



Phosphorus Solubilizing Microorganisms: An Eco-Friendly Approach for Sustainable Plant Health and Bioremediation

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Abstract

Phosphorus (P) is one of the essential macronutrients for plant metabolism. Regardless of its great quantity in inorganic and organic forms, it is generally inaccessible for plant utility due to bond formation with other ions present in soil. Due to the excessive use of agrochemicals, environmental issues have reached their peak. This has increased the interest of the scientific community in finding a sustainable alternative to chemical fertilisers. Diverse microbes like *Rhizobium* spp., *Serratia* spp., *Pseudomonas* spp., *Bacillus* spp., *Azotobacter* spp., *Penicillium* spp., *Rhizopus* spp., *Fusarium* spp., and various actinomycetes have been isolated and screened as phosphorus solubilizing microorganisms (PSMs). The PSMs also act as biological control agents (bioagents) and help to withstand extreme stress circumstances (like heavy metal toxicity) by producing ACC deaminase. With the advent of time, organic farming is gaining attention as this technology is highly eco-friendly, so utilisation of potential microorganisms for solubilisation of phosphorus will improve soil health and crop productivity. PSMs possess significant heavy metal remediation potential; therefore, they can be used in restoration of contaminated soil as well as in enhancing plant health. This review will provide in-depth knowledge about PSMs and their role in sustainable agriculture and bioremediation of toxicants.

Keywords Phosphorus Solubilizing Microorganisms · Bioremediation · Bioagents · Solubilisation · Soil Health

1 Introduction

There is a necessity for adequate food requirements to overcome the increasing population demand at global level. To increase the productivity, farmers are using chemical-based fertilizers that are improving crop yield, however it is proven that application of these chemicals have adverse impact on soil productiveness (Yattoo et al. 2021; Fatima et al. 2021). A profitable mode of availing phosphorus to plants is using PSMs (Kirui et al. 2022). Efforts to enhance

the soil biological system are essential to address the aforementioned issues. Although phosphorus (P) is a macronutrient, it is crucial for plant health and often required in significant amounts (Kirui et al. 2022; Rawat et al. 2021; Kalayu 2019), contributing to 0.2 percent dry weight of plant (Maharajan et al. 2018). It is one of the main components of phospholipids, phosphoproteins, and cofactors and is the constituent of skeletal structure of genetic material of living creatures (Ozane 1980; Bai et al. 2020; Timofeeva et al. 2022; Feng et al. 2024). P is the vital element associated in plant metabolism with many functions like cell division, nitrogen fixation, nucleic acid and protein formation, crop quality, disease resistance (Khan et al. 2014; Nesme et al. 2018; Koch et al. 2018). Though soil holds entire P in organic and inorganic form, maximum of them remains locked thus becomes unavailable to plants (Kalayu 2019; Dong et al. 2023).

Phosphorus deficiency distresses root architecture (Williamson et al. 2001). Phosphorus deficiency leads to pale, dull, blue-green leaves and delayed maturity (Bai et al. 2013). This macronutrient is utilized in an inorganic form either as $\text{H}_2\text{PO}_4^{4-}$ or HPO_4^{2-} or both (Hinsinger 2001;

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Divjot et al. 2021; Li et al. 2021). Numerous microorganisms produce low molecular weight organic acids, such as acetic acid, citric acid, oxalic acid, malic acid, and gluconic acid, which help solubilize P. These acids chelate cationic partners of phosphorus ions, thereby releasing phosphorus directly into the soil solution. Microorganisms, including various species of *Aspergillus*, *Fusarium*, *Penicillium*, *Serratia*, *Bacillus*, *Azotobacter*, *Rhizobium* and *Pseudomonas*, play a crucial role in this process. They assimilate phosphorus and prevent its immobilization or fixation, thus enhancing its availability to plants. This microbial activity is vital for maintaining soil fertility and promoting healthy plant growth (Khan et al. 2009a, b, c).

Microorganisms, through various processes such as mineralization, solubilization, and decomposition influences soil fertility. Microbes increase phosphorus availability by solubilizing the locked form of phosphorus (Chen et al. 2006; Kang et al. 2002). Microorganisms acts as a substitute for phosphorus fertilizers (Padmavathi and Usha 2012). From couple of decades numerous PSMs studies were under focus which include various species of *Serratia*, *Micrococcus*, *Enterobacter*, *Azotobacter*, *Rhizobium* and *Micrococcus* (Kirui et al. 2022; Chawngthu et al. 2020; Mohamed et al. 2018; Yadav et al. 2016) *Rhizobium*, *Arthrobacter* and *Rahnella aquatilis* HX2 (Chawngthu et al. 2020; Zhang et al. 2019; Liu et al. 2019), *Leclercia adecarboxylata* (Teng et al. 2019a), the other fungi function in same way which includes species of *Penicillium*, *Aspergillus*, *Fusarium*, and *Hymenella* (Zhu et al. 2011; Ichriani et al. 2018) are potential PSMs and can be used as an substitute for phosphorus fertilizers (Padmavathi and Usha 2012). Phosphate solubilizing microbes produce some essential phyto hormones like cytokinins, auxins, and gibberellins which have a role in cell division, differentiation, root and shoot development, germination, flowering (Puri et al. 2020).

Moreover, bioremediation has attracted a lot of scientific attention in recent years. Heavy metals like Cu, Pb, Ni, Hg, Cd, and Zn among others, play a role in several environmental problems. Heavy metals pose a significant challenge as pollutants that are not easily broken down. These pollutants can originate from either natural sources or human activities (Tan et al. 2021). Microorganisms like bacteria, fungi, yeast and actinomycetes are known for bioremediation of heavy metals. Microbes have demonstrated remarkable effectiveness in the remediation of environmental pollutants (Ahmed et al. 2022; Hamid et al. 2023a; Hamid et al. 2023b). Various phosphate solubilizing microbial strains which belong to genus *Bacillus*, *Pseudomonas*, *Paenibacillus*, *Staphylococcus*, *Aspergillus*, *Rhizopus*, *Trichoderma* and *Brevibacterium* have been reported as bioremediators (Khambhaty et al. 2008; Vala and Sutariya 2012; Yahaghi et al. 2018; Bashir et al. 2018a, b).

2 Phosphorus Solubilizing Microorganisms (PSMs)

PSMs are abundant in the soil and may be readily isolated from a diverse rhizospheric soils (Manoj et al. 2018). The number of P solubilizers present in a soil are based on many factors like organic content and properties of soil (Menezes-Blackburn et al. 2013). Phosphorus solubilizers are observed in rhizosphere where many chemical reactions occur (Mittra et al. 2020; Chawngthu et al. 2020). PSMs play central part in phosphorus cycling in the environment (Khan et al. 2024; Mittra et al. 2020; Saha and Biswas 2009). Since 1903, the PSMs (bacteria, fungi, actinomycetes) that occurs naturally as per reports of Khan et al. (2009a, b, c) play an important role in phosphorus solubilization in soil.

Phosphorus occurs either in organic form or as phosphite and many solubilizing microorganisms have been obtained and identified from varied habitats (Acevedo et al. 2014; Taktek et al. 2015; Bashir et al. 2018a; Chawngthu et al. 2020; Divjot et al. 2021). PSMs includes many species of *Azotobacter*, *Bacillus*, *Serratia*, *Enterobacter*, *Micrococcus*, *Rhizobium*, *Penicillium*, *Aspergillus*, *Rhizopus*, *Fusarium* etc. (Kour et al. 2020). These microbial species have been isolated and screened from aquatic and terrestrial habitats (De Souza et al. 2000; Chakdar et al. 2018). These were also isolated and identified from rhizosphere of rice, banana, vegetable, apple, pear, walnut (Chawngthu et al. 2020; Bashir et al. 2019a, b; Bashir et al. 2017, 2018a, b; Kumar et al. 2013; Naik et al. 2008). A part from many species of *Bacillus* and *Pseudomonas* other potential P-solubilizers are *Rhodococcus*, *Serratia*, *Arthrobacter*, *Chryseobacterium*, *Xanthomonas*, *Azotobacter*, *Klebsiella*, *Enterobacter*, *Acinetobacter* (Wani et al. 2007; Kumar et al. 2013; Chen and Liu 2019; Chawngthu et al. 2020; Zhao et al. 2023). Here are some examples of PSMs that have been studied (Table 1).

Among all PSMs in soil PSB constitutes 1 to 50%, fungi constitute 0.1 to 0.5% (Chen et al. 2006). Among actinomycetes, 20% of the genera *Micromonospora*, *Actinomyces*, and *Streptomyces* can solubilize P (Aallam et al. 2021; De Zutter et al. 2022). Soil is the hotspot for diverse microflora. Phosphorus solubilizers are the microorganisms that have ability of changing locked form of P in to a plant accessible form (Chawngthu et al. 2020; Silva et al. 2023; Khan et al. 2024). Their potency for solubilization of P can be analysed via both qualitative and quantitative approach (Mehta and Nautiyal 2001). These PSMs are diversified in nature, bacteria from the genera *Serratia*, *Leclercia adecarboxylata*, *Enterobacter*, *Pantoea*, *Bacillus*, *Pseudomonas*, *Arthrobacter* and fungi like *Aspergillus niger*, *Penicillium spp*, *Acremonium*,

Table 1 Phosphorus solubilizing microorganisms and their sources of isolation

S. No	Source of isolation	Phosphorus Solubilizing Microorganisms	References
1	Rhizospheric soil	<i>Aspergillus niger</i> , <i>Aspergillus flavus</i> , <i>Penicillium</i> sp., <i>Rhizopus</i> sp., and <i>Mucor</i> sp	Uzah et al. (2024)
2	Rhizospheric soil	<i>Epicoccum dendrobii</i> B-27	Zhan et al. (2023)
3	Rhizospheric soil	<i>Penicillium</i> sp., Sarita-12	Zhan et al. (2023)
4	Saline alkali soil	<i>Bacillus amyloliquefaciens</i>	Zhang et al. (2023a, b)
5	Rhizospheric soil	<i>Serratia marcescens</i>	Gong et al. (2022)
6	Rhizospheric soil	<i>Fusarium</i> spp.,	Liu et al. (2022)
7	Wheat rhizospheric soil	<i>Klebsiella variicola</i>	Kusale et al. (2021)
8	Rhizospheric soil	<i>Penicillium oxalicum</i>	Qarni et al. (2021)
9	Cereal crops rhizospheric	<i>Pseudomonas libanensis</i>	Kour et al. (2020)
10	Rhizospheric soil	<i>Gongronella hydei</i> , <i>Penicillium soli</i>	Mingkwon et al. (2020)
11	Peat	<i>Staphylococcus cohnii</i>	Hii et al. (2020)
12	Rhizospheric soil	<i>Klebsella variicola</i>	Nacoon et al. (2020)
13	Heavy metal contaminated soil	<i>Pseudomonas putida</i>	Teng et al. (2019b)
14	Rhizospheric soil	<i>Aspergillus niger</i> (strain SI-10URAg; SI-11URAg; SI-12URAg) <i>Panicillium oxalicum</i> and <i>Talaromyces pinophilus</i>	Islam et al. (2019)
15	Saline alkali soil	<i>Burkholderia cenocepacia</i>	Zhang et al. (2019)
16	Rhizospheric soil	<i>P. fulva</i>	Munir et al. (2019)
17	Saline alkali soil	<i>Arthrobacter defluvii</i>	Zheng et al. (2019)
18	Rhizospheric soil	<i>Aspergillus fumigatus</i> TS1 and <i>Fusarium proliferatum</i> BRL1	Bilal et al. (2018)
19	Gut of earthworm	<i>Bacillus megaterium</i>	Biswas et al. (2018)
20	Rhizospheric soil	<i>T. beigelii</i> and <i>R. aurantiaca</i>	Birhanu et al. (2017)
21	Rhizospheric soil	<i>Aspergillus tubingensis</i> SANRU	Jamshidi et al. (2016)
22	Himalayan soil	<i>Acinetobacter rizosphaerae</i> , <i>Tetrathobacter</i> sp.,	Kumar et al. (2013)
23	Rhizospheric soil	<i>Fusarium</i> spp., <i>Micromonospora</i> spp	Srinivasan et al. (2012)
24	Rhizospheric soil	<i>Enterobacteria</i> sp.,	Park et al. (2011)
25	Rhizospheric forest soil	<i>B. subtilis</i>	Krishnaswamy et al. (2009)
26	Cold desert Himalayan soil	<i>B. cerus</i>	Chatli et al. (2008)
27	Heavy metal polluted soil	<i>Streptomyces</i> spp.,	Dimkpa et al. (2008); Mansoor et al. (2023b)
28	Rhizospheric soil	<i>Penicillium</i> sp.,	Mittal et al. (2008)
29	Rhizospheric soil	<i>A. tubigenis</i>	Richa et al. (2007)
30	Rhizospheric soil	<i>P. fluorescens</i>	Peix et al. (2009)

Hymenella and *Neosartorya* are potent PSMs (Kirui et al. 2022; Biswas et al. 2018; Bashir et al. 2018a, b; Zhang et al. 2019; Teng et al. 2019a; Ichriani et al. 2018; Rojas et al. 2018; Sulbaran et al. 2009). Phosphate solubilizers have been reported as N₂ fixers and regulate plant hormone levels (Unnikrishnan and Binitha 2024). There are various reports on isolation and characterization of diverse phosphorus solubilizers from different environmental sources. These PSMs by their metabolic activities perform a dynamic role in soil. These microbes act as potent biofertilizers that enhance agriculture produce and maintain soil fitness (Rajwar et al. 2018).

Phosphorus solubilizers produce various hormones like auxins, cytokinins, gibberellins that enhance seed germination, cell differentiation, shoot elongation and flowering (Puri et al. 2020). An innovative choice strain

like *Pseudomonas plecoglossicida* isolated from rhizospheric soil of soybean, also produced growth promoting hormones like Indole-3-Acetic Acid (IAA) (Astriani et al. 2020). Studies suggested that *Trichoderma harzianum* can also solubilize P, the strain produced IAA, improved root and shoot biomass, leaf number and size observed on *Solanum lycopersicum* L. (Bader et al. 2020). Various microorganisms, including bacteria and fungi, are known for their ability to produce organic acids. *Pseudomonas* produces gluconic acid to increase phosphate solubility, which has become an important technology for improving phosphate fertilizer management in modern agriculture (Wang et al. 2022; Rai et al. 2023). Here are some common organic acids and the microorganisms that often produce them (Table 2).

Table 2 List of microbes secreting organic acids

S. No	Microbes	Organic Acids	References
1	<i>Pseudomonas anuradhapurensis</i> UFPI B5-8A	Citric acid, malic acid	de Almeida Leite et al. (2024)
2	<i>Bacillus cereus</i> and <i>B. subtilis</i>	Acetic acid, malic acid	Chawngthu et al. (2020)
3	<i>Trichoderma</i> sp.,	Ascorbic, lactic, fumaric acids	Bononi et al. (2020)
4	<i>Pantoea agglomerans</i> NCTC9381; <i>Pseudomonas azotoformans</i> NBRC12693; <i>Pantoea vagans</i> LMG24199	Succinic acid, oxalic acid, ascorbic acid, gluconic acid	Rfaki et al. (2020)
5	<i>Burkholderia</i> ; <i>Achromobacter</i> ; <i>Pseudomonas sphingobacterium</i>	Acetic acid, Malic acid, tartaric acid, gluconic acid	Nacoon et al. (2020)
6	<i>Leclercia adecarboxylata</i> B3	succinic acid, formic acid	Teng et al. (2019b)
7	<i>Bacillus megaterium</i> ; <i>B.licheniformis</i> ; <i>B. subtilis</i>	Lactic acid, citric acid, Propanoic acid	Do carmo et al. (2019)
8	<i>Kosakonia cowanii</i> and <i>B. megaterium</i>	Gluconic acid	Chakdar et al. (2018)
9	<i>Penicillium oxalicum</i> and <i>A. niger</i>	Citric acid, Formic acid, Tartaric acid, Malic acid	Li et al. (2016)
10	<i>A. niger</i> FSI and <i>P. islandicum</i> FS30	Gluconic acid, Citric acid, Oxalic acid	Mendes et al. (2013)
11	<i>A. awamori</i> S19	Malic acid, Oxalic acid, Citric acid, Fumaric acid	Jain et al. (2012)
12	<i>Enterobacter</i> sp., FS.11	Citric acid, gluconic acid	Shahid et al. (2012)
13	<i>A. niger</i> and <i>Pencillium</i> sp,	oxalic acid, Citric acid	Arwidsson et al. (2010)
14	<i>P. Trivalis</i> (BIHB 769)	Formic acid, lactic acid, malic acid	Vyas and Gulati (2009)
15	<i>Penicillium</i> sp and <i>Fusarium oxysporum</i>	Lactic acid, Malic acid, Gluconic acid, Acetic acid Fumaric acid	Akintokun et al. (2007)
16	<i>A. flavus</i>	Oxalic acid, citric acid, Gluconic acid, Succinic acid	Maliha et al. (2004)
17	<i>A. candidus</i> and <i>A. flavus</i>	Gluconic acid, Oxalic acid	Shin et al. (2006)
18	<i>Serratia marcescens</i> (CC-BC14)	Citric acid, Lactic acid	Chen et al. (2006)
19	<i>Chryseobacterium</i> (CC-BC05)	Malic acid, Citric acid	Chen et al. (2006)
20	<i>P. regulosum</i>	Gluconic acid, Citric acid	Reyes et al. (2001)
21	<i>A. niger</i>	Citric acid, Succinic acid	Vazquez et al. (2000)

3 Mechanisms of Inorganic Phosphorus Solubilization

The PSMs uses various strategies for phosphorus solubilization. Out of which the principal mechanism is low molecular weight (MW) secretions which include organic acids (Citric acid, Malic acid, Gluconic acid, and Oxalic acid) (Saeid et al. 2018; Marra et al. 2015; Buch et al. 2008; Liu et al. 2024). Gluconic acid is the main acid secreted by these PSMs (Zhang et al. 2023a, b). The generation of these low MW secretions causes acidification of microbial cells as well as its surroundings (Lin et al. 2006; Chen et al. 2006; Silva et al. 2023; Khan et al. 2024). Subsequent ionization of acid occurs, and proton released becomes responsible for expelling phosphorus from phosphate via proton substitution for calcium, aluminium, and iron or chelate cations from carboxylic anions and releasing phosphate anions (Aliyat et al. 2022). The release of organic acids has also been well established (Park et al. 2009; Lin et al. 2006). Studies suggested that there occur some genes which are indirectly or directly involved in secretions of these low molecular weight organic acids (Babu-Khan et al. 1995; Buch et al. 2010; Pang et al. 2024). The -COOH and -OH functional groups of these

acids compete with Ca^{2+} , Al^{3+} and Fe^{2+} , make bonds with metal ions (chelation) and thus transforms phosphorus from insoluble to soluble state (Kpombrekou and Tabatabai 1994). The estimation of these compounds (acids) can be done by HPLC (Wei et al. 2017; Park et al. 2009). Siderophores i.e., Fe^{2+} chelating agents, phosphatases and extracellular polysaccharides (EPS) synthesized by PSBs results in availability of P in its soluble form from fixed phosphate form (Sharma et al. 2013; Yi et al. 2008; Chen and Arai 2023; Thampy et al. 2023). Thus, the various chelating agents, low molecular weight organic acids and enzymes produced by PSMs are main compounds that cause solubilization of inorganic phosphorus.

4 Mechanism Involved in Organic Phosphorus Mineralization

Organic matter is the key basis of phosphorus availability in the soil, various organic phosphorus compounds are nucleic acids, phospholipids, and phosphodiester and so on (Rodríguez and Fraga 1999). Besides pesticides, antibiotics, that are released in to the environment also contain organic

phosphorus. Phosphorus mineralization means solubilization of organic phosphorus. Microorganisms solubilize P by secretion of various enzymes as among them are those that dephosphorylate the phosphoester or phosphoanhydride bond in organic compounds. PSM, mostly release phosphomonoesterases or phosphatases (Nannipieri et al. 2011), these enzymes i.e., phosphomonoesterases can occur in both acidic as well as in alkaline forms (Jorquera et al. 2011). Other class of enzyme secreted by phosphate solubilizers in the process of mineralization of organic P is phytase (Silva et al. 2023; Khan et al. 2024). This phytase enzyme releases the phosphorus from organic materials like plant seeds and pollen. The phytase during degradation process releases phosphorus in a form which is available for plant uptake (Richardson and Simpson 2011).

5 Phosphate Solubilizers as Plant Growth Enhancers

Microorganisms that solubilize phosphates exert indirect or direct influences on plant health and their yield (Zveushe et al. 2023). Direct process comprises improved solubilization of minerals such as K, P, Si and Zn etc. (Prakash and Arora 2019; Bashir et al. 2017; Hayat et al. 2010). The substances /chemicals released by PSB that enhance plant growth are mentioned in (Table 3).

The PSBs have showed good performance for plant development (Prakash and Arora 2019; Wen et al. 2019). These phosphate solubilizing microbial strains increase plant health and yield as they improve the biogeochemical cycling (Fig. 1) (Mitra et al. 2020; Hutchins et al. 2019), prevents from pathogen infestation (Bononi et al. 2020; Saravana et al. 2008), yield some vitamins like riboflavin, biotin, niacin etc., for plant development (Jaiswal et al. 2021; Revillas et al. 2000), phytohormones (Mažylytė et al. 2022; Kalayu 2019; Prakash and Arora 2019), and iron scavenging molecules (Purwaningsih et al. 2021; Prakash and Arora 2019) (Table 4).

6 Phosphate Solubilizing Microbes as Biocontrol Agents

Increased application of chemical pesticides has given rise to environmental contamination, reduced beneficial soil biota, and enhanced vulnerability of crops to disease (Yatoo et al. 2021, 2022). The strategy to combat disease is currently being explored, with a focus on using PSMs as biological control agents. In addition to giving plants vital nutrients, PSMs operate as plant growth-promoters and hinder the growth of a variety of diseases, including nematodes (Thomas et al. 2005; Khan and Kounsar 2000; Oyekanmi et al. 2008; Khan et al. 2009a, b, c). PSMs are efficient

Table 3 Plant growth promoting substances released by phosphorus solubilizing bacteria

S. No	Bacteria	Secretions by bacteria that promote plant health	References
1	<i>Lysinibacillus fusiformis</i> yj 4	Gibberellins, Cytokinins, Indole-3- acetic acid	Jha and Mohamed (2023)
2	<i>Acinetobacter</i> sp.	Indole-3- acetic acid / Phosphatase secretion	Timofeeva et al. (2022)
3	<i>Rhizobium</i> sp	Indole-3- acetic acid, Gibberellins, cytokinins, ACC deaminase, Phosphatase secretion	Jaiswal et al. (2021)
4	<i>Bacillus subtilis</i> and <i>Bacillus cereus</i>	Indole-3- acetic acid, Acid phosphatase	Chawngthu et al. (2020)
5	<i>Streptomyces laurentii</i>	Siderophore, Indole-3- acetic acid, ACC deaminase, phosphatase enzyme	Kour et al. (2020)
6	<i>Bacillus</i> sp. STJP	Siderophores, Indole-3- acetic acid, Hydrogen cyanide production	Prakash and Arora, (2019)
7	<i>Pseudomonas fluorescens</i>	Indole-3- acetic acid, peroxidase, ascorbate peroxidase secretion, Phosphatase secretion	Kadmiri et al. (2018)
8	<i>Serratia</i> sp. 5D	Indole-3- acetic acid, phosphatase enzyme	Zaheer et al. (2016)
9	<i>Bacillus</i> sp	Indole-3-AceticAcid / Hydrogen cyanide /Siderophores, Phosphatase secretion	Kumar et al. (2013)
10	<i>Azotobacter</i> sp	Indole-3- acetic acid /Siderophores/Phosphatase secretion	Farajzadeh et al. (2012)
11	<i>Rhizobium leguminosarum</i>	Indole-3- acetic acid/phosphatase enzyme	Stajkovic et al. (2011)
12	<i>Bradyrhizobium</i>	Gibberellic acid / (Indole-3- acetic acid)/ phosphatase enzyme	Afzal et al. (2010)
13	<i>Rhizobium</i> strain TAL 1145	ACC deaminase/Phosphatase secretion	Tittabutr et al. (2008)
14	<i>Rhizobium</i> sp	Gibberellic acid/ Indole acetic acid /Zeatin/ Phosphatase secretion	Boiero et al.(2007)
15	<i>Brevibacterium</i> sp	Indole-3- acetic acid /phosphatase enzyme	Vivas et al. (2006)
16	<i>Xanthomonas</i> sp	Indole-3- acetic acid / phosphatase enzyme	Sheng and Xia (2006)
17	<i>Pseudomonas putida</i>	Siderophores/ phosphatase enzyme	Tripathi et al. (2005)
18	<i>Pseudomonas fluorescence</i>	Siderophore/ Indole-3- acetic acid / phosphatase enzyme	Gupta et al. (2005)

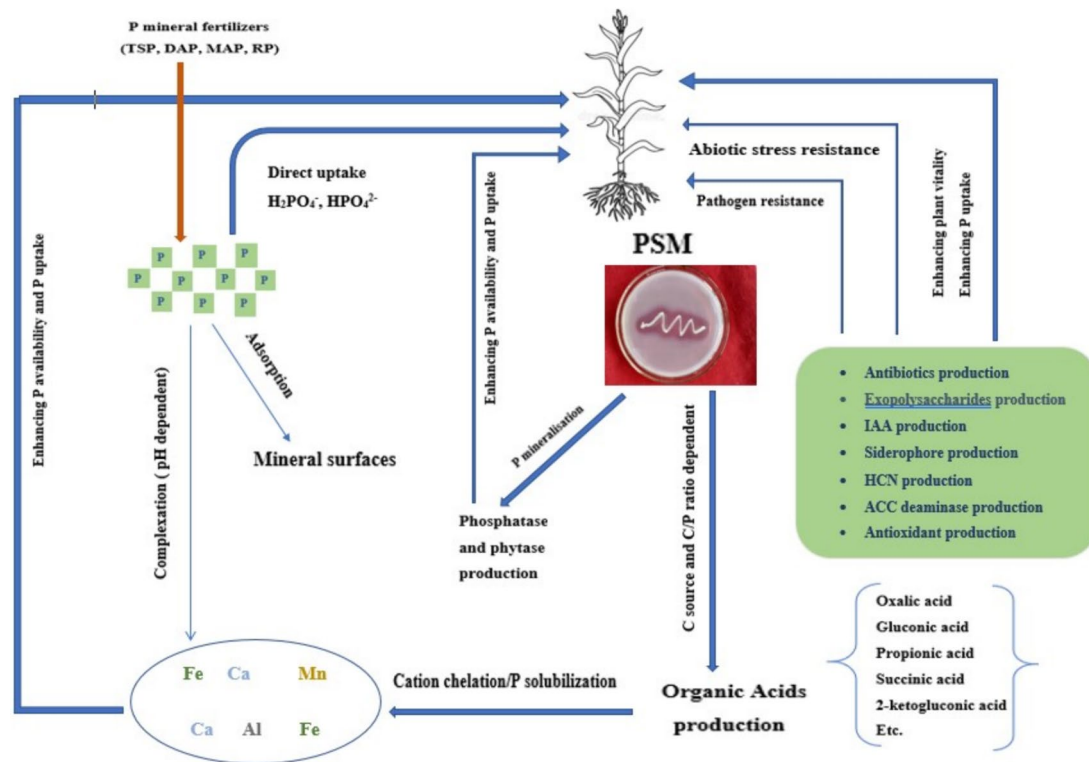


Fig. 1 Phosphorus solubilizing microbes with different plant growth promoting potential

Table 4 Phosphorus solubilizing bio-inoculants and their benefited crops

S. No	Bio-inoculant (PSM)	Benefited Crop	References
1	<i>Pseudomonas moraviensis</i> and <i>Bacillus cereus</i>	Wheat (<i>T. aestivum</i> L.)	Hassan and Bano (2016)
2	<i>Sinorhizobium meliloti</i> , <i>Bacillus flexus</i> and <i>B. megaterium</i>	Maize (<i>Zea mays</i> L.)	Jesús et al. (2017)
3	<i>Phosphobacteria</i>	Potato (<i>Solanum tuberosum</i> L.)	Lallawmkima et al. (2018)
4	<i>Rhizobium</i> sp	Peanuts (<i>Arachis hypogaea</i> L.)	Guimarães et al. (2019)
5	<i>Bacillus simplex</i> UT1 and <i>Pseudomonas</i> sp FA1	Wheat (<i>T. aestivum</i> L.)	Rezakhani et al. (2019)
6	<i>Rhizobium</i> sp	Brinjal (<i>S. melongena</i>)	Paulraj et al. (2020)
7	<i>Funneliformis mosseae</i> <i>Bacillus megaterium</i> 10011	Alfalfa (<i>Medicago sativa</i>)	Liu et al. (2020)
8	<i>Enterobacter</i> sp. J49	Maize and Soybean	Lucero et al. (2021)
9	<i>Funneliformis mosseae</i> <i>Apophysomyces spartima</i>	Palm (<i>Chamaerops humilis</i>)	Zai et al. (2021)
10	<i>Enterobacter ludwigii</i> AFFRO2 <i>Bacillus megaterium</i> Mj1212	Alfalfa (<i>Medicago sativa</i>)	Kang et al. (2021)
11	<i>A. pittii</i> and <i>E. coli</i>	Black Night Shade (<i>S. nigrum</i> L.)	He et al. (2022)
12	<i>Rhizophagus aggregatus</i>	Sun choke (<i>Helianthus Tuberosus</i>)	Nacoon et al. (2022)
13	<i>Lysinibacillus sphaericus</i> YJ5	Maize (<i>Zea mays</i> L.)	Jha and Mohamed (2023)
14	<i>Acinetobacter rhizosphaetae</i> EU-KL44	Wheat (<i>T. aestivum</i> L.)	Kour and Yadav (2023)
15	<i>Rhizophagus irregularis</i>	Barrel clover (<i>Medicago truncatula</i>)	Duan et al. (2023)
16	<i>Azospirillum brasilense</i>	Sugarcane (<i>Saccharum officinarum</i>)	Fernandes et al. (2023)

biocontrol agent for plant diseases. They affect directly different stages of development in nematodes; eggs, larvae and adults (Pocasangre et al. 2007; Pant and Pandey 2001; Oyekanmi et al. 2008; Sharon et al. 2009).

A PSB, *Bacillus amyloliquefaciens* can inhibit the growth of *F. oxysporum* can prevent the growth of *F. oxysporum* through the production of antifungal components 1-amino-cyclo-propane-carboxylic-aciddeaminase, and enzymes like chitinase and cellulase (Gowtham et al. 2016). Chitinase enzymes can inhibit *F. oxysporum* attack on chilli seeds (Suryanto et al. 2014), and *G. philippii* (Widyastuti and Sumardi 1998) causing red roots in acacia plants.

Several bacteria from the genera *Azotobacter*, *Pseudomonas* and *Bacillus* are recognised to be vital in the solubilization of soil minerals and to inhibit plant diseases (Khan et al. 2005; Mardhiansyah 2011; Gill et al. 2016; Bashir et al. 2017; Bashir et al. 2018a; Prihatini et al. 2018; Bashir et al. 2018b; Bashir et al. 2019a, b., Bashir et al. 2019b; Gowtham et al. 2016). To suppress parasitic nematodes, different phosphate solubilizing bacteria were used in various plants. For example *Azospirillum lipoferum* was used against *Meloidogyne incognita* in green gram (*Vigna radiata*) (Khan and Kounsar 2000), *Bacillus subtilis* was used against Root-knot nematode (*Meloidogyne* spp.) of tomato (*Solanum lycopersicum*) (Jiménez-Aguirre et al. 2023), *Pseudomonas fluorescens* against *Heterodera schachtii* in sugar beet (*Beta vulgaris*) Oostendrop and Sikora (1989), *B. subtilis* was used against *M. incognita* in ornamental plants (Khan et al. 2005b), *P. fluorescens* was used against *Heterodera schachtii* in sugar beet, *Beijerinckia indica* was used against *M. incognita* in green gram (Khan and Akram 2000; Khan et al. 2009a, b, c). These bacteria suppress nematode pathogenesis, as well as encourage plant development by solubilizing minerals in the soil (Khan et al. 2009a, b, c).

Phosphate solubilizing bacteria suppress the growth of plant pathogens by adapting different mechanisms. Bacteria gets attached to roots by means of pili in case of *Pseudomonas fluorescens* on wheat roots (Patil et al. 2002; Khan et al. 2009a, b, c) or involve development and multiplication on the root surface. Various antifungal components are also produced by bacteria that are active against various pathogens including nematodes, these include iturin, mycosubtilin, surfactin, bacilysin, fengymycin HCN, mycobacilin, ammonia, 2,4-diacetylphloroglucinol, xantobaccin, butyrolactones, oomycin, kanosamine, oligomycin, phenazine-1-carboxylicacid, viscosinamide, pyrrolnitrin, zwittermycin A etc. (Khan et al. 2009a, b, c). They stimulate the systemic resistance (SR) in the host against the pathogenic microbes. After inoculating with the biocontrol bacteria, they bring the following changes in the host; increased the level of enzymes like phenylalanine ammonia lyase, polyphenol oxidase, peroxidase and chitinase (M'Piga et al. 1997; Chen and Dickson 2004; Mansoor et al. 2023a), increased production of

phytoalexins, enhanced gene expression related to response to stress, deposition of barriers and strengthening of cell walls outside infection sites including phenolics, lignin and cellulose (Khan et al. 2009a, b, c). Bacteria produce a large number of siderophores or iron chelators that have high affinity for iron. They sequester the iron present in the rhizosphere making it inaccessible to pathogens, thus limiting their growth (Khan et al. 2009a, b, c). *P. fluorescens* and *B. subtilis* promote growth of plants directly as well as indirectly. Growth promotion via indirect means is based on the suppression of plant parasites (soil borne) and pathogenic microorganisms in the rhizosphere, whereas direct growth promotion is primarily exerted through the release of growth factors. *B. subtilis* and *P. fluorescens* synthesizes plant growth promoting hormones such as gibberellins, indole acetic acid, zeatin and cytokinins that enhances plant growth (Khan et al. 2009a, b, c).

Various P solubilizing fungi inhibits the growth of various microbes including nematodes (Khan and Kounsar 2000; Oyekanmi et al. 2008) and other pathogenic fungi (Padmavathi and Madhumathi 2009). In addition to supplying vital nutrients in plants (Thomas et al. 2005), imparts a vital role on solubilizing insoluble phosphorus (Turan 2006) allowing plants to use it (Mittal et al. 2008; Oyekanmi et al. 2008; Khan and Kounsar 2000). Some fungi *Aspergillus niger*, *Penicillium digitatum*, *Penicillium anaticum*, *Trichoderma viride* and *Trichoderma harzianum*, play a major part in phosphate solubilisation and have been used in biomanagement of different pathogenic fungi and nematodes in different plants like *A. niger* was used in controlling *Meloidogyne incognita* in tomato (Tayade et al. 2019), okra (Sharma et al. 2005), *Paecilomyces lilacinus* was used in controlling *Meloidogyne* spp. in tomato (Schenek 2004), tobacco, *P. anaticum* was used in controlling *Globodera rostochinensis* in potato (Jatala 1986), *Trichoderma harzianum*, and *P. lilacinus* was used in controlling *M. incognita* in chickpea (Pant and Pandey 2001), *Trichoderma harzianum* and *Pseudomonas fluorescens* against *M. javanica* in tomato (Siddiqi and Shaikat 2004). The many developmental stages of nematodes, including eggs, larvae, and adults, may be directly impacted by phosphorus solubilizing fungi (PSF) (Pocasangre et al. 2007, Pant and Pandey 2001; Oyekanmi et al. 2008; Sharon et al. 2009). *Trichoderma*, a main biocontrol fungus is found in almost all soils and in a diversity of habitats. They are the most common culturable fungi found in soil and colonize plant roots. *Trichoderma* sp. invade, parasitize, or feed on other fungi. Because it is usually abundant in healthy roots, they evolved many mechanisms to combat other fungi and encourage the growth of plants and roots (Benítez et al. 2004).

The effect of *Trichoderma harzianum* on different isolates of *Xanthomonas* was studied and it was observed that *Xanthomonas* was completely lysed by *T. harzianum* and

inhibited their growth (Padmavathi and Madhumathi 2009). The phosphate-solubilizing fungi adapt different mechanisms to suppress plant pathogens. According to Lipping et al. (2008), antibiosis gives phosphate-solubilizing fungus species of *Trichoderma*, *Penicillium* and *Aspergillus*, a competitive saprophytic advantage. Different species of *Trichoderma* and *Aspergillus* produce low molecular weight compounds both volatile and non-volatile that impedes the growth of harmful microbes including in the root zone. Some of the compounds produced by *Aspergillus* sp. and *Trichoderma* sp. include harzianic acid, viridin, tricholin, alamethicins, glisoprenins, peptaibols, massoilactone, heptelidic acid, antibiotics, 6-penthy-pyrone, oxalic acid, gliovirin, and enzymes (Khan et al. 2009a, b, c).

It is believed that the antagonistic action of phosphorus dissolving fungus, like strains of *Trichoderma*, *A. niger* and *P. digitatum*, on the invading pathogen allows them to defend plants against various pathogens (Khan et al. 2009a, b, c). *Trichoderma* strains have the potential to cause plants to exhibit hypersensitive reactions systemic generated resistance as well as acquired systemic resistance (Harman et al. 2004). Different species of *Trichoderma* induces resistance in their host by stimulating the production of genes that stimulate the production of phytoalexins, Pathogenesis-related (PR) proteins and other chemicals that increase plant pathogen resistance. *Trichoderma harzianum* induced resistance in various plants like cucumber, bean, and cotton (Khan et al. 2009a, b, c). *Trichoderma* releases growth factors that enhance plant growth, crop yield as well as seed germination rates (Benítez et al. 2004). *Trichoderma* sp and *A. niger* also produces phytohormones like zeatin and gibberellic acid, and their production might enhance bio fertilization. Thus, with increased nutrient absorption and the synthesis of these plant hormones directly influence plant development, control of different pathogens and enhancing defence mechanism of plants (Khan et al. 2009a, b, c).

7 Phosphate Solubilizers and Bioremediation

Bioremediation has fascinated a lot of scientific attention in recent years. Its mechanisms are based on redox transformations, absorption, and changes in the reaction of the medium. Presently, the most common methods of microbial removal of heavy metals are bioleaching, biomineralization, biosorption, bioaccumulation, and production of biosurfactants, oxidation–reduction, and biovolatilization (Rahman and Singh 2020). Some specific genera of microorganisms called extremophiles are involved in such processes, these specific microbial strains, are able to develop protective systems to avoid negative effects of heavy metal based pollution. Therefore, the ability of microorganisms to remain viable under

the influence of heavy metals in the restoration of disturbed areas is of pivotal importance (Ayangbenro and Babalola 2017; Hamid et al. 2023a, b). According to literature data, it is possible to use Bacteroidetes and Firmicutes for As-contaminated areas. Their abundance positively correlates with this pollutant in contaminated areas. It is also noted that proteobacteria are resistant to high concentrations of Zn, as well as Pb (Fajardo et al. 2019). Under the heavy metal stress some microbial strains are able to secrete or release extracellular substances such as proteins, polysaccharides, lipids containing various heavy metal binding sites (Tarfeen et al. 2022). Diverse phosphate solubilizing microbial communities have been reported which play important role in heavy metal remediation.

Considerable attention is being given to the microbial breakdown of agricultural chemicals such as pesticides, insecticides, fungicides, chemical fertilizers, and other toxic compounds (Rafa and Chiampo 2021). Besides this microbial community benefit the plants by direct or indirect way like phosphate solubilization, potassium solubilization, zinc solubilization, silicate solubilization, nitrogen fixation, 1-aminocyclopropane-1-carboxylate deaminase (ACCD) production, HCN, siderophore (iron chelating agents) production and phytohormone secretions (Glick et al. 2007; Bashir et al. 2017, 2018a, b; Gouda et al. 2018; Kalam et al. 2020; Park et al. 2021; Saeed et al. 2021; Kaur et al. 2024).

Several research reports have shown that PSMs strains including *Bacillus* spp, *Azospirillum lipoferum*, *Pseudomonas fluorescense*, *Rhizobium* spp that remediate chemicals and also secrete gibberellic acid (GBA) that induce plant health (Bottini et al. 2004; Gouda et al. 2018). These rhizobacterial phosphate solubilizers also secrete EPS which showed effect on growth and development of plant and drought tolerance (Naeem et al. 2018; Bashir et al. 2021; Kaur et al. 2024). Numerous plant growth-promoting features of phosphate solubilizers such as organic acid production (citric, malic, oxalic, propionic acids), secretion of iron chelating agents (siderophores), indole acetic acid production and ACC deaminase activity enhances the phytoremediation capability of plants (Park et al. 2009; Cui et al. 2022). Plentiful P solubilizing strains belonging to the genera of *Pseudomonas*, *Bacillus*, *Paenibacillus*, *Brevibacterium*, and *Staphylococcus* have been reported to solubilize phosphate as well as dissolves the Lead (Pb) mineral. PSM in addition to chelating agent Ethylene diamine tetra acetic acid when added to Arsenic contaminated soil, phytoremediation property of *Echinochloa frumentacia* is enhanced and it has been reported within 85 days from the seeding of *Echinochloa frumentacia*, arsenic contamination in the soil decreases when compared with initial concentration (Yahaghi et al. 2018). Inoculation with both *Brevibacterium frigoripolerans* YSP40 and *Bacillus paralicheniformis* YSP151

and their consortium have been reported to enhance the growth and Pb uptake of *Brassicajuncea* plants grown in metal contaminated soil. Hence, phosphate solubilizers have an effective role to play in bioremediation (Yahaghi et al. 2018).

8 Conclusion

Phosphorus is an indispensable mineral element amongst the macronutrients needed for different plant metabolic functions. Phosphorus is available in soil as inorganic as well as in organic form, but due to its limited accessibility since it occurs in an insoluble form. Because of its complex formation and meagre soil solubility only few percent of total phosphorus are available to plants. Phosphorus accounts for around 0.2–0.8% of the dry weight of the plant. To fulfil the needs of crop nutrition, phosphorus is generally added to soil in chemical form but the synthesis of phosphorus fertilizer is expensive and effortful process. In addition, plants utilize a small quantity of this phosphorus and 75–90% of added phosphorus forms metal-cation complexes, gets precipitated and is quickly locked in soils. Microbiologists and experts in soil science have setup a way to make phosphorus available to crops, a replacement for crop fertilization that is economically successful. Such ecological concerns result in exploration of crop nutrition for a sustainable way of phosphorus. In this regard, Phosphorus solubilizing microorganism is seen as the best environmentally sustainable means for crop phosphorus nutrition, which farmers can afford. Bioremediation being an interesting and highly applied tool for decontamination of heavy metal polluted soils and sites, number of microbes possess remediation capacity and are utilized at large scale. Phosphorus solubilizing microorganisms has proven to be a potential bio-remediating agent and can be applied in agriculture soils for solubilisation as well as remediation purpose. Future insight about improving bioremediation potential of phosphorus solubilizing microorganisms need to be explored for enhancing quality of soil health and plant health.

Abbreviations ACC: 1-Aminocyclopropane-1-carboxylic acid; EDTA: Ethylene diamine tetra acetic acid; EPS: Exopolysaccharides; HCN: Hydrogen cyanide; IAA: Indole-3-acetic acid; PAL: Phenylalanine ammonia lyase; PSMs: Phosphorus solubilizing microorganisms; PSF: Phosphorus solubilizing fungi; PSB: Phosphorus solubilizing bacteria; ACCD: 1-Aminocyclopropane-1-carboxylate deaminase; MW: Molecular weight

Declarations

Conflicts of Interests Authors declare no conflict of interest.

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