



Relevance of phosphate solubilizing microbes in sustainable crop production: a review

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Abstract

Phosphorus (P) is one of the most important factors regarding plant growth and development. Its deficiency can be compensated by adding chemical fertilizers which are expensive and have an overall negative impact on the ecosystem. Their continuous use leads to the depletion of soil fertility, accumulation of toxic elements which will affect the normal soil micro flora, leading to an imbalance in equilibrium. Phosphate solubilizing microbes (PSM) may be an alternative way to overcome the P deficiency without causing any harm to environment. For this, their biodiversity, mode of action, colonizing ability and their careful relevance should be used as trustworthy components in sustainable agricultural systems. Due to variability in the performance of these microbes, their exploitation in the area of nanotechnology becomes a challenge in sustainable agriculture. In this review, we have discussed the use of PSM as biofertilizers, responsible factors and the strains that are used for the synthesis of different nanoparticles whose implementation will not only promote sustainable agriculture but also be helpful in commercial applicability.

Keywords Crops productivity · Phosphate solubilizing microbes · Mineralization · Solubilization · Nanotechnology · Sustainable agriculture

Introduction

The universal need to increase crop yields from a slowly diminishing and degrading soil resource had drawn significant attention to the agroecosystem around the world. In the coming years, increasing crop production for the growing population in all developing countries, particularly countries like India, will be a major challenge for agro-scientists. The most popular method for improved growth is the use of chemical fertilizers, which reflects a 50 percent boost in crop production, while the other half results in increased soil alkalinity, leading to loss of soil quality and environmental

degradation (Lin et al. 2019). These chemically synthesized fertilizers contain heavy acids, like nitric acid, sulfuric acid and hydrochloric acid in their composition that upon accumulation tends to reduce the soil's useful microbial population, increase soil acidity and ultimately interfere with the growth of plants. However, their continuous use may reduce the population of these beneficial microbes. Their adverse effects on the environment and increasing costs prompted the researchers to use alternate methods to increase crop production that would be environmentally sustainable and cost-effective. Implementations of plant growth-promoting microorganisms (PGPMs) may thus be seen as an effective way of minimizing the usage of chemical fertilizers within the agricultural boundaries (Dobbelaere et al. 2003).

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Availability of phosphate in soil

Phosphorus (P) is an essential macronutrient known for biological and physiological development known for the cellular organization, stimulation of root development, formation of seed and in earlier maturation of crops. In nature, two forms of available P are present in the soil, *viz.*, inorganic



and organic phosphates. Mostly in some types of soil only 0.1 % is utilized by the plant (Beever and Burns 1980). Still, a large proportion of phosphates remains present in unavailable form (Fig. 1). This inorganic insoluble form of P is apatite, oxyapatite and hydroxyapatite. However, under favorable conditions, they can be solubilized and become available. Depending on the soil properties, phosphate anions (PO_4^{3-}) are found to be extremely reactive and can be immobilized *via* precipitation with the Mg^{2+} , Ca^{2+} , Al^{3+} , or Fe^{3+} cations. A huge amount of P when applied as fertilizer reacts with reactive cations in acidic soil and Ca^{2+} in calcareous or normal soils *via* precipitation reaction (Richardson et al. 2011). Richardson (2011) suggested that organic matter should also exist as the main reservoir (30%–80%) of immobilized P mostly in the form of orthophosphoric acid, phytin, inositol phosphates, phospholipids, nucleic acids, etc., degraded by the activity of enzymes like acid phosphatase, phytase and nucleases.

Plant growth-promoting microorganisms (PGPM)

Agricultural activities now take more acceptable and environmentally sustainable approaches, such as the use of plant growth-promoting microbes (PGPMs), as the excessive use of chemical fertilizers and pesticides has

adverse effects on the soil ecosystem as well as human health (Leach and Mumford 2011). Various important microbes have been reported to be associated within a plant's rhizospheric region which has beneficial effects on plant growth known as microbe-promoting plant growth (PGPM) (Mustafa et al. 2019). These positive effects are mediated by a series of mechanisms which includes enhancement of plant tolerance against abiotic and biotic stress, improvement in mineral nutrition, nitrogen fixation, phosphate solubilization, iron sequestration, root modification, as well as suppression of soil-borne diseases, synthesis of phytohormones, modulation of plant ethylene levels, and control of phytopathogenic microorganisms (Olanrewaju et al. 2017; Ramamoorthy et al. 2001; Ali et al. 2014; Chabot et al. 1996) as represented in Fig. 2. Microbial strains like *Pseudomonas*, *Rhizobium*, *Acetobacter*, *Bacillus amyloliquefaciens*, *Vibrio proteolyticus*, *Xanthobacter agilis*, *Enterobacter aerogenes*, *E. asburiae*, *E. taylora*, *Aspergillus flavus*, *Trichoderma harzianum*, *A. niger*, *Penicillium rugulosum*, etc., were also identified as PGPM (Table 1). Specific bacterial rhizospheric strains such as *Rhizobium*, *Pseudomonas* and *Bacillus* are among the strongest strains with phosphorous solubilizing capacity (Sharma et al. 2013; Antoun and Pre´ Vost 2005). Kaur et al. (2015) stated that the combined inoculation of PSB with rock phosphate solubilization could serve as an alternative to the application of chemical fertilizers in sustainable agricultural systems.

Fig. 1 Ground phosphorus balance within the soil

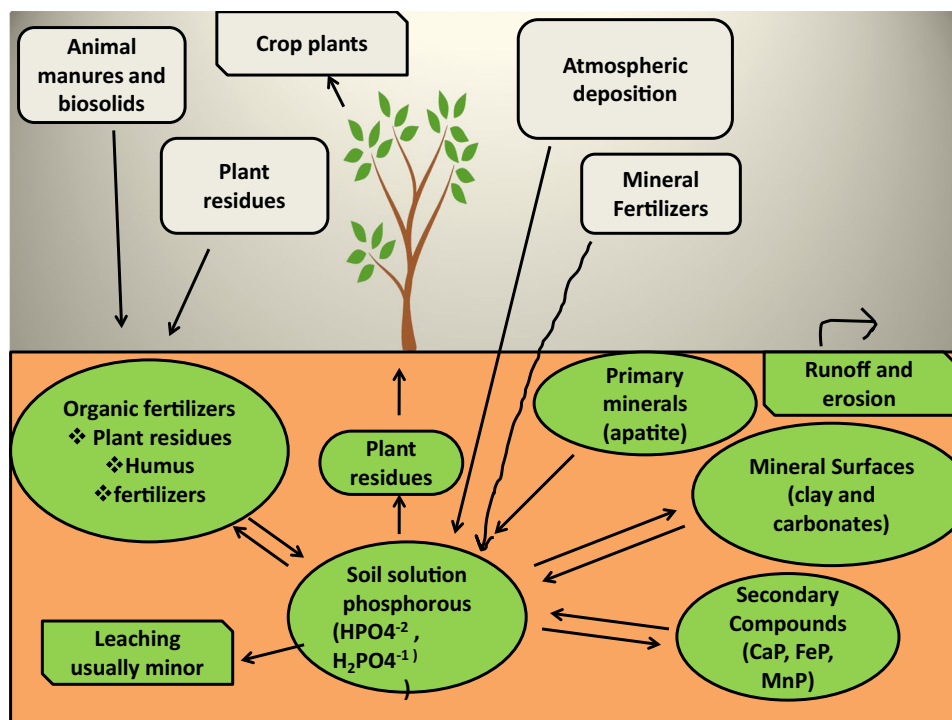


Fig. 2 Processes associated with the promotion of plant growth through microbial mediation by direct and indirect mode

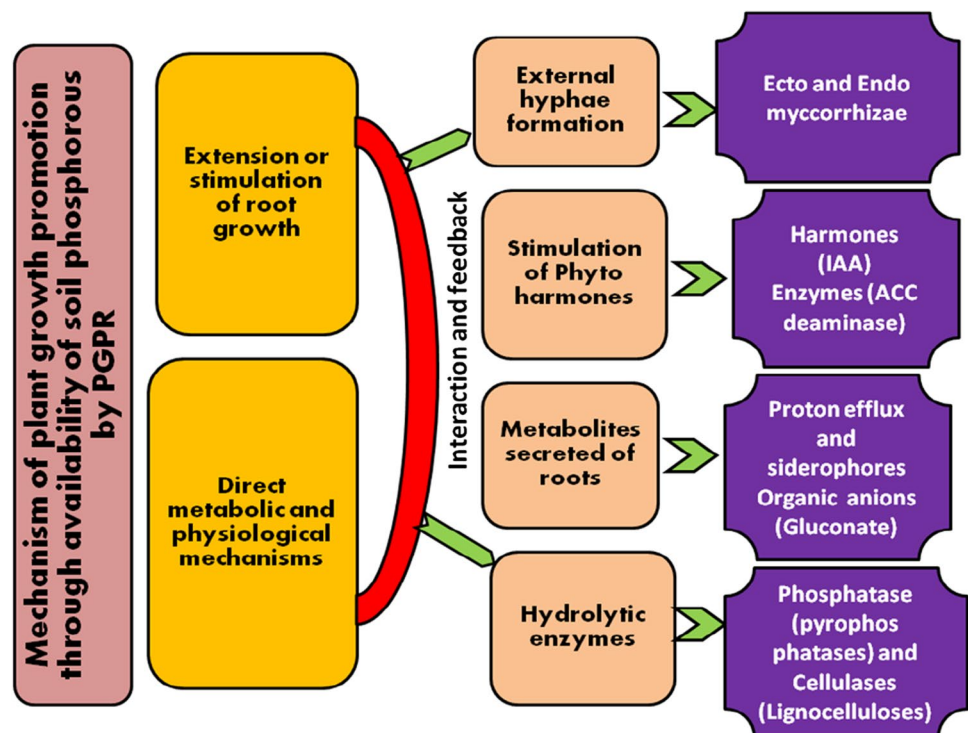


Table 1 List of crops and important plant growth regulators (PGPRs)

| Crops used for the study | Phosphate solubilizing bacteria as PGPR | Phytohormones secreted | References |
|--------------------------|---|--------------------------|--|
| Rice | <i>R. leguminosarum</i> | Indole-3-acetic acid | (Kim et al. 2018) |
| Maize | <i>Azotobacter sp.</i> | Indole-3-acetic acid | (Khalid et al. 2001) |
| Wheat, Brassica, Wheat | <i>Rhizobacterial spp.</i> | Auxins, IAA Acetamide | (Muratova et al. 2005); (Asghar et al. 2002) |
| Wheat | <i>Azospirillum lipoferum</i> | Auxin | (Ahmad et al. 2005); (Egamberdiyeva 2005) |
| Wheat, maize | <i>Pseudomonas denitrificans</i> | Auxin | (Ahmad et al. 2005) |
| Mung bean | <i>Pseudomonas rathonis</i> | Indole-3-acetic acid | (Ahmad et al. 2005) |

Phosphate solubilizing microbes (PSM)

Various microbes such as bacteria, actinomycetes, fungi and algae are capable of solubilizing and mineralizing the P. A variety of rhizospheric bacteria that help to solubilize and mineralize immobilized P are *Pseudomonas spp.*, *Bradyrhizobium*, *Serratia*, *Agrobacterium spp.*, *Bacillus circulans*, *Rhodococcus*, *Sinomonas*, *Salmonella*, *Thiobacillus* (Chakraborty et al. 2009), *Erwinia* (Farajzadeh et al. 2012), *Azotobacter* (Kumar et al. 2012), *Bacillus spp.*, (Raza et al. 2008), *Paenibacillus* (Rashid et al. 2012), *Burkholderia* (Badawi et al. 2011), *Rhizobium* (Kuckey 1983) whereas the fungal strains carrying this ability are *Curvularia*, *Phoma*, *Alternaria*, *Glomus*, *Micromonospora*, *Arthrotrichum*, *Aspergillus*,

Helminthosporium, *Oidiodendron*, *Rhizoctonia*, *Penicillium*, *Cephalosporium*, *Fusarium*, *Achrothcium*, *Cladosporium*, *Cunninghamella*, *Chaetomium*, *Mortierella*, *Sclerotium*, *Myrothecium*, *Paecilomyces* and many more. Kucey (1983) reported that fungus is claimed to be stronger phosphate solubilizers as compared to bacteria because they do not lose their P dissolving activity when subculturing and can traverse long distances through their hyphae thus producing more acids such as lactic acid, citric acid, gluconic acid, oxalic acid, 2-ketogluconic acid, acetic acid and tartaric acid than bacteria. Recently, actinomycetes have also attracted special attention due to their P solubilizing ability, production of phytohormones, antibiotics and are capable of surviving in extreme conditions, e.g., *Actinomyces*, *Micromonospora* and *Streptomyces* (Sharma et al. 2013; Khan et al. 2007). It has been



documented that *Kushneria sinocarni*, a halophytic bacterium isolated from stressed environments from the Daqiao saltern east coast of China, has also shown to exhibit P solubilization properties (Zhu et al. 2011).

Mechanisms of phosphorus solubilization

A number of the mechanism has been reported for P solubilization by rhizospheric bacteria and fungi. The ability of PSM to release metabolites like low molecular weight organic acids/inorganic acids (Seshachala and Tallapragada 2012), and decrease the pH (Alori et al. 2017a). A general sketch of P solubilization is represented in Fig. 3. Besides these acid systems, phosphate deprivation also activates the phosphate solubilization system (Gyaneshwar et al. 1999). In addition, releasing root exudates such as organic ligands helps in modification of P concentration within soil (Geelhoed et al. 1999). Consequently, the process responsible for mineralizing and solubilizing organic and inorganic phosphates is discussed as: -

Solubilization and mineralization of organic P

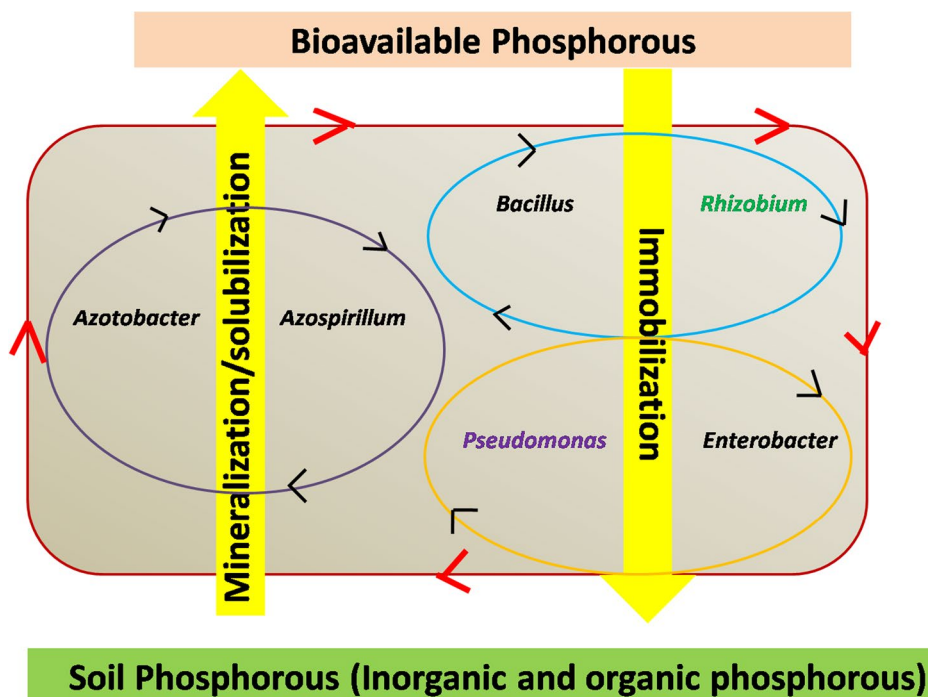
In soil, organic P constitutes around 35–50%, which is present either in the form of inositol phosphate (soil phytate) or in phosphodiester, phospholipids, nucleic acids, pesticides, antibiotics, detergents additives and flame retardants (Singh

and Satyanarayana 2011). These forms are usually resistant toward chemical hydrolysis and thus require conversion into soluble form (Pi , HPO_4^- , H_2PO_4^-). Halvorson et al. (1990) stated that sink phenomenon could be responsible, claiming that the value of P present in the biomass is significantly related to the decay of P present in the organic compounds. Different classes of enzymes such as phosphomonoesters (phosphatases), non-specific acid phosphatases (NSAPs) whose principal role is to dephosphorylate the phosphoanhydride or phosphodiester bond present in organic compounds.

Solubilization of inorganic phosphates

Organic acid production also plays an important role in inorganic P solubilization which involves pH reduction, enhance cation chelation, competition with P for adsorption sites or complex formation with metallic ions and insoluble P (Fe, Ca, Al). Trolove (2003) stated that the release of organic acids is represented by a direct oxidation mechanism via the pH decrease within the medium. The mechanism behind the production of these organic acids is either due to fermentation of sources presence of organic carbon (e.g., glucose, sucrose) or oxidative respiration (Kimberley et al. 2019). The organic acid formation within the rhizospheric area acidifies its surroundings that ultimately results in the release of PO_4^- ions (Goldstein and Liu 1987a). The prominent forms of acids are gluconic acid (Goldstein 1994), aspartic acid, lactic acid, tartaric acid (Bar-Yosef et al. 1999), citric acid and oxalic

Fig. 3 Process of inorganic and organic phosphorus by solubilization and by mineralization means



acid (Venkateswarlu et al. 1984) used for solubilization. It is also reported that the ability of phosphate solubilization was done by various methods like chelation /reduction processes and H₂S gas production (Kim et al. 1997). Various studies have indicated that inorganic phosphate solubilization in the liquid media by bacterial and a fungal strain is due to carbon dioxide production. Solubilization of Fe⁺ and Al⁺ occurs via proton release mechanism in which adsorption of negatively charged P ions occurs. It is tested that proton release decreases P adsorption upon acidification because it increases H₂PO₄⁻ in relation to HPO₄²⁻ which have a higher affinity toward reactive soil surfaces. Studies show that it is through rhizospheric microbes having high affinity toward iron uptake system, releasing iron-chelating molecules, *i.e.*, siderophores (Whitelaw 2000).

Genetic engineering of PSM

There is still little information about the genetics of phosphate solubilization (Altomare et al. 1999). However, certain genes involved in organic and mineral phosphate solubilization also need to be isolated and characterized. Microbial biotechnology, genetic engineering and molecular studies have created an entirely new way of modifying a number of rhizobacterial strains which improve their phosphate solubilizing ability. Insertion or over-expression of phosphate solubilizing genes in rhizospheric microbes is a novel approach for improving their ability to work as agricultural biofertilizers.

The gene cloning from the Gram-negative bacteria *Erwinia herbicola* was reported which encodes for the pyrroloquinoline quinone (PQQ) synthase gene involved in phosphate solubilization (mps). Clones containing those recombinant plasmids showed higher clearing halos with insoluble phosphate within the plates. These findings were the first study on the application of genetic modification to increase the performance of phosphate solubilization from microbial strains that can be used as biofertilizers (Goldstein and Liu 1987b). Additional studies were also carried out to investigate the function of these pqqE gene inhabiting rhizobacteria in the production of organic acid and phosphate solubilization. The pqqE successfully amplified and sequenced in genome of *Pantoea* sp. as well as *Pseudomonas* sp. Organic acids such as acetic, malic, gluconic, citric, and succinic acid were produced by these microbes. The effectiveness of phosphate solubilization was also tested by *Pantoea* sp. in the broth culture that was found as is 311 ± 4 and $204 \pm 3 \mu\text{g ml}^{-1}$, while *Pseudomonas* sp. showed 176 ± 3 and $298 \pm 5 \mu\text{g ml}^{-1}$ of phosphate that is solubilized. The amount of acetic acid and gluconic acid was also greater in the exudates of treated plants. Maximum value was also reported for chlorophyll quality, germination rate, leaf area

index, grain weight and P content in plants inoculated with these organisms. In the field trials, grain yield was improved by 10–12 % over non-inoculated control. These findings lead us to the conclusion that organic acids were produced by the rhizobacteria inhabiting the pqqE gene and phosphate was solubilized *in vitro* and *in vivo* condition (Tahir et al. 2020).

Similarly, Kim et al. (1997) reported an increase in phosphatase enzyme activity of the recombinant strain was achieved when the gene of *napA* phosphatase from the rhizospheric bacterium *Morganella morganii* was transferred into *Burkholderia cepacia IS-16* (Ishige et al. 2003). Several genes, such as *ushA* (nucleotidase), *phoA* (alkaline phosphatase), *phyC* (phytase), *pst* (Pi-specific transporter) and *glpQ* (glycerophosphoryldiester phosphodiesterase) involved in uptake of PO₄⁻ and solubilization of organic phosphate were stimulated during phosphate starvation (Kim et al. 1997; Ishige et al. 2003). Sequences of different phytase genes were also studied for optimal expression in *Proteobacteria*, synthesized and further engineered into the genomes of three different root-colonizing bacteria. The results showed that engineered strains showed high levels of phytate hydrolysis. Recently, *Chryseobacterium* sp., a phosphate solubilizing endophytic bacterial strain, shows plant growth promotion and biocontrol activities against *Phytophthora* blight and anthracnose on pepper using the draft genome sequence that includes genes linked to phosphate solubilization, plant growth promotion and biocontrol features (Fraga et al. 2001). These studies demonstrate that molecular approaches could be used to generate plant-associated strains with novel phosphate solubilizing capabilities (Jeong et al. 2018). Despite that, some hurdles like metabolic machinery dissimilarity and different regulating mechanism among donor and acceptor strains should be solved first to achieve successful gene introduction when using this approach. Last but not least, more studies are required to study better utilization of these PSMs under different environmental conditions and to make them favorable for farmers to boost agricultural production.

Parameters affecting phosphate solubilization

Carbon sources

The carbon source plays a very important role because of the heterotrophic nature of microorganism and of the fact that they solubilize insoluble phosphate by releasing organic acids. In the liquid medium, glucose was found to be the best energy source for microbes. PSM which can solubilize rock phosphate used various types of carbon-rich residues as sources of energy. The amount of soluble phosphate, however, varies with the form of source used



for solubilization. *Pseudomonas striata* were reported to consume glucose, galactose, sucrose and arabinose as their energy while for *Aspergillus awamori*, the preferred carbon source was sucrose, followed by arabinose, glucose, mannitol, galactose, and xylose (Shulse et al. 2019). A fungus *Penicillium digitatum*, use glucose, sucrose, mannitol, arabinose, fructose, xylose and galactose and shows maximum P solubilization efficacy.

Nitrogen sources

Microorganisms require nitrogen for the synthesis of amino acids, proteins and nitrogen bases, which may occur either in the form of ammonium salts, nitrite and nitrate, or in the form of amino acids, depending on the type of enzyme produced. Strains of *Pseudomonas striata* utilized diverse forms of nitrogen sources except for nitrites (Rudresh et al. 2004). A bacteria *Staphylococcus occidentalis* can make use of nitrogen if present either in ammonium or amino-nitrogen forms as they lack in nitrate-reducing enzymes. Ammonium sulfate and ammonium nitrate were found as the best sources among all the nitrogen sources consumed by microbial strains.

Hydrogen ion concentration

Studies show that PSM's behavior and growth are greatly influenced by pH shift within the liquid medium. Bacteria have a maximum solubilizing pH of 5.5–6 while fungal strains have a range of 5–6. The pH activity of fungal isolates was greatly reduced at pH 7 to 8. In several studies, it was reported that at pH 4.0, fungal strains show maximum solubilization of tri-calcium phosphate.

Temperature

Temperature plays a vital role in the growth and physiological activity of PSMs. Strains of *P. striata* shows appropriate growth at a range between 25 and 30 °C that while for *Aspergillus awamori* and *Penicillium digitatum*, 30 °C was found as the favorable optimum temperature for P solubilization. The behaviors of certain PSMs were substantially reduced at higher temperatures (35 °C and 40 °C). Wani et al. (2007) stated that 30 °C is a suitable temperature for tricalcium phosphate solubilization by *P. digitatum*, *P. striata* and *A. Awamori* whereas bacterium *Bacillus polymyxa* can solubilize at a range between 35 and 40 °C. It was also observed that the culture medium was found a less acidic at higher temperature.

Aeration

Shake culture exhibited better solubilization of rock phosphate when compared to static culture. It has been noted often that *S. occidentalis* and *P. digitatum* solubilized less rock phosphate under shake culture. Several studies suggest a persistent rise in phosphate solubilization up to 9–14 days. According to several reports, after 24 hours of incubation, *Aspergillus niger* and *Pseudomonas fluorescence sp.* solubilized TCP and reached at maximum on the 7th day and 14th day (Wani et al. 2007).

Humic substances

Humic substances also have an impact on phosphate solubilization. *B. megaterium* can solubilize insoluble TCP if fulvic acid and sodium humate are present. Thus, the mechanism of phosphate solubilization is directly proportional to the number of humic substances present within the soil. Humic substances behave as strong chelating agents, and this feature of humic substances is of great use increasing the effectiveness of phosphatic fertilizers, which are rendered insoluble via fixation mechanisms (Muratova et al. 2005).

Relevance of PSM as commercial bio-fertilizer

Implementation of chemical fertilizers made farmers satisfied with rising farm yields. Yet gradually there are negative impacts such as water contamination, leaching out, fauna and flora devastation which make crops more vulnerable to microbial infections leading to a decline in soil fertility causing irreparable harm to the biosphere. Then, there comes an existence of biofertilizer, a substance containing living microorganisms which help in plant growth promotion by either increasing the availability of the nutrients or by biological control. The primary biofertilizer sources are bacteria, fungi and cyanobacteria (blue-green algae) as they have a number of capacities that could be applied to enhance agricultural practices as microbes can fight diseases, degrade/convert complex soil compounds into their simpler forms that are further used by plants to develop and grow. This proves that these microbes have a beneficial role in increasing soil fertility by producing essential nutrients for the plant and soil (Souad et al. 2018).

An alternative strategy for the application of these PSMs as inoculants is their use in either in the form of mixed cultures or as co-inoculation in combination with other beneficial microorganisms. For example, the combined effect of microbial strains (*Rhizobium*+ *Bacillus megaterium*+ *Trichoderma* spp.) on nutrient uptake growth, and yield of chickpea showed an increase in nutrient uptake, the number



of branches increased in plant height, yield of pea, nodulation and total biomass of chickpea when compared with the individual inoculations or control (Muratova et al. 2005). Co-inoculation of PSB isolates with rock phosphate promote the maize and wheat growth in terms of the height of shoot, dry biomass, the yield of grain and their total P uptake when compared with control (Quan et al. 2008).

In 2003, Nav Shakti Biotech developed a biofertilizer, Phosphobacteria which contains highly biopromoting PSB (*Bacillus megaterium*) that helps to secrete organic acids and making the unavailable phosphate into the soluble form. A biofertilizer, “Phylazonit-M” which contains a combination of three bacteria, viz., *Bacillus megaterium* + *Azotobacter chroococcum*, increases N and P supply to the plants. The primary role of these biofertilizers is to suppress the growth and activities of soil-borne pathogenic microbes in plants.

Since these microbes constitute a massive and crucial reservoir within microbiota, it can act as an innovative alternative to agricultural practices. Not only that, they also reflect the richest range of high biodiversity that helps to sustain biogeochemical cycles and food chains that can be used to grow and conserve food, manage pests, bioleaching, increase soil fertility, generate biofuels, control contaminants and serve as instruments for the therapeutic industry, such as antimicrobial agents, enzyme inhibitors, pesticides, immunomodulators/immunosuppressants and antitumor agents (Suleman et al. 2018; Fatima et al. 2015).

To solve the agricultural problems and to advance the crop biotechnology, there is an essential need to study the biodiversity of these beneficial microbes as the gene responsible for phosphate solubilization gives information related to their biochemical, evolutionary, taxonomical and metabolic and their regulatory networks. Ojuederie et al. (2017) reported that these microbes could also degrade toxic chemical pollutants and help in cleaning of polluted sites proving that these microbes act as self-sustaining and inexpensive ways. Further work is required to research the biodiversity of indigenous PSMs which can degrade various chemical contaminants and make the environment clean. Thus, more efforts have been made to characterize the microbial communities related to PSMs and their affective responses to chemical pollutants, acting as potential degraders and to identify those genes that are involved in particular degradation mechanism.

PSM performance as biocontrol agents

Phytopathogens born from soil are among the biggest issues in sustainable crop growth worldwide. To mitigate the harmful effects of pathogens on crop yields, enormous quantities of poisonous chemicals, particularly pesticides, are employed in conventional agronomic practices, which are

incredibly harmful to the environment too (Ojuederie and Babalola 2017). The undesirability of implementing enormous levels of chemicals within the fields results in contamination, thus increasing resistance among soil phytopathogens. This lack of pathogen-resistant agricultural crops has compelled researchers to find alternatives to the issues with pesticides. To this end, biocontrol agents strategies consisting of biological formulations are considered the most promising choice for the use of costly destructive pesticides and the environment. In general, microorganisms with phosphate solubilizing ability were found to synthesize a broad range of metabolites with relevant biocidal and fungicidal capacities. The usage has both direct and indirect effects on plant growth and development. PSM controls pathogens by producing antimicrobial compounds such as phenolics compounds, PAL and flavonoids, antibiotics, cyanide hydrogen, indoleacetic acid (IAA), siderophores and several lytic enzymes, all of which suppress the growth of pathogens in plants (Saud and AL-Ahmadi (February 21st 2019; Köhl et al. 2019). The assessments of *Streptomyces* isolates against *B. glumae* (Zaidi et al. 2014) *Trichoderma* strains against phytopathogens (Suárez-Moreno et al. 2019) and *Trichoderma harzianum* isolate against *Sclerotinia sclerotiorum* in soybean (Bononi et al. 2020) were found as an effective biocontrol agent. However, *Burkholderia cepacia*, *Citrobacter freundii*, *Enterobacter aerogenes*, *Klebsiella pneumonia*, *Proteus vulgaris* and *Acinetobacter lwoffii* *Alternaria alternata*, *Macrophomina phaseolina*, *Fusarium oxysporum* and *Sclerotium rolfsii* were also posse’s biocontrol capacity (Zhang 2016) by exerting antagonistic activities against pathogens by synthesizing antimicrobial peptides, secreting lytic enzymes and inducing systemic resistance against pathogenic microbes (Ullah et al. 2018).

Effectiveness of PSM for enhancing crop production under stress

Due to increasing populations and rising food demands, it has now become vital to mitigate the adverse soil conditions in order to increase agricultural production and, ultimately, meet the food demands. Soil and its related environmental stresses not only impact the residual microbial population species and habitats but also the productivity and yield of plants. The primary stress on the soil is metal contamination, alkalinity/salinity and drought (Kang et al. 2015). Various methods are pursued to solve this problem, and one of those solutions includes leveraging this microbial capacity for the benefit of plants. Significant agronomic features of these PSMs are to produce exopolysaccharide (EPS) (Fatima et al. 2018, 2021), various phytohormones, 1-aminocyclopropane—1 carboxylate



(ACC) deaminase, volatile compounds, enhancement of nutrient uptake, induction of accumulation of osmolytes, upregulation or downregulation of the stress responsive genes or bringing about alterations in root morphology that exaggerate the improvement in soil properties, assist in plant growth, development and biocontrol activities (Meena et al. 2017). There are multiple studies on the enhancement of microbial-mediated plant growth under stress-free conditions while fewer studies are available on their impact under stressful environment.

It demonstrates the microbial ability to improve plant tolerance in stressed soils, and their effects as a mixture on various crops. The key idea here is to integrate the fact that PSM alliance can be used primarily in stressed soil, with the goal of rehabilitating soil conditions to promote crop productivity (Köhl et al. 2019). *Bacillus*, *Pseudomonas* spp. (Panwar et al. 2014) and *Providencia rettgeri* sp. *Bradyrhizobium japonicum*, (Jiang et al. 2018), *Bacillus amyloliquefaciens* (Han and Lee 2005), *Bacillus megaterium* (Shao et al. 2015) and *Rhizobium* (Thant and Aung 2018) were able to possess strong capacity for dissolving calcium phosphate under saline conditions *Bacillus halodenitrificans* and *Hallobacillus* sp. also showed more than 90 % higher root elongation and 17.4 % higher dry weight than untreated control wheat seedlings at 320 mM NaCl stress that suggests a substantial reduction in the detrimental effects of NaCl (Surange et al. 1997). The bacterial species of *Pseudomonas fluorescens* and *Azospirillum brasilense* also showed auxin production and inorganic phosphate solubilization under hypersaline conditions (Ramadoss et al. 2013), *Pseudoalteromonas* sp. showed halo-alkali and thermostable properties proved to have potential industrial activity (Kadmiri et al. 2018). However, *Talaromyces aurantiacus* and *Aspergillus neoniger* could survive in acidic environments and both fungi had a considerable ability to release soluble P by decomposing recalcitrant P-bearing compounds in alkaline conditions (Makhdoumi et al. 2015). Same results were found in the case of *A. niger* (Zhang et al. 2018) and *A. terreus* strains that had the potential to deal with salinity and drought stress (Li et al. 2015).

Interaction of exogenous phosphorus-solubilizing bacteria with rhizospheric microbial community

Phosphate solubilizing bacteria have made substantial use in the form of biological fertilizers (PSB). However, less understanding of its effect on the general microbial ecosystem has been shown. In several studies, a mixture of PSB was inoculated in conjunction with the manure fertilizer in tomato plant. The growth parameter findings showed that the mixture of PSB and compost could be significantly

induced the growth of tomato. Adding PSB could significantly increase pH, available phosphate and many types of trace minerals, both in the rhizosphere and non-rhizosphere soil. The results of quantitative PCR and high-throughput sequencing showed that the rhizosphere-inoculated PSB did not become the dominant strain. However, the structure of the soil microbial species gets modified. Some indigenous bacteria, such as *Pseudomonas*, have declined in number, while several bacteria have expanded in the population, including members of *Anaerolineaceae*, *Bacillus*, *Gemmatimonadaceae* and *Cytophagaceae*. The PSB secreted low-molecular organic compounds and changed soil properties in order to dissolve inorganic phosphorus, which indirectly altered the root system's microbiota community. The results of the durability analysis showed that the soil's properties had a significant effect on the endogenous bacterial population (Liu et al. 2020).

Furthermore, in phosphorus poor soils or soils with rock phosphate, PSM associates well with arbuscular mycorrhizal fungi. Certain phosphatic ions that are accessed and transferred by the arbuscular mycorrhizal fungal hyphae to the plant may be produced by PSM from some of the more sparingly soluble phosphorus reservoirs. In addition, compared to non-mycorrhizal roots, PSM persists better around mycorrhizal roots and works symbiotically with AMF, contributing to increased plant growth, particularly where rock phosphate is added to the soil. In some cases where the soil is phosphate, combined dual inoculation of AMF and PSM has been shown to growth of plants more than inoculation of either microorganism individually. The simpler understanding of this finding is that in abundance, success and survival, the mycorrhizal endophyte may be stimulated. Increased nutrient absorption, especially phosphorus, is the main effect of this mycorrhiza in enhancing plant growth due to the discovery of the existing hyphae of the soil far beyond root-hair region where phosphorus gets reduced. In addition, by PSM inoculation, root exudation and plasticity can alter, which could also influence the growth of AMF. In the root region, the AMF also produces plant hormones and enhances the development of nitrogen-fixing species. However, for the optimum use of these interactions with regard to growth and development, a more comprehensive evaluation of the dynamics among soil microorganisms is required (Alori et al. 2017b).

Canavalia ensiformis, a forage legume popularly used as organic fertilizer, similar studies have been reported. An agronomically effective and sustainable solution applied to economically important crops would be the use of AMF and phosphorus solubilizers. Mycorrhizal colonization, phosphorus availability and ultimate phosphorus solubilizers will be promoted by the interaction of AMF and phosphorus solubilizers. An improvement of 3.07 mg/Kg of soluble P in the soil favored this interaction. The number of nodules varied



from 46 to 76. The use of interactions between AMF and PSF increased mycorrhizal colonization, soil phosphorus availability and C growth (Padrón-Rodríguez et al. 2020). AMF and PSB combine synergistically when PSB solubilizes orthophosphate into sparingly accessible phosphorous compounds that can be consumed and transferred to the host plant by AMF. In conjunction with rock phosphate, the co-inoculation of KV with RI showed the biggest improvements in growing plants and tuber inulin quality relative to both unfertilized and fertilized controls. This strong cumulative effect may have had the opportunity for prospective farmers to use this association as a biofertilizer for inulin production in *Helianthus tuberosus* L (Nacoon et al. 2020).

In Chickpea (*Cicer arietinum*) several bio-inoculants are encouraged as natural “nutrient” resource. Bio-inoculants diazotroph *Pseudomonas palleroniana* and a phosphate solubilizer strain of *Pseudomonas jesenii* were evaluated for their plant growth-promoting potential. Furthermore, denaturing gradient gel electrophoresis (DGGE) and real-time PCR (qPCR) techniques were also implemented to analyze the microbial diversity and dynamics. Comparative agronomical and biochemical crop parameters revealed that organic soils co-inoculated with bio-inoculants and phosphate solubilizers have improvement in morphological and physiological content, respectively, over the control. Furthermore, microbial soil dynamics based on qPCR and DGGE showed the survival of strains until around the end of harvesting time without disrupting the indigenous microflora. Conclusively, their co-inoculation has demonstrated considerable promise for the growth and production of chickpeas under organically controlled soils and would also offer further motivation for their bio-formulation to progress toward zero budget natural farming (Rawat et al. 2019).

Performance of PSM in biosynthesis of metallic nanoparticles

As a strong technology, nanoscience enables us to look at the atomic and molecular levels and build structures on a nanometer scale. Nanotechnology offers agricultural productivity for the larger population of agriculture and food processing, and it promotes and frames the next stage of growth of genetically engineered plants, sustainable agriculture inputs, agricultural chemicals and advanced farming techniques of research and development (Jalili et al. 2020). In recent times, the nanomaterials have been developed using physical and chemical approaches. These methods are expensive and use harmful chemicals under ultraviolet irradiation, laser ablation and aerosol spray during the synthesis of nanoparticles. While such techniques are widely used, there is concern over the use of hazardous chemicals. (Prasad et al. 2017). Microbial synthesis of metallic

nanoparticles is being investigated to overcome this problem. The physical solution of lower synthesis limits for the production of nanoparticles needs greater energy usage, and expenses are indeed very high. Industrial solutions, however, are low cost but include the use of hazardous solvents and a trace of chemical waste with hazardous by-product production (Thakkar et al. 2010). Biological approach that includes bacteria, fungi, yeast and viruses therefore provides high production, low-cost and environmentally safe nanoparticles synthesis (Narayanan and Sakthivel 2010).

Microbial nanoparticle synthesis would be a green chemistry method and is regarded an extremely interesting field for potential applications (Mandal 2006). Microbial production with enriched microbial biodiversity, using specific microbial cultivation, can be accomplished under cellular, biochemical and molecular processes, the rate of synthesis and improvement of nanoparticulate properties. The relationship between microbial and metals is well recognized in biotechnological applications such as bioleaching, biomineralization, biocorrosion and bioremediation (Mohanpuria et al. 2008). The properties of microbially generated nanostructured mineral particles and metallic nanoparticles are close to those of chemically synthesized nanomaterials. Most unicellular and multicellular organisms, such as bacteria (prokaryotes) and fungi (eukaryotes), make inorganic materials either intracellular or extracellular (Mandal 2006; Gericke and Pinches 2006a). The intracellular processes include the movement of positive ions through the cell wall by contact with negative cell membrane ions. Furthermore, cell wall enzymes reduce the metal ion to nanoparticles, and later, these nanoparticles spread across the bacterial cell wall. The extracellular generation of nanoparticles in the case of fungi is the nitrate reductase-mediated production in the presence of enzyme nitrate, which helps to bio-reduce metal ions into nanoparticles (Duygu et al. 2019; Hulkoti and Taranath 2014). It provides a short description of recent PSM work involving in metallic nanoparticles synthesis.

The synthesis method (GS) of various metallic nanoparticles (MNPs) has reassessed microorganisms for their universal ability to turn heavy metal ions into neutral atoms at no cost to toxic chemicals. Microbial-mediated biosynthesis provides advantages of improved biocompatibility as compared to chemically synthesized MNPs and hence has greater potential for biological as well as agricultural applications. Microbial-mediated biosynthesis includes microorganisms such as fungi, bacteria and algae. They produce MNPs such as gold (Au), silver (Ag), zinc oxide (ZnO), iron (Fe₂O₃), nickel oxide (NiO) palladium (Pd), copper oxide (CuO), platinum (Pt) and magnesium oxide (MgO) that play a significant role as nanofertilizer (Mandal 2006), nanopesticides, nondiagnostic agents (Fatima et al. 2021), nano-induced resistance, etc. (Fatima et al. 2020). The tolerance of bacteria toward metal ions and formation

of metal nanoparticles depends on physical and chemical growth parameters, such as particle size, pH, temperature, culture time, composition of growth medium and growth in light or dark conditions. PSM and different fungal species have also shown their abilities in the reduction of metal ions. However, not a thumb rule, most of the reducing agents sourced from living world also act as capping agents and render MNPs less toxic or more biocompatible. Various examples are given in Table 2.

Thus, in the field of agriculture, nanotechnology has been used to heighten the crop production with quality enrichment by improving farming systems. The emergence of biologically synthesized nanomaterials by PSM and their actions within the frame of sustainable agriculture have revolutionized world agriculture canvass dramatically by novelty, fast growth and enormity to meet the projection of global food demand (Singh and Prasad 2017). Therefore, further research is urgently needed to unravel the behavior and fate of these PSM in altered agriculture inputs and their interaction with biomacromolecules present in living systems and environments.

Conclusion

The inoculation of PSM in soil indicates to be a successful way to turn the insoluble P compounds into the plant-available P type, resulting in improved plant growth,

crop production and performance. The most important P solubilizers for increasing the bioavailability of P in the soil are *Bacillus*, *Pseudomonas*, *Rhizobium*, *Aspergillus*, *Penicillium*, and *AMF*. By supplying readily absorbable P type, manufacturing plant hormones and antibiotics such as IAA and GA, PSM causes immediate crop production. PSM promotes plant growth by siderophore development and improves nitrogen fixation ability. In addition, through the synthesis of antibiotics, hydrogen cyanate (HCN), and antifungal metabolites, PSM acts as a disease control toward pathogenic bacteria. There are also possible replacements for inorganic phosphate fertilizers in order to satisfy plant P specifications, improving yields in sustainable farming. An economical and environmentally sustainable approach is their implementation. Further analysis, therefore, is critical in the field study to explore productive biofertilizers-PSM with several growth-stimulating attributes. The diverse form of PSMs has proved an important functional activity in agricultural sector as they constitute an important role by recycling the nutrients, pollutants degraders, waste treatment, a biocontrol agent and as an important source for the production of nanoparticles in the form of nanofertilizers that boost the agricultural crop production in the coming era. However, still there is an urgent need to study these environment-friendly microbes that can solve and show a new way to advance biotechnology. Despite knowing the significance of phosphate solubilizing microbes, still the information related to their diversity

Table 2 Role of PSM in production of different nanoparticles

| Microbial species | Type of NP | Size of NPs | References |
|-------------------------------------|-----------------------|--|--|
| <i>Bacillus subtilis</i> | Au | 5–25 nm, octahedral | (Egamberdiyeva 2005) |
| <i>Lactobacillus sp.</i> | Au, Ag, Au–Ag, Ti | 20–60 nm, hexagonal/contour/ Spherical | (Beveridge and Murray 1980) |
| <i>Pseudomonas aeruginosa JP-11</i> | CdS | 5–200 nm | (Nair and Pradeep 2002) |
| <i>Shewanella loihica PV-4</i> | Pt | 30–0.3 nm, spherical, chains, dendritic | (Chakraborty et al. 2018) |
| <i>Pseudomonas stutzeri AG259</i> | Ag, Ag ₂ S | < 200 nm, nano-crystals | (Ahmed et al. 2018) |
| <i>Fusarium oxysporum</i> | Au | 20–40 nm spherical, TRIANGULAR | (Naik et al. 2017) |
| <i>F. oxysporum</i> | Zr | 3–11 nm quasi-spherical | (Mukherjee et al. 2002) |
| <i>F. oxysporum</i> | Au–Ag | 8–14 nm | (Ishida et al. 2014) |
| <i>F. oxysporum</i> | Pt | 10–50 triangle, hexagons, square, rectangles | (Senapati et al. 2005) |
| <i>Verticillium sp.</i> | Ag | 25 spherical | (Syed and Ahmad 2012) |
| <i>V. luteoalbum</i> | Au | < 10 nm spherical | (Mukherjee et al. 2001) |
| <i>A. flavus</i> | Ag | 8.9 nm | (Nicomrat et al. 2016) |
| <i>Coriolus versicolor</i> | Ag | 25–75 nm, 444–491 nm spherical | (Gericke and Pinches 2006b) |
| <i>Trichoderma viride</i> | Ag | Spherical | (Vigneshwaran 2007) |
| <i>A. fumigatus</i> | Zn | 60–80 nm spherical | (Fayaz et al. 2009); (Srivastava et al. 2016) |
| <i>Aspergillus oryzae</i> | FeCl ₃ | 10–24.6 | (Raliya 2013) |
| <i>Aspergillus flavus TFR7</i> | TiO ₂ | 12–15 | (Raliya et al. 2015) |
| <i>Aspergillus flavus</i> | Ag | 50 nm | (Raliya et al. 2015);(Fatima et al. 2016); (Chaudhary et al. 2020) |



is very insufficient. Thus, their evaluation, exploration and exploitation are needed for scientific purposes as well as further work is urgently required to unravel the actions and fate of these PSMs in altered inputs from agriculture and their association with biomacromolecules present in living systems and ecosystems for the betterment of humankind.

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Declarations

Conflict of interest The authors declares that they have no competing of interest.

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