and increasing the production of reactive oxygen species. Therefore, the availability of this nutrient in the soil directly influences crop productivity [21].

In general, P is found in the soil in two forms. The first is the organic form, where its atom is covalently bonded to a carbon, either directly or via phosphodiester bonds [22]. However, it is predominantly found in inorganic forms, including orthophosphate anions in solution, bound in minerals, or adsorbed on mineral surfaces and organic matter [22,23].

As a result of the immobilization of P in different complexes and adsorbents, only approximately 0.1% of it is available for assimilation by plants in the soil [24,25]. Phosphorus dynamics is related to the balance between its organic and inorganic forms in the soil, in addition to the balance of insoluble organic phosphorus and its adsorbed and/or precipitated forms [26]. Several factors can influence this process, such as soil type, management practices, and climate [26]. Globally, two-thirds of soils have limited phosphorus availability, where the low rate of P diffusion in solution and the high rates of specific adsorption in oxidic minerals are the main factors that make phosphorus less accessible to plants and lead to low yield in field conditions [4,23].

According to Sims and Pierzynski [27], several factors of the P cycle affect its solubility and concentration in soil. Among these factors are (1) the sorption–desorption ratio (interaction between P and solid surfaces); (2) mineralization–immobilization (biological conversion of P between organic and inorganic forms), and (3) dissolution–precipitation (related to the mineral balance) [28]. Thus, the P found in soluble form in the soil quickly precipitates with metals, forming insoluble complexes with calcium in alkaline soils, with iron, silicate, and aluminum in acidic soils, or also adsorbing on clay [29–31].

The P demand of crops is often met using fertilizers with relatively elevated levels of P, which may be organic or inorganic. However, the majority of phosphate fertilizers are applied in their inorganic form, that is, approximately 70–80% of the P found in agricultural areas is from this source [32]. Among the various inorganic fertilizers, rock phosphate, nitric phosphates, phosphoric acid, ammonium phosphates, ammonium polyphosphate, and calcium orthophosphates can be mentioned [33].

When applied, the P in the fertilizer is converted into water-soluble forms such as the orthophosphate ions HPO_4^{2-} and $H_2PO_4^{-}$, which are readily assimilable [34,35]. However, a large part of the P once available can be lost due to the speed of the specific adsorption processes, which in the case of phosphorus, have limited reversibility, and can also be lost due to surface runoff and leaching processes [36]. Another process that leads to nutrient loss is erosion, where P bound in organic matter, in mineral particles, or precipitated in poorly soluble salts is lost along with the eroded soil [12,37,38].

In this context, the use of P by crops has an average efficiency between 20% and 25% of the total amount of phosphate fertilizers applied [39,40] and may reach values below 10% in some vegetables under intensive management. Therefore, an excessive amount of P fertilizers is required to increase the phosphorus available and thus increase crop productivity. In terms of comparison, the annual use of phosphate fertilizers increased from 4.6 million tons in 1961 to approximately 21 million in 2015 [41]. This indiscriminate use has adverse effects on the soil, altering its biological, chemical, and physical properties, impacting its quality, and potentially compromising the future of agricultural production [8,19].

The effects of long-term fertilization at high doses were also discussed. Chen et al. [42] studied the effects of excessive phosphorus fertilization on pomelo orchards. The concentrations and relationships between total soil P, quantifiable P, and its fractions (such as organic P, soluble P, and adsorbed P) were examined and the authors observed that in non-cultivated areas the most common form of P is organic, corresponding to 57% in superficial horizons (0–20 cm deep) and 57% in deep horizons (20–40 cm deep). In orchards with cultivation time longer than 10 years, it was noted that there was a P input of 947 kg P_2O_5 ha^{-1} yr^{-1}, an output of 132 kg P_2O_5 ha^{-1} yr^{-1}, and a surplus of 774 kg P_2O_5 ha^{-1} yr^{-1}. The highest proportions of P in surface soils corresponded to Al-P: 39% and Fe–P: 20%, while P-organic represented 19%. In deep horizons, this proportion was Al–P: 43%, Fe–P: 23%, and P–organic 15%. The authors warn about the excessive use of P in agriculture, especially in the conversion of its forms in the soil, since there is a greater loss of this essential nutrient in soils with higher proportions of inorganic forms.

The effect of excess fertilizer on the physical and biological properties of the soil was described by Beauregard et al. [43]. They observed that phosphate fertilization for 8 years in alfalfa (*Medicago sativa*) mono-crop increased the flux and amount of soluble P in the environment, but reduced microbial activity and soil moisture.

Another concern is the exploitation of phosphate rocks, which are raw materials for fertilizer manufacture. According to USGS [44], the world has about 71 billion metric tons (bmt) of phosphate rocks. The phosphate in these rocks can be provided in the form of carbonate apatite $[3Ca_3(PO_4)_2{\cdot}CaCO_3]$, hydroxyapatite $[Ca_{10}(PO_4)_6(OH)_2]$, fluorapatite

[$Ca_{10}(PO_4)_6F_2$], and sulpho-apatite [$3Ca_3(PO_4)_2 \cdot CaSO_4$] [45]. The countries with the largest reserves of this resource are Morocco and Western Sahara (50 bmt), China (3.2 bmt), Egypt (2.8 bmt), Algeria (2.2 bmt), and Brazil (1.6 bmt). In addition, IFASTAT [46] indicates that in 2020 the regions that consumed the most phosphate were: East Asia with 15,112 thousand tons of P_2O_5 (kt P_2O_5), South Asia (11,011 kt P_2O_5), Latin America (8 541 kt P_2O_5), North America (5256 kt P_2O_5), and Western and Central Europe (2992 kt P_2O_5). In 2020, globally there was a consumption of around 48,975 kt P_2O_5.

These numbers point to a very worrying trend regarding the conservation of the natural reserves of phosphate rocks, a non-renewable resource [28,41]. Several studies indicate that we are facing a crisis regarding phosphate sustainability [47–50]. Furthermore, some authors suggest that at this current frequency of consumption, phosphate rock reserves will deplete in the next two centuries. Appalling projections indicate that the end of this resource could even happen in the next 50 years [51,52]; especially, these projections are based on known mines. The remaining potential reserves are of lower quality, with higher exploration costs and less accessibility [53]. Other authors indicate that phosphate reserves will persist into the future, where 40–60% of known resources will still be exploited by 2100 [54,55]. However, amid these contrasting views, there is a certainty that currently the value of phosphate fertilizer commodities is increasing, being consistent with greater economic competitiveness and greater environmental exploitation [56–58].

The accumulation of toxic metals in the environment may be associated with the inadequate application of phosphate fertilizers, as these metals may be present in their source rocks. Li et al. [59] look at the cadmium input in Chinese provinces where in 2016 there was a deposition of 10.52 t. In Brazil, according to estimates by Vieira da Silva et al. [60], 24–30 t of cadmium is deposited annually from phosphate fertilizers. Previous studies also indicated the accumulation of toxic metals in the environment, such as the accumulation of arsenic in groundwater in the state of São Paulo (Brazil) [61].

Therefore, this scenario raises awareness regarding the rational use of phosphate rocks and their impact mitigation in natural and anthropic environments. At the same time, new strategies, methods, and technologies are needed to increase the efficiency of the use and application of fertilizers in crops, taking advantage of every fraction of the nutrient and increasing its assimilation by plants. In this context, phosphate-solubilizing microorganisms are fundamental vectors for the sustainability of modern agriculture.

3. Phosphate-Solubilizing Microorganisms

Phosphate solubilizing microorganisms (PSM) are a group of organisms composed of actinobacteria, bacteria, fungi, arbuscular mycorrhizae, and cyanobacteria capable of hydrolyzing organic and inorganic phosphorus into soluble forms, thus making it bioavailable to plants [12,62]. They are quite abundant in the soil, and commonly associated with the rhizosphere of plants [63]. Djuuna et al. [64] performed a sampling of these microorganisms in Indonesia. Agricultural soils with a relevant history of growing vegetables, cereals, and legumes from different regions were collected. The results showed a population of solubilizing bacteria ranging between 25×10^3 and 550×10^3 CFU g^{-1} of soil and solubilizing fungi between 2.0×10^3 and 5.0×10^3 CFU g^{-1} of soil in all areas examined.

There is also great diversity in PSM. Bacteria have several representatives of the genera *Azospirillum*, *Bacillus*, *Pseudomonas*, *Nitrosomonas*, *Erwinia*, *Serratia*, *Rhizobium*, *Xanthomonas*, *Enterobacter*, and *Pantoea* [12,63]. Among the non-mycorrhizal fungi are the genera *Penicillium*, *Fusarium*, *Aspergillus*, *Alternaria*, *Helminthosporium*, *Arthrobotrys*, and *Trichoderma*, [62,65]. Examples of mycorrhizal fungi are *Rhizophagus irregularis*, *Glomus mossea*, *G. fasciculatum,* and *Entrophospora colombiana* [28,66].

Among actinobacteria, the genera *Streptomyces*, *Thermobifida* and *Micrococcus* are examples of PSM [67–70], and cyanobacteria, *Calothrix braunii*, *Westiellopsis prolifica*, *Anabaena variabilis*, and *Scytonema* sp. [12,63].

4. Phosphate Solubilization Mechanisms

Phosphate-solubilizing microorganisms have several mechanisms to increase the availability of this element in the soil. Figure 1 brings together the mechanisms and processes involved in the nutrient dynamics in the soil and the various interactions with the microbiota. The main roles of microorganisms in P solubilization include (1) the release of extracellular enzymes (biochemical mineralization), (2) the release of P during substrate degradation (biological mineralization), and (3) the secretion of mineral-dissolving complexes or compounds (siderophores, protons, hydroxyl ions, organic acids) [28,71].

Microorganisms interact in diverse ways in terms of the bioavailability of nutrients in plants. Mycorrhizal fungi, for example, can provide an increase in the root surface from the proliferation of their mycelium, helping in the exploitation of nutrients in the soil, thus accessing soil portions, such as microaggregates, previously not accessible to the plant only by root exploration [72,73].

In addition, PSM presents several mechanisms to make phosphate available in its soluble form. When the substrate is organic, the processes are described as mineralization, which is a step in the decomposition process of organic matter, while inorganic substrates undergo solubilization processes [12,28,74].

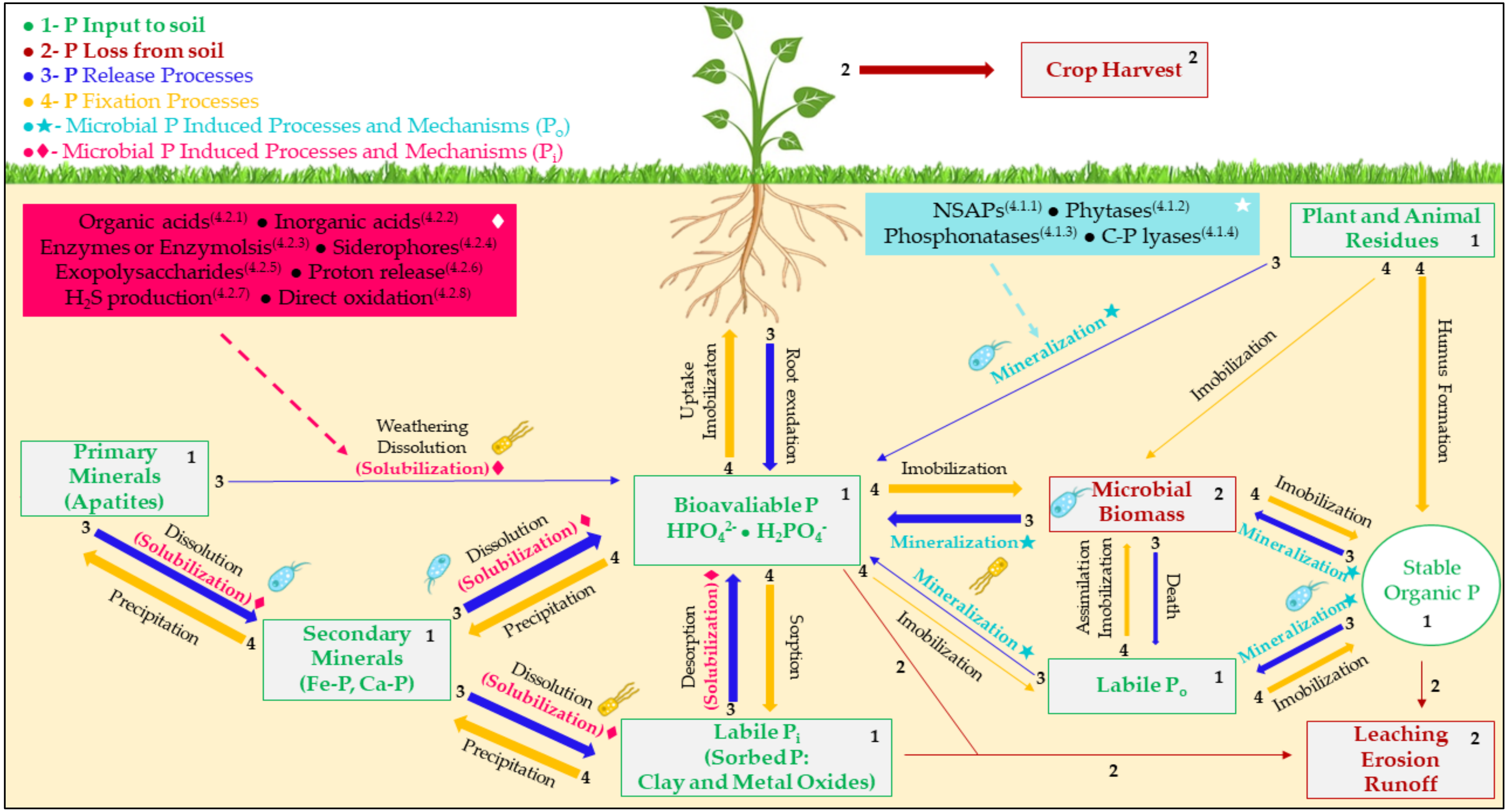

Figure 1. Phosphorus cycle and nutrient mobilization. The numbers and symbols at the base of the arrows are related to the P mobilization process described in the heading of the figure. The numbers related to the mechanisms correspond to the topics in which they are explained. NSAPs (4.1.1), phytases (4.1.2), phosphonatases (4.1.3), C–P lyases (4.1.4), organic acids (4.2.1), inorganic acids (4.2.2), enzymes or enzymolysis (4.2.3), siderophores (4.2.4), exopolysaccharides (4.2.5), proton release (4.2.6), H_2S production (4.2.7), and direct oxidation (4.2.8).

4.1. Organic Phosphate

Organic phosphate corresponds to 20–30% of the total amount found in the soil [28]. Its main source of entry into the environment is biomass, being present in animal and plant debris, and in microbial cell membranes, that is, they constitute biomolecules such as phosphides, nucleotides, phosphoproteins, co-enzymes, sugar phosphates, phosphonates and can be immobilized in the form of humus [75–77]. Figure 2 shows some organic molecules that contain phosphorus in their composition.

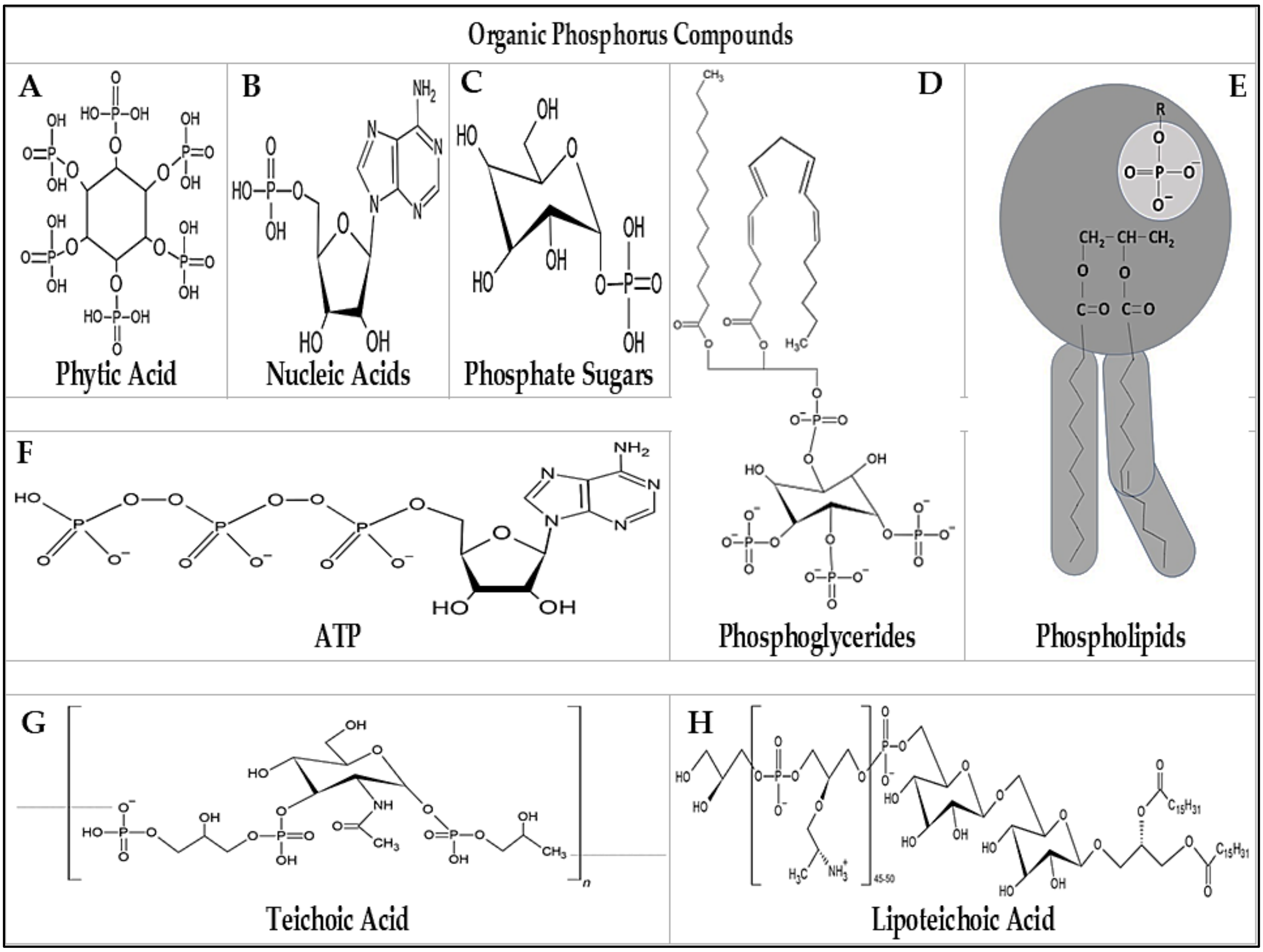

Figure 2. Organic phosphate compounds in the soil. (**A)** phytic acid, (**B**) adenine nucleotide, (**C**) galactose 1-phosphate, (**D**) phosphatidyl inositol 3,4,5-triphosphate, (**E**) phospholipid, (**F**) adenosine 3-phosphate, (**G**) teichoic acid, (**H**) lipoteichoic acid.

4.1.1. Non-Specific Acid Phosphatases (NSAPs)

NSAPs are a class of enzymes bound to the lipoprotein membranes of microorganisms or secreted extracellularly [78,79]. Also known as phosphomonoesterases, they act according to the optimal pH of the environment, and can therefore be acidic or alkaline [80,81]. These enzymes can dephosphorylate a wide variety of phosphoesters (RO–PO_3), solubilizing around 90% of organic phosphate in soils [82,83]. Figure 3 shows how the catalytic reaction of NSAFs occurs.

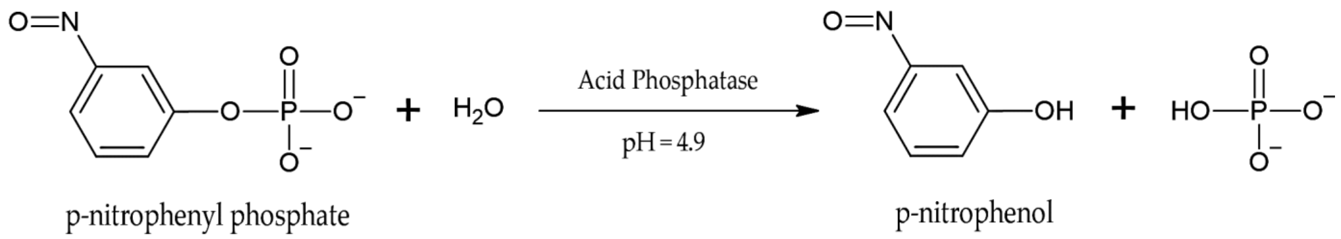

Figure 3. Acid phosphatase catalytic reactions.

The proportion of phosphatases is relative to the abundance of P in the soil and consequently influences the availability of this nutrient to plants. Fraser et al. [84] indicated that in soybean (*Glycine max*) fields labile P in bulk soil was negatively correlated with *phoC* and *phoD* genes abundance (acid and alkaline phosphatase encoders, respectively) and phosphatase activity. According to the authors, the activity of NSAPs is greater in the rhizosphere than in other soil portions. A positive correlation was also observed between phosphatase activity, P uptake by plants, and nodule weight.

4.1.2. Phytases

Phytic acid is the major form of organic P present in the soil and is a component of seeds and pollen [12,85,86]. However, because they form complexes with cations or are adsorbed on various soil organic components, they are not readily available for plant assimilation [12]. Phytase enzymes are phosphatases produced by soil microorganisms. They are capable of hydrolyzing phytic acid by acting on the phosphomonoester bonds present in the compound, originating two subgroups, myo-inositol hexaphosphate or phytate (salt form). This process means that, in addition to P, other nutrients associated with it also become available, such as zinc and iron [87,88]. Figure 4 shows the catalysis of phytases.

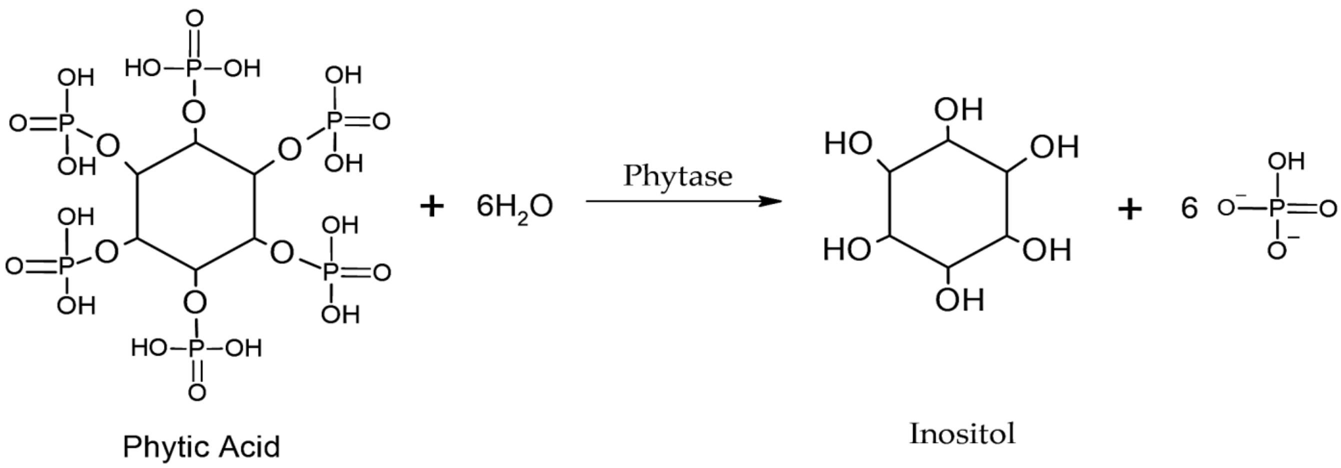

Figure 4. Phytase catalytic reaction.

Wang et al. [89] investigated the effect of mycorrhizal hyphae-mediated phytase activity. Maize (*Zea mays*) cultivars inoculated and non-inoculated with the arbuscular mycorrhizal fungi *Glomus mosseae* or *Claroideoglomus etunicatum* were evaluated, and the plants were separated into two compartments, one with only roots and the other with hyphae of the tested fungi supplemented with different concentrations of calcium phytate. The effect of phytase and acid phosphatase on phytate mineralization was analyzed. The authors observed that at higher phytate addition, the rate decreased, and lower phytate addition caused an increased hyphal length density; phytate addition increased phytase and acid phosphatase activity resulting in greater P uptake and plant biomass. It was concluded that the observed increases in P uptake were primarily due to phytase activity rather than phosphatase activity.

4.1.3. Phosphonatases

Phosphonates are organic phosphoric compounds rich in hydrolytically stable C–P bonds that are chemically inert and resistant to thermal and photolytic decomposition [90,91]. The enzymes that promote the breaking of this bond are known as phosphatases (phosphonate hydrolases) and act by catalyzing this reaction from a group β-carbonyl electron scavenger that allows heterologous cleavage between nutrients [91]. Phosphonatases act on several substrates, including phosphoenolpyruvate, phosphonoacetate, and phosphoenol-acetaldehyde. Figure 5 shows the mechanisms of phosphonatases.

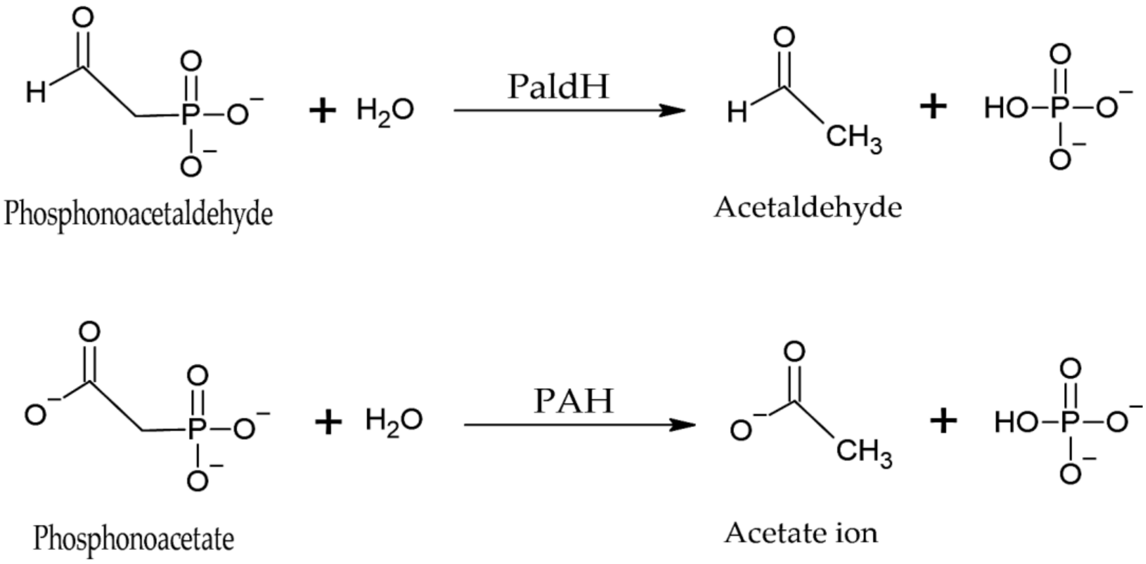

Figure 5. The catalytic reaction of phosphonatases. PaldH: phosphonoacetaldehyde hydrolase, PAH: phosphonoacetate hydrolase.

Furthermore, organophosphoric compounds are the active components of many pesticides, as they interfere with the catalytic activity of key enzymes in the target organism (such as acetylcholinesterase and phosphate synthases) [92,93]. However, studies indicate that these compounds are very persistent in the environment and may harm the quality of soil, water, and even the germination of non-target plants [94–96]. Soil microorganisms act on the bioremediation of these xenobiotics, using them as a source of P [97], thus contributing to the reduction of toxicity in the soil while converting the inert P of the phosphonate into a nutrient assimilable to plants.

Chávez-Ortiz et al. [98] studied the effects of glyphosate and commercial formulation (CH) on soil nutrient dynamics and microbial enzymatic activity. Two plots were used: one with a 5-year history of glyphosate application (NP) and the other with a history of agricultural management without glyphosate application (AP). The authors found that the application of CH in the AP soil favored the specific activity of the phosphonatase. The study shows how the application of the herbicide shapes the microbial community, and how it adapts to metabolize the xenobiotic.

4.1.4. Carbon–Phosphorus Lyases

Carbon–phosphorus lyases are a complex of membrane enzymes that also allow the release of P, cleaving the C–P bonds of several classes of phosphonates (i.e., alkyl, amino-alkyl, and aryl phosphonates), producing hydrocarbons and inorganic phosphate [99,100]. This complex is the main mechanism for the use of phosphonates by microorganisms [101].

The enzymes and proteins of C–P lyases are complex and specific to their substrates. In *Escherichia coli*, they are all encoded by the 14-cistron operon (*Phn* CDEFGHIJKLMNOP), which is activated under conditions of phosphate deficit allowing the use of phosphonates [102]. Figure 6 shows the reaction of a C–P lyase.

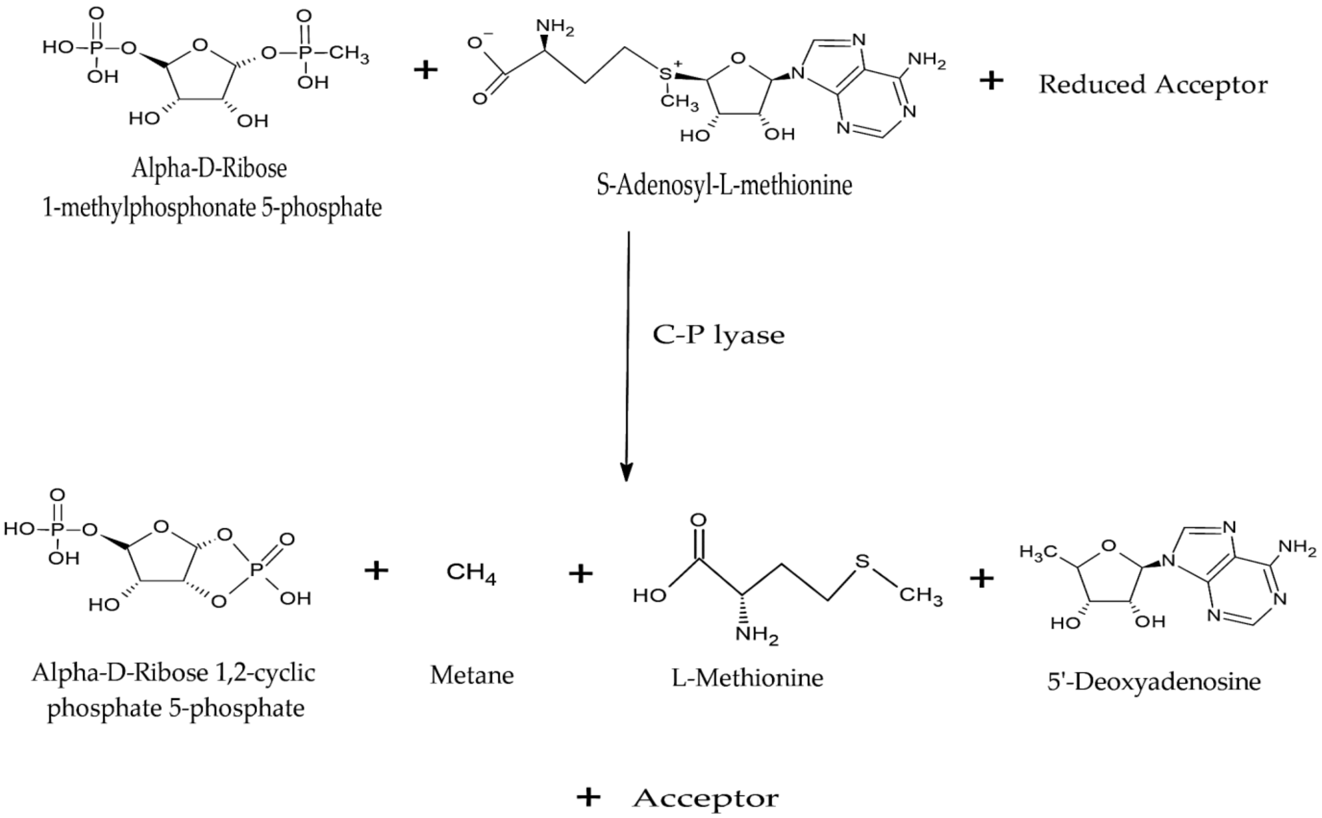

Figure 6. The catalytic reaction of α-D-ribose-1-methyl phosphonate-5-phosphate C–P lyase (methane-forming).

Kryuchkova et al. [97] analyzed the effect of several growth-promoting bacteria on glyphosate degradation. Among the bacteria analyzed, *Enterobacter cloacae* K7 proved to be both resistant to a 10 mM concentration of the herbicide and enabled its degradation in vitro (40% of the initial 5 mM content). The authors also analyzed the intermediate metabolites involved in the degradation and verified, using thin-layer chromatography, the activity of C–P lyase in the conversion of glyphosate to sarcosine, and later oxidation to glycine.

4.2. Inorganic Phosphate

In turn, inorganic P is the most abundant conformation of phosphorus found in soil, 70–80% of its total [12]. In soil, it can be a constituent of primary or secondary minerals or adsorbed on metallic oxides and clay, as shown in Figure 7 [103,104].

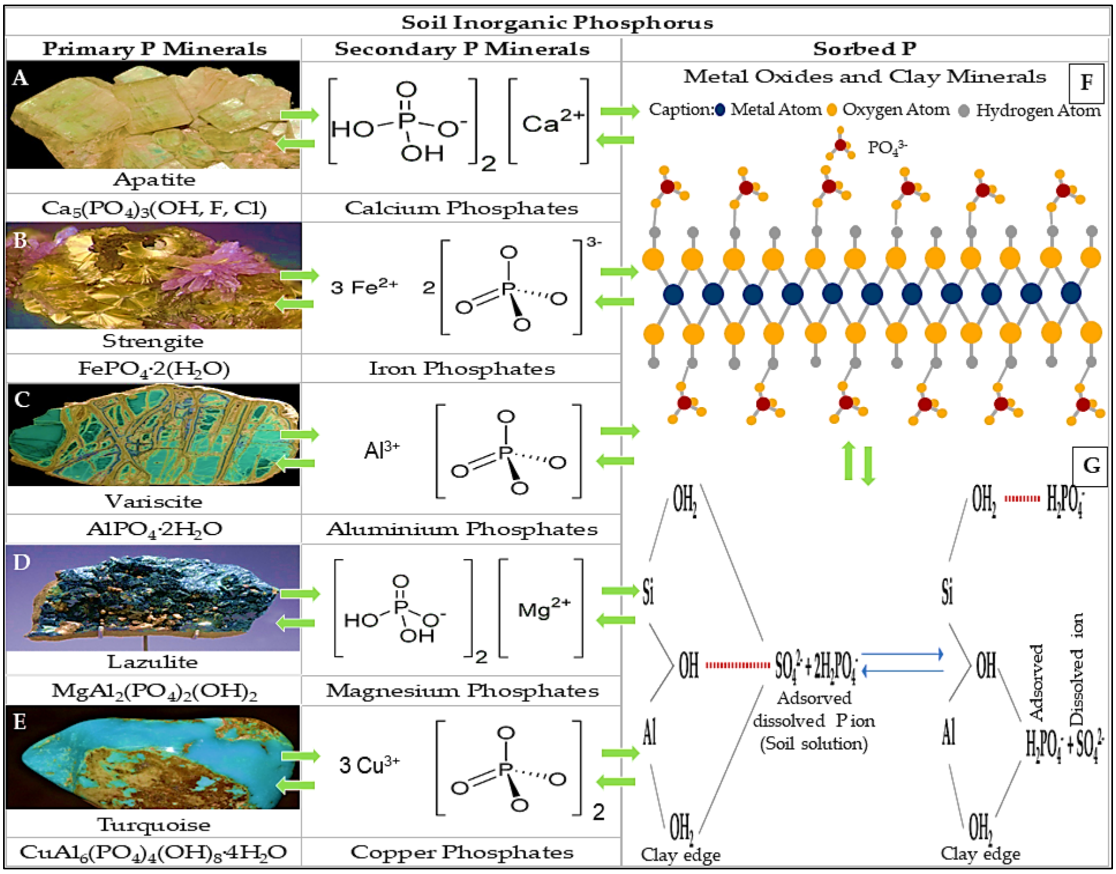

Figure 7. Inorganic phosphorus in soil. (**A**) Apatite (Image author: Parent Géry, Source: Wikimedia Commons, Public domain), (**B**) Strengite, cacoxenite (Image by: Modris Baum, Source: Wikimedia Commons, Public domain), (**C**) Variscite (Image author: Jstuby at Wikipedia, Source: Wikimedia Commons, Public domain), (**D**) Lazulite (Image author: Marie-Lan Taÿ Pamart, Source: Wikimedia Commons, Reprinted/adapted with permission from the author. 2020, © Marie-Lan Taÿ Pamart, Own work, License and link: Creative Commons Attribution 4.0 International CC BY 4.0), (**E**) Turquoise (Image author: Parent Géry, Source: Wikimedia Commons, Public domain). All photographs of rocks have had their brightness increased. (**F**) Conformation of a soil metal oxide and P adsorption mechanisms, (**G**) Conformation of soil clay and P adsorption mechanism [105,106].

4.2.1. Organic Acids

Organic acids are low-molecular-weight compounds secreted by PSM and produced in oxidative metabolic pathways [34]. They are described as the main mechanism for inorganic phosphate solubilization [107]. The main organic acids produced are gluconic and 2-keto gluconic [62,108]. In addition, the release of oxalic, acetic, fumaric, malic, succinic, and tartaric acid, among others, may also occur [109,110].

In general, when released, organic acids acidify the rhizosphere, which causes a drop in pH, and the cations linked to phosphorus are chelated from their hydroxyl and carbonyl groups [111,112]. In addition, these acids can compete with P-adsorption sites and form complexes with P-bound metal ions [12,113,114].

Mendes et al. [115] analyzed the effectiveness of organic acids commonly associated with P solubilization by microorganisms for the solubilization of phosphate rocks with different degrees of reactivity. Increasing concentrations of oxalic, gluconic, citric, malic, and itaconic acids were used in vitro, and their effectiveness in solubilization was compared with that of sulfuric acid. The authors saw that oxalic acid was the most effective for the solubilization of rocks composed of apatite and was superior to sulfuric acid. On average, each mmol of oxalic acid released 21 mg of P, while sulfuric acid solubilized 14 mg of P $mmol^{-1}$.

Patel et al. [116] analyzed the ability of *Citrobacter* sp. DHRSS for solubilization of phosphate rocks. The researchers used different carbon sources to produce the organic acids responsible for solubilization. It was seen that on sucrose and fructose, the bacteria released 170 and 100 µM of phosphate and secreted 49 mM (2.94 g/L) and 35 mM (2.1 g/L) of acetic acid, respectively. With glucose and maltose, *Citrobacter* sp. DHRSS produced approximately 20 mM (4.36 g/L) of gluconic acid, and the released phosphate was 520 and 570 µM, respectively. This study shows the role of different carbon sources and different organic acids in phosphate solubilization.

4.2.2. Inorganic Acids

In general, inorganic acids act in an equivalent way as organic acids, lowering the pH of the environment and acting as chelators; however, they are less effective in the same pH range [12,117]. Examples of these acids include sulfuric, nitric, carbonic, and hydrochloric [118,119].

Cantin et al. [120] conducted a series of experiments to figure out the effectiveness of the combination of a mixture containing commercial elemental sulfur + sewage sludge inoculated with different combinations of bacteria of the genus *Thiobacillus* in the solubilization of apatite P. The combinations used were (1) *T. thioparus* ATCC 23645, (2) *T. thioparus* C5 + *T. thioparus* ATCC 8085, and (3) *T. thioparus* ATCC 23645 + *T. thiooxidans* ATCC 55128. The phosphate solubilization capacity was verified in apatite–sulfur culture medium (ASM) with 1, 10, or 20% (P/V) of apatite. The results showed that *T. thioparus* ATCC 23645 alone lead to a decrease in pH in vitro (from 6.8 apatite 1; or 7.8 apatite 2 to 3.9), confirming that the bacterium is capable of oxidizing sulfur into sulfuric acid. Furthermore, the researchers saw that the consortia of combinations 2 and 3 were more effective for phosphate solubilization than the inoculum with isolated bacteria. In addition, researchers evaluated the release of P from the inoculum when applied to municipal wastewater sludge and incubated with concentrations of 1, 10, or 20% (P/V) of apatite for 33 days. It was seen that 28% of the initial P concentration was solubilized when the apatite–sulfur-sewage-sludge contained 20% apatite, this proportion increased to 86% when the mixture consisted of 1% apatite. The authors suggest that combinations such as pellet form of sulfur, apatite, and stabilized sewage sludge as a source of *thiobacilli* for agricultural use, would provide an effective P fertilizer source.

4.2.3. Enzymes or Enzymolysis

The ability of microorganisms to solubilize phosphate via this mechanism is briefly described in the literature [34].

Zhu et al. [121] evaluated the ability of the bacterium *Kushneria* sp. YCWA18 in the solubilization of P in two culture media, where the first contained calcium phosphate $Ca_3(PO_4)_2$ as the only source of P and the second lecithin as the exclusive source of P. The results showed that for the medium containing $Ca_3(PO_4)_2$ in 11 days of cultivation, there was the release of 283.16 µg/mL of P, and the pH varied from 7.21 to 4.24 in about 4 days. As for the medium containing lecithin, there was solubilization of 47.52 µg/mL of P in 8 days; however, the pH remained stable at approximately 7.0, a value similar to that of the control. Thus, the authors suggest that enzymolysis is the mechanism responsible for the solubilization of P from lecithin because compared to the culture medium containing $Ca_3(PO_4)_2$ (where the solubilization possibly occurred through the release of organic acids), the acidity of the medium does not change. Thus, P is released through catalysis performed by enzymes that convert the substrate to choline.

4.2.4. Siderophores

Siderophores are low-molecular-weight secondary metabolites produced by PSM that have a high affinity for inorganic iron and function as metal chelators [122,123]. They have three functional groups, hydroxamates, catecholates, and carboxylates, and catalyze the reduction of Fe^{3+} to Fe^{2+} [124]. They act at neutral to alkaline pH; however, the mechanisms of this reaction are still not fully understood [125]. Microorganisms use siderophores to obtain the iron used in their cell, and so, during the breakage of its bond, they can release the P bound of the metal, making it assimilable to plants [12,124].

As discussed earlier, in acidic soils, much of the P is fixed in metals such as iron. Cui et al. [126] evaluated the ability of *Streptomyces* sp. CoT10 endophytic activity of *Camellia oleifera* on P mobilization in acidic and deficient soils. The authors saw a release of 72.49 mg/L for $FePO_4$, which was prominent in the production of different siderophores. Moreover, the application of *Streptomyces* sp. aided in Fe-P mobilization improving P availability by 15% in the soil. The authors conclude that the production of siderophores leads to the observed results, including the promotion of plant growth.

4.2.5. Exopolysaccharides

Exopolysaccharides are compounds with high molecular weights that act indirectly on the solubilization of P in soil [127]. They are secreted by microorganisms under stress conditions. In bacteria, they form biofilms, which have a great affinity for binding with metallic ions in the soil, thus competing with free P, providing its availability [128,129]. It is seen that different exopolysaccharides have varying binding affinities with different metals, and there are also different binding strengths between the metals themselves [130,131].

Yi et al. [127] evaluated that *Enterobacter* sp. EnHy-401, *Arthrobacter* sp. ArHy-505, *Azotobacter* sp. AzHy-510 producing exopolysaccharides (EPS) have a higher tricalcium-phosphate solubilization capacity than *Enterobacter* sp. EnHy-402 which does not produce EPS. The authors analyzed that under the same conditions, *Enterobacter* sp. EnHy-402 solubilized 112 mg/L of P, the medium pH ranged from 7.0 to 4.5, had an organic acid production of 258 mg/L, and did not produce EPS. Meanwhile *Enterobacter* sp. EnHy-401 solubilized 623 mg/L of P, the medium pH varied from 7.0 to 4.3, had an organic acid production of 2092 mg/L, and produced 4 g/L of EPS. The authors suggest that EPS potentiates phosphate solubilization mainly by benefiting the production and activity of organic acids.

4.2.6. Proton Release

The release of protons is another mechanism that promotes rhizosphere acidification. Soil microorganisms use various sources of nitrogen to form amino acids, one of which is ammonium (NH_4^+) which, when metabolized, generates ammonia (NH_3) [132,133]. At the end of the reaction, the excess H^+ protons generated are released into the soil, allowing the desorption of P immobilized in metals [134].

Studies have shown different ways in which proton extrusion favors phosphate solubilization. Öğüt et al. [135] reported an increase in proton extrusion in maize roots after being inoculated with *Bacillus* sp. 189 causing acidification of nutrient solution supplemented with ammonium. The bacteria contributed to the increase in evaluable P by 8.0 mg/Kg, while in the control the concentration of evaluable P was 6.3 mg/Kg. The authors suggest that the increase in proton release was due to (1) stimulation of plasmalemma ATPase of plant roots, (2) proton release by the PSM associated with the release of organic acid anions, and (3) proton release by the PSM in response to NH_4 uptake.

Habte and Osorio [136] verified the influence of various sources of nitrogen on the solubilization of phosphate rocks by *Mortierella* sp. The results showed that in the presence of NH_4Cl and NH_4N_3, the pH of the solution decreased from first value of 7.6 to 3.4 and 3.7, respectively. When the N source was KNO_3, the pH decreased to 6.7. As for P solubilization, it was seen that supplementation with NH_4Cl was responsible for the release of 130 mg/L of P, with NH_4N_3 it was 110 mg/L of P, and with KNO_3 only 0.08 mg/L of P. The authors also indicated that excess NH_4^+ negatively affected fungal growth. However, this may have promoted a greater pumping of H^+ that significantly decreased the pH of the solution and consequently favored the solubilization of P.

4.2.7. H_2S Production

Hydrogen sulfide is a compound produced by sulfur-oxidizing and acidophilic bacteria. It is released from metabolic pathways such as sulfate reduction and organic matter decomposition [12,137]. This compound interacts with minerals that have phosphate, releasing it into the soil solution [128]. An example is ferric phosphate, which forms ferrous sulfate with the release of immobilized phosphorus in the soil [138,139].

Phosphate solubilization mediated exclusively by the production of H_2S does not have many practical examples in the literature. However, some studies have analyzed the synthesis of compounds by bacteria [140–142].

4.2.8. Direct Oxidation of Glucose

The direct oxidation of glucose is another strategy used by PSM to make P bioavailable. In bacteria, this mechanism begins with the oxidation of glucose in the periplasmic space by the enzyme glucose dehydrogenase, generating gluconic acid, which is eventually converted to 2-keto gluconic by the enzyme gluconate dehydrogenase [28,143]. Subsequently, the release of these acids to the outside of the cell occurs, acidifying the medium. As seen previously, these acids function as ferric ion chelators, releasing the P from its bond [144].

Phosphate solubilization by the direct oxidation pathway is a mechanism that is extremely restricted by the effectiveness of glucose dehydrogenase. Therefore, studies seek to identify the enzyme in microorganisms using molecular methods, as was the case with the work by Mei et al. [145] who identified the enzyme in the bacteria *Pantoea vagans* IALR611, *Pseudomonas psychrotolerans* IALR632, *Bacillus subtilis* IALR1033, *Bacillus safensis* IALR1035 and *Pantoea agglomerans* IALR1325.

In addition, studies have also highlighted the importance of gluconic acid in plant growth. Rasul et al. [146], showed that *Acinetobacter* sp. (MR5) and *Pseudomonas* sp. (MR7) producing gluconic acid were responsible for promoting rice growth, increasing grain yield (up to 55%), plant-associated P (up to 67%), and soil available P (up to 67%), with 20% reduced fertilization. The authors confirmed the activity of the enzyme based on the construction of new primers designed to amplify the *gcd*, *pqqE*, and *pqqC* genes responsible for glucose dehydrogenase-mediated phosphate solubilization.

Other studies have pointed out the reasons for the failure or reduction of phosphate solubilization from the inhibition of glucose dehydrogenase catalysis. The work by Bharwad and Rajkumar [147] and Iyer and Rajkumar [148] describe how succinate inhibits enzyme activity in *Acinetobacter* sp. and *Rhizobium* sp. respectively.

5. Applications of Phosphate-Solubilizing Microorganisms as Plant Growth Promoters

In addition to making P available, microorganisms can also promote plant growth in complementary ways. They have direct and indirect mechanisms of action for plant growth promotion, including biological nitrogen fixation [149] and phytohormone production [150,151].

They can stimulate tolerance to environmental stresses such as drought [152] and low soil fertility [153]. They can also induce host plant defense from the production of antibiotics and secondary metabolites [154,155], and biosurfactant compounds [156,157].

In addition, the application of isolated microorganisms or consortia can modulate the physiological response of plants and aid their growth and development. Thus, the inoculation of microorganisms plays a notable role in reducing the time required for the acclimatization of seedlings [158], improving foliar gas exchange [159], and the accumulation of fresh and dry matter, as well as increasing plant root growth [160].

Thus, the use of microorganisms and their versatility in growth promotion mechanisms constitute a notable resource to produce bioinoculants, and consequently, for sustainable agricultural production. Table 1 summarizes studies in which the microorganisms used can solubilize and make phosphate available. They were inoculated into different crops and their effects were described.

Table 1. Applications of growth-promoting microorganisms capable of phosphorus solubilization in cultures.

Microorganism/Consortia	Crop	Mechanism of Action	Highlights	Reference
Glomus mosseae +/or *Bacillus megaterium*	Alfalfa (*Medicago sativa*)	Increased the mycorrhizae infection rate, shoot biomass, chlorophyll content in leaves, and soluble sugar content	AMF and PSB significantly promoted the nutritious quality of alfalfa under different phosphorus application conditions	Liu et al. [161]
Advenella mimigardefordensis, *Bacillus cereus*, *Bacillus megaterium*, and *Burkholderia fungorum*	Barley (*Hordeum vulgare*)	Improved levels of assimilated phosphate, dry weight of ears, and total starch accumulated on ears	The use of PSB is a promising strategy to take advantage of non-accessible soil P reserves	Ibáñez et al. [52]
Acinetobacter pittii +/or *Escherichia coli* +/or *Enterobacter cloacae*	Betel nut (*Areca catechu*)	The strains significantly improved plant height, shoot and root dry weight, and nutrient uptake. Moreover, the co-inoculation enhanced the solubilization of tricalcium and aluminum phosphate.	The strains can be potentially applied as inoculants in tropical and aluminum-rich soils	Liu et al. [162]
Azotobacter sp. SR-4 +/or *Aspergillus niger*	Calabash (*Lagenaria siceraria*) and Okra (*Abelmoschus esculentus*)	Increased plant height, leaf length/width, fruit size, and the number of fruits per plant. Consortium shows better results	Selected strains may replace costly and the environment-toxic chemical fertilizers	Din et al. [13]
Pseudomonas donghuensis JLP2, *Pseudomonas grimontii* JRP22, *Pantoea roadsii* HRP2, *Enterobacter hormaechei* SSP2, *Paraburkholderia caffeinilytica* JRP13, *Novosphingobium barchaimii* JRP23 and *Ochrobactrum pseudogrignonense* JRP24	Chinese fir (*Cunninghamia lanceolata*)	Improved plant height, stem diameter, biomass, and nutrient content. Also enhanced soil nutrient content and enzyme activity	PSB could be used as biological agents instead of chemical fertilizers for agroforestry production	Chen et al. [140]
Bacillus megaterium +/or *Bacillus cereus*	Common bean (*Phaseolus vulgaris*)	Single and dual inoculation increases root length, plant height, root and shoot dry weight, P content in plants and photosynthetic pigments even in salt stress conditions	Decreased the harmful effects of salinity and improve plant growth in stress conditions	Abdelmoteleb et al. [163]
Bacillus subtilis Q3 and *Paenibacillus* sp. Q6	Cotton (*Gossypium* sp.)	Increased root length, shoot and root fresh and dry weight, and root/shoot ratio	Selected strains are potential candidates for promoting cotton growth under alkaline conditions	Ahmad et al. [164]

Table 1. *Cont.*

Microorganism/Consortia	Crop	Mechanism of Action	Highlights	Reference
Enterobacter sp.	Eggplant (*Solanum melongena*)	Eggplant recruited *Enterobacter* PSBs during fruiting stages	The rhizosphere bacterial community was susceptible to farming strategies and was largely shaped during the plant development stages	Li et al. [165]
Achromobacter, Agrobacterium, Bacillus, Burkholderia, Erwinia, Flavobacterium, Micrococcus, Pseudomonas, and *Rhizobia*	Maize (*Zea mays*)	Improved growth, its P concentration, and uptake	PSB inoculation may nullify the negative effects of liming (such as decreased maize growth and P uptake, and increased post-harvest soil salinity and calcification) on plant growth and P availability	Adnan et al. [166]
Citrobacter amalonaticus M16 +/or *Bacillus safensis* M44	Maize (*Zea mays*)	Increased the length of the root and sprout, also the underground and aboveground biomass. Enhanced plant amino acids, metabolites, and other molecules	This study supplies a theoretical basis for the application of PSB in sustainable agriculture	Shen et al. [167]
Bacillus sp. ACD-9	Maize (*Zea mays*)	Improve growth (9%) and phosphorus uptake (15%) and decrease the accumulation (70%) and toxic effects of herbicide acetochlor	The strain may be useful in the degradation of acetochlor in soil and the promotion of the growth and phosphorus uptake of maize	Li et al. [168]
Bacillus sp. RZ2MS9 and *Burkholderia ambifaria* RZ2MS16	Maize (*Zea mays*) and Soybean (*Glycine max*)	Increases in root and shoots dry weight of both plants when compared to non-inoculated control	The PSB isolated of guarana (*Paullinia cupana*) a tropical plant shows the ability to endophytically colonize plants of agricultural interest	Batista et al. [169]
Bacillus velezensis Ag75	Maize (*Zea mays*) and Soybean (*Glycine max*)	Increased maize and soybean yield by 18% and 27%, respectively, while also being a biocontrol agent.	The bacterium has multifunctional traits for promoting plant growth and makes it possible to reduce the demand for phosphate fertilization	Mosela et al. [170]

Table 1. *Cont.*

Microorganism/Consortia	Crop	Mechanism of Action	Highlights	Reference
Enterobacter sp J49 and *Serratia* sp. S119	Maize (*Zea mays*), Soybean (*Glycine max*) and Peanut (*Arachis hypogaea*)	Promote plant growth and P tissue uptake and increased the phosphate-solubilizing ability of the rhizosphere. Root exudates of the plants showed to produce changes in the pectinase and cellulase activities of the strains	The strains analyzed constitute potential sources for the formulation of biofertilizers for application in agricultural soils with low P content	Lucero et al. [171]
Penicillium guanacastense JP-NJ2	Masson pine (*Pinus massoniana*)	Extracellular metabolites and fungal suspension from the strain promoted the shoot lengths by 60% and 98%, respectively, while root crown diameters increased by 28% and 47%	The strain might be used to improve soil fertility in nurseries and forestry practice	Qiao et al. [172]
Bacillus megaterium UFMG50, *Klebsiella variicola* UFMG51, *Pantoea ananatis* UFMG54, *Microbacterium* sp. UFMG61, *Pseudomonas* sp. UFMG81 and *Ochrobactrum pseudogrignonense* CNPMS2088	Millet (*Pennisetum glaucum*)	Increased P both in soil and in the plant. Organic acids and the production of phytohormones are among the mechanisms of plant growth	RP and the isolates described here are used as adjuvants to a P-fertilization strategy in tropical soils.	Silva et al. [21]
Pseudomonas spp.	Mung bean (*Vigna radiata*)	Increased seed yield, 1000-grain weight, biological yield, shoot and root P concentration, and uptake	PSB inoculation with less P fertilization	Bilal et al. [4]
Bacillus megaterium MF 589715, *Staphylococcus haemolyticus* MF 589716, and *Bacillus licheniformis* MF 589720	Mung bean (*Vigna radiata*)	Isolated PSBs from earthworm gut is capable of plant growth promotion and metal resistance	Integrated use of earthworms and associated bacteria as the powerful biofertilizer in the sustainable crop production	Biswas et al. [173]
Burkholderia cepacia strains 5.5, 2EJ5 and ATCC 35254, *Burkholderia uboniae*, *Gluconacetobacter diazotrophicus* PAl 5	Mung bean (*Vigna radiata*)	The PSB improved root and shoot lengths, and seedling vigor	Bacterial strains could potentially be included in bio-fertilizer formulations for crop growth on acid soils	Tang et al. [174]
Pseudomonas sp. +/or *Serratia* sp.	Onion (*Allium cepa*)	Consortium increases the seeds germination rates (90% of evaluated) and plant's total dry weight	Consortium application twice a week for two months favored onion total dry weight increase in comparison with controls	Blanco-Vargas et al. [8]

Table 1. *Cont.*

Microorganism/Consortia	Crop	Mechanism of Action	Highlights	Reference
Providencia rettgeri TPM23	Peanut (*Arachis hypogaea*)	Combined application of RP and PSB increased plant length, biomass, and uptake of NPK. Decrease of soil Na^+, Cl^-, and pH. Also increased soil beneficial enzymes and microbial diversity	The combination of PSB and RP might be a low-cost and environmentally safe strategy to remediate the problem of low nutrient availability in saline soils.	Jiang et al. [175]
Bacillus pumilus	Potato (*Solanum tuberosum*)	In vitro increased root (68%) and stems (79%) length. Also, duplicate the fresh weight of plants	Growth promotion under in vitro conditions is a step forward in the use of innocuous bacterial strain biofertilizer	Yañez-Ocampo et al. [176]
Bacillus licheniformis QA1 and *Enterobacter asburiae* QF11	Quinoa (*Chenopodium quinoa*)	The strains significantly improve germination rate and seedling height and weight. Also reduces Na^+ uptake under saline conditions	Isolation of potential biofertilizers PSB strains from the rhizosphere of quinoa from Moroccan soil	Mahdi et al. [177]
Bacillus sp. LTAD-52, LRCP-2, LRCP-3, LRCP-4, *Serratia* sp. LRCP-29, *Pantoea* sp. LRCP-17 and *Arthrobacter sp.* LRCP-11	Rapeseed (*Brassica napus*)	Increased significantly plant growth and crop yield (from 21% to 40%), reaching values like or even higher than the fertilized control	Extend the knowledge of the diversity of bacteria associated with rapeseed plants. Contributes to the development of biotechnological strategies	Valetti et al. [178]
Enterobacter ludwigii GAK2	Rice (*Oryza sativa*)	Enhanced plant fresh, shoot and root weight, plant height, and chlorophyll content	The strain solubilizes the silicate and phosphate in the soil and thereby promotes the growth of plants in cadmium-contaminated soil	Adhikari et al. [179]
Acinetobacter sp. RC04 + *Sinorhizobium* sp. RC02	Safflower (*Carthamus tinctorious*)	Improved seed germination and, when co-inoculated, improved seedling growth	Reveal the potential of *Acinetobacter* sp. and *Sinorhizobium* sp. as biofertilizer agents.	Zhang et al. [180]
Trichoderma spp.	Soybean (*Glycine max*)	Increased soybean growth from 2% to 41% as well as in the efficiency of P uptake-up to 141%	Reveal the potential of *Trichoderma* spp. from the Amazon biome as a promising biofertilizer agent.	Bononi et al. [181]

Table 1. *Cont.*

Microorganism/Consortia	Crop	Mechanism of Action	Highlights	Reference
Acinetobacter pittii	Soybean (*Glycine max*)	Promoted plant growth. Increased activities of phosphatase, phytase, and indole acetic acid	*A. pittii* promotes inorganic and organic P use and increases the function of P-cycling-related enzymes of the rhizosphere bacterial community.	He and Wan [182]
Klebsiella variicola + *Rhizophagus intraradices*	Sunchoke (*Helianthus tuberosus*)	Increased plant growth and tuber inulin content	Dual inoculation may be a promising strategy to both reduce expensive synthetic fertilizers and enhance insulin production	Nacoon et al. [183]
Klebsiella variicola +/or *Rhizophagus intraradices*	Sunchoke (*Helianthus tuberosus*)	In 2016 (year) the consortium improved the growth and production of the plant more than the inoculation of AMF or PSB alone. In 2017 showed that the inoculation of AMF alone played a more significant role in enhancing plant growth and production	Different years of sunchoke plantation could result in distinct levels of plant response and PSB and AMF status in soil	Nacoon et al. [184]
Bacillus aryabhattai JX285 +/or *Pseudomonas auricularis* HN038	Tea-Oil Camellia (*Camellia oleifera*)	Improved plant growth, photosynthetic ability, the N and P content of the leaves, and the available N, P, and K content of rhizosphere soil	The inoculation effect of mixed PSB strains was better than that of single strains	Wu et al. [185]
Arthrobacter sp. and *Bacillus* sp.	Tomato (*Solanum lycopersicum*)	Enhanced plant growth in P-deficient and salt-affected soils by 47–115%. The PGPB effect was increased in higher salt stress conditions	Selected bacteria solubilize phosphate in the presence of high salt concentrations, promoting plant growth even under combined P and salt stresses	Tchakounté et al. [186]
Methylobacterium sp. PS and *Caballeronia* sp. EK	Tomato (*Solanum lycopersicum*)	In acid sulfate soils treated with each bacterial strain led to 38% to 60% increased germination (52 days), a 2–3-fold increased number of leaves (52 days), and 19–45% increased soil tATP levels (50 days)	Strains of PSB described have the potential for use as biofertilizers that promote vegetation growth in acid sulfate soils	Kim et al. [187]

Table 1. *Cont.*

Microorganism/Consortia	Crop	Mechanism of Action	Highlights	Reference
Pseudomonas fluorescens PSB1 and PSB11, *P. koreensis* PSB18 +/or *Rhizoglomus irregulare* (One PSB + AMF consortium)	Tomato (*Solanum lycopersicum*)	PSB and AMF increased the plant biomass. Also, PSB increased hyphal length and colonization	Plants inoculated with the combination of fungus and bacteria had significantly higher plant biomass compared to single inoculations	Sharma et al. [188]
Burkholderia gladioli +/or *Pseudomonas* sp. +/or *Bacillus subtilis*	Tomato (*Solanum lycopersicum*) and Fenugreek (*Trigonella foenum-graecum*)	Seed germination, plant height, and weight significantly increased	Reveals the strains and consortium ability to solubilize insoluble inorganic and organic P into absorbable form for plant	Kumar et al. [189]
Paenibacillus beijingensis BJ-18 + *Paenibacillus* sp. B1	Wheat (*Triticum aestivum*)	Increase plant biomass, improve plant nutrition and rhizosphere soil physicochemical properties	PSB and diazotrophic bacteria can improve the sustainability of agriculture.	Li et al. [25]
Consortium 1 (*Enterobacter* spp. ZW9, ZW32, and *Ochrobactrum* sp. SSR). Consortium 2 (*Pantoea* sp. S1, *Enterobacter* sp. D1, and *Ochrobactrum* sp. SSR). Consortium 3 (*Ochrobactrum* sp. SSR, *Pseudomonas* sp. TJA, and *Bacillus* sp. TAYB)	Wheat (*Triticum aestivum*)	Alleviation of P stress through induced sequential production of root exudates, modification of root architecture, and mitigation of oxidative damage by induced activities of antioxidant enzymes	P-solubilizing bacteria employed beneficial impact on morpho-physiological attributes of inoculated plants	Yahya et al. [190]
Bacillus sp. MWT-14	Wheat (*Triticum aestivum*)	Increased number of productive tillers, 1000-grain weight, grains per spike	Combined use of Bio-organic P and PSB can increase the soil fertility, crop growth, and productivity of wheat	Tahir et al.[191]
Streptomyces alboviridis P18, *Streptomyces griseorubens* BC3, *Streptomyces griseorubens* BC10, and *Nocardiopsis alba* BC11	Wheat (*Triticum aestivum*)	Improved root length (2–24%), root volume (42–72%), root dry weight (47–162%), shoot length (9–24%) and shoot dry weight (3–66%)	Significant ability to solubilize mica and RPs under the in vitro condition. BC10 and BC11 are promising candidates for the implementation of efficient biofertilization	Boubekri et al. [192]
Bacillus sp.	Wild mint (*Mentha arvensis*)	Increased in the plant growth parameters, oil yield, and P uptake	PS Bacillus enhanced the menthol content of M. arvensis	Prakash and Arora, [193]

AMF: Arbuscular mycorrhizal fungi, PSB: phosphate-solubilizing bacteria, PGP: plant growth promotion, PGPB: plant growth promoting bacteria, RP: rock phosphate, NPK: nitrogen–phosphorus–potassium fertilizer, when the microorganisms listed are separated by commas (,), the different species were inoculated individually. The +/or signs indicate their application in a consortium or individually.

The examples cited in Table 1 show the versatility of PSMs as growth promoters. In general, it is possible to observe that the inoculation of microorganisms favors plant development at all stages of the plant, favoring germination, accumulation of biomass in roots and shoots, increasing the concentration of chlorophylls, increasing crop productivity, reducing biotic and abiotic stress, and increasing the availability and assimilation of nutrients.

Furthermore, studies have strongly shown the use of PSMs as bioinoculants, either in isolated formulations or in consortia. The activity of microorganisms makes it possible to reduce the use of chemical fertilizers, both when applied together and when applied together with phosphate rocks. Microorganisms also benefit from improving soil quality, benefiting the dynamics of the rhizosphere of plants, enabling the solubilization of phosphate in acidic and alkaline soils, and degrading xenobiotic compounds.

Figure 8 shows the information presented in topic 4 "Phosphate-solubilizing microorganisms" and Table 1. A total of 55 articles were reviewed.

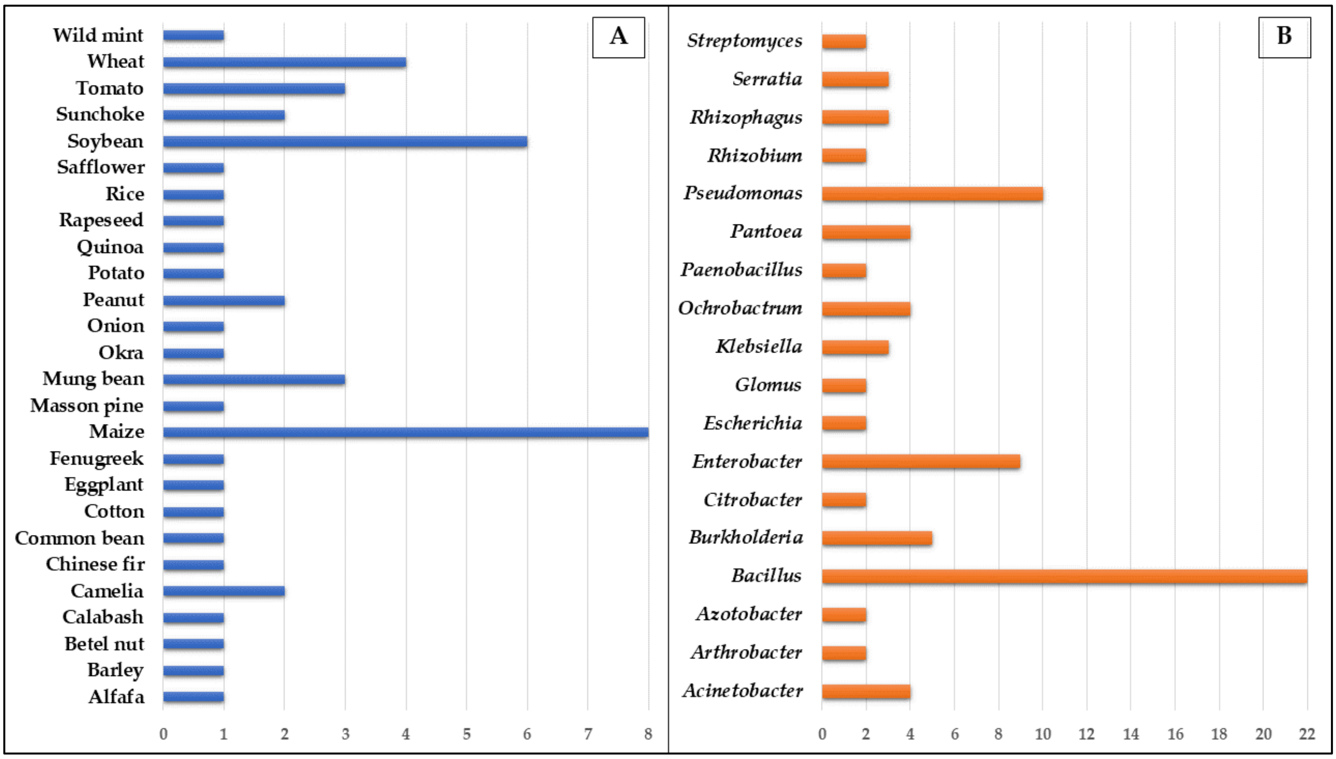

Figure 8. (**A**) Primary cultures were inoculated with phosphate-solubilizing microorganisms. (**B**) The main microbial genera studied for phosphate solubilization. To compress the graph, only the genres that were present in more than one work were selected.

We gathered 48 studies that used plants to verify the ability of PSM to promote growth. Among them, 26 different crops were studied, of which maize (n = 8), soybean (n = 6), and wheat (n = 4) were the main research focuses (Figure 8A).

Among these microorganisms, 41 different genera were studied. Among these, the genera *Bacillus* (n = 22), *Pseudomonas* (n = 10), and *Enterobacter* (n = 9) were the most studied, and possibly those that demonstrated the best potential for the development of bioinoculants (Figure 8B).

6. Market and Agricultural Practices with Phosphate-Solubilizing Microorganisms

Production of biological inoculants is the main way to explore the potential of PSM in agriculture. Forecasts say that the biofertilizer market will register a compound annual growth rate of almost 14% until 2023. In 2016, the global market size of biofertilizers reached

USD 1106.4 million and is projected to grow at the rate of 14% to reach USD 3124.5 million by the end of 2024 [194].

In general, for a microorganism to be selected as a bioinoculant, it must be multifunctional, present several mechanisms of growth promotion, and be a generalist, interacting with several cultures [195]. The work by Owen et al. [196] and Mącik et al. [197] lists several commercial bioinoculants, the microorganisms that compose them, and their modes of action.

Bioinoculants can be used in several ways. As seen throughout the text, the main method of using it is directly in the soil, favoring the release of the P part that is inaccessible to plants. Moreover, the inoculants can be applied together with phosphate rocks [21,45], in the treatment of wastewater [198], and in fermenting animal detritus [199], these being external sources of P.

As shown in Table 1, the potential for some microorganisms to release P from the soil and promote plant growth is unequivocal. However, unlike what occurs with some N-fixing symbionts, such as those from the genera *Rhizobium* and *Bradyrhizobium*, the amount of P made available by PSM does not seem to be well regulated by plants. As a consequence, and allied to the fact that P is not in the air as N, PSM does not supply P in amounts corresponding to high levels of productivity of crops. For this reason, often capitalized farmers choose to apply high doses of phosphate fertilizers instead of applying or managing PSM in the soil. After all, using only PSM these farmers will not be able to reach yields comparable to the use of synthetic fertilizers, and by applying high doses of phosphate fertilizers the action of PSM tends to be minimized, as is the case with arbuscular mycorrhizal fungi. Thus, if the prices of synthetic phosphate fertilizers are not counterproductive at the current level of use, or there is a wide rupture in the productivity paradigm, with a greater appreciation of sustainability over productivity, inoculation with PSM will remain a market niche.

7. Conclusions

In this study, we examined how microorganisms make up a highly viable resource for improving soil and plant nutrition, especially phosphate solubilization. Constant global awareness of the perpetuity of natural resources and their rationalization for future generations is necessary.

Additionally, it is essential to conduct research on the development of innovative technologies for phosphate-solubilizing microorganisms. It is necessary to further understand the nutrient availability mechanisms, and how the process can be perfected under different soils and abiotic conditions. Likewise, the development of innovative technologies can help in the identification, isolation, and prospecting of new microorganisms.

Finally, the use of microorganisms as biological inoculants is a viable, sustainable, and promising alternative for the agriculture of the future, agriculture with greater socio-biodiversity and less use of non-renewable resources external to farmers' properties. The formulation of new bioinoculants, if they are accessible and appropriated by farmers, will help both in agriculture and in socio-economic development.

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