



Prospects of phosphate solubilizing microorganisms in sustainable agriculture

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Abstract

Phosphorus (P), an essential macronutrient for various plant processes, is generally a limiting soil component for crop growth and yields. Organic and inorganic types of P are copious in soils, but their phyto-availability is limited as it is present largely in insoluble forms. Although phosphate fertilizers are applied in P-deficit soils, their undue use negatively impacts soil quality and the environment. Moreover, many P fertilizers are lost because of adsorption and fixation mechanisms, further reducing fertilizer efficiencies. The application of phosphate-solubilizing microorganisms (PSMs) is an environmentally friendly, low-budget, and biologically efficient method for sustainable agriculture without causing environmental hazards. These beneficial microorganisms are widely distributed in the rhizosphere and can hydrolyze inorganic and organic insoluble P substances to soluble P forms which are directly assimilated by plants. The present review summarizes and discusses our existing understanding related to various forms and sources of P in soils, the importance and P utilization by plants and microbes, the diversification of PSMs along with mixed consortia of diverse PSMs including endophytic PSMs, the mechanism of P solubilization, and lastly constraints being faced in terms of production and adoption of PSMs on large scale have also been discussed.

Keywords Phosphorus · Phosphate-solubilizing microorganisms · Arbuscular mycorrhizal fungi · Phytases

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Introduction

Phosphorus (P) is amongst the most vital essential macronutrients necessary for promoting the growth and well-being of plants along with nutrient cycling in soil systems (Maharajan et al. 2018; Billah et al. 2019; Wang et al. 2022a). On an average, the P level in soil is nearly 0.05% (w/w), out of which merely 0.1% is available to be taken up by plants (Zhu et al. 2011; Iftikhar et al. 2024). It comprises 0.2–0.8% of the total plant biomass and ranks second among the most limiting factors, after nitrogen (Tak et al. 2012; Sharma et al. 2013). Phosphorus is present in several biomolecules, such as nucleic acids, ATP, enzymes, coenzymes, phosphoproteins, nucleotides, and phospholipids (Malhotra et al. 2018; Timofeeva et al. 2022; Feng et al. 2024). It performs imperative functions in almost all essential plant metabolic processes, such as cell division and enlargement, photosynthesis, respiration, carbohydrate metabolism, energy production, storage and transfer reactions, redox-homeostasis, and signalling, growth of root and stem, development of flower and seed, crop ripening, nitrogen fixation in leguminous

plants, and tolerance to plant diseases (Malhotra et al. 2018; Nesme et al. 2018; Elhaissofi et al. 2020; Siedliska et al. 2021), ultimately contributing to increased yields.

Plant roots take up P as orthophosphates (HPO_4^{2-} or H_2PO_4^-), but these ions are present in the soil at the micromolar level (Timofeeva et al. 2022). Due to soils being generally P deficient, inorganic P fertilizers are required as P deficiency can cause significant reductions in plant growth and (up to 15%) yield (Elhaissofi et al. 2022). Generally, worldwide food production inevitably relies on chemical fertilizers (conventionally N and P fertilizers) to boost crop outputs. Consequently, P addition continues to be one of the vital agricultural practices for achieving plant nutritional requirements (Bindraban et al. 2020). Soils having a small amount of total P can be treated with P fertilizers; nevertheless they are not capable of holding the supplemented P. Phosphate anions present in inorganic fertilizers are highly reactive and immediately get fixed owing to associations with Ca^{2+} , Fe^{3+} , and Al^{3+} ions in the soil (Kumar et al. 2018; Ma et al. 2021; Timofeeva et al. 2022). Therefore, the formation of insoluble complexes of analogous phosphate salts results in low P uptake by plants (10–25%) from chemical phosphate fertilizers (Schnug and Haneklaus 2016; Weeks and Hettiarachchi 2019; Dong et al. 2023). Hence, effective P transfer for plant uptake continues to be challenging and raises concerns about global food security.

There are worldwide concerns regarding energy and expenditure in mining phosphate minerals and their transportation from production sites to cultivated crop fields. Mining rock phosphate and distributing P fertilizers on the land is neither ecological-friendly, cost-effective nor sustainable as it possesses certain constraints, for example, (i) release of fluorine as a highly explosive and lethal hydrogen fluoride gas, (ii) dumping of gypsum and (iii) accretion of heavy metals such as cadmium (Cd) in soil and crop plants because of recurring utilization of P fertilizers (Sharma et al. 2013). Undoubtedly, additions of synthetic P fertilizers to farming lands have increased the crop yield but simultaneously long-term utilization of P fertilizers has resulted in negative influences on the environment, such as carbon footprint, water pollution, eutrophication, and depletion of soil fertility (Bhattacharyya et al. 2015; Liu et al. 2018; Kalayu 2019; Cheng et al. 2023). Pollution caused by P fertilizers has gained intense attention of researchers globally. Thus, it is of great interest to explore management approaches that can increase P fertilization efficiency, improve crop output, and decrease environmental contamination (Heathwaite et al. 2005; Sharpley et al. 2007). Until now, numerous strategies have been exploited to decrease the detrimental effects of chemical P fertilizers on soil ecosystems, for example, lessening P fertilizer supplementation, upgrading planting methods, proper intercropping,

and utilizing eco-friendly fertilizers (Wu et al. 2015). One of the most promising approaches in this direction is the addition of phosphate-solubilizing microorganisms (PSMs) possessing various P sources exploiting capabilities. PSMs have distinct mechanisms that facilitate the solubilization of immobile inorganic P, such as acidification owing to the secretion of H^+ , inorganic acids, and organic acids, production of siderophores and exopolysaccharides (Sharma et al. 2013; Jiang et al. 2020; Elhaissofi et al. 2022). Enzymes such as C–P lyases, phosphatases, and phytases assist in solubilizing organic phosphate (Chawngthu et al. 2020; Bargaz et al. 2021). Potential PSMs have been developed as biofertilizers and added in agricultural fields to promote plant growth and health (Wang et al. 2023). Interestingly, their phosphate solubilization behaviour has gained enormous applications, especially in phytoremediation. For this reason, PSMs should be used in farming practices to reduce the price and use of chemical P fertilizers, ultimately lessening the load on farmers, boosting crop yield, and accomplishing sustainable agricultural goals. The present review focuses on various forms of P in soils along with their sources, importance of P for the growth of microbes and plants, effect of P deficiency on plants, diverse microbes (including mixed consortia) implicated in P solubilization, various mechanisms employed by them to solubilize insoluble phosphate, ultimately leading to sustainable agriculture. In addition, a comparison of sources of chemical phosphate and phosphate released by PSMs and various constraints being faced in terms of bulk production of PSMs and their adoption by farmers has also been highlighted.

Forms and sources of phosphate in soils

Although P transfers in a cyclic manner in soil, water, sediments, rocks, and organisms, it does not exhibit quick cycles compared to carbon, nitrogen, and sulfur (Anantharaman et al. 2016). In time, rainfall and weathering trigger rocks to liberate phosphate ions and other minerals which is then distributed in water and soils. Although most soils contain significant concentrations of P, a large fraction is combined with soil components (over 80% of P is static) and is not readily available for plant absorption (Xu et al. 2020; Tian et al. 2021; Barrow 2022). In soil, not all P is the same. P is present in diverse forms in soil, mostly inorganic P (Pi) and organic P (Po) (Bünemann et al. 2015; Pang et al. 2024), with quantities of Pi and Po changing with the ageing of soils (Cross and Schlesinger 1995). Soil Pi generally occurs as relatively insoluble and steady forms of primary (variscite, apatite, and strengite) and secondary (aluminium, calcium and iron phosphates) P minerals (Pierzynski and Hettiarachchi 2018; Hao et al. 2020a) which cannot be

absorbed by plants. On the other hand, soluble Pi mainly exists as hydrogen phosphate and dihydrogen phosphate ions (HPO_4^{2-} and H_2PO_4^-) (Hao et al. 2020a; Kour et al. 2021). Pi exists in high levels and represents 35–70% of the total P content of the soil (Jones and Oburger 2011; Lambers and Plaxton 2015). Pi occurs in diverse forms and amounts in soil, which can be leached into streams, accumulated P in ocean deposits, or absorbed by plants or soil microbes in the secondary Po cycle (Mathew et al. 2020). P has very low solubility, poor mobility in soil solution and less capacity to form insoluble salts with different mineral elements. Thus, mineral P, plant-available (soil solution) P and sorbed P, and are the major pools of Pi form.

Po consists of a large variety of compounds which are generally classified into four groups: organic polyphosphate, monoester phosphates, diesters phosphates and phosphonates (Huang et al. 2017). Organic polyphosphate includes compounds such as ADP and ATP, monoester phosphates occur mainly as inositol phosphates, phosphate diesters comprise nucleic acids (DNA and RNA), phospholipids and teichoic acids and phosphonates possess carbon-phosphorus bonds (C-PO_3^{2-}), a bond that gives them great chemical stability (Huang et al. 2017; Ducouso-Détrez et al. 2022). Phytate (myo-inositol hexakisphosphate, IP6) exists in six phosphorylation states with 1–6 phosphate groups (i.e., mono, bis, tris, tetrakis, pentakis, and hexakis; IP1–6), is added to the soil through various means such as plant residues, monogastric animal manures and microbial conversion from soil Pi (Gerke 2015a; Liu et al. 2022). The IP6 is found in soils in four isomeric forms i.e., *myo*, *D-chiro*, *scyllo*, and *neo*, but *myo* isomer (~56–90% of IP6) dominates, with small amounts of other stereoisomers (20–50% of *scyllo*, 6–10% of *D-chiro*, and 1–5% of *neo*) (Turner et al. 2012). Phytate is synthesized in plant seeds where it acts as the primary storage form of phosphate (up to ~90–100%). In soils, it can account for up to 50–80% of Po and ~80% of IP (Gerke 2015a), nevertheless, it is not easily accessible for plant absorption due to complexation with cations or adsorption on various soil organic components, with sorption capacity being ~4 times that of orthophosphate in soils (Gerke 2015a; Liu et al. 2022). In acidic soils, phytate is bound to Fe/Al-oxides whereas alkaline soils contain phytate bound to Ca/Mg minerals (Gerke et al. 2010). It is worth mentioning that complexation of phytate with Fe^{3+} is stronger than Ca^{2+} , thus Fe-phytate is more stable than Ca phytate. Moreover, Ca-phytate can be transformed to Fe-phytate in soils over time (House and Denison 2002). Many factors affect phytate stability in soils such as organic matter, clay type and content, pH, and metal oxides (Menezes-Blackburn et al. 2013). Other phosphate esters, including DNA, RNA or sugar phosphates, react moderately with the soil solid phase, thus contributing less towards soil Po pool

(Turner 2007). Moreover, most organic P pools present in soils cannot be absorbed directly by plants. According to Barrow (2022), much of the Po has not yet been identified. Po matters (for example, polyphosphates, orthophosphate esters, and phosphonates) are mainly temporary compounds consisting of about 65% of the total P in most soils (Fabianska et al. 2019). However, it can vary from 5% (occurring in mineral soils) to 95% in organic soils (>20–30% organic substances) (Margalef et al. 2017). In contrast to Pi, Po is leached more quickly due to weak associations with the soil constituents (Gebrim et al. 2010). Further, Po in the soil exists in a quick cycling pool (rapid Po) and a gradual cycling pool (sluggish Po), depending on the source (Dodd and Sharpley 2015). The quick pool comprises the stable Po obtained from the soil solution, immobilized within the microbial cell, and redelivers the gradual pool after cell mortality. Soluble orthophosphate ions in soils can be immobilized in microbial biomass to increase cell growth. It has been reported that most of the PSM-mediated P mineralized from organic P is assimilated into the microbial cells as cellular P (Tao et al. 2008). At the same time, these soil microbes may promptly liberate Po into the gradual pool after cell breakdown, cell death, and predation by soil fauna (Müller and Bünemann 2014; Dodd and Sharpley 2015).

Plant remains, dead microorganisms, and animals along with Po fertilizers (for example, animal dung and dry straw) are the regular gradual Po sources that can quickly restore the soil orthophosphate levels via geochemical or biological degradation, ultimately proving to be beneficial for available-P supply to plants and improving soil quality (Sun et al. 2020; Bai et al. 2020). Therefore, management of the orthophosphate liberation from sources of the soil Po is a crucial soil P cycle that can raise the accessibility of soil Po for plant absorption and decrease the dependence on the application of chemical P fertilizers. Soil microorganisms, particularly PSMs, can increase the soil Po cycle by decomposition and mineralization of Po. Through examining soil P levels and oxygen isotope proportions in P, Bi et al. (2018) proposed that soil microorganisms could boost the soil P cycle by increasing extracellular hydrolysis of Po substances and assisting in the turnover of available P (NaOH-Pi , $\text{H}_2\text{O-Pi}$, and $\text{NaHCO}_3\text{-Pi}$). These biogeochemical processes are chiefly regulated by phosphatase enzymes present in PSMs and soils (Sun et al. 2020). Hedley et al. (1982) developed a technique [improved by Tiessen and Moir (2006)] that distinguished inorganic and organic P into three forms, viz. stable P (SP), labile P (LP) and moderately labile P (MLP). SP is more or less inaccessible to the plant; LP form represents a rapid-cycling P pool that is available for short-term plant uptake; MLP fraction denotes a gradual-cycling pool that can be easily transformed into LP form under particular chemical conditions (Audette et al. 2016).

With time, the minute level of steady P reacts biologically or chemically and turns into soluble and labile P. Majority of the stable P continues to exist in this form indefinitely.

Different P forms in the soil can be classified as insoluble inorganic phosphates, organic phosphates, and soluble orthophosphates. Due to the great reactive nature of orthophosphate ions with various soil components, they can be easily converted into insoluble organic and insoluble inorganic fractions. Thus, its mobility is the least in most soils, making it inaccessible for plant uptake. Previous pieces of literature have reported that insoluble Pi can be converted into soluble form via low molecular mass organic acids, (for example, gluconic and citric acids) synthesized and liberated by phosphorus solubilizing fungi (PSF) and bacteria (Ogbo 2010; Patel et al. 2011) and Po can be broken down with the help of extracellular enzymes (for instance phytase and phosphatase) primarily produced and released by microorganisms (Tan et al. 2016; Neal et al. 2017).

In most environments, geochemical processes, comprising adsorption/desorption, weathering, solid-phase conversions, and precipitation/dissolution-ascertain the P forms (accessible or inaccessible to plants) along with its distribution in soils over long-term time scales ($> 10^3$ years) (Hou et al. 2018). Nevertheless, in the short-term (ranging from $10^{0.2}$ to 10^0 years), biological processes impact P distribution as majority of the available P for the plants comes from organic substances present in the soil, which in turn is mineralized and immobilized by soil microorganisms (Tamburini et al. 2012). At the same time, geochemical processes' role in regulating P availability in soils is somewhat well understood, however, little is known about the significance of biological processes in influencing soil P availability (Tamburini et al. 2012).

Phosphorus additions to the soil for farming reasons are mostly from supplementing inorganic chemical fertilizers and organic reserves, such as manure and compost. Manure and fertilizers are essential sources of nutrients for crop growth and yield. The P in most fertilizers occurs as an inorganic or soluble fraction that is readily available for plants. The nonstop addition of rock phosphate (RP) to soils as a source of P fertilizer has been carried out for more than 100 years. Rock phosphate is among the fundamental raw materials required for manufacturing chemical phosphatic fertilizers such as single diammonium phosphate, superphosphate and nitrophosphates. Rock phosphate exists in nature as apatites (containing minerals) deposits together with other minerals like silicates, quartz, carbonates, sesquioxides and sulfates. In general, PR sources are categorized as igneous or sedimentary. Sedimentary PR possesses a greater replacement of carbonates and about 20 times higher specific surface area than igneous rocks (Van Kauwenbergh and McClellan 2004). Higher carbonate

substitutes and specific surface area enhance P solubility; thus, sedimentary RP sources are highly suitable for direct addition to soils. Manure has organic compounds containing P and soluble or inorganic phosphates. Only a small fraction of P in manure is accessible to crop plants during the input year (20–80% of P in soils) (Richardson 1994). The fraction accessible to plants (i.e. 0.1% of the entire P) is tiny owing to complexation and minimum solubility (Mahidi et al. 2011). The P present in manure, not consumed in the primary year of addition (residual P), remains in the soil and is accessible to successive crops. Soluble P present in manure, when supplemented to the soil, is easily accessible to plants for uptake. In contrast, P should be made accessible to the plant through mineralization (i.e. degradation of organic substances by soil microbes), which causes some of the P present in manure to remain in soil for few years. Composts and manures are good quality sources of P, having excellent plant availability. Although both are organically derived nutrient sources, the more significant part of P is inorganic, making up 75–90% of the entire P found in compost and manure (Eghball et al. 2002). In contrast to nitrogen, P is preserved during the composting process. Based on this process, the soluble P present in aged compost may be similar to that of the initial manure source (Adler and Sikora 2003). Guano and bone meal are not normally mentioned as P sources; nevertheless, they can possess high P levels (varying from 1 to 9% and 7–12%, respectively). Besides being commonly used as a nitrogen fertilizer, guano can also be utilized as a P source. It is produced from repeated deposition of bat or bird droppings underneath resting sites. Bone meal is made by crushing raw animal bones and is amongst the most primitive P sources employed in agriculture. It is frequently quoted as an organic P source but has several drawbacks such as high cost, less supply (Bekele and Hofner 1993), and limited research on its effectiveness. Besides these sources, soil organic P, which constitutes a large fraction of entire soil P, is derived chiefly from living tissues where P comprises an essential part of organic substances, for example, nucleotides, phytins, phospholipids, coenzymes, and phosphoproteins (Billah et al. 2019; Ducouso-Détrez et al. 2022). The extensive application of Po-comprising products, for example, fire extinguishers, plasticizers, pesticides, and antifoam agents has led to their common occurrence in the ecosystem as modern Po sources, consequently augmenting the quantities and varieties of Po fractions in soils (Hoffman et al. 2017; Fabianska et al. 2019). Soil nutrient cycling processes are accountable for the re-allocation of initial Pi into Po fractions over 10^4 – 10^6 years (Adams and Pate 1992). Conversely, Po is changed to Pi via the mineralization process. On the contrary, Pi immobilization is the opposite of mineralization. In immobilization, soil microbes transform inorganic phosphate into

organic forms, which are subsequently absorbed into their cells. Both immobilization and mineralization of P takes place at the same time in the soil. Eventually, the C: P proportion ascertains whether there is net immobilization or net mineralization.

Phosphate solubilizing microorganisms (PSMs)

Crop production is largely affected by an insufficient supply of phosphorus (P), since P functions in various plant physiological processes and overall well-being and growth of plants (Rosita et al. 2023; Silva et al. 2023). The orthophosphate ions (H_2PO_4), which are the most dominant form of P transported by plant roots, must be available at least $>0.1\%$ (w/w) in soils for proper plant growth and health (Vance et al. 2003). The available form of P in soils is majorly dependent on the microbes linked with the rhizosphere of plants. Therefore, it is critical to investigate and manage the microbiomes found in the rhizosphere to increase crop growth potential and development. In this context, PSMs have a great potential to enhance P availability while maintaining the soil's biochemical balance. Where there is restricted access to chemical fertilizers, PSMs are essentially applicable. PSMs are generally not host-specific and can be employed in various crops. A few commercially available PSMs used as biofertilizers at global level have been listed in Table 1. Additionally, patents granted for utilizing PSMs as potential biofertilizers have been summarized in Table 2.

The various types of PSMs have been discussed in the following sub-sections:

Phosphate solubilizing bacteria (PSB): underground living machinery for generation of the available form of phosphorus

The quick uptake and assimilation of P by plants largely depends on converting the insoluble fraction of P to soluble fraction by PSB in the soils. PSB account for 1–50% of the total PSMs found in nature (Fatima et al. 2022). The significant members of PSB aiding in this conversion include *Actinomyces*, *Aspergillus*, *Bacillus*, *Calothrix braunii*, *Pseudomonas*, *Rhizobium*, *Streptovorticillium* and *Streptomyces*. (Kumar et al. 2012; Kalayu 2019). Other P mineralizing and solubilizing bacteria comprise diverse strains of *Azotobacter* (Kumar et al. 2014), *Burkholderia* (Istina et al. 2015; You et al. 2020), *Enterobacter* and *Erwinia* (David et al., 2014). From rhizobial strains, two species of nodulating chickpea, *Mesorhizobium mediterraneum* and *Mesorhizobium ciceri*, are known for their high phosphate-solubilizing efficiency (Rivas et al. 2006). In plant tissue, in general, endophytic P-solubilizing bacterial populations have been reported between 10^2 and 10^4 viable bacteria

per gram (Kumar et al. 2013; Saini et al. 2015). Moreover, endophytic PSB in a single plant host are not restricted to a single species but comprise several genera and species (Mehta et al. 2015). Using morphological analysis and 16 S rRNA sequencing, Panda et al. (2016) discovered 42 PSB belonging to the genera *Pseudomonas*, *Bacillus*, *Staphylococcus*, *Micrococcus*, *Delftia*, and *Microbacterium* in the rhizosphere of rice, maize, large cardamom and ginger raised in various areas of Sikkim (India). Depending upon 16 S rRNA sequence and morphological examination from Chinese fir, Chen et al. (2021) screened seven endophytic PSB belonging to genera *Burkholderia*, *Pseudomonas*, *Paraburkholderia*, *Ochrobactrum* (HRP2, SSP2, JRP22) and *Novosphingobium*. Kumar et al. (2016a) screened several strains of *Pseudomonas* sp., *Bacillus* sp., and *Rhizobium leguminosarum* from the rhizosphere and nodules of common bean. They demonstrated the inorganic phosphate solubilizing capability of three plant growth-promoting bacteria (PGPB) strains (BPR7, RPN5, and PPR8), besides enhancing growth and productivity. Likewise, inoculation of PSB genera such as *Pseudomonas*, *Klebsiella*, *Burkholderia*, and *Chryseobacterium* was reported to regulate other microbial communities and aid in improving growth of *Ulmus chinensis* (Song et al. 2021). PSB endophytes *Enterobacter* sp. J49 or *Serratia* sp. S119 from peanut plants significantly promoted soybean and maize plant growth on a microcosm scale (Lucero et al. 2021), which indicated that PSB could be used in different plant species for improving phosphate use efficiency. Three endophytic isolates belonging to *Pseudomonas fluorescens* from the bioenergy crop *Miscanthus giganteus* showed moderate to high phosphate solubilization capacities (~ 400 – 1300 mg L^{-1}) (Oteino et al. 2015). *Aneurinibacillus* sp. and *Lysinibacillus* sp. isolated from banana have been reported to possess high P solubilization indexes (Matos et al. 2017). Borah et al. (2017) isolated rice endophytes viz., *Pantoea ananatis*, *Pseudomonas putida*, *Brevibacillus agri*, *Bacillus subtilis* and *Bacillus megaterium* that were able to efficiently solubilize different sources of phosphate viz. TCP, $AlPO_4$, and $FePO_4$. *Bacillus subtilis* (LP31 L03) showed highest phosphate solubilising activity (57.58 ± 0.65 , 6.10 ± 0.65 , $7.65 \pm 0.30\text{ }\mu\text{g/ml}$) in TCP, $AlPO_4$ and $FePO_4$ respectively. Mei et al. (2021) reported five endophytic PSB *Pantoea vagans* IALR611, *Pseudomonas psychrotolerans* IALR632, *Bacillus subtilis* IALR1033, *Bacillus safensis* IALR1035 and *Pantoea agglomerans* IALR1325 having high P solubilization efficiency. *Brevibacillus brevis* has been reported to be a PSB endophyte associated with endemic legume *Humboldtia brunonis* Wall (Shendye and Thamizhsaran 2022).

Prototypically, two Gram negative PSB viz., *Pantoea* sp. MR1 and *Ochrobactrum* sp. SSR were also reported to aid in the solubilization and mineralization of both organic

Table 1 Commercially available phosphate solubilizing microorganisms (PSMs) used as biofertilizers at global level

Product Name	PSM employed	Crop plant	Manufacturing company	Manufacturing country	References
Symbion van Plus Anubhav liquid formulation	<i>Bacillus megaterium</i> <i>B. coagulans</i>	- All crops	T. Stanes and Co. Ltd Anand Agricultural University	India India	Celador-Lera et al. (2018) Vyas et al. (2017)
Azo-N*	<i>Azospirillum brasilense</i> <i>Azospirillum lipoferum</i> <i>Azotobacter chroococcum</i> PGPR consortia	Major crops	Biocontrol Products SA (Pty) Ltd	South Africa	Rodrigues et al. (2008)
Bioativo*	<i>Aotobacter</i> , <i>Pseudomonas fluorescens</i> , <i>Phosphobacteria</i>	Bean, Maize, Sugarcane, Rice, Carrot, Cotton, Maize, Citrus, Tomatoes, Soybean	Embrafos Ltd	Brazil	Odoh et al. (2019)
Biomix, Gmax PGPR	<i>B. megaterium</i> var: <i>phosphaticum</i>	Several plants and field crops	GreenMax Agrotech	India	Odoh et al. (2019)
Biophos, Get-Phos, Reap P, Phosphonive Ecosoil	<i>P. aureofaciens</i>	All crops	KCPMC AgriStore	India	Thomas and Singh (2019)
FZB 23®	<i>B. amyloliquefaciens</i> sp. <i>planetarium</i>	Cucumber, tomato, wheat, barley	ZECH Umwelt GmbH	Germany	Patel and Goswami (2020)
Likuiq Semia*	<i>Bradyrhizobium elkanii</i>	Vegetables	AbiTEP GmbH	Germany	Odoh et al. (2019)
Gmax, Phosphomax, Astha PSB	<i>B. megaterium</i> , <i>P. striata</i>	All crops	Varsha Bioscience and Technology	India	Pallavi et al. (2017)
Rhizosom P SoiFix*	<i>B. megaterium</i> <i>Bravibacillus laterosporus</i> , <i>Paeni-</i> <i>bacillus chitinolyticus</i> , <i>Lysiniba-</i> <i>cillus sphaericus</i> , <i>Sporolactobacillus</i> <i>laevolacticus</i>	- -	Biosym Technology BioControl Products SA (Pty) Ltd	Spain South Africa	García-Fraile et al. (2015) Grady et al. (2016)
Twin N	<i>Azorhizobium</i> sp., <i>Azoarcus</i> sp., <i>Azospirillum</i> sp.	Legumes, Cereals	Mapleton Ltd	Australia	Mehnaz (2016)
JumpStart® P Sol B® - BM	<i>Penicillium bilaii</i> <i>B. megaterium</i> , <i>Pseudomonas striate</i>	-	Novozymes AgriLife	United States India	Satyaprakash et al. (2017) Beminger et al. (2018)
CBF Phylazonit M	<i>B. mucilaginosus</i> , <i>B. subtilis</i> <i>B. megaterium</i> , <i>Pseudomonas putida</i> , <i>Azotobacter chroococcum</i> , <i>Bacil-</i> <i>lus circulans</i>	All crops All arable and horticultural plants	CBF China Bio-Fertilizer AG Phylazonit Ltd	China Hungary	Celador-Lera et al. (2018) https://phylazonit.com/wp-content/uploads/2020/08/Phylazonit-product-catalogue-2020.pdf Sessitsch and Mitter (2015)
CataPult	<i>Bacillus</i> spp., <i>Glomus intraradices</i>	Wide range of crops	Mapleton Agri Biotec	Australia	Uribe et al. (2010)
Fosforina®	<i>Pseudomonas fluorescens</i>	Wide range of crops	Labiofam	Cuba	

($109 \pm 10 \mu\text{g mL}^{-1}$ and $222 \pm 11 \mu\text{g mL}^{-1}$) and inorganic P ($110 \pm 12 \mu\text{g mL}^{-1}$ and $109 \pm 15 \mu\text{g mL}^{-1}$) in soils (Rasul et al. 2021). Moreover, several studies have unveiled that inoculation of PSB species to experimental plants can enhance growth and metabolism even under stressful conditions (for more details, refer to Supplementary Table). For instance, inoculation of PSB strain N3 was reported to alleviate cadmium (Cd) toxicity in tomato plants (Zhang et al. 2021). Likewise, in ryegrass PSB such as *Acinetobacter pittii*, AP was reported to enhance the phytoextraction of Cd from the rhizosphere (Zhao et al. 2023). The inoculation of PSB species like *Bacillus aryabhatai* IA20, *Bacillus subtilis* IA6, *Paenibacillus polymyxa* IA7, and *Bacillus* sp. IA16 in the rhizosphere of cotton enhanced the growth in the semi-arid environment (Ahmad et al. 2021). These reports suggest the multi-dimensional roles of PSBs in enhancing plants' tolerance capabilities in extreme environmental conditions. Besides frequent distribution in the rhizosphere, the PSB have been dominantly localized in marine and freshwater ecosystems, particularly in sediments (Liu et al. 2015a).

Bacterial species largely mobilize P by the process of solubilization through the release of organic acids having low molecular mass. The acids released include formic, acetic, fumaric, glycolic, propionic, succinic, lactic acid, and acidic phosphatases such as phytase. The inorganic acids produced by PSB include carbonic acid, nitric acid, sulphuric, and various chelating agents that aid in P mineralization (Alori et al. 2017). Specifically, these acids' carboxyl and hydroxyl groups aid in chelating phosphate-bound cations to convert them into soluble forms of P (Lee et al. 2012). In addition, a few bacterial genera like *Bacillus* and *Streptomyces* mineralize the complex organophosphates by releasing enzymes such as phospholipases, phosphodiesterases, phytases, and phosphodiesterases to make a readily available form of P (Walpolo and Yoon 2012). Among PSB, *Bacillus*, *Streptomyces*, and *Pseudomonas* have been reported to be most effective in accelerating the mineralization of organic phosphates (Khan et al. 2009).

Soil fungi: the masters of catching the hidden treasure of insoluble P (moulds and yeast)

Prototypical to bacteria, soil fungi (accounting for 0.1–0.5% of the total PSMs) also assist in solubilizing the phosphate compounds to provide a repository of available P for easy uptake and transport through plant roots (Fatima et al. 2022). Among PSF, 20% belong to Ascomycota and the least represented phyla are Mucoromycota (1%) and Basidiomycota (3%) (Kour et al. 2021). However, soil fungi can pass through longer distances through soil than bacteria and are more crucial for solubilizing inorganic phosphate in soils because they usually synthesize and release more acids

than bacteria, including citric, gluconic, 2-ketogluconic, lactic, acetic, oxalic and tartaric acid (Sharma et al. 2013). In particular, PSF, for instance, *Aspergillus* (*Aspergillus niger*), *Gongronella*, *Fusarium*, *Penicillium* (*Penicillium oxalicum*), and *Talaromyces*, are widely studied to investigate their role in solubilization and availability of P (Li et al. 2016; Doilom et al. 2020) (Supplementary Table), among which *Aspergillus* is the most reported, followed by *Penicillium* (Kour et al. 2021; Etesami et al. 2021). For instance, at least 359 fungal species, including *Aspergillus*, *Fusarium*, and *Penicillium*, have been reported to solubilize the inorganic phosphate to soluble P in several plant species like cabbage, faba bean, haricot bean, sugarcane, and tomato (Elias et al. 2016a). Moreover, *Yarrowia lipolytica* yeast has been demonstrated to possess the ability to solubilize P (Goncalves et al. 2014). The fungal species solubilize and transport the nutrients by secreting siderophores and IAA (Zhang et al. 2018a). Sharif and Claassen (2011) reported the role of hyphal extension as an essential attribute of fungi to enhance P uptake in *Capsicum annum* L. It is worth mentioning that hyphae of PSF can even transport PSB to the site of the rhizosphere to aid in transforming insoluble P to soluble form for convenient mineralization and transport process (Jiang et al. 2021a). The mineralization of P by PSF is aided by the release of phosphatase enzymes, such as phytase, which hydrolyses organic phosphate to release P (Satyaprakash et al. 2017; Kumar et al. 2018). The P derived from phytate is only possible through the intervention of a wide range of PSMs (Richardson and Simpson 2011). Fungal species capable of procuring P from phytate by releasing phytase enzymes include *Aspergillus parasiticus*, *Aspergillus fumigatus*, *Aspergillus terreus*, *Aspergillus candidus*, *Aspergillus rugulosus*, *Aspergillus niger*, *Pseudeurotium zonatum*, *Penicillium simplicissimum*, *Penicillium rubrum*, *Trichoderma harzianum* and *Trichoderma viride* (Tarafdar et al. 2003). Similarly, the inorganic form of phosphates is solubilized by *Aspergillus awamori* (S29) (phosphate solubilizing activity in liquid 1,110 mg/L for TCP) found in the rhizosphere of mung bean (*Vigna radiata*) (Jain et al. 2012). PSF, such as *A. niger*, *A. fumigatus*, and *Penicillium pinophilum* have been demonstrated to effectively solubilize the TCP and RP, thereby augmenting the availability of P in soils (Wahid and Mehana 2000). The inoculation of these species helped to enhance the yield in faba bean and wheat crops (Wahid and Mehana 2000).

Phosphorus solubilizing fungal endophytes pertaining to diverse genera including *Acremonium*, *Aspergillus*, *Paecilomyces*, *Cryptococcus*, *Curvularia*, *Rhodotorula*, *Cladosporium*, *Phaeomonilla*, *Chaetomium*, *Berkleasium*, *Geomyces*, *Leptospora*, *Phyllosticta*, *Microdochium*, *Neotyphodium*, *Ophiognomonia*, *Penicillium*, *Rhizopus*, *Trichoderma*, *Xylaria*, and *Wallemia* have been isolated

Table 2 Patents granted for utilization of phosphate-solubilizing microorganisms (PSMs) as potential biofertilizers

Patent no.	Application filed by	Country	Patenting Year	Web link
CN103952356A	CHONGQING BEER GROUP YIBIN BEER Co Ltd, Sichuan University of Science and Engineering	China	2014	https://patents.google.com/patent/CN103952356A/en
AU2015210432B2	Novozymes Biologicals Inc	Australia	2012	https://patents.google.com/patent/AU2015210432B2/en?q=(phosphate+solubilising+bacteria)
CN103834584A	Soybean Tech Development And Research Center Heilongjiang Prov	China	2012	https://patents.google.com/patent/CN103834584A/en
CN111954712B	Walagor AG	China	2018	https://patents.google.com/patent/CN111954712B/en?q=(phosphate+solubilising+bacteria)&coq=phosphate+solubilising+bacteria
US9615584B2	Michigan State University MSU	United States	2014	https://patents.google.com/patent/US9615584B2/en?q=(phosphate+solubilising+bacteria)
CN110438037B	Northwest A&F University	China	2019	https://patents.google.com/patent/CN110438037B/en?q=(phosphate+solubilising+bacteria)
AU2022202612B2	Carbon Technology Holdings LLC	Australia	2016	https://patents.google.com/patent/AU2022202612B2/en?q=(phosphate+solubilising+bacteria)&page=4
CN111849815B	Guangxi University for Nationalities	China	2020	https://patents.google.com/patent/CN111849815B/en?q=(phosphate+solubilising+bacteria)&page=9
EP3105198B1	Biofl Mikrobiologjai Genticologiai Es Biokemiai Kft	European Patent Office	2014	https://patents.google.com/patent/EP3105198B1/en?q=(phosphate+solubilising+bacteria)
CN104450552B	Xi'an Jinborui Ecological Technology Co Ltd	China	2014	https://patents.google.com/patent/CN104450552B/en?q=(phosphate+solubilising+bacteria)

from various host plants (Yadav et al. 2018; Mehta et al. 2019; Sujatha et al. 2020). A dark septate root endophytic fungus *Curvularia geniculata* isolated from *Parthenium hysterophorus* roots has been reported to improve plant growth through P-solubilization and phytohormone production (Priyadharsini and Muthukumar 2017). Researches have been conducted globally to investigate the ability of endophytic PSF to solubilize insoluble phosphates. In this regard, five endophytic fungi, isolated from the roots of *Taxus wallichiana*, belonging to *Penicillium* and *Aspergillus* spp. were studied for their ability to solubilize insoluble phosphates in the presence of tricalcium (TCP), aluminium (AlP), and iron phosphate (FeP). Maximum phosphate solubilization was recorded in the case of the fungal isolate *P. daleae* being 83.42 ± 3.41 $\mu\text{g/ml}$ TCP, 57.63 ± 0.79 $\mu\text{g/ml}$ AlP, and 57.76 ± 1.70 $\mu\text{g/ml}$ FeP (Adhikari and Pandey 2019). In another study, three strains of endophytic fungi namely, *Penicillium simplicissimum* CN7, *Talaromyces flavus* BC1, and *Trichoderma konilangbra* DL3 isolated from the roots of *Stevia rebaudiana* (Bert.) Hemsl., *Polyscias fruticosa*, and *Angelica dahurica* in some localities in Vietnam have been demonstrated to possess the ability to solubilize phosphate to 341.90, 1498.46, and 390.79 ppm (Huong et al. 2022). The endophytic fungal isolates *Trichoderma asperellum* isolate, *Curvularia chiangmaiensis*, and *Fusarium solani* collected from rice plant tissue displayed phosphate solubility in range of 2.74 to 17.61 $\mu\text{g/ml}$ (Putri et al. 2022). Out of 35 endophytic fungal isolates from wild

Zingiberaceous species, 4 PSF, namely, *Pestalotiopsis thailandica* He06, *Trichoderma atroviride* E101, *Trichoderma brevicrassum* displayed the amount of solubilized P in the order: *P. thailandica* (4.61 mg/L), followed by *T. scalesiae* (1.85 mg/L), *T. brevicrassum* (1.38 mg/L) and *T. atroviride* (1.33 mg/L) (Munir et al. 2022). Recently, Parvez et al. (2023) assessed P-solubilization capacity of fungal endophyte *Rhizopus oryzae* associated with coriander roots, collected from water stressed soil and reported that among the 6 supplemented P-sources, the highest solubilization was observed for tricalcium phosphate (51.45 ± 2.3 mg/L). The multifunctional property of soil fungi in phosphate solubilization and plant growth has been illustrated in Fig. 1.

Arbuscular mycorrhizal fungi (AMF) networking for facilitating plant growth and development

The AMF establish a symbiotic relationship with plant roots. This association exerts beneficial impacts on plants in terms of enhancing the uptake of nutrients, boosting growth, health, and yield, and also alleviating several abiotic stressors (Liu et al. 2021; Zen El-Dein et al. 2022; Kaur et al. 2023) (Supplementary Table). Moreover, a large number of studies have reported the role of AMF in improving the availability of P in the rhizosphere of a wide range of plants by colonizing the roots intracellularly, thereby promoting overall growth and well-being (Mitra et al. 2020, 2023; Basiru et al. 2023; Chatterjee and Margenot 2023).

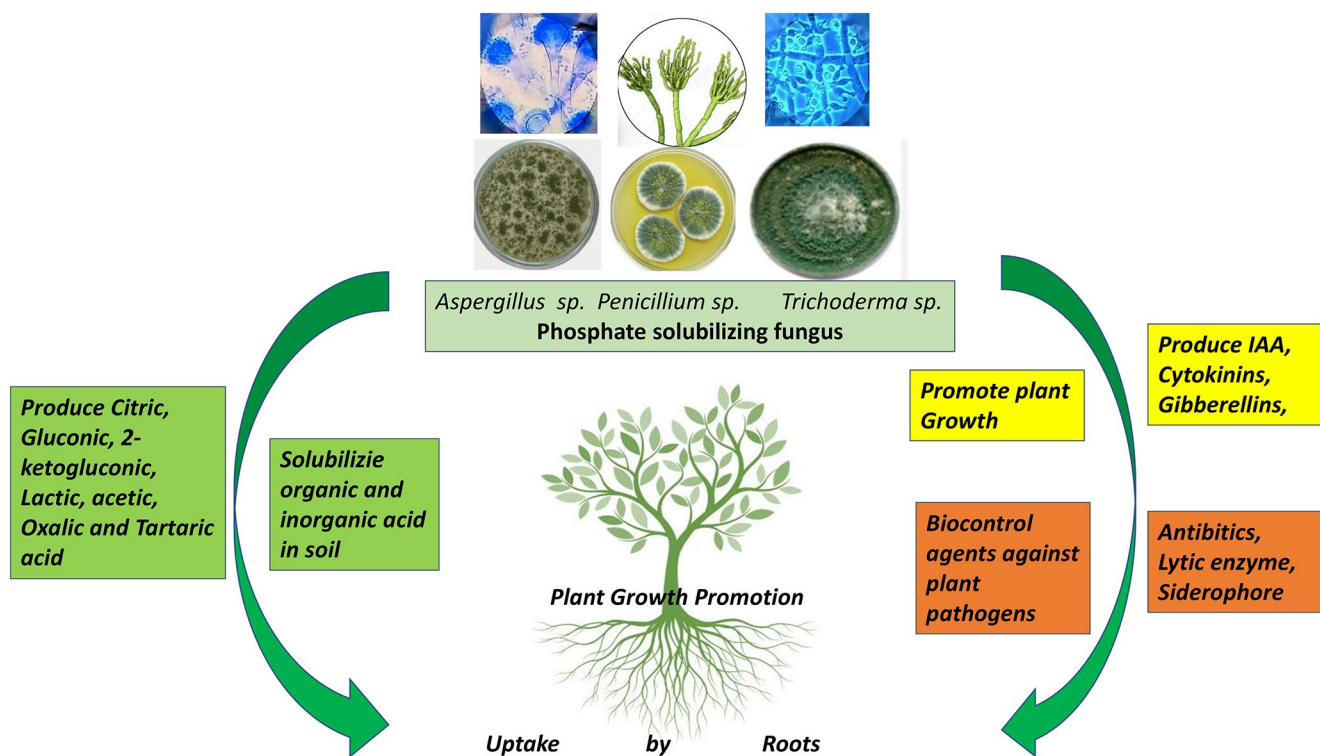


Fig. 1 Soil fungi: the architecture of plant growth promotion with different strategies

AMF have been reported to scavenge P from soils through the AM pathway to deliver P to the cortical cells in roots quickly, hence bypassing the direct uptake pathways (Smith et al. 2011). This reported AM pathway for the transport of P involves different cell types, specific areas of roots, and P transporters for an efficient transport process (Smith et al. 2011; Johri et al. 2015). These studies suggest that AMF have adopted novel means to transport P directly to the root systems. Plants in symbiosis with AMF secrete H^+ or organic anions to liberate P_i from rocks containing P minerals, boosting the uptake of P_i by both AMF and plants. This is accomplished by the development of dense “cluster roots.” In rice plants, AMF significantly improved P uptake under aerobic conditions, and this association also reported biomass enhancement (Maiti et al. 2011). Similarly, AMF *Rhizophagus irregularis* colonization greatly enhanced the P absorption performance of wheat from soluble P, burned sewage sludge, and dehydrated sewage sludge raised in pots containing ^{33}P labelled pool dilution (Mackay et al. 2017). Additionally, in nutrient-limited conditions, AMF can increase plant uptake of P by enriching soil PSB in the extended hyphae, allowing for a more significant physical exploration of P-depleted soil (Tian et al. 2021). A huge repository of studies back up the role of AMF in regulating plant metabolism by enhancing P solubilization and uptake in the rhizosphere. Therefore, AMF need special attention and engineering to be included in syncoms for sustainable agricultural growth. Figure 2 describes the Arbuscular

Mycorrhizal Fungi (AMF) networking with PSB for facilitating phosphate solubilization and plant growth.

Actinomycetes

These are highly ubiquitous organisms with high disseminating potential through spores, either singly or in chains. They possess bacterial properties and also have complex life cycles. Recently confirmed as bacteria, due to their spore-forming capability, they dominate a broad range of soil habitats, acting as phytoenhancers under extreme environmental conditions. Among actinomycetes, 20% of the genera *Micromonospora*, *Actinomyces*, and *Streptomyces* can solubilize P (Alori et al. 2017; Aallam et al. 2021; De Zutter et al. 2022). Eighteen actinomycetes strains were recovered by Faried et al. (2019) from rhizospheric soils collected from an experimental farm grown with wheat, faba bean, and clover. Actinomycetes, such as *Actinoplanes*, *Frankia*, *Microbispora*, *Micromonospora*, *Nocardia*, *Rhodococcus*, and *Streptomyces*, have been described to boost plant growth and development by inducing the release of antimicrobials, siderophores, and phytohormones (Menendez and Carro 2019). Recently, Elshafie and Camele (2022) demonstrated the function of phosphate-Actinomycetes as biofertilizers and biopesticides, thereby aiding in the preparation of bioformulations. Actinobacteria isolated from *Laminaria ochroleuca* were able to impede the growth

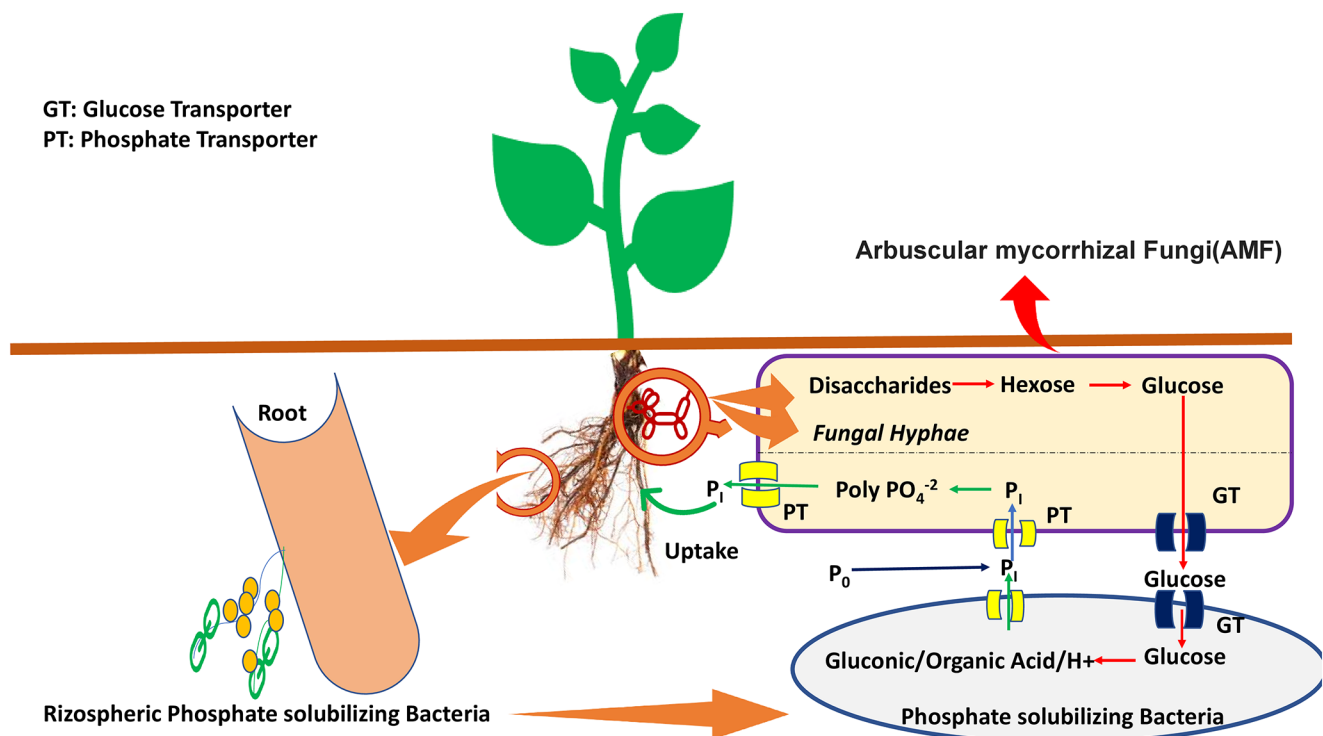


Fig. 2 Arbuscular Mycorrhizal Fungi (AMF) networking with phosphate solubilizing bacteria for facilitating phosphate solubilization

of *Staphylococcus aureus* and *Candida albicans*, hence authenticating their antimicrobial potential (Girão et al. 2019).

The plant-growth-promoting *Streptomyces* increased plant growth potential by inducing phosphate solubilization, phytohormones production, and alleviating abiotic stress conditions (Sousa and Olivares 2016). It has been demonstrated that endophytic Actinobacteria stimulate plant growth by inducing the secretion of phytohormones, for example, IAA (Manulis et al. 1994; Dochhil et al. 2013). The *Frankia*, a mutualistic Actinobacteria, aids in nitrogen fixation, enhances nutrient availability, and helps in solubilizing immobilized potassium and phosphorus. In addition, reports suggest that actinobacteria improve organic matter decomposition by releasing cellulases, glucanases, lipases, proteases, chitinases, and xylanase and trigger the production of ammonia, siderophores, and hydrogen cyanide to combat biotic and abiotic stressors in plants (Mitra et al. 2022). More recently, Bouizgarne (2022) evaluated the actinomycetes' high potential for producing metabolites, suitability for formulations, adaptability to hostile environments, and versatility. A few studies have been conducted to investigate P solubilizing capability of endophytic actinomycetes. For instance, Gangwar et al. (2012) isolated 35 endophytic actinomycetes strains from the roots, stems and leaves tissues of healthy wheat plants and identified them as *Streptomyces* sp. (24), *Actinopolyspora* sp. (3), *Nocardia* sp. (4), *Saccharopolyspora* sp. (2) *Pseudonocardia* (1) and *Micromonospora* sp. (1). The authors further reported 17 endophytic actinomycetes isolates possessing abilities to solubilize phosphate in the range of 5 to 42 mg/100 mL. Similarly, Passari et al. (2015) isolated 42 endophytic actinomycetes from medicinal plants out of which 14 isolates showed the solubilization of inorganic phosphate ranging from 3.2 to 32.6 mg/100 ml. In another study, the actinomycetes showed P solubilization activity ($1,916 \text{ mg L}^{-1}$) and produced phytase (0.68 U mL^{-1}), chitinase (6.2 U mL^{-1}), IAA (136.5 mg L^{-1}), and siderophore (47.4 mg L^{-1}). Furthermore, inoculation of *Streptomyces* mhcr0816 and mhce0811 with *Triticum aestivum* significantly improved plant growth, biomass (33%), and mineral (Fe, Mn, P) content in non-axenic conditions (Jog et al. 2014). Mesta et al. (2018) isolated 11 phosphate solubilizing endophytic actinomycetes from two mangrove plants *Rhizophora mucronata* and *Sonneratia caseolaris* amongst which the highest amount of phosphate solubilized was recorded for Isolate RO 11 about $1410 \text{ }\mu\text{g/mL}$. Taken together, it is essential to highlight and unravel the potential of Actinomycetes in regulating plants' growth and overall well-being.

Archaea

Archaea refers to a domain of single-celled organisms that lack nuclei and are therefore categorized under prokaryotes. They inhabit a wide range of habitats, especially thermal vents, psychrophilic, hypersaline, arid, semi-arid, and dry environments, and highly acidic and alkaline habitats (Timonen and Bomberg 2009; Ahmad et al. 2011; Huang et al. 2019; Naitam and Kaushik 2021). Several species belonging to Archaea are reported to be associated with plant microbiome, aiding in improving plant health (Taffner et al. 2019). For instance, Archaea (*Natronoarchaeum*, *Natrialba*, *Natrinema*, *Haloterrigena*, *Halolamina*, *Halosarcina*, *Haloarcula*, *Halobacterium*, *Halococcus*, *Haloferax* and *Halostagnicola*) have been described to play crucial roles in phosphate solubilization, sulfur cycling, nitrogen fixation, IAA and siderophore release, dissimilatory nitrate reduction and ammonia-oxidation (Navarrete et al. 2011; Yadav et al. 2015, 2017; MacLeod et al. 2019). *Natrinema* sp. and *Halococcus hamelinensis* have been reported to solubilize phosphate 134.61 mg/L and 112.56 mg/L respectively (Yadav et al. 2017). Moreover, Archaea help in driving soil stoichiometry in habitats having P deficiency and also aid in regulating the C/N/P cycling in subtropical habitats (Wang et al. 2022b). Hence, Archaea play a vital role in improving the production of crops and sustainability in semi-arid and arid habitats (Alori et al. 2020).

Cyanobacteria

Cyanobacteria exist as unicellular, colonial, or multicellular filamentous forms and are considered a significant subset of the bacterial kingdom. They help in nitrogen fixation, reduce CO_2 levels, help in phosphate solubilization, and trigger the release of plant hormones, amino acids, siderophores, and important polysaccharides (Elagamey et al. 2023). Reports suggest that metabolites released by cyanobacteria aid in soil decontamination, soil fertilization, and resilience to biotic and abiotic stressors (Górka et al. 2018; Ronga et al. 2019). Most of these bioactive compounds induce gene expression, accumulate biomolecules important for plant growth, and help mediate tolerance against environmental stressors (Han et al. 2018; Pan et al. 2019).

Inoculating cyanobacteria directly on seeds or soil increases germination rate and yields in several cereals and horticultural crop plants (Singh et al. 2017; Toribio et al. 2021). The application of Cyanobacteria such as *Anabaena sphaerica* ISB23, *Anabaena torulosa*, *Anabaena oscillarioides* ISB46, *Nostoc calcicola*, and *Trichormus ellipsosporus* to *Mentha piperita* under saline conditions stimulated oil content and also enhanced plant growth (Shariatmadari et al. 2015). Similarly, the soils inoculated with *Spirulina*

meneghiniana and *Anabaena oryzae* in lettuce plants helped alleviate the drought stress (Ibraheem 2007). Seed priming with *Nostoc* sp. and *Microcoleus* sp. enhanced seed germination and growth of *Acacia hilliana* and *Senna notabilis* seedlings (Muñoz-Rojas et al. 2018). Additionally, Cyanobacteria assist in regulating soil vigor by increasing soil physiochemical properties, such as aeration aggregation, and help release nutrients (Singh et al. 2016). Rai et al. (2019) reported that cyanobacteria could facilitate the solubilization and mobilization of insoluble organic phosphates like aluminium phosphate, tricalcium diphosphate, and ferric phosphate into soluble and available forms of phosphorus in plants, primarily due to the presence of phosphatase enzymes. Hence, it is evident from the above studies that cyanobacteria can aid in accomplishing agricultural sustainability by improving plants' overall physiology and development. Therefore, they are the best candidates to be explored for enhancing crop production and sustainable agricultural development.

Effect of consortia of diverse PSMs on phosphorus solubilization and plant acquisition

The combined inoculation of two or more phosphate solubilizing microbial species has often been reported to exert positive effect on growth and yield of various crops. For example Saxena et al. (2015) demonstrated significant positive impact of dual inoculation of a PSB *Bacillus* sp. RM-2 and a free living PSF species *Aspergillus niger* S-36 on growth and development of chickpea plants than their respective individual inoculations. Similarly, the addition of consortium containing PSB (BRC-AP and BRC-AK) and IAA producing fungi (*Humicola* sp. R.Dn) improved the growth of elephant grass (Imaningsih et al. 2019). Co-inoculation with *Trichoderma viride*, *Humicola* spp., *Paecilomyces lilacinus*, *Gluconacetobacter diazotrophicus*, *Azospirillum brasilense*, and *Bacillus subtilis* improved nutrient cycling and soil fertility, thereby promoting sugarcane root development (Tayade et al. 2019). Similarly, inoculation with *Azospirillum brasilense* and *Bacillus subtilis* improved the quality and yield of sugarcane crop (Rosa et al. 2020). The composite inoculation of *Bradyrhizobium japonicum* 5038 and *Paenibacillus mucilaginosus* 3016 in soybean caused significant increase in the abundance of phosphorus cycle genes, soil available phosphorus and phosphatase activity (Xing et al. 2022). Nandimath et al. (2017) isolated, identified and developed a consortium of five thermo-tolerant phosphate solubilizing actinomycetes for producing a multipurpose bio-fertilizer which released soluble phosphate of up to 46.7 $\mu\text{g ml}^{-1}$. Kumar et al. (2020) performed qualitative and quantitative analyses of inorganic and organic P solubilization by three PSR consortia (*Burkholderia*

gladioli, *Pseudomonas* sp. and *Bacillus subtilis*) on various culture media containing six different sources of insoluble inorganic phosphate such as tri-calcium phosphate (TCP), di-calcium phosphate (DCP), zinc phosphate (ZP), ferric phosphate (FP), sodium di-hydrogen phosphate (SP), and aluminum phosphate (AP), and two organic P such as calcium and sodium phytate and reported P solubilization of 37.9 mg/100 ml of TCP, 40.01 mg/100 ml of DCP, 15.79 mg/100 ml of FP, 43.02 mg/100 ml of SP, no solubilization of ZP and AP, 39.75 mg/100 ml of calcium phytate and 24.01 mg/100 ml of sodium phytate. The authors further reported that after bio-priming of seeds in pot assay, the level of P in soil increased by 54% in consortium treated soil compared to control soil. In another study, Kumar et al. (2016a) observed solubilization of TCP, DCP, ZP on different media by consortia *Bacillus* sp., *Pseudomonas* sp. and *Rhizobium leguminosarum*.

Effect of consortia of rhizospheric and endophytic PSMs on plant phosphorus efficiency

Besides rhizospheric communities, huge and diverse population of microbes reside within plant tissues without causing any visible signs of disease and are called endophytes (Deng and Cao 2017). Limited reports are available in the literature regarding co-inoculation of rhizospheric and endophytic PSMs and their effect on P efficiency of plants. For instance, dual inoculation of *Rhizobium* and PSB in wheat resulted in yield increases of 29% and 25% with and without P fertilizer respectively (Afzal and Bano 2008). It has been proposed that rhizospheric and endophytic bacterial inoculation could improve P efficiency of plants by increasing P bioavailability and extension of root system via IAA production. In this context, Emami et al. (2020) selected 22 isolates from rhizosphere and inside root of wheat (*Triticum aestivum* L.) plants based on their plant growth promoting traits and demonstrated their significant ability to solubilize P from tri-calcium phosphate and production of IAA under in vitro condition. In pot experiments, the authors reported synergistic interaction between PGPR and plant growth promoting endophytes in increasing P uptake, growth and yield in two wheat cultivars, Marvdasht and Roshan. The uptake of P was 3.61 mg pot⁻¹ for Marvdasht cultivar and 6.44 mg pot⁻¹ for Roshan cultivar. The co-inoculation of N-fixing bacteria (*Bradyrhizobium japonicum*) and PSMs (*Saccharomyces cerevisiae* and *Saccharomyces exiguus*) increased P utilization and atmospheric nitrogen fixation in soybean, leading to enhanced soil fertility and crop productivity (Zveushe et al. 2023). Similarly, Tennakoon et al. (2019) reported that application of N₂ fixing and PSB dual inoculants reduced application rate of N by 33% and P by 50%. Meena et al. (2010) analyzed inoculation of chickpea with

endophytic fungus, *Piriformospora indica*, in combination with PSB, *Pseudomonas striata* and reported their synergistic effect on population buildup of *P. striata* and plant dry biomass compared to individual inoculations.

Mechanism of phosphate solubilization by phosphate solubilizing microorganisms

After nitrogen, P has been considered the second most censored macronutrient, which significantly enhances plants' growth, metabolism, and overall health (Silva et al. 2023). Even though P is present in significant amounts in organic and inorganic fractions in soil, its complex formation with metal ions generally leads to reduced plant uptake (Rawat et al. 2020). Furthermore, the agrochemical-mediated increased P requirement for improving crop yield has deteriorated the soil ecosystem and the balance of soil microbiota. To overcome this issue, there is a pressing need to adopt environment-friendly strategies that can enrich the soil with P, ultimately making the P readily available for plants (Rawat et al. 2020). One of the most promising strategies is the addition of microorganisms, which aid in the solubilization of insoluble phosphates in the soil (Wang et al. 2023). These microorganisms secrete various enzymes, siderophores, and organic acids, which facilitate the dissociation of metal ions from the phosphate-metal complex, consequently making the phosphate readily accessible to plants for uptake (Rawat et al. 2020, 2021; Silva et al. 2023; Khan et al. 2024). It has been demonstrated that diverse PSMs can transform insoluble P into readily available fractions for the plant. Moreover, their abundant presence in the soil and P-solubilization ability can be analyzed via different quantitative and qualitative methods. It is worth mentioning here that in most experiments, microorganisms intended to solubilise soil phosphate are selected on their ability to produce a clear halo around the colony on a plate when they are grown on a medium containing sparingly-soluble phosphate compounds which involves production of acidity. Barrow and Lambers (2022) are of the opinion that if plants are inoculated with such microbes, any benefit arising from increased acidity is likely to be as a result of increased rate of P uptake by plant roots rather than from increased desorption of phosphate from soil.

The dynamics of soil P status depend on various factors such as (i) precipitation and dissolution, (ii) desorption and sorption, and (iii) the reaction that stimulates the interconversion between inorganic and organic P (Sims and Pierzynski 2005). The PSM-mediated immobilization, mineralization, and solubilization of P in soil up-regulate the dissemination of soil P, which is impacted by the availability of inorganic minerals in the soil. The enhanced exudation of organic acids, siderophores, protons, extracellular enzymes,

and the mineralization-assisted degradation of substrates are the strategies adopted by PSMs through which the soil phosphate dissolution occurs (Rawat et al. 2020) (Fig. 3).

Solubilization of soil inorganic phosphates

The various ways through which PSMs assist in the solubilization of inorganic phosphates (like Fe-P, Ca-P, and Al-P) present in the soil have been discussed in the following sub-sections:

Secretion of organic acids

PSMs produce organic acids via physiological secretion and decomposition of organic matter (Schneider et al. 2019). It has been demonstrated that the PSMs-mediated exudation of organic acids such as gluconic, tartaric, lactic and citric acid solubilize the soil inorganic phosphates via chelation of cations complexed with phosphate, decrease in pH, formation of a complex with phosphate bound metals and disturbance in P adsorption region (Rawat et al. 2021; Li et al. 2023). The low molecular mass organic acids assist in the hydroxylation and carboxylation mediated chelation of cations bound to Pi, reduced rhizospheric pH via exchange of O₂ and CO₂ and balancing of proton bicarbonate, ultimately creating a favourable soil environment for the release of bound Pi (Mander et al. 2012; Wei et al. 2018). It has been reported that P mobilization via citric acid and its acquisition is very strong in cluster root rhizosphere such as those found in white lupin and yellow lupin, because of the strong accumulation of citric acid and efficient uptake of the mobilized P (Adams and Pate 1992). Several PSMs have been reported to secrete carboxylates which increase the solubility of P in soils (Jayakumar et al. 2019). Nevertheless, P mobilization by carboxylates depends on the chemical reactions occurring at the solid phase of soils (Gerke 2015b). Adsorption of P to the soil solid phase may inhibit its degradation by microbes which partially describes the long-term impact of carboxylates on P solubility in soil (Gerke 2015b). Additionally, citrate and to some extent oxalate are more efficient in mobilizing P as compared to other carboxylates (Barrow and Lambers 2022). Zaheer et al. (2019) reported secretion of oxalic acid, gluconic, citric, acetic, and lactic acid from the AZ15 strain of *Pseudomonas* species, which enhanced the P solubilization up to 109.4 µg mL⁻¹. The researchers also observed increased growth and yield traits in chickpeas due to application of this particular bacterial strain (Zaheer et al. 2019). Similarly, various strains of *Trichoderma* like AMS 31.15, AMS 1.43, and AMS 34.39 have been demonstrated to aid in the solubilization of P in soybean by secreting various organic acids (gluconic acid, malic acid, phytic acid, citric acid, and ascorbic acid) and supplementation

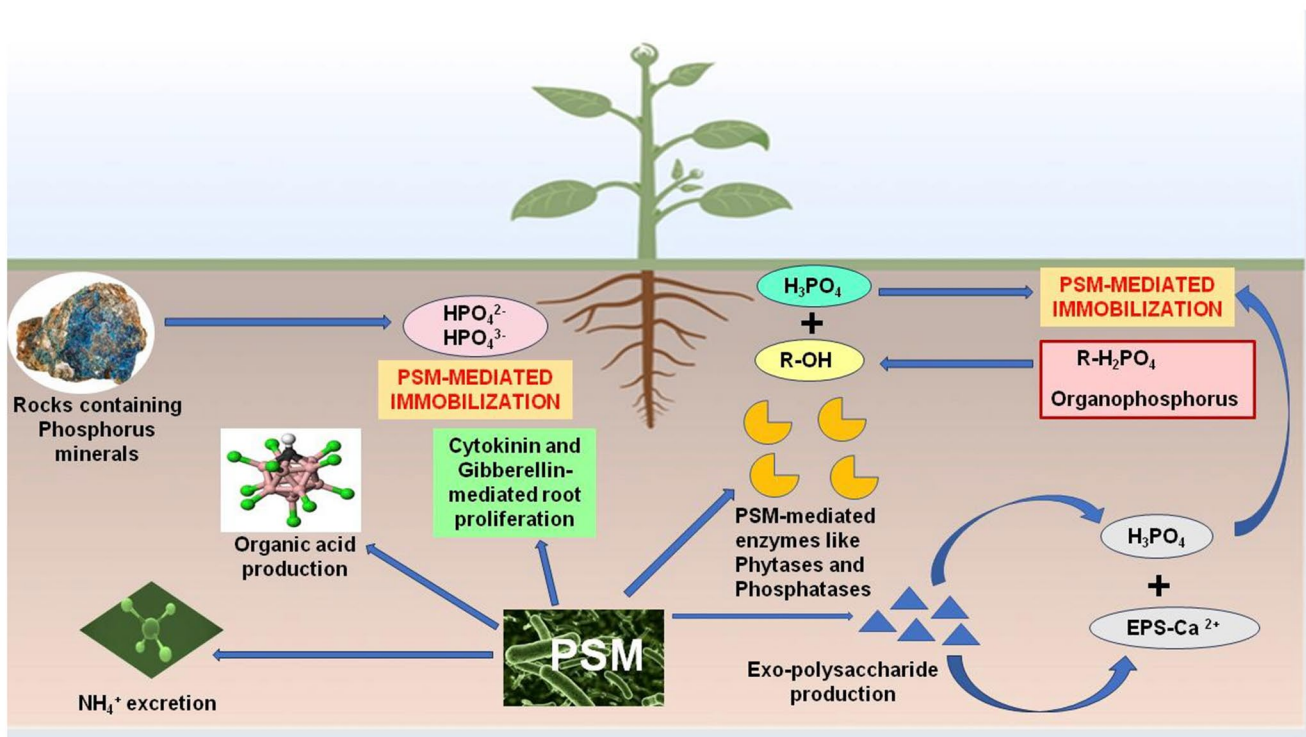


Fig. 3 Various mechanisms of phosphate solubilization in soil adopted by phosphate solubilizing microorganisms (PSM)

of these strains enhanced the growth of plants up to 40% as compared to uninoculated plants (Bononi et al. 2020). Despite beneficial influence of PSMs-induced organic acid secretion at desorbing phosphate from soil and making it available for plant uptake under controlled conditions, Barrow and Lambers (2022) are of the opinion that the effects of the production of organic acids under field conditions are probably over-estimated. Apart from this, carboxylate groups present in organic acids also assist in mobilizing Po, especially phytate via three mechanisms: (i) desorption of P anions from soil through ligand exchange via replacing P with a carboxylate anion, (ii) solubilization of Fe and Al via H^+ , thereby destroying P sorption sites and (iii) solubilization of organic matter binding to P through Fe/Al-bridges, with P being solubilized as organic matter-Fe/Al-P complex (Gerke 2010).

Secretion of inorganic acids and hydrogen sulfide (H_2S)

Apart from organic acids, diverse PSMs secrete different types of inorganic acids like nitric acid, sulfuric acid, hydrochloric acid, and carbonic acid to solubilize phosphate, though with less efficiency than organic acids (Siddique et al. 2021; Pang et al. 2024). *Nitrobacter* and *Thiobacillus* species secrete inorganic acids such as sulfuric acid and nitric acid, respectively, which assist in the dissolution of P (Shrivastava et al. 2018). It has been reported that the

production of metabolic byproduct, H_2S , by sulfur- and acidophilic bacteria facilitate the production of ferrous sulphate by reacting with ferric phosphate, thus liberating the bound P (Florentino et al. 2016). Roy and Roy (2019) observed that about 1 g L^{-1} elemental sulfur was oxidized to 203 mg L^{-1} sulfate, and 20 mM thiosulfate was oxidized to 220 mg L^{-1} sulfate with the help of the SR4 strain of sulfur-oxidizing bacteria of *Delftia* species. Further, the inoculation of this strain to *Brassica juncea* enhanced P-solubilization efficiency by up to 116% compared to the control plants (Roy and Roy 2019).

Extrusion of the proton from ammonium ion (NH_4^+)

The PSM-mediated synthesis of amino acids via assimilation of soil ammonium (NH_4^+) leads to enhanced proton (H^+) concentration in the microbial cytoplasm. This acidifies the surrounding microbial cell medium and enhances the dissolution efficiency of insoluble phosphates (Gand 2016). The extrusion of H^+ reduces the soil pH, depending on the nitrogen source. It has been reported that utilizing NH_4^+ enhances the dissolution of P as a nitrogen source compared to NO_3^- (Sharan and Darmwal 2008). FA7 strain of *Bacillus marisflavi*, an alkalophilic bacterium, plays a pivotal role in the H^+ -extraction-mediated dissolution of phosphate. It was observed that this particular strain maximized the dissolution of TCP when NH_4Cl was used as an inorganic source

of nitrogen in the media (Prabhu et al. 2018). In addition to this, the BPM12 strain of *Bacillus subtilis* enhanced the solubilization of P up to $272.02 \mu\text{gmL}^{-1}$ when $(\text{NH}_4)_2\text{SO}_4$ as a source of nitrogen was supplemented to the media (Wang et al. 2020).

Production of siderophores

The low molecular mass siderophores are the iron-chelating substances obtained from iron-stressed plants and microorganisms. They form the strongest complex with ferric ions (Verma et al. 2012; Rizvi et al. 2021), and presently about 500 known siderophores are obtained from both microbes and plants (Sharma et al. 2013). It has been reported that the release of PSM-mediated siderophores in soil aids in iron chelation from the Fe-P complex (Collavino et al. 2010; Cui et al. 2022). Several types of PSMs, like *Rhizobium radiobacter*, *Bacillus megaterium*, *Pantoea allii*, and *Bacillus subtilis*, have been reported to produce siderophores varying from 80 to $140 \mu\text{mol L}^{-1}$ that enhance the solubilization of P and create an environment for the survival of organisms (Ferreira et al. 2019). Recently, a novel fungus, *Beauveria brongniartii*, has been reported to produce siderophores in the range of 59.8% Fe³⁺-Chrome azurol-S degradation, which enhanced the solubilization of P by about 158.95 mg L^{-1} (Toscano-Verduzco et al. 2020).

Solubilization of soil organic phosphates

About 20–30% of organic phosphates have been reported in soil, and their dissolution occurs via mineralization through enzymatic processes (Kumar and Shastri 2017). Three broad enzymatic reaction mechanisms have been reported through which PSM-mediated dissolution of organic phosphates occurs. These mechanisms have been discussed as follows:

Phosphomonoesterases or non-specific acid phosphatases (NSAPs)

Acid and alkaline phosphatases are the two main types of NSAPs produced by PSMs, whose categorization is based on the optimal pH at which they function (Liang et al. 2020; Cheng et al. 2023). Acidic soil contains acid phosphatases, whereas alkaline to neutral soil contains alkaline phosphatases (Cheng et al. 2023). The activity of alkaline phosphatases is hindered by inorganic phosphates in the environment, while acid phosphatases activity is not inhibited by high levels of phosphates (Li et al. 2021; Xie et al. 2021). Phosphatases catalyze the dephosphorylation of phosphoanhydride or phosphoester linkages of organic phosphate compounds and are exuded by the microorganisms which show high affinity towards soil organic phosphate

compounds (Sharma et al. 2013). It has been reported that about 90% of the soil's organic P is hydrolyzed by alkaline phosphatases, making P readily accessible to plants (Chen and Arai 2023). It was observed that alkaline phosphatases extracted from the MTCC 2312 strain of *Bacillus licheniformis* when supplemented with the soil-grown *Zea mays*, enhanced the percentage of P in the root by about 2.35 fold and in the stem by about 1.76-fold (Singh and Banik 2019). The co-inoculation of the L7B strain of PSF (*Talaromyces helices*) and AMF (*Rhizophagus irregularis*) increased the activity of soil alkaline phosphatase in comparison to the uninoculated soil which in turn enhanced the P solubilization by about 50% than uninoculated controls (Della Monica et al. 2020).

Phytases (myo-inositol hexakisphosphate phosphohydrolases)

One of the abundant forms of soil organic P is the phytate compounds from which the P is removed via the catalytic activity of phytases. These phytate compounds are the reservoir of inositol and the house of seed and pollen P (Sharma et al. 2013). Plants show low efficacy of P uptake directly from the phytate since it is strongly bound to soils. It has been reported that the concentrations of soluble phytate-P in the soil solution are typically very low ($4\text{--}14.3 \mu\text{g L}^{-1}$) (Shand et al. 1994). Phytases are extracellular enzymes secreted by soil microorganisms and/or plant roots and participate in phytate mineralization. Phytase liberates orthophosphate from phytate organic compounds, thereby changing P into a phyto-available form (Ortega-Torres et al. 2021; Timofeeva et al. 2022). Depending on catalytic mechanism, phytases are classified as histidine acid phosphatase (HAP), purple acid phosphatase (PAP), Cys phosphatase, or β -propeller phosphatase, with HAP and PAP being more prevalent (Lei et al. 2007). HAPs originate mainly from plants and show specific activity toward phytate whereas PAPs originate from both plants and microbes and can hydrolyze various Po forms besides phytate (Hegeman, and Grabau 2001). Phytase activity in soils is affected by soil pH, with optimal activity at 2.5–8.0 pH and then decreasing with increasing pH, thus, it is higher in acidic soils than alkaline soils.

When the *phyA* gene from *Aspergillus niger* was transferred into the *Arabidopsis* plant, the genetically-modified *Arabidopsis* showed P-mediated enhanced growth and development (Richardson 2001). In addition, inoculation of phytases-producing bacteria to different cereal crops increased the rate of P uptake without exogenous supplementation of phosphate fertilizers (Martinez et al. 2015). Similarly, inoculation of the fungus *Aspergillus niger* to *Lagenaria siceraria* and *Abelmoschus esculentus* enhanced the morphological characters like leaf area, fruit number,

and plant height in both the plants when compared to their respective uninoculated plants (Din et al. 2019). Ben Zineb et al. (2020) described that phytase-producing strains of *Serratia liquefaciens* (LR88) and *Pseudomonas corrugate* (SP77) displayed their phytase activity by about 24.84 and 23.02 U mL⁻¹ respectively, which in turn exhibited their rate of phosphate solubilization efficiency by about 306.74 and 714.96 µg mL⁻¹ respectively. A close analysis of literature revealed contrasting results regarding the role of phytases in P acquisition from phytate. A few researchers have reported that hydrolysis by phytases is not the limiting step in P acquisition from phytate in a strong P deficient soil (Tarafdar and Claassen 1988). On the contrary, another group of researchers argued that even under conditions of high P solubility, the enzymatic hydrolysis via phytases is the limiting step in P acquisition from phytate (Hayes et al. 2000; George et al. 2004). These contrasting reports might be attributed to the differences in the soils that were used for experiments by the two groups of researchers. According to the results of Adams and Pate (1992), phytate P acquisition is limited by its fixation to the soil solid and that inadequate phytase activity is not the limiting factor in P acquisition. Similarly, Lung and Lim (2006) also advocated the solubility of phytate to be the limiting factor in phytate P acquisition in soil and not the hydrolysis of its ester bond. As such, there is no agreement regarding the limiting step in phytate-P acquisition by plants.

Carbon–Phosphorus (C–P) lyases /Phosphonates

These enzymes extract phosphate from organophosphates by catalyzing the breakdown of C–P linkage, thereby generating P readily accessible to plants (Rodriguez et al. 2006). Several phosphate solubilizing bacteria (*Acinetobacter*, *Enterobacter*, *Burkholderia*, *Rhizobium*, *Bacillus*, and *Pseudomonas*) have been demonstrated to have C–P lyases activity (Vazquez et al. 2000; Teng et al. 2019). Further, some endophytic fungi (*Piriformospora*, *Curvularia*, *Aspergillus*,

and *Penicillium*) have been reported to encode C–P lyase enzymes (Mehta et al. 2019). Mechanism of action of C–P lyase and phosphonate has been described in Fig. 4.

Molecular background of PSM-mediated phosphate solubilization

The molecular aspects of PSM-mediated phosphate solubilization revealed that a small number of genes are responsible for the dissolution of phosphate (Table 3), known as pyrroloquinoline quinone genes (*pqq*). The PQQ gene family contains about six genes, *pqqA*, B, C, D, E, and F, which encode a tiny redox active molecule and co-factor for PQQ and quinoprotein enzyme glucose dehydrogenase, respectively (Wu et al. 2022a). The latter enzyme plays a pivotal role in producing gluconic acid from glucose, which is considered an essential PSM-released organic acid responsible for P dissolution (Wan et al. 2020; Joshi et al. 2023). Previously, it was shown that mutations in *pqqA* in *Rahnella aquatilis* HX2H led to a reduced content of gluconic acid, thereby decreasing soluble P (Li et al. 2014). Various investigations have reported that bacterial and fungal-mediated solubilization of inorganic phosphate is the outcome of the *pqq* genes (Chen et al. 2016; Suleman et al. 2018). Additionally, *pqqE* is extremely conserved and critical for the biosynthesis of PQQ (Lo et al. 2023). *Pantoea* sp. and *Pseudomonas* sp. possessing *pqqE* can solubilize P and enhance crop yields (Tahir et al. 2020). The *pqq* genes can be transferred to other microorganisms present in the soil to increase their P solubilization efficiency. The genetically engineered transformation of *pqq* genes into *Rhizobium* has been reported to enhance their capabilities of P solubilization and nitrogen fixation. The expression of *pqq* genes in different soil microbes reduced the need for an association for the same objective (Sharma et al. 2013). The membrane-bound quinoprotein glucose dehydrogenase (PQQGDH) is the key enzyme responsible for regulating the synthesis of gluconic acid coupled with dissolution of insoluble

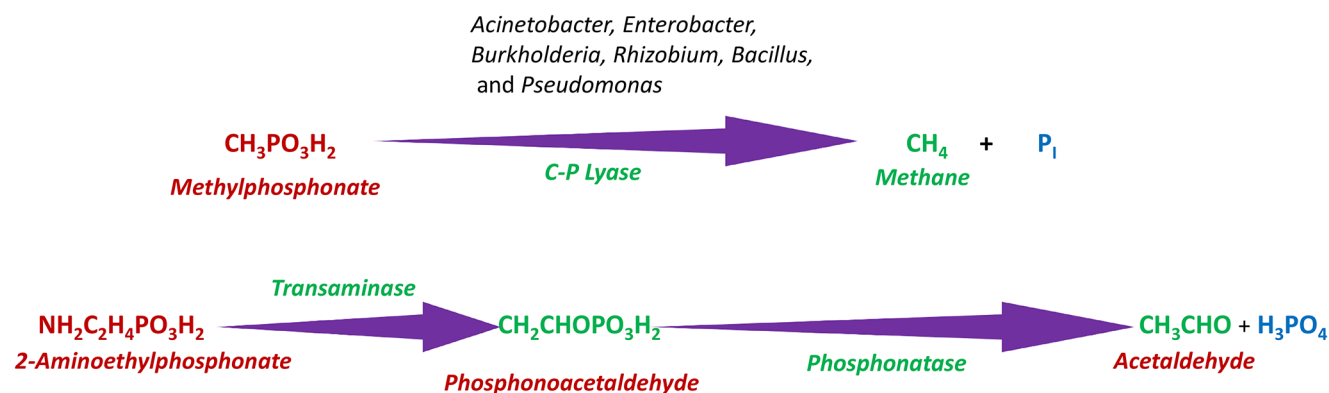


Fig. 4 Mechanism of action of C–P lyase and phosphonate

Table 3 Genes responsible for acidolytic and enzymolytic action of different phosphate solubilizing bacteria (PSB)

PSB	Genes	Gene product and functions	References
<i>Ochrobactrum haematophilum</i>	<i>CS, ACO, ODGH, SFD, FH, MDA</i>	Tricarboxylic acid cycle related genes reduce the pH of medium by releasing H ⁺ ions which leads to the dissolution of insoluble phosphorus	Ding et al. (2021)
	<i>POX, LDH</i>	Genes play a pivotal role in the regulation of acetic acid and lactic acid	
<i>Pseudomonas putida</i>	<i>gcd</i>	Gene codes for enzyme glucose dehydrogenase which plays pivotal role in the solubilization of inorganic phosphorus	Luo et al. (2019)
<i>Pseudomonas</i> sp.	<i>gcd</i>	Gene codes for enzyme glucose dehydrogenase, which plays pivotal role in the solubilization of inorganic phosphorus and enhance the production of gluconic acid	Suleman et al. (2018)
<i>Acinetobacter</i> sp.	<i>gcd</i>	Gene codes for enzyme glucose dehydrogenase which plays pivotal role in the solubilization of inorganic phosphorus and enhance the production of gluconic acid	Xie et al. (2021)
<i>Acinetobacter pittii</i> gp-1	<i>gcd</i>	Gene codes for enzyme glucose dehydrogenase and plays essential role in the solubilization of inorganic and organic phosphorus	He and Wan (2021)
<i>Acinetobacter</i> spp., <i>Pseudomonas</i> spp	<i>phoD, bpp, pqqC, pqqE</i>	Upregulation of solubilization of organic as well as inorganic phosphorus Genes responsible for the regulation of gluconic acid production	Rasul et al. (2019)
<i>Ochrobactrum</i> sp.	<i>pho</i>	Upregulation of solubilization of organic as well as inorganic phosphorus	Maria et al. (2021)
<i>Arthrobacter</i> sp.	<i>Ppx, ppxk</i>	Increase in the transcriptome level of exonuclease polyphosphate kinase and exonuclease polyphosphatase	He and Wan (2021)
<i>Pseudomonas</i> sp.	<i>bpp</i>	Genes responsible for the synthesis of phytases	Cotta et al. (2016)
<i>Aryabhatai</i> sp.	<i>Phn, pho,</i>	Upregulates the phosphorus metabolic pathway	Xing et al. (2022)
<i>Pantoea agglomerans</i>	<i>phy</i>	Increase in phytic acid dissolution	Maria et al. (2021)

phosphate and is encoded by the *gcd* gene (Wu et al. 2022a). The genes related to gluconic acid production include *gabY* and *mps* (Rawat et al. 2021). The abundance of *gcd* genes has been reported to be significantly correlated with several environmental factors such as dissolved total phosphorus, dissolved oxygen and phosphorus hydrochloride (Li et al. 2019). Hence, *gcd* gene could act as a genetic marker for evaluating the potential of microbes to dissolve inorganic phosphate. Rice plants inoculated with *Pseudomonas* sp. MR7 (DSM 106634) and *Acinetobacter* sp. MR5 (DSM 106631) carrying *gcd* gene displayed increased P biofortification and growth parameters. The higher P content and grain yield (67% and 55% respectively) was recorded in rice plants as compared to control, which in turn led to a decrease in fertilizer input by about 20% (Rasul et al. 2019). ‘gab Y gene’ reported from *Burkholderia cepacian* encodes an enzyme apo glucose dehydrogenase responsible for producing gluconic acid that participates in solubilizing inorganic P (Zhao et al. 2014). In another study, the enolase encoding gene, known as the ‘eno gene’, isolated from strain 71–2 of *B. cepacian* assisted in the solubilization of P (Liu et al. 2019). Novel enzymes, such as bacterial phosphatases, aid in producing orthophosphates from phospho-monoesters and phosphodiester via hydrolytic process and are encoded by *PhoA*, *PhoD*, and *PhoX* (Zhou et al. 2021; Yuan et al. 2023). Bacterial phosphatases have been extensively studied in terms of biosynthesis, genetic control, and catalytic properties (Park et al. 2022; Wijeratne et al. 2022). Two bacterial phosphatase genes known as *phoC* and *phoD* have been quantified through quantitative real-time

PCR. Fraser et al. (2017) demonstrated a positive correlation between the transcriptome level of phosphatase gene, the up-regulated activity of phosphatase in the rhizosphere, and enhanced P uptake by plants. The specific acid phosphatase genes (ACP) along with non-precise acid phosphatase genes (*napA* and *phoC*) screened from *Burkholderia pyrrocinia* and *Morganella morganii*, respectively are considered to be responsible for solubilizing organic P (Rodriguez et al. 2006; Zhu et al. 2019). The *phoD* gene is generally used as a marker gene to assess the abundance and community composition of organic PSMs (Azene et al. 2023). It has been reported that exudates from the hyphae of AM fungus *R. irregularis* MUCL 43194 increased the transcriptome level of a phosphatase gene present in *Rahnella aquatilis* HX2, a phosphate solubilizing bacterium (Zhang et al. 2018b). Association of P cycling genes (*bbb*, *pqqC*, *phoD*, *phoX*) containing bacteria and hyphae of *Penicillium* increased the expression level of *pqqC*, *phoX*, *phoD*, *bbb* when compared to the native soil inhabitants (Hao et al. 2020b), suggesting an indirect role of fungi in enhancing the potential of P solubilization in closely associated bacteria. Two strains of rhizospheric bacteria were developed through an artificial biological approach using *Pseudomonas putida* KT2440, *Pseudomonas simiae* WCS417r and *Ralstonia* sp. strain UNC404CL21Col in which the engineered phytase gene was used. Both strains containing the phytase gene produced an increased amount of inorganic P when cultured on the phytate-containing liquid culture media (Shulse et al. 2019). Genetic transformation of maize using the phytase gene (*phyA2*) of *Aspergillus ficuum* resulted in improved growth

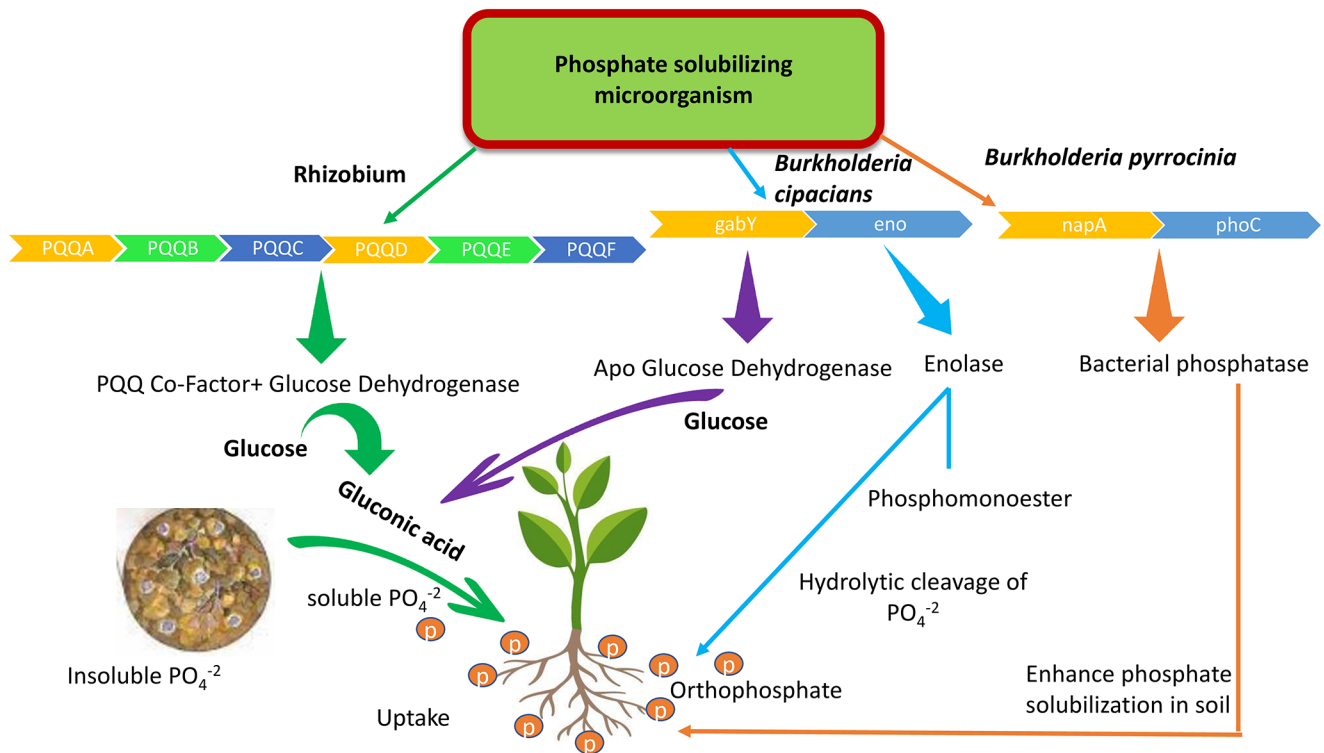


Fig. 5 Comparison of phosphate solubilizing genes of *Rhizobium*, *Burkholderia cepacians* and *Burkholderia pyrrocinia*

and ability to obtain P from phytates (Jiao et al. 2021). Several studies have reported isolation of various genes with P-solubilization ability from different species, such as *mMDH* from *Penicillium oxalicum* C2 (Lü et al. 2012), *vgb* from *Vitreoscilla hemoglobin* (Yadav et al. 2014), *Zymomonas mobilis* (*invB*), and *Saccharomyces cerevisiae* (*suc2*) (Kumar et al. 2016b). Comparison of phosphate solubilizing genes of *Rhizobium*, *Burkholderia cepacians* and *Burkholderia pyrrocinia* with their enzymatic activity and phosphate solubilization pathways has been represented in Fig. 5.

Utilization of phosphate by plants and microbes

The orthophosphates (HPO_4^{2-} and $H_2PO_4^-$) are the primary forms of P absorbed by plants, although plant uptake of HPO_4^{2-} is considered gradual compared to $H_2PO_4^-$ uptake (Kumar et al. 2018). $H_2PO_4^-$ is the dominant form present in soil, especially when the soil pH is below 7.0. Though less widespread, a few organic P fractions can be easily absorbed by plants. It is believed that Po is initially mineralized with the help of extracellular phosphatases before plants take it up. Phosphatase activity is typically maximum when P levels in the soil solution are low since phosphatases are the enzymes synthesized when there is a requirement for P by soil microbes and roots of plants. Elevated activities of phosphatases are typically observed in the rhizospheric soil rather than in the non-rhizosphere region due to the higher

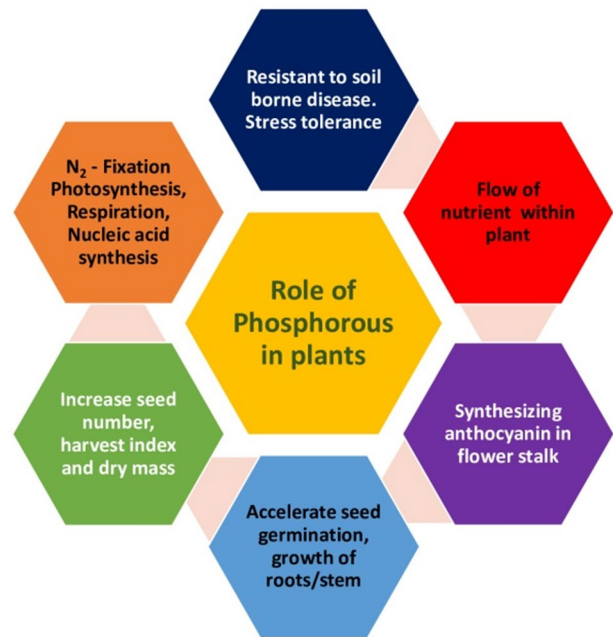


Fig. 6 Multipurpose role of phosphate in plant Growth

microbial density and plant root phosphatases in the former (See Fig. 6).

Arbuscular mycorrhizal fungi (AMF) and PGPB are amongst the most widespread microbes in the rhizosphere. AMF and PGPB, particularly the PSB, aid in overcoming P

deficiency in plants. AMF and PSB are the critical components of biogeochemical cycles (Sharma et al. 2013; Etesami 2021). AMF can boost P uptake by host plants through (i) enhancement in the P uptake per unit of AMF colonized root owing to the great efficiency of hyphal surfaces to absorb P from the soil, in contrast to root surfaces having cylindrical shape (Sharif and Claassen 2011); (ii) expansion of the hyphal networks to stretch outside the rhizospheric region, absorption of Pi via AMF through Pi transporters around 25 cm close to the roots, translocation of Pi to intracellular AMF structures colonizing root cortical region (Garg and Pandey 2015); (iii) storage of P as polyphosphates, so that AMF can maintain internal Pi concentration comparatively low, successfully transporting P from soil to AMF hyphae via formation of appressoria and from extra-radical to intraradical mycelium (Pepe et al. 2020); (iv) small diameter of hyphae (2–20 μm) which helps AMF to explore minute soil interiors for P, and attain higher P absorption rates for a specific surface area (Jakobsen et al. 2001); and (v) reduction in the depletion area around the hyphae or roots (Garg and Pandey 2015). Bacteria acquire P chiefly as Pi and assimilate it in the cytoplasm as adenosine triphosphate (ATP) (Bruna et al. 2021). Microbes should strictly control Pi acquisition and consumption since P absorption is necessary; however, surplus Pi in cytoplasm proves to be toxic (Lubin et al. 2016; diCenzo et al. 2017). Soil microbes are a sink for P because they can immobilize available P from the soil. As soon as P is absorbed by microbial cells, it gets integrated into cellular constituents (for example, organic P-esters, nucleic acids, coenzymes, free Pi, and excess P, which can accumulate as polyphosphates) (Hallama et al. 2019). Numerous reports have indicated that immobilized P is considerably distributed into diverse P pools (for instance, resin-extractable P, water-extractable P, and microbial P) after its liberation from microbial biomass (Bünemann et al. 2012; Bi et al. 2018). Furthermore, soil microorganisms have been reported to compete with plants for the accessible P, and microbial cells symbolize a critical transient immobilized assemblage of P, which could be mobilized and discharged in the soil solution in the form of available P (Richardson and Simpson 2011).

Storage of phosphate within cells

Phosphate is a necessary nutrient for every cell in nature. The growth and development of microorganisms is suppressed by P deficiency, while its surplus levels negatively affect phosphate metabolism regulation. Pi's intracellular concentration is tightly controlled inside microbial cells. Microorganisms living in varied environments possess diverse mechanisms for adaptation to P excess and deficiency. The Pi transport system, which has diverse affinities

and modes of action, is one such mechanism. An alternative pathway by which microbes adapt to the variations in accessibility of P in the environment is the production of reserve P compounds, which are stored or used under excess or deficiency of P sources in the medium, respectively. Low-soluble phosphates, such as $\text{MgPO}_4\text{OH}\cdot 4\text{H}_2\text{O}$ produced by the halophilic archaea *Halobacterium salinarium* and *Halorubrum distributum* (Smirnov et al. 2002; Sminov et al. 2005), as well as $\text{NH}_4\text{MgPO}_4\cdot 6\text{H}_2\text{O}$ produced by *Brevibacterium* bacteria and *Acetobacter xylinum* (Smirnov et al. 2005; Ryazanova et al. 2009), are the best examples of simplest reserve P compounds. During their growth, the archaea *H. distributum* and *H. salinarium* concentrate P (Pi) from aqueous solutions, and when Pi is in excess, its large portion accumulates inside the microbial biomass (Smirnov et al. 2002, 2005). It has been reported that several species of *Brevibacteria* store P as low-soluble salts, and during their growth, these *Brevibacteria* almost completely consumed the medium's Pi at its concentration of about 11 mM (Smirnov et al. 2005; Ryazanova et al. 2009).

Inorganic polyphosphates (polyP), which are straight anionic polymers of orthophosphoric acid and contain three to several hundreds or even thousands of phosphate residues connected via energy-rich phosphoanhydride bonds, play the role of P reserve in the majority of microorganisms (Kulakovskaya 2015). However, Mandala et al. (2020) recently reported substantial amounts of cyclic polyphosphates in *Xanthobacter autotrophicus*. Reports suggest that these polymers are present in all cells, although their concentration and length usually differ. PolyP was initially discovered by Arthur Meyer in microbes in 1904. However, it was named volutin because of its pink colour obtained when stained with blue dyes and was recognized as polyP in 1947 by J. M. Wiame (Kornberg 1995). Because the energy in the phosphodiester bond of polyP is the same as in an ATP molecule, it functions as an energy reserve and does not affect osmotic pressure. Numerous microorganisms ranging from a variety of taxa, from archaea to fungi, have demonstrated the function of polyP as a phosphate reserve (Wood and Clark 1988). Their functions in living organisms are extensive, including metal chelation, energy storage, Ca^{2+} storage influencing bacterial transformation, regulation of osmotic pressure, alkali buffering, increased biological phosphate exclusion, chaperon protecting protein, stress response, survival, and assisting factor in gene regulation (Rao et al. 2009; Achbergerova and Nahalka 2011; Gray et al. 2014). Furthermore, polyP is directly related to bacterial physiological processes such as signalling and regulation, DNA replication, cell proliferation, production of poly-3-hydroxybutyrate, mobility, quorum sensing, biofilm formation, and pathogen virulence (Rashid et al. 2000; Tumlirsch et al. 2015; Albi and Serrano 2016). Wang et al.

(2018) proved the relationship of polyP with virulence and durability in bacteria.

Several ultra-structural studies have demonstrated the presence of polyP granules in archaeobacteria, e.g. *Archaeoglobus fulgidus*, *Sulfolobus* sp., *Methanospirillum hungatei*, *Metallosphaera sedula*, and in members of Methanosarcinaceae (Toso et al. 2011, 2016). In some archaea, the accumulation of polyP is an essential resistance mechanism against metals (Rivero et al. 2018) and oxidative stress (Jasso-Chávez et al. 2015). Recently, polyP has been shown to play a role in heterochromatin formation in bacteria (Beaufay et al. 2021). These polymers are low under P deficiency and high under adequate phosphate content in the medium (Nesmeyanova 2000). Bacteria belonging to the genera *Mycobacteria* and *Corynebacteria* store large amounts of polyP as cytoplasmic granules (Lindner et al. 2010). *Mycobacteria* and *Corynebacteria* have enzymes that directly use polyphosphate energy for substrate phosphorylation, such as polyphosphate glucokinase (Hsieh et al. 1996), NAD kinase (Mori et al. 2004), fructose and mannose kinases, in addition to polyphosphate kinase, the essential enzyme involved in polyP synthesis in prokaryotes (Mukai et al. 2003).

In yeast, the function of polyP as a phosphate-storing reserve material is well established (Vagabov et al. 2000), where it functions as a buffer and maintains intracellular phosphate levels when external P is transiently limiting (Thomas and O'Shea 2005). Additionally, polyP plays a pivotal role in oxidative stress response (Hothorn et al. 2009; Reddi et al. 2009) and accumulates in response to the scarcity of some nutrients in yeast (Breus et al. 2012). PolyP is primarily synthesized and accumulates in yeast vacuoles with the vacuolar transporter chaperone (VTC) complex (Gerasimaite et al. 2014). PolyP can be non-covalently connected to lysine residues of proteins as a non-enzymatic post-translational modification (PTM), suggesting their role in regulating protein interactions (Azevedo et al. 2015; McCarthy et al. 2019). PolyP has also been considered to facilitate adequate deoxynucleoside triphosphates (dNTPs) and check the genome's constancy during yeast replication (Bru et al. 2016). A few yeast species, for example, *Candida humicola* (McGrath et al. 2005), *Hansenula fabiani*, and *Hansenula anomala* have been reported to accumulate considerable amounts of polyP and were isolated from wastewaters containing excess levels of polyP (Watanabe et al. 2008). Even the enzymes involved in polyP metabolism are well characterized in yeast (Hothorn et al. 2009). It has been reported that phosphate uptake-consumption balance generates an intracellular free P content of about 20 mM in yeast (Pinson et al. 2004; van Heerden et al. 2014). Besides PolyP, some bacteria have also reported the presence of organic P reserves. Teichoic acids, made up of repeating polyol or glycosylpolyol residues linked by phosphodiester

linkages constitute the polymeric compounds in Gram-positive bacterial cell walls. These polymers participate in adhesion and bacterial cell morphogenesis and regulate the ionic composition of cell walls and autolysin activity (Brown et al. 2013). These polymers are consumed in a P-deficient medium and may constitute up to 30% of the cells' total P (Grant 1979). Hence, it is believed that one of the functions of teichoic acids is phosphate reservation.

Besides bacteria, AMF contain significant amounts of Pi and polyP granules or volutin granules in cell vacuoles (Dhalaria et al. 2020). AM fungi take up Pi from the soil via Pi transporters present on the plasma membrane of extraradical hyphae (Xie et al. 2016), which is quickly changed into polyP and then sequestered into tubular vacuoles (Kikuchi et al. 2014). Scattered polyP has been discovered in the extra-radical and intra-radical mycelium of *Gigaspora margarita*, indicating a strong link and substantiation of polyP confinement in AMF vacuoles (Nayuki et al. 2014). Studies on obligate mycorrhizal fungus have revealed that polyP builds up in fungal cells and is hydrolyzed to provide phosphate to symbiotic plants (Ohtomo and Saito 2005). Pi is liberated from polyP with polyphosphates present in the vacuole, exported to the cytosol via vacuolar Pi exporter (PHO91), and subsequently integrated into ATP (Kikuchi et al. 2014). Using these processes, the fungi can accumulate enormous quantities of polyP (up to 64% of total phosphorus in cells) within several hours without disturbing the cellular Pi level (Hijikata et al. 2010), indicating strict regulation of Pi homeostasis in fungi. The polyP content in the fungus varies during mycorrhizal development and can be exploited as an indicator of fungal activity as a phosphate supplier for the plant. It has been reported that the obligatory mycorrhizal fungus has polyP-synthetase activity when ATP is present (Tani et al. 2009). Mycorrhizal fungi are essential for providing P to symbiotic plants (Plassard and Dell 2010) due to their capacity to concentrate Pi from soil, release organic acids that cause the dissolution of low-soluble mineral phosphorous compounds, and accumulate polyP.

Deficiency of phosphorus in soil and its effects on microbes and plants

Phosphorus plays a critical role in agricultural production whose status is non-substitutable. This element has been found to regulate the growth and endurance of plants and their allied microorganisms, most especially in the rhizosphere. Against this background, the correlation and interdependency of P, microbes, and plant growth are discussed in this section to unravel its role in enhancing food production. A large number of studies have focused on the influence of P on microbial organization and diversity in diverse soil types and their role in mining the unavailable P (Dai et al. 2020;

Enebe et al. 2021; Ducouso-Détrez et al. 2022). In addition, P is found to promote plant-microbe interaction and improve soil aggregation in arid habitats (Rillig and Mumme 2006; Smith and Schindler 2009). Reports suggest that P facilitates the growth of almost all organisms, even though it is scarcely found in many ecosystems (Van Mooy et al. 2009; George et al. 2016). P availability drastically changes the dynamics of the soil microbiome in the rhizosphere. For instance, Ling et al. (2017) highlighted the significance of P in changing scenarios of soil microbial communities. The authors concluded that microbes play a critical role in regulating nutrient cycling to accelerate the organic matter decomposition in terrestrial ecosystems. On the contrary, a few studies have demonstrated an insignificant correlation between increased P availability and composition of microbial communities in soil; rather, their abundance is related to several other factors such as plant species, type of fertilizer applied, and physicochemical conditions of soil (Huang et al. 2016; Lagos et al. 2016; Shi et al. 2020). A close literature analysis revealed that P exerts negative, neutral, and positive impacts on soil microbiomes, influencing plant growth and well-being (Thirukkumaran and Parkinson 2002; Groffman and Fisk 2011). For instance, the composition of fungal and bacterial communities altered in temperate meadow soils upon P addition, with increased operational taxonomic unit (OTU) of fungi and a decline in OTU richness of bacterial communities (Yan et al. 2021). Plant-linked microorganisms stimulate growth, aid in the up-regulation of nutrient uptake, and, more importantly, help plants in alleviating biotic and abiotic stressors (Trivedi et al. 2020). The diversity and richness of plant-associated microbial communities are grossly dependent on the nutrient composition of the rhizosphere. For example, reports suggest that rhizosphere bacterial genera, for instance, *Arthrobacter*, *Devosia*, and *Bacillus*, varied upon nitrogen supply, and the same is least influenced by increasing the levels of P in wheat (Chen et al. 2019). Reports in the literature revealed that P availability is an essential aspect for controlling the richness of soil microbiomes in grassland ecosystems, and its dependency is also found to be associated with fertilization frequencies, soil types, and soil use systems (Dong et al. 2020; Yan et al. 2021; Wu et al. 2022b). It is reported that the P status of soils impacts the diversity and incidence of soil bacteria involved explicitly in P cycling (Ikoyi et al. 2018; Widdig et al. 2019). Recently, Chen et al. (2023) demonstrated that variation in organic and inorganic P pools greatly influenced the microbial composition of the rhizosphere in paddy-rice red soil. This study further reported that there was a shifting of microbial communities after adding P fertilizers. For example, *Thiobacillus*, a class of dominant PSB, was found to be abundant after adding P fertilizer. Similarly, the abundance of PSF such as *Aspergillus*, *Flavobacterium*, and

Trichoderma increased upon administration of nutrient-rich fertilizers (Kraut-Cohen et al. 2021).

Constraints in bulk production of phosphate solubilizing microorganisms and adoption by the farmers

Biofertilizers are the substitute of synthetic or chemical fertilizers and have gained significant attention in sustainable agriculture. But still there are many challenges in commercializing these alternative fertilizers including bulk production, technical complexities, regulatory hurdles and adaptation by the farmers (Yadav and Yadav 2024). At present the main problem associated with the PSMs is selection of efficient strain, standardization and scale up of the strain for bulk production, optimization of process parameters for mass production. PSMs also do not persist in soil for long time and may lose viability due to competition from other microorganisms in the soil and soil conditions such as temperature, pH, heavy metal toxicity and salinity limiting their effectiveness over long time. The other factors that limit the application of PSMs are the high production cost and also its application require technical support (Wang et al. 2023). At the same time many farmers are not aware of PSMs. They must be extensively educated about the role of biofertilizers and PSMs in agriculture, how their use improves the quality and quantity of crop production. If farmers are convinced the availability and distribution network should be strong so that PSMs reach to the farmers on timely even in remote area.

Genetically engineered PSMs and its regulatory hurdles

Genetically engineered PSMs are produced by chromosomal integration of the gene for higher solubilization capability and stability but full proof strategies should be implemented to avoid the horizontal gene transfer in other soil microbes (Ingle and Padole 2017). Getting approvals for the use of genetically modified PSMs is also time consuming and costly process. Different countries have their own regulatory standards for the application of recombinant microorganisms in agricultural application. As we are directly inoculating large amount of recombinant microbes in the environment, therefore comprehensive research and study required to ensure the ecological and environmental safety. For the widespread application of PSMs the government should provide funding for the research and development, joint venture of private-public partnership can also accelerate the commercialization of PSMs. Government also streamlined the regulatory frameworks so the approval process would be easy and convenient for the safe use of

genetically modified PSMs. For the better adoption of this type of fertilizers government should give incentives, tax rebate and grants to encourage the farmers to adopt these biofertilizers. In future it is expected that PSMs widely adopted by farmers in crop production, but still there is breach and we have to close this gap by improving the efficiency and effective of PSMs through innovation and research, introducing novel strain, reducing production cost, farmers participation in training and education to aware them about PSMs, by strengthen and smoothing the regulation and policy and ensuring environmental safety. In conclusion by addressing these hurdles and following the strategic interventions the PSMs potentially improve the agriculture productivity in sustainable manner (Silva et al. 2023; Wang et al. 2023; Prasad et al. 2023).

Conclusions and future prospects

Within the soil-plant nutrition cycle, P is a limiting nutrient. While exogenous chemical fertilizers can meet crop P requirements during critical growth phases, their detrimental effects on soil, plants, humans, and environment force us to use natural alternatives like PSMs, which can solubilize and mineralize insoluble phosphate and thereby increase crop yields while preserving environmental sustainability. PSMs use several mechanisms to solubilize different kinds of P, both inorganic and organic. PSMs can be used on agricultural land for providing required organic P to plants. In a nutshell it can be concluded that utilization of PSMs is an essential biotechnological tool for raising agricultural output and has a vast array of possible uses.

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Declarations

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