Phosphate-Solubilizing Rhizobacteria: Mechanisms, and Prospects in Sustainable Agriculture

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ABSTRACT

Phosphorus (P) is the second-most important element after nitrogen that is required for plant growth. Although this element is abundant in most soils, it is rarely available in plant-accessible forms since most of it normally exists in soil in insoluble forms such as phosphates. In conventional agriculture, P is normally supplied as chemical fertilizer to satisfy plant P requirements. This, to a large extent, boosts plant production. However, chemical fertilizers are costly, have a huge carbon footprint, and are environmentally-unsustainable owing to the high energy requirements during their synthesis. Besides, P-containing agricultural run-offs contribute hugely to the eutrophication of water bodies and environmental degradation. Moreover, plants can consume only a small amount of chemically-supplied P since between 75 and 90% of this form of P normally get precipitated into complexes and rapidly become fixed in soil. These issues and concerns necessitate research into alternative and viable ways of supplying P to plants. Rhizobacteria have for decades been investigated *in vivo* and *in planta* as suitable tools in sustainable agriculture due to the plant-growth-promoting activities such as nutrients' solubilization, nitrogen fixation, and production of phytohormones. Although a lot of research has been done on different nutrients solubilizing rhizobacteria and their potential in sustainable agriculture, their mechanisms of action and prospects in sustainable agriculture remain to be fully understood. This review particularly focuses on the P solubilizing rhizobacteria and evaluates their diversity, mechanisms of action, and prospects in sustainable agriculture based on the present and future scenario of their application. Such information is useful in determining their potential and evaluating their prospects in promoting sustainable agricultural systems.

Keywords: phosphorus solubilization; plant growth promotion; biofertilizers; sustainable agriculture; phosphorus solubilizing bacteria; rhizobacteria

1. Introduction

Phosphorus (P) is the second-most important nutrient after nitrogen in terms of plant growth and development (Kalayu, 2019; Mitra et al., 2020). This nutrient element is important in virtually every metabolic process in plants from photosynthesis, biosynthesis of macromolecules, and respiration to energy transfer and signal transduction (Billah et al., 2019;). It is a fundamental component of enzymes, proteins, coenzymes, nucleotides, phospholipids, and nucleic acids (Alaylar et al., 2020; Kafle et al., 2019; Kalayu, 2019). According to Mitra et al., (2020), P availability also improves other basic plant functions such as cell division, cell enlargement, and transformation of starches and sugars.

Although P is present in most soils in large quantities, its accessibility to plants is largely limited since it occurs in complex and insoluble forms and only about 0.1% is available for plant use (Alori et al., 2017;). According to Alaylar al (2020), P anions are highly reactive get immobilized through complex formation with different cations like Mg^{2+}, Al^{3+}, Ca^{2+}, and Fe^{3+}, especially under low pH and the fraction that is available to plants is generally very low. Consequently, P is often a major limiting plant nutrient in most soils, and artificial P fertilizers have for long been employed to cater for P deficits in agricultural farms (Mitra et al., 2020). According to FAO, (2017) approximately 52.3 billion tons of P-based fertilizers are applied each year in agricultural lands. These synthetic fertilizers present a lot of problems in the environment. For instance, increased P from agricultural farms has been identified as a major course of eutrophication of surface body waters (C. Bhattacharyya et al., 2020). Contrary to the expectation, the continuous application of P fertilizers has even been shown to contribute to loss of soil fertility through the constant disturbance of natural microbial ecosystems in soil. The efficiency of applied chemical P fertilizers is also reported to rarely exceed 30% due to its fixation in the form of iron/aluminium phosphate in acidic soils or calcium phosphate in neutral/alkaline soils (Kalayu, 2019). About 75 – 90% of the added chemical P fertilizer is precipitated by metal-cation complexes and rapidly becomes fixed or immobilized in soils and has long-term impacts on the environment in terms of eutrophication, soil fertility depletion, and carbon footprint (Zhang et al., 2017). Moreover, P is a finite resource and due to its great demand, and it is estimated that the word's known reserves could be depleted.

The realization of the aforementioned potential problems associated with chemical P fertilizers, together with the high costs involved in their manufacture has led to the search for alternative plant fertilization mechanisms. Plant Growth-Promoting Rhizobacteria (PGPR) are plant-root residing bacteria in symbiotic interactions that have for decades been investigated as alternative environmentally friendly and cheap plant fertilization tools (P. N. Bhattacharyya et al., 2016). Phosphate solubilizing bacteria (PSB) are a subset of the PGPR with the ability to solubilize complex P forms into plant accessible forms. Although a lot of research has been done on different nutrients-solubilizing rhizobacteria and their potential in sustainable agriculture their mechanisms of action and prospects in sustainable agriculture remain to be fully understood. This review focuses on the diversity, mechanisms of action, and prospects of PSB in sustainable agriculture based on the present and future scenario of their application. Such information is useful in determining their potential and evaluating their prospects in promoting sustainable agricultural systems.

2. The diversity of P solubilizing Rhizbacteria

Numerous microorganisms, including fungi, are capable of releasing P from soil through solubilization and mineralization in the natural soil environment (Kafle et al., 2019). It is estimated that 50% of all bacteria in soil are capable of solubilizing P, and several strains of rhizobacteria have been described and investigated in detail for their P solubilizing capabilities. These organisms are ubiquitous but vary in density and P solubilizing abilities from soil to soil (Awais et al., 2019; Kalayu, 2019). These bacteria can be isolated from rhizospheres, rhizoplane, and even non-rhizosphere soils. However, they are known to be more metabolically active and better P solubilizers in plant rhizospheres (P. Kaur & Purewal, 2019; Rafi et al., 2019).

Table 1: Examples of rhizobacteria with P solubilization potential in various plants

Host/Tested Plant	Bacteria	Reference
Bamboo (*Dendrocalamus asper*)	*Bacillus spp., Lactobacillus spp., Burkholderia spp.*	(Suleiman et al., 2019)
Chilli (*Capsicum annum* L.)	*Pseudomonas aeruginosa*	(Linu et al., 2019)
	B. megaterium, P. putida and P. fluorescens	(Baliah et al., 2016)
Common bean (*Phaseolus vulgaris*)	*Bacillus sp.*	(Abdelmoteleb & Gonzalez-Mendoza, 2020)
Faba bean (*Vicia faba* L.)	*Serratia plymuthica*	(Borgi et al., 2020)
Lettuce (*Lactuca sativa*)	*Pseudomonas spp.*	(Jo et al., 2019)
Maize (*Zea mays*)	*Bacillus subtilis*	(Wang et al., 2020)
	Burkholderia cenocepacia	(You et al., 2020)
	Bacillus spp., Pseudomonas spp.	(Akintokun et al., 2019)
Mung bean/Green gram (*Vigna radiata* L.)	*Pantoea agglomerans, Burkholderia anthina Bacillus aryabhattai, B. subtilis*	(Ahmad et al., 2019)
Rice (*Oryza sativa*)	*Bacillus spp., Burkholderia spp., Paenibacillus sp.* *Bacillus, Pseudomonas*	(Eramma et al., 2020)

Soybean (*Glycine max*)	*B. acidiceler, B. megaterium, B. pumilus, B. safensis, B. simplex, Lysinibacillus fusiformis, Paenibacillus cineris and P. graminis*	(Kadmiri et al., 2018)
	Pseudomonas plecoglossicida	(Astriani et al., 2020)
Sugarcane (*Saccharum offcinarum*)	*Burkholderia cepacia, Proteus vulgaris, Pasteurella mulocida, Stenophomonas maltophilia, Burkholderia mallei, Burkholderia pseudomallei, Citrobacter freundii,* *Acienotbacter lwoffi, Pseudomonas fluorescens,* *Enterobacer cloacae, Klebsiella pneumoniae, Klebsiella oxyoca*	(Awais et al., 2019)
Wheat (*Triticum aestivum*)	*Pantoea, Pseudomonas, Serratia, Enterobacter*	(Rfaki et al., 2020)
	Pantoea, Pseudomonas, Serratia, Enterobacter	(Rfaki et al., 2020)
	P. fluorescens, B. megaterium, Serratia marcescens, B. subtilis	(El-Deen et al., 2020)
	Pseudomonas, Streptomyces, Phyllobacterium	(Breitkreuz et al., 2020)

The PSB are present in almost all soils but their numbers vary depending upon soil and climatic conditions. Species of *Pseudomonas, Agrobacterium, Bacillus* (Babalola & Glick, 2012), *Rhizobium*, *Enterobacter*, *Alcaligenes sp., Aerobactor aerogenes, Achromobacter sp.,* and *Burkholderia sp.* are among the most common plant root residing P solubilizers. Others include *Rhodococcus*, *Arthrobacter*, *Serratia*, *Chryseobacterium*, *Gordonia*, *Phyllobacterium*, *Delftia* sp., *Enterobacter, Pantoea*, *Klebsiella*, *Micrococcus, Flavobacterium, Enterobacter, Vibrio, Chryseobacterium, Xanthobacter, Erwinia, Acinetobacter, Pantoea, Burkholderia,* and *Achromobacter*.

Mesorhizobium, *Aeromonas, Mycobacterium, Acetobacter, Corynebacterium, Gluconacetobacter, Achromobacter, Escherichia* and *Ralstonia,* have also been associated with P solubilization and the subsequent increase in plant growth and yield (P. Kaur & Purewal, 2019). Furthermore, many plant root residing PSB have also been isolated from stressed environments for example the halophilic bacteria *Kushneria sinocarni* isolated from the sediment of Daqiao saltern on the eastern coast of China, which may be useful in salt-affected agricultural soils.

Table 1 provides examples of root residing bacteria with P solubilization potential in various plants as reported by several authors. Studies show that the diversity of the PSB is highly varied in different ecological niches and there is ample scope to identify many new potent isolates from varied environments in the coming times. The bacteria involved in P solubilization are numerous and probably more than 99% of them have not been successfully cultured. In this regard, culture-independent methods that are more precise, reproducible, and nondependent on culture conditions could be handier in understanding their functions and ecology (Alaylar et al., 2020). However, such methods cannot exhaustively indicate the quantity of P solubilizers in soils, and much of these bacteria remain unexplored.

Symbiotic nitrogenous rhizobia which are known to be widely associated with the root nodules of various leguminous plants can also solubilize P (Bechtaoui et al., 2019). Some of these species have been shown to produce various organic acids which are highly associated with P solubilization. For instance, while characterizing rhizobia isolated from *Arachis hypogaea* grown under stressed environments, Khalid et al., (2020), established the P solubilization potential of eight rhizobia through the production of organic acids. Similar results have also been reported by Harsitha et al. (2020), Nagalingam et al., (2020), and Sijilmassi et al., (2020) in different plants.

3. Mechanisms of P solubilizing Plant Root Residing Bacteria

The mechanisms of P solubilization depends on the P forms in soil, whether organic or inorganic. While inorganic P forms occur in soil as insoluble mineral complexes, mostly after the application of chemical fertilizers, organic P is mostly constituted in organic matter. According to Alori et al., (2017), organic P can be as high as 30 - 50% of the total P in soil. The most common form of organic P is phytate/inositol P but are largely unavailable to plants because they lack phytase activities (Kafle et al., 2019). Other organic P compounds that have include phosphomonoesters, phosphodiesters, phospholipids, nucleic acids, and phosphotriesters.

Rhizobacteria of many plants have been shown to possess the ability to mineralize both organic and inorganic complex P compounds. For instance, the ability of several rhizobacterial genera to solubilize inorganic P compounds such as tricalcium phosphate, dicalcium phosphate, and rock phosphate is largely documented (Billah et al., 2019; El-Deen et al., 2020). From experiments, the principal mechanism is the production of mineral dissolving compounds such as organic acids, siderophores, protons, hydroxyl ions, and CO_2 (Satyaprakash et al., 2017). Nevertheless, the main mechanism of inorganic P solubilization is largely proposed to be by organic acids (Billah et al., 2019), whose carboxyl and hydroxyl ions act by lowering soil pH, chelating cations like iron, aluminum, and calcium ions bound to P, competing with P for adsorption sites in soil and/or forming soluble complexes with metal ions associated with P (P. N. Bhattacharyya et al., 2016; Billah et al., 2019). These acids that compete for fixation sites of Al and Fe insoluble oxides are called chelates (Kulayu et al., 2019). One such acid which is a powerful chelator of calcium is 2-ketogluconic acid. Organic acids may also directly dissolve mineral P by anion exchange. These acids are products of microbial metabolism such as oxidative respiration or fermentation of organic sources (Satyaprakash et al., 2017)

The organic acids that solubilize phosphates are primarily citric, lactic, gluconic, 2-ketogluconic, oxalic, glyconic, acetic, malic, fumaric, succinic, tartaric, malonic, glutaric, propionic, butyric, glyoxalic, and adipic acid (Satyaprakash et al., 2017).

Others include isovaleric acid, lactic acid, isobutyric acid, and oxalic acid. Table 2 shows different forms of organic acids produced by several PSB associated with different plants. Among these organic acids, gluconic acid is the most common one implicated in P solubilization (Alori et al., 2017). Different organisms produce different types and quantities of organic acids (Kalayu, 2019; Rafi et al., 2019) which is also dependent on the type of carbon available for the microbes (D. Patel & Goswami, 2020). Subsequently, they differ extensively in their P solubilization efficiency (Rafi et al., 2019). (Kalayu, 2019).

The efficiency of P solubilization is greatly dependent on the type of organic acid produced and its concentration. However, evidence suggests that the quality of acids rather than their quantity is more important for P solubilization because the efficiency of solubilization is dependent upon the strength and nature of acids (Kalayu, 2019) . In the same light, tri- and dicarboxylic acids are more effective as compared to monobasic and aromatic acids, and aliphatic acids are also found to be more effective in phosphate solubilization.

Gram-negative bacteria are reportedly more effective P solubilizers than Gram-positive bacteria due to the release of diverse organic acids into the surrounding soil (A. Kumar et al., 2018), but more light needs to be shed on this. Apart from organic acids, other chelating substances, and inorganic acids such as sulphiridic, sulfuric, nitric, and carbonic acids (Pande et al., 2017) are also considered as alternative P solubilizing mechanisms of PSB, but their contribution and effectiveness in this regard are limited (Alori et al., 2017). Nevertheless, this explains why P solubilization by rhizobacteria can occur without the production of organic acids (Chen et al., 2006).

A second and major component of soil P is organic matter which contains organic P forms which may constitute 15 - 85% of the total P in most soils (Dash et al., 2017). The solubilization of organic P forms occurs through mineralization by several PSB (Dash et al., 2017). The mineralization process is mediated by enzymes such as phosphatases and phytase. Phosphatases, which may be acid or alkaline in nature based on their pH optima, are nonspecific enzymes that are secreted by bacterial cells and require P as substrates (Beech et al., 2001) and function by dephosphorylating phospho-ester or phosphor-anhydride bonds of organic matter (Alori et al., 2017; Dash et al., 2017). These enzymes have been studied in many bacterial genera including *Bacillus, Citrobacter, Enterobacter,* *Klebsiella, Proteus, Pseudomonas, Rhizobium*, and *Serratia* (P. N. Bhattacharyya et al., 2017). Phytases, on the other hand, mediate the degradation of phytate or phytic acid which is the major component of organic P in soil (Dash et al., 2017). Plants generally cannot acquire phosphorus directly from phytate, however, the presence of PSM in the rhizosphere may compensate for this. Some plant root residing bacteria that can mineralize complex organic phosphates through the production of extracellular enzymes like phosphor-esterases, phosphor-diesterases, phytases, and phospholipases are members of *Bacillus* and *Streptomyces* spp.). Other enzymes involved in organic P mineralization include phosphonatases (Dash et al., 2017), and lyases (Dash et al., 2017) which function by cleaving organo-phosphonates. Considering the positive impact of such enzymes in the dissolution of complex organic P forms into plantusable forms, it highly desirable that PSB that reduces such enzymes be developed into inoculants for plant biofertilization practices.

Apart from inorganic P solubilization by acidification and organic P solubilization by bacterial enzymes, several other bacterial mechanisms have also been suggested to bring about P solubilization. One important theory of the solubilization of organic P is the sink theory. Microorganisms in the presence of labile C serve as a sink for P, by rapidly immobilizing it even in low P soils; PSB become a source of P to plants upon its release from their cells. Release of P immobilized by PSB primarily occurs when cells die due to changes in environmental conditions, starvation, or predation (S. B. Sharma et al., 2013). Apart from this, bacterial siderophores which are complexing agents with a high affinity for iron have also been considered to take part in P solubilization (Satyaprakash et al., 2017). However, this mechanism of P solubilization has not been widely investigated, and the production of siderophores by PSB has not yet been directly linked to P solubilization. Considering the dominance of mineral dissolution over ligand exchange by organic acid anions as a P solubilization mechanism the potential role of siderophore in P solubilization should be given more attention.

Microbial exopolysaccharides (EPS) which are polysaccharide polymers excreted by microbes into their environment (Das et al., 2017) have also been linked to P solubilization. The authors established a strong indication of P solubilization by *Arthrobacter*, *Azotobacter*, and *Enterobacter* spp. that produced EPS were also shown to increase the quantities of soluble P. This is indeed an interesting phenomenon but more studies are necessary to understand the relationship between EPS production and phosphate solubilization.

It is clear that P solubilization by PSB has been a subject of analysis and research for a long time and yet still seems to be in its infancy. It occurs through different mechanisms and there is considerable variation amongst the organisms in this respect. Each organism can act in one or more than one way to bring about the solubilization of insoluble P. Though it is difficult to pinpoint a single mechanism, the production of organic acids and consequent pH reduction appears to be of great importance.

4. Prospects of P solubilizing Rhizobacteria in Sustainable Agricultures

There is no doubt that artificial P fertilizers can improve plant mineral P nutrition but the resources used to make these fertilizers are finite and dwindling. Moreover, P availability to plants is still limited even in chemical-P supplied soils due to fixation. About 75 – 90% of the added chemical P fertilizer is precipitated by metal-cation complexes and rapidly becomes fixed in soils and has long-term impacts on the environment in terms of eutrophication, soil fertility depletion, and carbon footprint (S. B. Sharma et al., 2013).

For decades, researchers worldwide have vigorously been searching for alternative plant fertilization mechanisms. This has paved ways for the identification of efficient PGP rhizobacteria and their development into biofertilizers by formulating them into different carrier materials. The use of such organisms is greatly advocated for in this regard because they are environmentally friendly and relatively cheap compared to their artificial counterparts. According to Pradhan et al, (2017) these microorganisms can also protect plants against phytopathogens and have a high cost-benefit ratio because of low-cost production technologies. This is because their formulation largely involves the use of agribusiness waste products which are readily and cheaply available. The use of these waste products in the formulation of biofertilizers including the PSB not only contribute to environmental sustainability by providing eco-friendly plant fertilization mechanism but also by reducing the quantity of wastes in the environment.

Microorganisms are an integral part of the phosphorus cycle (Kalayu, 2019), and the beneficial effects of PSB inoculation have been described in many plants and they are already being applied as effective inoculants in agronomic practices to increase the productivity of many crops (P. N. Bhattacharyya et al., 2016; Pradhan et al., 2017). According to Alori et al., (2017), the PSB technology can improve soil fertility and help in the realization of sustainable agriculture with minimized usage of artificial fertilizers and P use efficiency in agricultural lands can be improved through inoculation of PSM (Alaylar et al., 2020; Kalayu, 2019).

The use of PSB as biofertilizers for agriculture enhancement has been a subject of study for several years now (Kalayu, 2019; Wang et al., 2020; Zhang et al., 2017). The inoculation of PSB in soil or seed is widely reported to enhance the solubilization of applied and fixed P in soil, resulting in better crop yield (Alori et al., 2017; Billah et al., 2019; S. B. Sharma et al., 2013; Wang et al., 2020; Zhang et al., 2017). Many studies have reported correlations between the inoculation of PSB in soil with plant height, biomass production, and phosphorus content in plants that have been reported (Zhang et al., 2017).

Several PSB are commercially available in the market in India as formulated products or biofertilizers (Goswami et al., 2016). The first commercial biofertilizer called "Phosphobacterin" was formulated using *Bacillus megaterium* var. *phosphaticum* in the former Soviet Union and later on was frequently applied in East European countries and India. Table 3 presents forms of commercially available PSB biofertilizers in India and their trade names. Although several Gram-negative PSB such as *Pseudomonas* are known to competent P solubilizers, their formulation into biofertilizers is problematic because they do not bear spores, thus, have short shelf lives (D. Patel & Goswami, 2020).

5. Future Trends and Research Focus on P solubilizing Rhizobacteria

Microbial mediated P management is an eco-friendly and cost-effective approach for the sustainable development of crops (S. B. Sharma et al., 2013). The involvement of rhizobacteria in P solubilization is well documented. Most of the studies have however centered on the isolation of these microorganisms from the rhizospheric soil and the in vitro evaluation of their activities, with limited investigations under filed conditions (Pradhan et al., 2017).

Apart from P solubilization, various rhizobacterial PSB possess other PGP traits such as nitrogen fixation, production of PGP hormones and siderophores as well as the solubilization of other plant required nutrients like zinc and potassium. Such PSB can be more advantageous to plants as opposed to those that possess only the P solubilization function. For instance, PSB that produce PGP hormones apart from increasing P availability in the rhizosphere can also increase root development to enhance the uptake of more P. An alternative approach for the use of PSM as microbial inoculants is either the use of mixed cultures or co-inoculation with other microorganisms with other capabilities.

Molecular research has identified and characterized some genes that are involved in mineral and organ P solubilization. Nevertheless, studies on P solubilization and PSB at the genetic level are still inconclusive (Pradhan et al., 2017). The manipulation of such genes through genetic engineering and their expression in selected rhizobacterial strains opens a promising frontier for obtaining PSB with improved P-solubilizing abilities as agricultural inoculants (Pradhan et al., 2017). Indeed, such advances can be superior since a single engineered inoculant can be suitable for the inoculation of several crops. Molecular-based techniques offer the new prospect for the quantification of target gene expression with high potential in plant rhizosphere soils (Alaylar et al., 2019, 2020). Microarrays can also provide a further application for the estimation of the diversity surrounding particular traits or functional groups of microorganisms (Richardson & Simpson, 2011), including the PSB. Together, these tools deliver new opportunities in the ecology of microbial communities and assess the survival and perseverance of specific inoculants under diverse environmental conditions. Biotechnological approaches can develop more knowledge about PSB mechanisms of actions of PSB and pave way for the development of more successful potential in them.

As far as field trials are concerned the establishment and performance of these PSM inoculate developed in the laboratory are largely hampered by environmental variables including salinity, pH, moisture, temperature, and climatic conditions of the soil. Moreover, the inocula developed from a particular soil fail to function as effectively in soils having different properties (S. B. Sharma et al., 2013). Hence the necessity to study PSM activity in correlation with these factors before PSM application as a biofertilizer. The growing need for the discovery of new strains of PSMs necessitates the replacement of the time-consuming and less sensitive conventional methods with alternative approaches that are more accurate, reliable, less time consuming, and show reproducible results (Alaylar et al., 2020). The current approaches and developments in our understanding of the functional diversity, rhizosphere colonizing ability, and mode of actions of PSB are likely to facilitate their application as reliable options in the management of sustainable agricultural systems.

6. Conclusion

Phosphorus is an important limiting factor in agriculture. Considering the cost and the negative effects of chemical fertilizers, efforts should be focused on PSB technology which offers an excellent opportunity to reduce chemical-based agriculture. Although the potential exists for developing such inoculants, their widespread application remains largely limited by the lack of understanding of their diversity, ecology, and population dynamics in soil, and by inconsistent performance over a range of environments. Current and future developments in understanding them fully are likely to facilitate their use as reliable components in agricultural systems. Furthermore, researchers need to address issues like efficacy, delivery systems, and nutritional aspects to reap maximum benefits from their application.

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