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Phosphate-Solubilizing Rhizobacteria: Diversity, 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

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1 Introduction

Phosphorus (P) is the second-most important nutrient after nitrogen in terms of plant growth and development (Alori et al., 2017; Kalayu, 2019; Mitra et al., 2020; Pradhan et al., 2017). 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; M. S. Khan et al., 2010; S. B. Sharma et al., 2013). 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 (S. B. Sharma et al., 2013), and only about 0.1% is available for plant use (Alori et al., 2017; Zhu et al., 2011). According to Mahidi et al., (2011) and 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 (Santana et al., 2016), and artificial P fertilizers have for long been employed to cater for P deficits in agricultural farms (Mitra et al., 2020; S. B. Sharma et al., 2013). 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; Youssef & Eissa, 2014). 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 (Gyaneshwar et al., 2002). 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 (Alori et al., 2017; Kalayu, 2019; A. Kumar et al., 2018; Satyaprakash et al., 2017). 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 (S. B. Sharma et al., 2013; 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 (Leghari et al., 2016) in the current century (Cordell et al., 2009).

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 (Alori et al., 2017; Zaidi et al., 2009). 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; P. N. Bhattacharyya & Jha, 2012). Phosphate solubilizing bacteria (PSB) are a subset of the PGPR with the ability to solubilize complex P forms into plant-accessible forms (Pande et al., 2017; Zaidi et al., 2009). Although a lot of research has been done on different nutrients-solubilizing rhizobacteria and their potential in sustainable agriculture (Chen et al., 2006; M. S. Khan et al., 2010), 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 (Alori et al., 2017; P. N. Bhattacharyya & Jha, 2012; Kafle et al., 2019). It is estimated that 50% of all bacteria in soil are capable of solubilizing P (S. B. Sharma et al., 2013), and several strains of rhizobacteria have been described and investigated in detail for their P solubilizing capabilities. According to Sharma et al., (2013), these organisms are ubiquitous but vary in density and P solubilizing abilities from soil to soil (Awais et al., 2019; Chen et al., 2006; Kalayu, 2019; Vessey, 2003). These bacteria can be isolated from rhizospheres, rhizoplane, and even non-rhizosphere soils (S. B. Sharma et al., 2013; Zaidi et al., 2009). However, they are known to be more metabolically active and better P solubilizers in plant rhizospheres (P. Kaur & Purewal, 2019; A. A. Khan et al., 2009; Rafi et al., 2019; Vessey, 2003).

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

Host/Tested Plant	*Bacteria*	*Reference*
Apple (*Malus domestica*)	*Pseudomonas spp.*	(R. Sharma et al., 2017)
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)
Coffee (Coffea arabica L.)	*Pseudomonas sp., Bacillus sp., Enterobacter sp. and Stenotrophomonas sp.*	Teshome et al., 2017
	Pseudomonas chlorophis, Erwinia rapontici, Bacillus sp., Serratia marcescens	(Muleta et al., 2013)
Common bean (*Phaseolus vulgaris*)	*Bacillus sp.*	(Abdelmoteleb & Gonzalez-Mendoza, 2020)
Cotton (*Gossypium sp.*)	*B. megaterium, P. putida and P. fluorescens*	(Baliah et al., 2016)
Drumstick tree (*Moringa oleifera*)	*Azotobacter chroococcum, Saccharomyces cerevisiae, and Bacillus megaterium*	(Zayed, 2012)
Eggplant (*Solanum melongena*)	*B. megaterium, P. putida and P. fluorescens*	(Baliah et al., 2016)
Faba bean (*Vicia faba* L.)	*Serratia plymuthica*	(Borgi et al., 2020)
Lentil (*Lens culnaris*)	Enterobacter, Bacillus, Pseudomonas spp.	(Midekssa et al., 2015)
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)
	Bacillus spp., Lactobacillus spp., Burkholderia spp.	(Suleiman et al., 2019)
	Pseudomonas plecoglossida, Acromobacter insolitus, Enterobacter hormaechei	(Oo et al., 2020)
	Bacillus aryabhattai, B. subtilis	(Ahmad et al., 2019)
	Bacillus safensis, B. pumilus, Kocuria rosea, Enterobacter aerogenes, Aeromonas veronii	(Mukhtar et al., 2020)
	Burkholderia cepacian	(Zhao et al., 2014)
	Pseudomonas sp., Anthrobacter nicotinovorans	(Pereira & Castro, 2014)
	Lysinibacillus fusiformis	(Rafique et al., 2017)
	B. flexus, B. megaterium, Sinorhizobium melitoti	(Ibarra-Galeana et al., 2017)
	P. fluorescens, P. putida, Enterobacter sp., B. megaterium, B. firmus, P. agglomerans	(Sarikhani et al., 2020)
	B. acidiceler, B. megaterium, B. pumilus, B. safensis, B. simplex, Lysinibacillus fusiformis, Paenibacillus cineris and P. graminis	(Kadmiri et al., 2018)
	Alcaligenes aquaticus, Burkholderia cepacia	(Pande et al., 2017)
Mung bean/Green gram (*Vigna radiata* L.)	*Pantoea agglomerans, Burkholderia anthina*	(Walpola & Yoon, 2013)
	Bacillus aryabhattai, B. subtilis	(Ahmad et al., 2019)
	Bradyrhizobium sp., Rhizobium sp.,	(Yaqub & Shahzad, 2011)
	Various PSB	(Kolekar et al., 2017)
	Pseudomonas plecoglossida, Acromobacter insolitus, Enterobacter hormaechei	(Oo et al., 2020)
Mushroom (*Agaricus busporus*)	*Acinetobacter baumanii, B. megaterium, Paenibacillus taichungensis*	(Zhang et al., 2017)
Oil palm tree (*Elaeis guineensis*)	Pseudomonas fluorescens	(Fankem et al., 2006)
Okra (*Abelmoschus esculentus*)	*B. megaterium, P. putida and P. fluorescens*	(Baliah et al., 2016)
Rice (*Oryza sativa*)	*Bacillus spp., Burkholderia spp., Paenibacillus sp.*	
	Bacillus, Pseudomonas	(Eramma et al., 2020)

	Aeromonas hydropila, Klebsiella pneumoniae, E. aerogenes	(Awais et al., 2019)
	Paenibacillus sp.	(Qu et al., 2020)
Miscanthus giganteus	*P. fluorescens*	(Oteino et al., 2015)
Pine (*Pinus elliotii*)	*Burkholderia multivorans*	(Liu et al., 2020)
Potato (*Solanum tuberosum* L.)	*Klebsiella sp., Citrobacter sp., Serratia sp.*	(Aloo et al., 2020)
	Non-identified	(Jadoon et al., 2019)
Runner bean (*Phaseolus coccineus*)	*Pseudomonas lini, B. mycoides, B. pumilus*	(Mihalache et al., 2018)
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)
	Not mentioned	(Awais et al., 2019)
	Proteus vulgaris, Klebsiella pneumoniae, E. aerogenes, B. cepacian, Citrobacter freundii, A. lwaffii, P. fluorescens	(Sadiq et al., 2013)
Taro (*Colocasia esculenta*)	*Aquabacterium commune, Bacillus sp.*	(Thiruvengadam et al., 2020)
Tomato (*Solanum lycopersicum*)	*B. megaterium, P. putida and P. fluorescens*	(Baliah et al., 2016)
	B. subtilis, Serratia marcescens	(Akinrinlola et al., 2018)
Different legumes	Bacillus sp., Proteus sp., Pseudomonas sp., Azospirillum sp.	(Selvi et al., 2017)
Wheat (*Triticum aestivum*)	*Not specified*	(Batool & Iqbal, 2018)
	Non-identified	(Panhwar et al., 2020)
	Not mentioned	(Emami et al., 2020)
	Pantoea, Pseudomonas, Serratia, Enterobacter	(Rfaki et al., 2020)
	Serratia marcescens	(Sood et al., 2018)
	B. acidiceler, B. megaterium, B. pumilus, B. safensis, B. simplex, Lysinibacillus fusiformis, Paenibacillus cineris and P. graminis	(Kadmiri et al., 2018)
	Azotobacter spp.	(S. Kumar et al., 2014)
	Azospirillum, Azotobacter, Pseudomonas, Enterobacter, Bacillus	(Saleemi et al., 2017)
	Streptomyces sp., Rhodococcus sp.	(Jog et al., 2014)
	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)
	Several strains	(Batool & Iqbal, 2018)
	P fluorescens, Azospirillum brasilense	

The PSB are present in almost all soils but their numbers vary depending upon soil and climatic conditions (Rafi et al., 2019). Species of *Pseudomonas, Agrobacterium, Bacillus* (Babalola & Glick, 2012), *Rhizobium*, *Enterobacter* (Zaidi et al., 2009), *Alcaligenes sp., Aerobactor aerogenes, Achromobacter sp.,* and *Burkholderia sp.*(Pande et al., 2017) are among the most common plant root residing P solubilizers. Others include *Rhodococcus*, *Arthrobacter*, *Serratia*, *Chryseobacterium*, *Gordonia*, *Phyllobacterium*, *Delftia* sp. (Chen et al., 2006), *Enterobacter, Pantoea*, *Klebsiella* (Chung et al., 2005), *Micrococcus, Flavobacterium, Enterobacter, Vibrio, Chryseobacterium, Xanthobacter, Erwinia, Acinetobacter, Pantoea, Burkholderia,* and *Achromobacter* (S. B. Sharma et al., 2013).

Mesorhizobium (Oteino et al., 2015), *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 (Etesami & Maheshwari, 2018; Zhu et al., 2011).

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 (S. B. Sharma et al., 2013). 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 non-dependent 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 (A. Kumar, 2016).

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; A. A. Khan et al., 2009; Pande et al., 2017; Qin et al., 2011; Walpola & Yoon, 2013; Zaidi et al., 2009). 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 (S. B. Sharma et al., 2013). 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 (Alori et al., 2017; Kafle et al., 2019; A. Kumar, 2016). Other organic P compounds that have include phosphomonoesters, phosphodiesters, phospholipids, nucleic acids, and phosphotriesters (A. Kumar, 2016).

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; S. B. Sharma et al., 2013). Nevertheless, the main mechanism of inorganic P solubilization is largely proposed to be by organic acids (Billah et al., 2019; Pande et al., 2017; Rafi et al., 2019; Walia et al., 2017), 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; S. T. Patel & Minocheherhomji, 2018; Pradhan et al., 2017; S. B. Sharma et al., 2013). 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 (Walpola & Yoon, 2013). Organic acids may also directly dissolve mineral P by anion exchange (Satyaprakash et al., 2017). These acids are products of microbial metabolism such as oxidative respiration or fermentation of organic sources (Satyaprakash et al., 2017; Zaidi et al., 2009).

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 (A. Kumar et al., 2018; Satyaprakash et al., 2017).

Table 2: Organic acids produced by various phosphate-solubilizing rhizobacteria

Host/test plant	*Bacteria*	*Organic acid(s)*	*Reference*
Mangroves	*Bacillus amyloliquefaciens, Bacillus licheniformis, Bacillus atrophaeus, Paenibacillus macerans, Pseudomonas aeruginosa*	Lactic, isovaleric, isobutyric, acetic	(Vazquez et al., 2000)
Oil palm tree (Elaeis guineensis)	*Pseudomonas fluorescens*	Citric, malic, tartaric, gluconic	(Fankem et al., 2006)
Sunflower (Helianthis annuus L.)	*Enterobacter sp. Fs-11*	Malic acid, gluconic	(Shahid et al., 2012)
Several Legumes	*Bacillus sp., Proteus sp., Pseudomonas sp., Azospirillum sp.*	Citric, malic, succinic, fumaric, tartaric, gluconic, succinic, ketobutyric, glyoxalic, glutaric	(Selvi et al., 2017)
Coffea arabica	*Pseudomonas chlorophis, Erwinia rapontici, Bacillus sp., Serratia marcescens*	2-ketogluconic, gluconic, acetic, propionic	(Muleta et al., 2013)
Miscanthus giganteus	*Pseudomonads*	Gluconic	(Oteino et al., 2015)
Mangrove	*Serratia sp.*	Lactic, malic, acetic	(Behera et al., 2016, 2017)
Chickpea	*Burkholderia*	gluconic, acetic, and citric	(Valverde et al., 2006)
Lentil (Lens culnaris Medik.)	*Enterobacter, Bacillus, Pseudomonas spp.*	Not identified	(Midekssa et al., 2015)
Maize (Zea mays)	*Burkholderia cepacian, Alcaligenes aquatilis*	Gluconic, formic, citric	(Pande et al., 2017)
Rice (Oryza sativa)	*Bacillus, Pseudomonas*	Gluonic	(Eramma et al., 2020)
	Enterobacter sp.	Citric, lactic, tartaric	(Dash & Dangar, 2019)
Apples	*Pseudomonas spp.*	Schimic, succinic, malonic, citric, malic, quinic, tartaric, fumaric and lactic	(R. Sharma et al., 2017)
Runner bean	*Pseudomonas lini, B. mycoides, B. pumilus*	Isocitric, Tartaric, Succinic	(Mihalache et al., 2018)
Araucaria	*Pantoea agglomerans*	Gluconic, oxalic, tartaric, malic, acetic, citric, succinic	(Li et al., 2020)
Maize	*Not determined*	Malic	(Fitriatin et al., 2020)
Wheat (Triticum aestivum)	*Pantoea, Pseudomonas, Serratia, Enterobacter*	Oxalic, citric, gluconic, succinic, fumaric, acetic	(Rfaki et al., 2020)
Lettuce (Lactuca sativa)	*Pseudomonas*	Carboxylic, gluconic	(Jo et al., 2019)
Mung bean (Vigna radiata L.)	*Acinetobacter sp. Pseudomonas sp., Microbacterium sp.*	Gluconic, acetic	(Hakim et al., 2020)

Others include isovaleric acid, lactic acid, isobutyric acid, and oxalic acid (C. Kaur et al., 2016; Rawat et al., 2018). 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; S. B. Sharma et al., 2013). Different organisms produce different types and quantities of organic acids (Kalayu, 2019; Rafi et al., 2019; Satyaprakash et al., 2017), 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).

According to Delfim et al., (2018), 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 compared to phenolic, citric, and fumaric acids (Mahidi et al., 2011; Walpola & Yoon, 2013). Additionally, the simultaneous production of different organic acids may contribute to greater P solubilization potential (Marra et al., 2012).

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; Walpola & Yoon, 2013) are also considered as alternative P solubilizing mechanisms of PSB, but their contribution and effectiveness in this regard are limited (Alori et al., 2017; Pradhan 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 phytases (Behera et al., 2016, 2017; Dash et al., 2017; Maougal et al., 2014). Phosphatases, which may be acid or alkaline in nature based on their pH optima (Jorquera et al., 2011), 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; S. B. Sharma et al., 2013). These enzymes have been studied in many bacterial genera including *Bacillus, Citrobacter, Enterobacter, Klebsiella, Proteus, Pseudomonas, Rhizobium*, and *Serratia* (Behera et al., 2016, 2017; C. Bhattacharyya et al., 2020). 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; Pradhan et al., 2017). Plants generally cannot acquire phosphorus directly from phytate, however, the presence of PSM in the rhizosphere may compensate for this (Richardson & Simpson, 2011). 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. (A. A. Khan et al., 2009). Other enzymes involved in organic P mineralization include phosphonatases (Dash et al., 2017; V. Kumar et al., 2013), and lyases (Dash et al., 2017; Salimpour et al., 2010) which function by cleaving organo-phosphonates. Considering the positive impact of such enzymes in the dissolution of complex organic P forms into plant-usable 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 (A. Kumar et al., 2018; Parker et al., 2005; 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 (Parker et al., 2005), 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 (Walia et al., 2017) have also been linked to P solubilization (Yi et al., 2008). 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 (Babalola & Glick, 2012). 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.

Table 3: Examples of commercially available Phosphate Solubilizing Rhizobacterial biofertilizers in different countries

Product	Bacteria	Company	Crop	Country	Reference
Anubhav liquid formulation	*B. coagulans*	Anand Agricultural University	All crops	India	(Vyas et al., 2017)
Azo-N Plus*	*Azospirillum brasilense, Azospirillum lipoferum, Azotobacter chroococum*	BioControl Products SA (Pty) Ltd	Not specified	South Africa	(Rodrigues et al., 2008)
Azo-N*	*Azospirillum brasilense, Azospirillum lipoferum*	BioControl Products SA (Pty) Ltd	Not specified	South Africa	(Rodrigues et al., 2008)
Bac up*	*B. subtilis*	Biological control product Ltd	Not specified	South Africa	(Ahemad & Khan, 2010; Mohammadi & Sohrabi, 2012; Parmar & Sindhu, 2013)
Bio Gold*	*P. fluorescens, Azotobacter chroococcum*	Bio Power Lanka	Cardamom, potato, vegetables, fruits, cereals	Sri Lanka	(Mehnaz et al., 2016)
Bio Phos®	*B. megaterium*	Bio Power Lanka	Not mentioned	Sri Lanka	(Mehnaz et al., 2016)
Bioativo*	*PGPR consortia*	Embrafos Ltd	Bean, maize, sugarcane, rice, carrot, cotton, maize, citrus, tomatoes, soybean	Brazil	(García-Fraile et al., 2015; Odoh et al., 2019)
Phylazonit	*Azotobacter chroococcum, B. megaterium*	Ministry of Agriculture	Not specified	Hungary	(Dash et al., 2017)
Bio-phos, Humi-phos	*Various non-identified PSB*	Auriga Group of companies	Not specified	Pakistan	(Mehnaz et al., 2016)
Biomix, Gmax PGPR	*Aotobacter, P. fluorescens, Phosphobacteria*	GreenMax Agrotech	Several plants and field crops	India	(Odoh et al., 2019)
Bio-N*	*Azotobacter spp.*	Nutri-Tech Solution	Australia	Australia	(Adeleke et al., 2019)
Biophos	*Non-identified PSB*	Ajay Bio-Tech Ltd	Various crops	India	http://www.ajaybio.in/prodpro.htm
Biophos, Get-Phos, Reap P, Phosphonive	*B. megaterium var. phosphaticum*	Not mentioned	All crops	India	(Thomas & Singh, 2019)
B-RUS, Extrasol*	*B. subtilis*	Ag-Chem Africa (Pty) Ltd	Not specified	South Africa	(Ahemad & Khan, 2010; Mohammadi & Sohrabi, 2012; Parmar & Sindhu, 2013)
Calphorous	*Non-identified PSB*	Camson Bio Technologies Limited	Legumes, cereals, vegetables	India	http://wwwcamsonbiotechologies.com/products/bio_fertilizers_and_stimulants.htm
Composter*	*Bacillus sp.*	BioControl Products SA (Pty) Ltd	Not specified	South Africa	(Mohammadi & Sohrabi, 2012; Parmar & Sindhu, 2013)
Ecosoil	*P. aureofaciens*	ZECH Umwelt GmbH	Cucumber, tomato, wheat, barley	Germany	(D. Patel & Goswami, 2020)
Ferti-Bio*	*PGPR consortia*	Microbial Biotechnologies	Rice, wheat, corn, cotton, sugarcane, vegetables	Pakistan	(Kennedy et al., 2004; Mehnaz et al., 2016; Mishra & Arora, 2016)

Fosforina®	*P. fluorescens*	National Program Project Agricultural Biotechnology of Cuba	Tomato	Cuba	(Mishra & Arora, 2016)
FZB 23 ®	*B. amyloliquefaciens sp. plantarium*	AbiTEP GmbH	Vegetables	Germany	(Odoh et al., 2019; Yao et al., 2006)
Gmax FYTON, Ashtha PF	*P. fluorescens, Azotobacter, Phosphobacteria*	GreenMax Agro Tech	Tomatoes, chilli, orchads, vineyards, ornamentals, potato, cucumbers, eggplant	India	(G. Kumar & Sarma, 2016; Pallavi et al., 2017)
Histick*	*Bradyrhizobium jponicum*	BASF South Africa (Pty) Ltd	Not specified	South Africa	(Tairo & Ndakidemi, 2014)
Inomix	*B. subtilis, P. fluoresecens, B. polymyxa*	LAB (Labbiotech)	Cereals	Spain	https://en.iabiotec.com/products/microbial-inoculants/
LifeForce*, Biostart*, Landbac*, Waterbac*	*Bacillus sp.*	Microbial solution (Pty) Ltd	Not specified	South Africa	(Mohammadi & Sohrabi, 2012; Parmar & Sindhu, 2013)
Likuiq Semia*	*Bradyrhizobium elkanil*	Microbial solution (Pty) Ltd	Not specified	South Africa	(Tairo & Ndakidemi, 2014)
Mazospirflo*	*Azospirillum brasilense*	Soygro (Pty) Ltd	Not specified	South Africa	(Rodrigues et al., 2008)
NAT-P	*P. fluorescens*	BioControl Products SA (Pty) Ltd	Not specified	South Africa	(Parani & Saha, 2012)
N-Soy*	*Bradyrhizobum japonicum*	BioControl Products SA (Pty) Ltd	Not specified	South Africa	(Tairo & Ndakidemi, 2014)
Organo/Organico*	*Bacillus spp., Enterobacter spp., Pseudomonas, Stenotromonas, Rhizobium*	Amka Products (Pty) Ltd	Not specified	South Africa	(Ahemad & Khan, 2010; Mohammadi & Sohrabi, 2012; Parmar & Sindhu, 2013)
P Sol B® - BM	*B. megaterium, Pseudomonas striate*	AgriLife	Not mentioned	India	(Berninger et al., 2018; Mishra & Arora, 2016)
Phosphatika	*Not mentioned*	TNAU Agritech Portal	Not specified	India	http://agritech.tnau.ac.in
Phosphobacteria	*Not mentioned*	Monarch Bio-Fertilizers and Research Centre	Not specified	India	http://www.monarchbio.co.in/bio_fertilizers.html
Phosphobacteria	*B. megaterium var phosphaticum*	Agro bio tech Research Centre LTD	Not specified	India	http://www.abtecbiofert.com/products.html
Phosphobacterium	*Not mentioned*	SAFS Organinc Eneterprises	Not specified	India	https://www.indiamart.com/safsorganicenterprises/bio-fertilizer.html#bio-fertilizer-phosphobacterium

Gmax, Phosphomax, Astha PSB	*B. megaterium, P. striata*	Varsha Bioscience and Technology	All crops	India	(Pallavi et al., 2017) http://www.varshabioscience.com/products/phosphomax.html
Rhizosum® P	*B. megaterium*	Biosym Technologies	Not specified	India	(Mehnaz et al., 2016)
Sardar Biofertilizer	*Azotobacter, Azospirillum, and non-identified PSB*	Gujarat State Fertilizers and Chemicals	All types of crops	India	http://www.gsfclimited.com/bio_fertilizers.asp?mnuid=3&fid=32
Signum	*Rhizobacter sp., Bradyrhizobium sp.*	Rhizobacter S. A.	Legumes and cereals	Argentina	http://www.rhizobacter.com/argentian/productos/
Soil Vital Q*	*B. subtilis, B. thuringiensis, Azotobacter chroococum, Lactobacillus sp., Pseudomonas fluorscens*	Biological control Products SA (Pty) Ltd	Not specified	South Africa	(Ahemad & Khan, 2010; Mohammadi & Sohrabi, 2012; Parmar & Sindhu, 2013)
SoilFix*	*Bravibacillus laterosporus, Paenibacillus chitinolyticus, lysinibacillus sphaericus, Sporolactobacillus laevolacticus*	BioControl Products SA (Pty) Ltd	Not specified	South Africa	(Grady et al., 2016)
Soyflo*	*Bradyrhizobium japonicum*	Soygro (Pty) Ltd	Not specified	South Africa	(Tairo & Ndakidemi, 2014)
Symbion-P	*B. megaterium var phosphaticum*	T. Stanes & Company Limited	Cereals, legumes and vegetable crops	India	http://www.tstanes.com/products-symbion-p.html
Twin N	*Azorhizobium sp., Azoarcus sp., Azospirillum sp.*	Mapleton Ltd	Legumes and cereals	Australia	(Mehnaz et al., 2016; Mishra & Arora, 2016; Rodrigues et al., 2008)
Vault NP*	*Bradyrhizbium japonicum*	Becker Underwood	Legumes	USA	(Tairo & Ndakidemi, 2014)
Xin Cheng Li	*B. mucilaginous, B. subtilis, Phosphobacteria*	CBF China Bio-Fertilizer AG	Not mentioned	China	(Mishra & Arora, 2016)
Phylazonit M*	*Azotobacter chrococcum, B. megaterium*	Ministry of Agriculture	Not mentioned	Hungary	(Dash et al., 2017)

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; R. Sharma et al., 2017; 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 (Santana et al., 2016).

Several PSB are commercially available in the market 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 (Mohammad et al., 2007). Table 3 presents forms of commercially available PSB biofertilizers in different countries 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 (Varma et al., 2017; Yildirim et al., 2011; Zaidi et al., 2009). 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 (Etesami & Beattie, 2018; Etesami & Maheshwari, 2018). 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 (Walia et al., 2017). 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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