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Review

Trends in the Application of Phosphate-Solubilizing Microbes as Biofertilizers: Implications for Soil Improvement

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Abstract: The application of phosphate-solubilizing microbes (PSMs) as biofertilizers in agricultural systems has not satisfactorily solved the problem of reducing our reliance on chemical phosphorus (P) fertilizers. Ongoing efforts are continually trying to translate promising laboratory results to successful deployment under field conditions, which are typically met with failure. In this review, we summarize the state-of-the-art research on PSMs and their role in the terrestrial P cycle, including previously overlooked molecular and cellular mechanisms underpinning phosphate solubilization. PSMs capable of transforming either organic or complexed inorganic P compounds are discussed. By providing environmentally secure and environmentally friendly ways to increase the accessibility of phosphate, these bacteria effectively transform insoluble phosphate molecules into forms that plants can utilize, encouraging crop growth and increasing nutrient usage effectiveness. The use of PSMs in agriculture sustainably improves crop productivity and has enormous potential for tackling issues with global food security, reducing environmental damage, and promoting sustainable and resilient agricultural systems. Furthermore, due to resource shortages, the changing global climate and need to reduce environmental risks associated with the overuse of chemical phosphate fertilizer, PSMs have the potential to be sustainable biofertilizer alternatives in the agricultural sector. Phosphate-solubilizing microorganisms constitute a cutting-edge field in agriculture and environmental science. In addition, this paper elaborates on the groups and diversity of microbes hitherto identified in phosphate solubilization. Also, factors that had hitherto hindered the reproducibility of lab results in field settings are succinctly highlighted. Furthermore, this paper outlines some biofertilizer formulations and current techniques of inoculation according to the test crop/strain. Finally, laboratory, greenhouse, and field results are presented to acquaint us with the current status of the use of PSM-based biofertilizers.

Keywords: sustainable agriculture; soil improvement; biogeochemical circle; field solubilization; biofertilizer formulation; bioinoculants

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1. Introduction

All living biota require the macroelement phosphorus (P) to sustain anabolism and homeostasis. Plants and microbes compete for P in the soil; therefore, it is crucial that

agricultural crops have access to enough P to maximize their yields and nutritional quality [1]. P is critical for plant growth, and its absence reduces crop yield [2]. In the soil, P exists in numerous forms; however, plants can only take up the inorganic mineral orthophosphate anions HPO_2^{4-} and H_2PO^{4-} (Pi) through their roots [1]. Unfortunately, this form of bioavailable P represents <10% of the total soil P pool [1,3]. Whilst most soils have large reservoirs of total P, its precipitation and fixation with soil elements gives rise to significant P deficiencies and adversely affects growth and production of plants [4]. P is, therefore, scarce in agricultural settings and appears in insoluble forms that are unavailable to plants [5]. The large natural reserve of soil P is predominantly composed of two forms: either organic complexes [6] or as non-labile phosphates which usually react with other components such as minerals, organic matter, or metal ions because of their high reactivity [7–9]. The biological and geochemical mechanisms involved in the soil cycle of P make it a dynamic process (Figure 1).

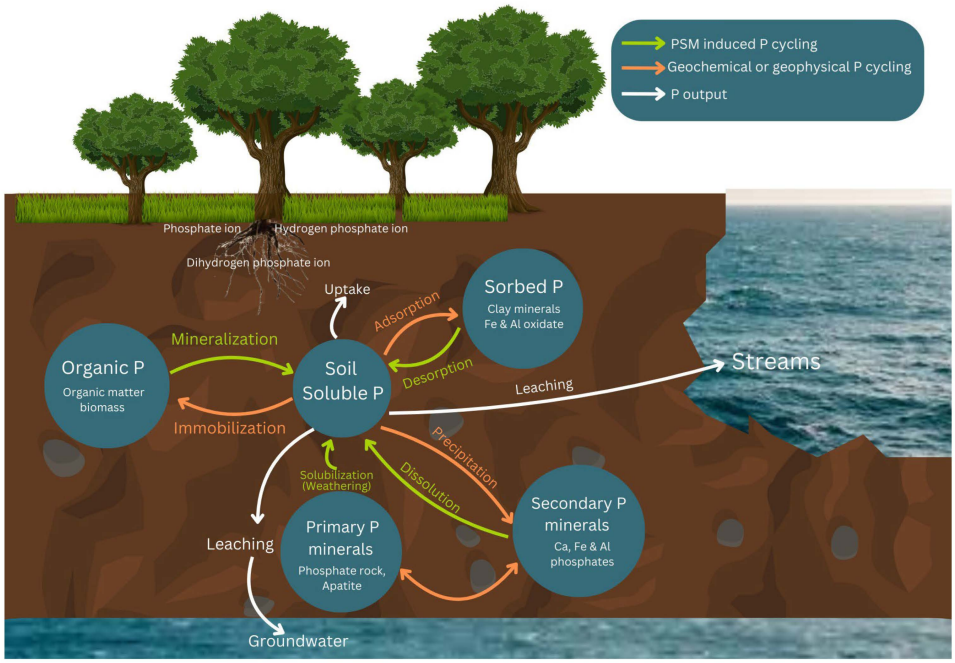

Figure 1. An illustration of the biogeochemical cycles of soil P. Microbe-induced P reactions and cycles are indicated by the yellow arrows. Fluxes connecting plants, streams, and groundwater are indicated by white arrows. Geochemical or geophysical P reactions and cycles are denoted by red arrows. Adapted from Tian et al. [10].

When specific microbes (often referred to as biofertilizers) are applied to the substrate, seeds, or the aerial parts of plants, they can enhance soil fertility, increase the quantity of nutrients available, and encourage plant growth and development [11]. These microbial inoculants may consist of a lone strain or a group of strains that have synergistic effects. Biofertilizers are typically effective colonizers of the plant phylosphere, rhizosphere, or endosphere, enhancing nutrient intake in their hosts, improving photosynthetic processes, and fostering plant growth and productivity [12]. Active or dormant microbes may serve as the basis for these microbe-based inoculants [13]. However, there is an overdue need to define a framework of their limitations and underline the huge prospects of their application. Few studies have presented field data, and the majority of conducted research has been undertaken under laboratory or greenhouse conditions and these usually differ significantly from comparative field results [4]. We currently lack fundamental and sufficient knowledge regarding the phosphorus metabolism of the diverse root-associated microorganisms and how these processes occur in-situ. As a result, there is a dichotomy between

results and observations recorded in the lab and in the field pertaining to microbe-based biofertilization processes. Furthermore, there is still a need to effectively manipulate microbial communities to improve plant phosphorus uptake. This review is therefore aimed at improving our knowledge on complex phosphate–microbe associations, the mechanisms of P solubilization and mineralization, microbial population dynamics, and suitable ways of inoculation based on the intended strain and/or crop. The overall aim of this study is to open an interdisciplinary research landscape that can close this current gap between laboratory/greenhouse and field microbe-based biofertilization outcomes.

2. Microbial Populations in Phosphate Solubilization

There are diverse populations of functionally active microorganisms comprising various bacteria and fungi as outlined in Table 1. These have the capacity to hydrolyze and solubilize either organic or inorganic P compounds [14,15]. According to some authors, a robust, dynamic microbial community is essential for ecosystem functioning in microbial P solubilization [15–17]. The bacterial communities comprising mainly the *Bacillus* spp., *Pseudomonas* spp., and *Enterobacter* spp. [18] and fungal communities comprising mainly *Penicillium* and *Aspergillus* spp. [14] are the two major communities widely acknowledged to be responsible for microbial P solubilization [4]. The Actinomycetes and Cyanobacteria are currently the smallest populations of PSMs reported in the literature, comprising very few species, including *Streptomyces albus, S. cyaneus, Streptoverticulum album, Micromonospora* spp. (Actinomycetes), and *Calothrixbraunii* spp. (Cyanobacteria) [14,19]. It was alluded that the population of phosphate-solubilizing bacteria (PSB) is about 1 to 50% of the total soil microbial population, while that of phosphate-solubilizing fungi (PSF) is 0.1 to 0.5% [4]. The populations of phosphate-solubilizing actinomycetes (PSAs) and phosphate-solubilizing cyanobacteria (PSC) were probably insignificant and, hence, were not compared with soil microbial populations as was realized with PSF and PSB. However, the expression of phytase genes and activity by *Euglena gracilis* and *Chlamydomonas reinhardtii* [15] suggests that some microalgae species are potential phosphate-solubilizing microbes (PSMs), though yet to be discovered. In another review, the potential PSMs were tabulated as 37 bacterial spp., 38 fungal spp., two actinomyces spp., and four cyanobacterial spp. [18]. Although more PSMs are being added to the directory following some recent research reports [10,19], the populations of PSAs and PSC remain significantly far less than PSB and PSF. Given the enormous diversity in soils, these numbers are likely very conservative.

Table 1. Diverse populations of phosphate-solubilizing microbes (PSMs) in the soil.

Phosphate Solubilizing Microbes	References
Pseudomonas, Aeromonas, Klebsiella, and *Enterobacter*	[20]
Acinetobacter, Pseudomonas, Massilia, Bacillus, Arthrobacter, Stenotrophomonas, Ochrobactum, and *Cupriavidus*	[21]
Bacillus sp., *Penicillium* sp., *Aspergillus fumigatus,* and *A. niger*	[22]
Bacillus safensis, Pseudomona moraviensis, and *Falsibacillus* sp.	[23]
Aspergillus, Penicillium, and *Trichoderma*	[24]
Rhizopus stolonifer var. *stolonifer, Aspergillus niger*, and *Alternaria alternata*	[25]
Mortierella sp.	[26]
Kushneria sp. YCWA18	[27]

Table 1. *Cont.*

Phosphate Solubilizing Microbes	References
Pseudomonas sp.	[28]
Chromobacterium sp., *Pseudomonas* sp., *Bacillus* sp., *Micrococcus* sp., *Caulobacter* sp., and *Aspergillus* sp.	[29]
Pseudomonas, Burkholderia, Paraburkholderia, Novosphingobium, and *Ochrabactrum*.	[30]

Factors Affecting Populations of PSMs in the Soil

It was reported in a study that the population density of PSMs varied significantly with rhizosphere soils of different crops [28]. In this study, the authors found that the rhizosphere soil of groundnut had a higher population density of PSMs than that of cotton, sorghum, and maize rhizosphere soils. In another study, the abundance of PSM populations isolated from the rhizosphere of wheat and mustard also varied [20]. It appears the plant species (roots system) together with some peculiar soil enzymes influence the physical and chemical properties of the soil rhizosphere, which are believed to affect the population dynamics of PSMs in the soil [4]. The root exudates of different plant species probably vary in concentration and chemical composition, influencing bacterial community composition in the rhizosphere [31]. Furthermore, the study by Dong et al. [32] revealed that soil amendment with organic fertilizer could lead to shifts in some specific soil microbial communities, thus affecting the microbial population dynamics of PSMs. Another opinion affirmed that higher populations of PSBs are found in agricultural and grazing land [4]. The total population of PSB isolated from agricultural soil was over 10-fold higher than the population of PSF at all locations, likely due to the nature of the soil. For instance, it was observed that the abundance of PSB was higher in soils in mild and moist climates than those in dry climates [29]. Factors directly or indirectly influencing the populations of PSMs, and thus affecting phosphate solubilization, were found to be nutrients (carbon and nitrogen sources), aeration, humic substances, hydrogen ion concentration, and temperature [19,33]. For instance, Ponmurugan and Gopi [28] reported that the population density of PSMs decreased as the depth of soil sampling increased due to decreased concentration of root exudates in the rhizosphere. These root exudates are phytometabolites, including secondary metabolites, amino acids, sugars, and organic acids that serve as a source of nutrients to microbes in the soil, and their impact on soil microbes depends on the chemical composition, concentration, and type of microorganism [31]. Djuuna et al. [29] concluded that there was no correlation between the populations of PSMs and some soil characteristics such as pH and total N and C. Similarly, it was reported that both phytase and phosphodiesterase gene concentrations remained the same at both low and high pH [34]. However, soil physicochemical characteristics were reported to influence bacterial populations as well as the stability and activity of the phosphatases produced [35–38]. The closer association of some bacteria, such as α-proteobacteria *Sphingopyxis* and *Asticcacaulis* and the β-proteobacteria *Ralstonia* and *Cupriavidus* (PhoD gene-haboring bacteria) with the sorghum rhizosphere, and α-proteobacterium *Bosea* (phosphate-solubilizing) and β-proteobacterium *Achromobacter* (non-specific acidic phosphatases (NSAPs) gene-harboring bacteria) with the maize rhizosphere, suggests different crop species could be one of the major factors that determine bacterial population and their phosphatases [34]. It does appear that diverse microbial communities producing the same phosphatases inhabit different types of soil [37], making soil type another factor affecting PSM populations in the soil. The effect of soil type could result from some components of the soil, such as mineral content. For instance, the dominance of some microbial communities in the soil was correlated with the presence or absence of Ca^{2+} which is believed to facilitate the abundance of alkaline phosphatases (PhoX and PhoD) and

NSAPs in the soil [35]. Some authors have also highlighted plant requirements as a factor that shapes the population of PSMs in the soil. Amy et al. [39] pointed out the nutritional preferences of plants as a factor for shaping the associated microbiome population in the rhizosphere of rapeseed, winter pea, and faba bean. They concluded that plants play a vital role in determining the quantity and type of PSMs in the associated rhizosphere, and they do this to fit specific P requirements. Similarly, Cai et al. [40] noted the role of the nutrient preferences of two plant species, tomato and cucumber, in variations in the soil microbiome employing a five-season continuous pot experiment. Their results revealed that these two plants assembled specific fungal and bacterial communities in their rhizospheres, and the soil nutrient status resulting from the plant nutrient preference was reported as a critical modulator in the development of a plant-specific microbiome.

3. Complex Microbe–Phosphorus Interactions

Under both field and laboratory conditions, several intricate microbe–phosphate associations can benefit plants and contribute towards soil P biogeochemical cycling [2,41]. Both bacteria and fungi are responsible for the solubilization and mineralization of inorganic P and organic P compounds, respectively [42–45].

3.1. Microbial Activities on Inorganic Phosphates

In soil, there are numerous insoluble forms of complexed inorganic phosphates which are unavailable to the plant without prior transformations [46]. PSMs have the potential to be extremely important to the invention of phosphate fertilizer systems for agriculture due to their capacity to liberate soluble Pi from rock phosphate ore [47]. However, the specific conditions required for effective functioning in soil systems are not well understood. Insoluble P complexes are typically associated with metal cations or as adhesions to soil mineral surfaces [42,48–50]. These can be solubilized, releasing Pi, by PSMs including both bacteria and fungi, making them bioavailable for plants and surrounding microbes [42,51,52].

PSMs solubilize inorganic phosphate complexes through proton secretion (Figure 2) and the production of organic acids. Different soil microbes have been reported to have phosphate-solubilizing attributes, and a few examples are listed in Table 1. Ligand exchange also leads to the blocking of phosphate adsorption sites on soil mineral surfaces, liberating Pi [33,43,45,53]. Rawat et al. [7] also reported that PSMs excrete siderophores which help to chelate metal ions to form complexes, thereby making insoluble soil phosphate available for uptake by plants [54]. Siderophores are complexing agents that facilitate phosphate solubilization and are produced by microorganisms in response to iron deficiency. Fundamentally, siderophores are low-molecular-weight iron-binding proteins that can bind to iron from organic compounds or minerals in conditions of iron scarcity. They can also help plants obtain iron from the environment, which can stimulate plant growth. PSMs also secrete growth-promoting hormones such as gibberellins, auxins, and cytokinins which promote plant growth and development [55]. Several studies revealed P solubilization by some microbial strains with a resultant improvement in growth hormone production; for instance, *Trichoderma harzianum* and *Pseudomonas plecoglossicida* solubilized up to 288.18 μg mL^{-1} and 75.39 mg L^{-1} P with 21.14 μg mL^{-1} and 38.89 ppm indole acetic acid production, respectively [56,57]. Similarly, PSMs can help in allied enzyme production for growth promotion. Olanrewaju et al. [58] highlighted the potential of PSMs to encourage the production of the enzyme 1-aminocyclopropane-1-carboxylate deaminase (ACC deaminase) which reduces plant's ethylene levels within stressed environments by converting ethylene precursor 1-aminocyclopropane-1-carboxylate (ACC) into α-ketobutyrate and ammonia to enhance the growth and survival of plants. Thus, assaying for the presence of these biomolecules can serve as a primary means of identifying PSM presence [7,59].

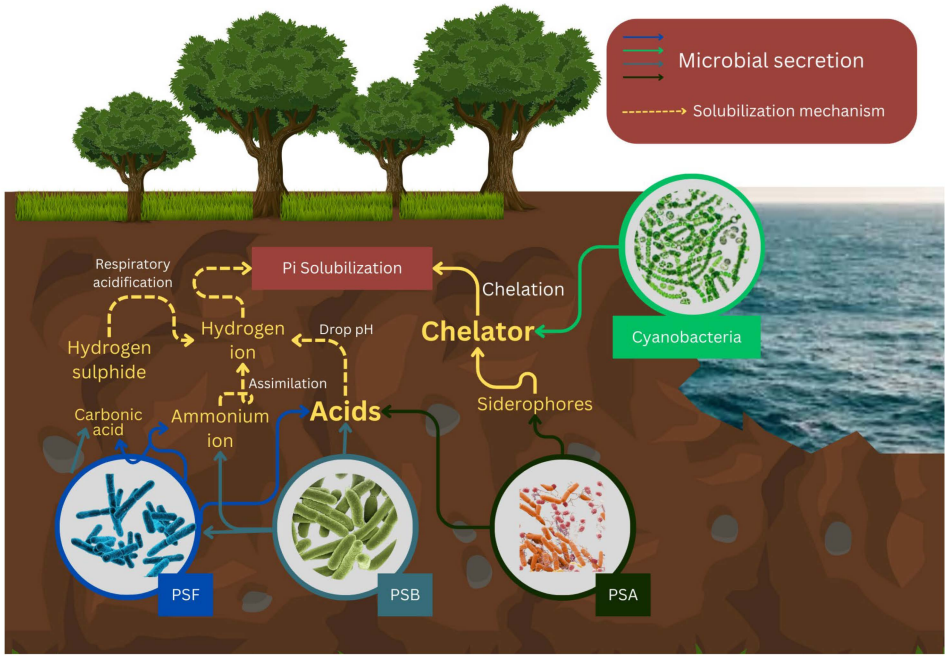

Figure 2. An illustration of the possible inorganic P solubilization mechanisms in PSMs. Different arrow colors represent probable agents of excretion by different groups of PSMs. Phosphate-solubilizing bacteria (PSB, Green), phosphate-solubilizing fungi (PSF, purple), phosphate-solubilizing actinomycetes (PSA, aqua), and cyanobacteria (PSC, cyan). Adapted from Tian et al. [10].

In PSMs, glucose dehydrogenase (Gcd) and pyrroloquinoline quinine (Pqq) encode the redox cofactors and enzymes [60] responsible for the solubilization of inorganic P compounds via the production of organic acids, most notably gluconic acids (GAs) [7,61]. PSMs primarily produce GA as the major organic acid they employ in mineral phosphate solubilization through chelation with phosphate-bound cations [49,62]. Metabolomic and HPLC analyses carried out by Yu et al. [8] during phosphorus solubilization showed 2-keto gluconic acid (2KGA) as the primary and major organic acid, with up to 19.33 mg mL^{-1} accumulated within 48 h of carrying out the process. Organic acids lower the soil solution pH as they separate into their proton and anion components in a pH-dependent equilibrium [59]. From Equation (1), H+ favors dissolution of the mineralized phosphate by changing the equation's equilibrium, with Pi being released into solution.

A simple equation of dissolution:

$$Ca_{10}F_2(PO^4)_6 + 12H \rightarrow 10\,Ca^{2+} + 6H_2PO^{4-} + 2F^- \quad (1)$$

Organic acid anions also stimulate the release of Pi from mineral surfaces by complexing with cations on the mineral surfaces to weaken their cation–oxygen bonds [63]. The role of siderophores, which are complexing agents, produced by PSMs in solubilizing Pi from minerals has also been reported [42,64]. However, microbial use of siderophores for Pi solubilization has not been widely documented. Extracellular polymeric substances (EPSs) found on microbial cell surfaces can affect the H+ or organic acid homeostasis involved in the solubilization process, sequestering the medium of free P and ultimately leading to the further liberation of Pi from inorganic P minerals [65]. However, the synergistic effects of inorganic P solubilization by EPSs and organic acids are not currently well understood. Also, diverse minerals of inorganic P have a spectrum of H^+ production and levels of inorganic P solubility that can be understood on the basis of their solubility product constant (Ksp) values, chemical equilibria, and acidity coefficients [10]. Under strong acidic conditions, PO_3^{4-} will first be dissolved from inorganic P minerals and become protonated

to form hydrogen phosphate (HPO_4^{2-} or H_2PO^{4-}). Metal ions (e.g., Ca^{2+}, Fe^{3+}, or Al^{3+}) are believed to ultimately capture the hydrogen phosphate to generate considerably higher Ksp values for metal hydrogen phosphates than their comparable metal phosphates [66]. Inorganic P minerals can, therefore, almost fully dissolve in extremely acidic environments. This gives further insight into the lower inorganic P solubilization efficiencies associated with monocarboxylic acids (acetic, lactic, gluconic, and formic acids) in comparison to di- and tri-carboxylic acids (malic, citric, and oxalic acids) with higher acidity coefficients [67]. By secreting malic and gluconic acids in a solution containing glucose, *Streptomyces* spp. was found to solubilize $Ca_3(PO^4)_2$ and phosphate rock in wheat rhizosphere soil [68]. Since Ca, Al, and Fe/phosphate or hydroxyapatite make up the majority of phosphate rock and other principal inorganic P minerals, siderophores and chelators may form chelates with these metals to liberate Pi that was previously bound to them [69].

Inorganic acids, such as sulfuric, carbonic, and nitric acids, which exhibit chelating properties, are also produced by PSMs to solubilize phosphates and enhance their application as biofertilizers [61,70]. These inorganic acids cause a pH reduction and dissociate to generate anions which in turn chelate cations bound to phosphates, increasing their solubility [71–73]. ATPase translocation of protons, extracellular cation exchange, and ammonium (NH^{4+}) assimilation were also reported to generate protons resulting in phosphate solubilization without organic acid production [49,74]. The production of hydrogen sulfide (H_2S) which reacts with ferric phosphate ($FePO_4$) to produce ferrous sulphate ($FeSO_4$) with the liberation of Pi has also been reported [42].

3.2. Microbial Biochemical Activities on Organic Phosphorus

In agricultural soil all over the world, organic P makes up an average of more than 40% of soil P content [75] and is important for the availability of P to plants. As we look to reduce our reliance on rock phosphate as a source of P fertilizer, we need to develop processes that facilitate the reuse of various waste streams, from crops, animal, and human sources [76,77]. Enzymes known as phosphatases catalyze the hydrolysis of phosphoester bonds. These can either act on phopshotri-, phopshodi-, or phopshomono-esters, with only hydrolysis of the latter releasing Pi (Table 2) [61,78]. PSM communities produce several classes of intracellular, periplasmic, and extracellular phosphatases that act on organic P compounds, including alkaline phosphatases (AlkPs), acid phosphatases (AcPs), and phytases [35,37,79]. Phytate is often the main form of organic P in soils and, in order to be accessed by plants, needs to be hydrolyzed. Phytase genes are abundant and diverse in the environment [34,80,81]. Kumar et al. [82] investigated phytase-producing bacteria as plant growth-promoting rhizobacteria (PGPR) to improve P intake and consequent plant growth due to high phytate content.

PhoA is a member of the phosphate stress response (Pho) regulon, which is a cascade of genes that code for proteins required for scavenging Pi or for the use of alternative P sources (such as phosphonates and phosphate esters). PhoA is a well-characterized alkaline phosphatase that hydrolyzes phosphate esters and is induced in Pi-deplete conditions. PhoA was once considered to not be abundant or diverse in the environment [79,83]. However, PhoA-like genes have now been identified in several bacteria including cyanobacterial species [84]. Indeed, PhoA appears to be a more phylogenetically diverse enzyme than previously thought, including a unique and environmentally abundant PhoA variant encoded in marine Gammaprotoebacteria related to *Alteromonas*, which exhibits mono-, di-, and tri-esterase activity [85]. *Flavobacterium* also possesses distinct PhoA homologs, which have been experimentally validated, with one also possessing a domain predicted to produce phosphodiesterase activity [86,87].

PhoX, an alkaline phosphatase originally identified in *Vibrio cholerae* [88] and further characterized in *Sinorhizobium meliloti* [89], is another member of the Pho regulon [90] but shares no homology to PhoA. PhoX is a monomeric enzyme activated by Ca^{2+} and has been shown to also require Fe^{3+}. In contrast, PhoA is a homodimer activated by Zn^{2+} and Mg^{2+} [88,91]. Another distinction between the two is that PhoA is secreted to the periplasm or the extracellular space through the Sec pathway [92], while for PhoX, this is achieved primarily through the twin arginine transport and type II secretion systems, capable of translocating fully folded proteins across membranes [36,93]. Importantly, in the soil isolate *Pseudomonas fluorescens*, PhoX encodes for the major inducible phosphatase [93]. This is also seen in the pathogens *Pasteurella multocida* X-73 [94], *Campylobacter jejuni* [95], the marine bacteria *R. pomeroyi* [83], *Ramlibacter tatouinensis* [96], *Phaoebacter* sp. MED193 [97], and *Flavobacterium* spp. [87]. Interestingly, *R. tatouinensis* possesses four phylogenetically distinct homologs.

A functionally unique phosphate-insensitive phosphatase, named PafA, which is prevalent in environmental Bacteriodetes, represents an overlooked enzyme in the soil P cycle [86]. In this study, using *Flavobacterium johnsoniae* as the model bacterium, PafA was discovered to be constitutively synthesized at a constant rate and facilitated growth on organic P as a sole carbon and energy source [86]. The net result was the rapid accumulation of Pi in the culture medium, hence demonstrating a highly efficient process for liberating plant-available P. This phenotype appears to be the 'hallmark' of soil Bacteroidetes suggesting organic P cycling is high when Bacteroidetes abundance is great [87,98,99]. Similarly, bacteria capable of utilizing 2-aminoethylphosphonate (2AEP) in a phosphate-independent manner have been shown to be abundant in both terrestrial and marine ecosystems and are a source of Pi regeneration [100–102]. Interestingly, PafA belongs to the same protein family (pfam01663) as the Pi-insensitive phosphonoacetate hydrolase (PhnA), an enzyme that hydrolase the C-P bond to release Pi [103]. As both function in the presence of Pi, perhaps this protein family represents a key target for future research into engineering efficient phosphatases to apply in agriculture.

PhoD represents a broad family of extra-cytoplasmic phosphodiesterases [104]. It is one of the most common phosphatases found in soil bacteria, however, this enzyme is typically considered a phosphomonoesterase by soil ecologists [79]. The existing genetic and biochemical data suggest that this enzyme is primarily a phosphodiesterase, and using PhoD as a marker of APase activity may be erroneous [105]. Nevertheless, the development of primers for genes (*phoD, phoX,* and *phoA*) encoding the enzymes (PhoD, PhoX, and PhoA) has enabled the study of PSM diversity in the soil [37,79,106–111]. For instance, Ragot et al. [79] reported the identification of 13 classes, 22 orders, 42 families, and 64 genera of microbes in the soil based on ALP primers. The dynamics of these microbial communities in the soil are believed to be influenced by factors that are environmentally dependent. Other enzymes such as C-P lyases and phytases cleave organophosphonates and phytic acid (phytate), respectively, also releasing Pi from these substrates (Table 2) [35,112]; however, primer sets for these enzymes have either not been generated or are infrequently used. A complementary approach is to utilize metagenomics coupled with phylogenomics to quantify and identify the diversity of all organic P-transforming genes in soil systems [34,36,86,113–115].

In addition to these promiscuous phosphomonoesterases, there are numerous specific phosphodiesterases, phosphotriesterases, phytases, and other phosphonate-hydrolysing enzymes that also contribute to soil organic P turnover [105]. Many of these enzymes target common phosphodiesters, including DNA and phospholipids that represent the bulk of organic P in soils, and typically have turnover times much shorter than molecules such as phytate [116,117].

By producing phosphatase, bacteria with phosphatase genes can mineralize organic P from soil which mostly correlates negatively [107,108,118] or positively with soil available P concentration as influenced by P fertilization [37]. It was discovered that an extensive input of mineral P fertilizer might impact the composition of the local community and decrease the number of bacteria that produce PhoD (as shown by the AlkP gene biomarker) [106,119]. In a recent study, it was demonstrated that PhoD-producing microorganisms in the microbiome had the capacity to immobilize organic P when the supply was adequate, while mineralizing organic phosphorus when the supply was deficient. However, it is unclear how much organic P will be present after the increased P addition. The results indicated that they can increase [120], decrease [121], or do not change [122] when P fertilization rates increased. Additionally, the majority of studies have concentrated on the correlation between soil P availability and PhoD gene copy numbers, but the correlation between organic P and PhoD richness has not been well defined. In acidic soil, organic P mineralization was carried out by soil fungi including *Geastrum* sp. and *Chaetomium* sp., which had a significant impact on the mineralization of organic P [123]. Thus, microbial inoculants mostly formed from PSMs that have unique solubilization and mineralization attributes are, therefore, applied to soil as alternatives to conventional inorganic fertilizers and are collectively part of the broader biofertilizers [124].

Table 2. Classification of bacterial phosphatases based on the substrate bond.

Category Name	Type of Bond	Product	Examples of Enzymes	References
Phosphoric monoester hydrolase (phosphomonoesterase)	P-O	Pi	Alkaline phosphatase (APase) Acid phosphatase Phytase Sugar phosphatase Nucleotidase	[125]
Phosphoric diester hydrolase (phosphodiesterase)	P-O	P-R	Phospholipase Exonuclease	[35]
Phosphoric triester hydrolase (phosphotriesterase)	P-O	R-P-R	Paraoxonase	[35]
Phospho-anhydrides hydrolase	P-O	Pi	Adenosine-triphosphatase Inorganic diphosphatase Nucleoside diphosphate-phosphatase Nucleoside triphosphate-phosphatase	[35]
Ribonuclease	P-O	P-R	Exodeoxyribonuclease Exoribonuclease Exonuclease Endodeoxyribonuclease Endoribonuclease	[35]
Enzymes hydrolysing P-N bonds	P-N	Pi	Phosphoamidase Protein arginine-phosphatase	[35]
Enzymes hydrolysing P-C bonds	P-C	Pi	Phosphonoacetaldehyde hydrolase Phosphonoacetate hydrolase Phosphonopyruvate hydrolase	[126]
Triphosphoric acid monoester hydrolase	P-O	P-P-P	dGTPase	[35]

Adapted from [35].

4. Crop and Strain-Specific Microbe-Based Biofertilizer Formulation and Inoculation Techniques

Generally, plant growth-promoting microbe (PGPM) technologies include proper inoculums formulations, choosing a reliable carrier, and following the proper delivery

protocol. PGPM inoculants are compositions with a single or more strains (or species) of beneficial microorganisms made with a convenient and affordable carrier material [127]. Microbe-based biofertilizer inoculants (made up of pure culture bacteria, fungi and archaea, or a mixed culture of any two or three of the former) [128] could exist in the form of a solid, a liquid, or other forms. Various materials are currently being used as carriers for microbe-based fertilizer inoculants, ranging from fly ash, clay, peat, coal, saw dust, wheat bran, and peat-supplemented chitin, as well as inorganic materials like vermiculite, perlite, silicates, kaolin, and betonies [129]. Carriers for inoculum preparation are selected and designed based on the needed microenvironment for the optimal activity of the PGPM. The form of the inoculant is also dependent on the type of carrier [129]. Malusá et al. [127] highlighted that availability, stability, eco-friendliness, economic viability, high pH-buffering, and moisture-holding capacities are the hallmarks of a desirable carrier [127,129]. Liquid inoculants could consist of a broth culture suspension, a suspension in mineral or organic oils, a suspension in humic acid solutions, or boiling water suspensions while for solid inoculants, depending on the size of the beads or granules can be employed to immobilize the microbe [127,129] onto absorbable solid materials. Notwithstanding that a lot of studies have highlighted the interrelationships between plants, soil, and microorganisms, the introduction of these microbes to plants through inoculation offers fresh opportunities for their use in agriculture. However, one of the fundamental challenges to the widespread use of biofertilizers is the standardization of methods for producing pure inocula in vast quantities with a high infectivity potential [127]. Thus, there is still a tremendous challenge in developing an inoculum that has a dependable and consistent response in field settings. However, there is an attempt in this literature to look at suitable technologies for plant-specific microbe-based biofertilizer formulation and inoculation.

4.1. Current Techniques for Enhancing Bioinoculant Formulations

Table 3 highlights the different microbe-based biofertilizer formulation technologies. Bioformulation of quality grade should have sufficient shelf-life, high water retention capacity, non-polluting attributes, and be readily biodegradable [13,127]. Bioinoculant formulation involves uniformly mixing a chosen beneficial strain with an appropriate carrier (vehicle of live dormant microbes which offer support and protection to the community of microbes) capable of providing stability and protection to the strain during transport and storage [130]. Bhattacharyya et al. [131] reported that the shelf-life and efficiency of biofertilizers could be enhanced via formulation process improvements. Chaudhary et al. [130] highlighted that different formulation types are formed based on their survival rate and efficiency.

Table 3. Some notable microbe-based biofertilizer formulations and inoculations.

Microbes/Inoculants	Plant	Formulation Material/Application	Formulation Type	References
Bacillus subtilis	Lettuce	Alginate	Polymer	[132]
Pseudomonas putida	Lettuce	Humic acid	Metabolite	[133]
Pseudomonas corrugate	wheat	Alginate	Polymer	[134]
A. brasilense	Legume crops	Alginate	Polymer	[135]
Sinorhizobium meliloti	Alfalfa Canola	oil Emulsion	Liquid	[136]
Klebsiella oxytoca	Cotton seeds	Alginate	Polymer	[137]
A. brasilense	Sorghum bicolour	Alginate	Polymer	[138]
Sinorhizobium meliloti and *Penicillium bilaii*	Alfalfa Canola		Liquid	[139]
Sinorhizobium meliloti	alfalfa and sweet clover	Alginate	Polymer	[140]

Table 3. *Cont.*

Microbes/Inoculants	Plant	Formulation Material/Application	Formulation Type	References
Azosporillium	Corn and wheat	turf In-furrow liquid, granule	Liquid and polymer	[124]
Gluconacetobacterdiazotrophicus	Multiple	In-furrow and foliage spray	Liquid	[124]
Azorhizobium caulinodans, *Azoarcusindigens* and *Azospirillum brasilense*	Multiple	Freeze-dried powder	Solid	[141]
Penicillium bilaiae	Multiple	In-furrow liquid as a wettable powder or in-furrow granular	Solid and liquid	[142]
Pseudomonas fluorescens	Multiple	Liquid seed coat	Liquid and metabolite	[143,144]
Bacillus amyloliquefaciens and *Trichoderma virens*	Corn, soy, wheat, and pulses	In-furrow wettable powder and granule	Solid and liquid	[145]
Bradyrhizobium spp., *Azospirillum* spp., *Penicillium* sp.	Soybean	Granular in-furrow inoculant	Solid and liquid	[146,147]
Cladosporium tenuissimum	Wheat and other cereals	Dry powder seed inoculant	Solid	[124]

4.1.1. Solid Formulation

In this formulation, a solid carrier (mostly peat, powder, biochar, or granules) is mixed with the beneficial strain to enhance the transition from the laboratory to the field and provide protection and a conducive environment for the proliferation of the available microbial colony [130]. Prior to sowing, the inoculated peat is applied to the surface of the seeds with the aid of machinery like cement mixers, huge troughs, and mechanical tumbling machines [130]. Peat's diversity in composition and quality is its biggest downside. Granules also have been used recently in solid formulations over peat as they offer certain advantages over the use of peat. Granules coated with viable microbes might be of calcite, marble, and silica grains; they are less dusty and are easier to handle, transport, and store than peat [130]. Inoculants in solid formulation using granules are positioned close to the seed surface on the furrow to facilitate lateral-root interactions. Despite the fact that some studies have shown less nitrogen fixation when granular inoculants are used, some research, however, revealed that peat inoculants and formulation by granules are superior in regards to total biomass, nitrogen metabolism and accumulation, and nodulation [130,148]. Granular inoculants have also been reported to have high stress tolerance due to their high capacity for inducing nodule formation and nitrogen fixation under conditions of stress.

Biochar inoculants have also been exploited with evidence of significant bioinoculant survival rates and eco-friendliness, being free from toxic elements [130]. Biochar and charcoal can be stored for a long time without sterilization because they contain little water and have no waxy material, providing good conditions for plants prior to field cropping.

4.1.2. Liquid Formulation

The liquid formulation technique comprises the formulation of a cocktail of microbes capable of solubilizing, mobilizing, and fixing essential plant nutrients in liquid medium. Examples include potassium-mobilizing microbes (KMMs), phosphate-mobilizing microbes (PMMs), and nitrogen-fixing microbes (NFMs) [130,149,150]. Liquid formulation holds some advantages over the carrier-based solid formulation, including an extended shelf-life of 19–25 months due to some strain-specific bioprotectant production, bulk sterilization, high moisture content, and temperature and other stress-tolerance potential [130,151]. One of the prevalent strains used in liquid formulation is *Azospirillum* (a free-living and microaerophilic plant growth-promoting rhizobacterium) [130]. Other

strains belong to the genera *Pseudomonas, Bacillus, Penicillium*, and *Aspergillus* [130]. Sahu and Brahmaprakash [150] reported that by modifying the nitrogen-free bromothymol blue meat broth with polyvinylpyrrolidone (PVP), glycerol, and trihalose, 108 cells per mL can be stored for 8-10 months. This might be due to the high water-retaining potential reported in PVP-protected microbes during stress conditions. Also, endospores of *B. megaterium* in glycerol, glucose, and PVP-supplemented broth can be explored in liquid formulation as it can last for 4-6 months [130]. Sahu and Brahmaprakash [150] also highlighted that a liquid formulation with PVP (3%) and trihalose (16 mM) improved the microbial population and shelf-life of *Azospirillum* and PSB strains unlike the one without PVP. Thus, PVP and trihalose can be said to be suitable bioinoculants with shelf-life enhancement capacities for both PSB and *Azospirillum* spp. at room temperature.

4.1.3. Metabolite Formulation

Metabolite bioformulation was reported to have been developed due to the bottlenecks of cell-based bioformulation [152]. This formulation is a very special kind of bioinoculant with a metabolite-rich milieu serving as bioregulators and biostimulators for other essential nutrients that provide inoculants with a competitive advantage over phytopathogens. Bioinoculants such as *Pseudomonas, Rhizobium, Mesorhizobium, Trichoderma*, and some mycorrhizal fungal strains have been used in this formulation [130]. Maillet et al. [153] reported that rhizobial strains, nodulation, and nitrogen fixation under conditions of stress were enhanced in the presence of flavonoids. Rhizobial strains are associated with lipochitooligosaccharide secretion in leguminous plant hosts, and this lipochitooligosaccharide has been reported to help in symbiosis in fields deficient in *Rhizobium*. More so, novozymes were significantly increased via lipochitooligosaccharide production and flavonoid induction in both leguminous and non-leguminous crops [153]. Wang et al. [154] showed that under hazardous and stressful situations, EPSs produced by plant growth-promoting bacteria (such as *Pseudomonas* spp. and *Rhizobium* spp.) not only help in biofilm development, but also improve root colonization and nodulation. Bioformulation with EPS supplementation generally protects microbial cells from extreme conditions such as radiation, extreme pH, osmotic shock, desiccation, predators, and toxic substances [130]. Timmusk et al. [155] reported that supplementation of the medium with tryptophan enhanced not only the indole-amino acid (IAA) production but also the grain yield of wheat, root hair formation, and plant biomass. In another report, plant growth-promoting rhizobium (PGPR) stimulated with ethylene precursor (L-methionine) and amended with amino acids, starch, wastewater, and molasses resulted in increased plant growth. Thus, these amendments in a harsh soil environment might improve the survival rate and shelf-life of beneficial strains [155]. Biosurfactants from PSB have also been reported to have antimicrobial, antiinsecticidal, and antiviral activities with emulsifying and wetting potential [156]. Most biosurfactants used in liquid bioinoculants are applied on plant aerial parts by spraying. Some of them (like pheromones) and metabolites (like glutamate, sucrose, and molasses) serve as attractants and are phagostimulatory for phytopathogens [130]. Antimicrobials such as pyrrolnitrin, fanzines, diacetyl chloroglucinol, and those with anti-phytopathogenic activities have also been reported in fluorescent *Pseudomonas* strains and *Bacillus* species, respectively [157]. High costs and bottlenecks in its large-scale production are some of the drawbacks of this formulation.

4.1.4. Polymeric Formulation

In this formulation, alginate made up of D-mannuronic acid and L-glucuronic acid synthesized from *Sargassum sinicola* (macroalga) and *Macrocystis pyrifera* (brown algae) are used [158]. The alginate bead formation is a complex and multi-step process carried out at

room temperature [159]. Alginate is a non-toxic and biodegradable compound. The alginate is pelleted into beads which can be of two types based on their diameter (microbeads (50–200 µm) and macrobeads (2–3 mm)), entrapping 109–110 $CFUg^{-1}$ (colony forming units per gram). However, for matrices of alginate, AMF is used for trapping [130]. This formulation impacts positively on bacterial chemotaxis, host plasmid proliferation, and the sustainability of mushroom cultivation. Chaudhary et al. [130] revealed that the bacterial strains mostly used in this formulation are *Azotobacter* and *Pseudomonas*. Other techniques using latent cell encapsulation in the gel matrix (which helps in shelf-life extension of usable strains under abiotic and biotic stressors) for polymeric formulation have also been highlighted recently. During the encapsulation, nutritional additives are also added to enhance growth under aerobic and anaerobic conditions [160]. This technique has been used for *Pseudomonas fluorescens, A. brasilense*, and *Aspergillus* strains (filamentous fungi) during formulation [161]. Zohar-Perez et al. [162] also reported on the positive impact of skimmed milk on strain viability enhancement when supplemented with glycerol, chitin-filled beads' porosity advantage over starch-filled beads' encapsulated cells, and the high survival rate under UV radiation in a glycerolized alginate bead encapsulation. Malusa et al. [127] opined that with soy oil and alginate, the cell viability and growth of *Sinorhizobium meliloti* can be enhanced up to 108 CFU mL^{-1} after 10 weeks of storage.

5. Laboratory, Greenhouse, and Field Results Examined

PSMs solubilize insoluble inorganic P in order to increase P availability for raising agricultural productivity and lowering reliance on synthetic fertilizers [4]. From an applied perspective, solubilization of insoluble inorganic P by PSBs has produced an alternative for chemical phosphate fertilizer, enhancing P availability and decreasing the consumption of chemical fertilizers [163]. However, this has rekindled researchers' interest in examining various ways P could be acquired more frequently by plants, including in laboratory, greenhouse, and field conditions. Under laboratory conditions, selected isolates carried out P-solubilization, producing indole acetic acid and hydrogen cyanide [164]. The P-solubilizing activity was followed by a simultaneous drop in the medium pH, from pH 7.0 to pH 3.0. In both calcareous and non-calcareous soils, combinations of PSB and poultry manure synergistically enhanced P availability [165]. The ecological tactic of utilizing PSB can boost P availability in soil [41]. Consequently, the idea of using organic fertilizers, such as a bioinoculant, has attracted enormous interest in recent times [163].

The benefits of combining chemical fertilizer with biofertilizers were investigated by Ajeng et al. [163], with a focus on soil fertility, nutrient uptake, and oil palm seedling development. Plants inoculated with *Mesorhizobium ciceri* C-2/2 alone exhibited the highest shoot dry weight according to Valverde et al. [166]. Shoot dry weight was 14% higher in the *P. jessenii* PS06-inoculated treatment than in the uninoculated control treatment. El-tarabily and Youssef [167] showed that adding *Oceanobacillus picturae* to sediments amended with rock phosphate considerably accelerated the growth of seedling roots and shoots compared to seedlings grown in sediment solely amended with rock phosphate. Furthermore, *Oceanobacillus picturae* significantly improved nutrient uptake parameters in roots and shoots, decreased available sediment pH, and enhanced stem circumference, the abundance of xylem vessels, the average xylem diameter, and the xylem vessel diameter in comparison to plants grown in uninoculated sediment amended with only rock phosphate. Chaiharn et al. [168] found that rice inoculated with *Streptomyces* had the tallest plants followed by those inoculated with *Burkholderia* strains and *Bacillus* isolates. Additionally, *Bacillus* isolates enhanced the dry mass of rice. According to Chaiharn et al. [168], all of the bacteria they recovered in their investigation showed optimal phosphate solubilization in tricalcium phosphate (TCP) medium, and the solubilization activities peaked at 37 °C,

pH 7.0, and after 15 days of incubation. The study by Kumar et al. [82] revealed a solubilization index of 193–642 for a range of pH, temperature, and salt concentrations. Delfim et al. [41] showed that PSB inoculation caused a rise in the P levels of the rhizosphere as well as increases in the sizes of aerial tissues and root tissues. This inoculation also increased the activity of the acid phosphatases, the biomass of soil microbes, and the biomass of plant roots. Mamta et al. [169] reported that *S. marcescens*-treated plants showed the greatest increase in root length (23.43%), fresh leaf weight (79.03%), dry gel weight (113.08%), and total gel volume (112.10%) compared with uninoculated plants. According to López-Ortega et al. [170], diazotrophic bacteria enhanced plant biomass by up to 39% and P accumulation by 10%. As a result, using diazotrophic PSB in fertilization systems for maize plants may provide an alternate method to chemical fertilizers [171]. PGPR-based inoculations boosted sugar beet root weight by 2.8% to 46.7%, depending on the species [172]. The bacterial inoculation boosted leaf, root, and sugar output by 15.5–20.8%, 12.3–16.1%, and 9.8–14.7%, respectively. Recently, enriched vermicompost with efficient PSB was critical as a natural fertilizer in calcareous soils for the propagation of vegetables and cereals [173]. Bacterial inoculation was found to significantly increase root, shoot, and plant biomass under greenhouse conditions and promoted bacterial numbers in the rhizosphere. As a result, these isolates show potential for further development and application in the field [164]. Numerous PSB strains that have potent abilities for phosphate solubilization and plant development promotion are present in the lentil rhizosphere, as seen from the enhancement in plant nodule quantity and improved shoot nitrogen content [166,174]. The majority of the potent strains should therefore undergo field testing using various soil types. The yield of field-grown maize grain rose by 85% and 64% after seed treatment in comparison with the uninoculated control [175]. By inoculating seeds of wheat types with phosphate-solubilizing and phytohormone-producing *A. chroococcum* under field conditions, Narula et al. [176] found that growth hormone production and phosphate solubilization percentage rose by 11.35% and 11–14%, respectively. Furthermore, sugar beet grown in two soil types with varying organic matter concentrations under both greenhouse and field conditions showed that all bacterial strains fixed nitrogen and considerably boosted sugar beet growth, with three bacterial strains dissolving P [172].

5.1. Factors Responsible for Laboratory/Greenhouse and Field Solubilization Results Dichotomy

PSMs are essential for improving soil fertility because they transform insoluble phosphate into soluble forms, which allow plants to absorb phosphorus. Although PSMs have been shown in lab tests to be able to solubilize significant amounts of phosphate, it has been difficult to translate these findings into real-world settings. This discrepancy can be attributed to various factors including environmental conditions, microbial interactions, soil properties, and methodological limitations. However, a meta-analysis by De Zutter et al. [177] comparing pot and field trials does not support the generally accepted notion that phosphate-solubilizing bacteria are less effective in field conditions. They selected a subset of papers where the same isolates were tested in both pot and field trials. The application of these isolates resulted in similar sizes in the field trials as in their respective pot trials.

5.1.1. Environmental Factors

Environmental conditions in laboratory settings are tightly controlled to optimize microbial activity and phosphate solubilization. These conditions, however, are unable to replicate the complexity and unpredictability of field situations. For example, temperature is important for the metabolism of microbes. Temperatures in laboratory research are usually kept between 28 and 30 °C, which is the ideal range for PSMs. However, temper-

atures might vary greatly in the field, which can hinder microbial activity. For example, the two studies by Ahmad et al. and Zeng et al. [178,179] found that when temperatures deviated from the ideal range, the ability of *Pseudomonas fluorescens* to solubilize phosphate was considerably reduced. Soil moisture is another critical factor. Laboratory conditions ensure consistent moisture levels, maintaining moisture at 50–60% [180], but in the field, soil moisture can vary due to weather conditions and irrigation practices. While dry conditions can completely limit microbial activity, excessive precipitation can cause anaerobic conditions that hinder aerobic PSMs [181]. Cheng et al. [182] emphasized how variations in soil moisture levels impacted the activity and survival of PSMs, decreasing their capacity to solubilize phosphate in field settings. Furthermore, soil pH in the lab is often adjusted to optimal levels for PSM activity, usually around a neutral pH. However, the strongly acidic to alkaline range of field soils can have a significant impact on the microbial solubilization of phosphate. Toxic aluminum ions, for example, can become more soluble in acidic soils and impede microbial development and phosphate solubilization [183]. When compared to neutral pH environments, the phosphate solubilization potential of PSMs was considerably lower in acidic soils (pH < 5.5). The ideal soil pH range for P availability is between 6 and 7.5. This is because pH ranges below 5.5 and between 7.5 and 8.5 prevent P from being fixed by calcium, iron, or aluminum and becoming unavailable for plant usage. The quantity of phosphate solubilized in *B. cepacia* SCAUK0330 was found to be negatively correlated with the pH drop that result from this action. Phosphate solubilization increases because of the pH decrease. Zhao et al. [184] reported that 452 $\mu g \cdot mL^{-1}$ of phosphorus was soluble at pH 3.12, and the pH reached 4.95 when 154 $\mu g \cdot mL^{-1}$ of P was soluble. Regarding organic P solubilization, the quantity of both organic P and residual inorganic phosphate can have dramatics effects on how efficiently microbial inoculants, or their enzymes, can increase P availability [185,186]. Furthermore, most field soils contain locally adapted strains that typically harbor these enzymes and/or mechanisms. Thus, it is naïve to assume an inoculant will establish and confer a beneficial phenotype in the field.

5.1.2. Soil Properties

The efficiency of PSMs is significantly influenced by the physical and chemical characteristics of the soil. Nutrient media or sterile, homogenized soils are frequently used in laboratory experiments, which do not adequately represent the complexity and diversity of field soils. For instance, the distribution and mobility of microorganisms are influenced by the texture of the soil. Clayey soils can restrict microbial movement and provide anaerobic conditions, whereas sandy soils promote better aeration and microbial dissemination. In a study by Bachtiar et al. [187], PSMs in sandy-loam soils outperformed clay soils because of improved root penetration and aeration in sandy-loam soils. Organic matter content in soil also significantly affects PSM activity. High organic matter can enhance microbial growth by providing additional nutrients. However, it can also lead to increased competition among microorganisms. For instance, soils with high organic content often have diverse microbial communities, which can outcompete introduced PSMs for resources. According to a study by Li et al. [188], native microbial communities considerably reduced the phosphate solubilization activity of PSMs in soils with a high level of organic matter because of competitive exclusion. However, according to Alori et al. [33], soil that is high in organic matter will encourage microbial development, which in turn will encourage microbial solubilization of phosphorus. Additionally, the availability of phosphate is influenced by the mineral makeup of the soil. Different types of insoluble phosphate are found in field soils; for example, calcium phosphate is found in alkaline soils, while iron or aluminum phosphate is found in acidic soils. Laboratory studies often use easily solubilizable phosphate compounds, which do not represent these complex forms. A recent study

by Ateş [189] highlighted that PSMs were less effective in solubilizing rock phosphate compared to tricalcium phosphate, a more soluble form often used in laboratory studies.

5.1.3. Microbial Interactions

In the field, PSMs must navigate a complex web of microbial interactions, unlike the simplified conditions of laboratory settings. These interactions can include competition for nutrients and space, as well as antagonistic relationships. Laboratory conditions often use pure cultures of PSMs, allowing them to thrive without competition. In contrast, the field environment hosts a diverse microbial community, which can inhibit the activity of PSMs. Antagonistic interactions are a significant challenge. The growth and activity of introduced PSMs can be inhibited by antimicrobial chemicals produced by native soil microbes. For example, Ramesh et al. [190] discovered that the introduced *Bacillus aryabhattai*'s ability to solubilize phosphate was dramatically decreased by soil bacteria that produce antibiotics. Moreover, PSM efficacy may be constrained by competition for resources like carbon and nitrogen sources. In nutrient-rich laboratory media, PSMs have ample resources to thrive, but in the nutrient-limited field environment, competition can be fierce. Synergistic interactions can also play a role. Co-inoculation with other beneficial microorganisms can sometimes enhance the activity of PSMs. For example, Magallon-Servin et al. [191] demonstrated that co-inoculation with mycorrhizal fungi improved phosphate solubilization by PSMs in the field, likely due to enhanced root colonization and nutrient exchange. However, such positive interactions are less predictable and harder to replicate consistently in different field conditions.

5.1.4. Methodological Limitations

The methods used to study phosphate solubilization in the laboratory often do not accurately reflect field conditions. Laboratory assays typically use synthetic media or easily solubilizable phosphate compounds, which do not represent the complex forms of phosphate found in natural soils. As previously mentioned, research frequently use tricalcium phosphate or dicalcium phosphate as substrates due to their greater solubility compared to the rock phosphate or aluminum phosphate typically present in field soils [189,192]. Furthermore, the techniques used in the lab to measure phosphate solubilization—such as molybdenum blue colorimetric assays—might not be readily transferable to field settings. Because these procedures are carried out in ideal circumstances that are rarely replicated in the field, they may overstate the solubilization potential. The limits of existing laboratory approaches were highlighted by Bakhshandeh et al. [193], who showed that the phosphate solubilization assessed in vitro was much higher than that reported in field testing. For example, regarding the solubilization of complexed inorganic P, laboratory studies often use specific solid media or liquid broth assays that typically contain abnormally high concentrations of carbon substrates, such as glucose. The conversion of excess glucose to an organic acid, such as 2-ketogluconurate, observed in laboratory conditions would rarely be replicated in the natural soils where microbes are typically limited for carbon and energy.

Another methodological limitation is the scale of application. Laboratory experiments are often conducted on a small scale, using petri dishes or small pots, which do not account for the spatial variability and scale of field conditions. Field applications involve larger areas and more heterogeneous conditions, making it difficult to achieve uniform distribution and activity of PSMs. Goswami et al. [194] noted that while PSMs showed high phosphate solubilization activity in small-scale pot experiments, their effectiveness was significantly reduced when applied to larger field plots.

6. Conclusions and Recommendations

While PSMs are promising candidates for phosphate solubilization, their use as biofertilizers is still arguably comatose. Some PSM-based biofertilizer formulations and different inoculation strategies were highlighted alongside the variation in PSM populations and their respective phosphate-solubilizing potentials. The inconsistencies in transferring phosphate solubilization results from the laboratory and greenhouse to the field were discussed. To develop efficient biofertilizers, efforts should be geared towards strain improvement of PSMs. Studies should also be aimed towards closing the gap that exists between laboratory and field results of phosphate solubilization.

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