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Improving Phosphorus Fertility in Soil through Microbial Mediators

Vishal Prasad*, **Shivani Chaudhary and Anjali Singh**
Institute of Environment and Sustainable Development, Banaras Hindu University, Varanasi, 221005, Uttar Pradesh, INDIA

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Corresponding author:
Dr. Vishal Prasad
Mob.: +91-9161863763
Email: ways2good@gmail.com

Abstract

Microbes are an important element of the phosphorus cycle operative in the soil and play significant roles in transference of phosphorus between various soil phosphorus pools. Therefore, there has been continued interest in the usage of soil microbes to improve the phosphorus nutrition of plants and increase the overall efficiency of phosphorus use in agricultural systems. This interest originates from the fact that insufficiency of phosphorus is a common problem in soils all over the world, that a foremost cost for agricultural production is due to phosphate fertilizers and that the efficacy of phosphorus used by plants from soil applied phosphate fertilizers is very poor. Hence, with such issues the role of soil microbes in increasing phosphorus fertility in soils becomes more important. In this review several such aspects concerning the solubilisation and mobilization of soil phosphorus by microorganisms for enhancing soil fertility are discussed.

1. Introduction

Phosphorus (P) is one of the fundamental elements after nitrogen required by plants which limits growth and development of plants. It is involved in almost all major metabolic processes occurring in plants such as in the form of ATP for energy transfer, in photosynthesis, respiration, signal transduction pathways, biosynthesis of macromolecules like nucleotides, proteins and cell membranes and biological nitrogen fixation (Khan *et al*., 2010; Sharma *et al*., 2013). In soil phosphorus is mostly abundant in both organic and inorganic forms but due to its unavailability to plant roots it serves as a major restraining factor for growth of plant. In cultivated soils around 70% to 80% of P exists in inorganic form applied in form of P fertilizers (Foth, 1990). After application to soil these P fertilizers gets converted to water-soluble Pi within hours as orthophosphate ions $H_2PO_4^-$ and HPO_4^{2-} (Schulte and Kelling, 1996). Available soil moisture starts dissolving the fertilizer particles as the fertilizer reaches the soil (Busman *et al*., 2002).These negatively charged inorganic phosphate ions form relatively insoluble complex by reacting readily with iron (Fe^{3+}), aluminium (Al^{3+}), and calcium (Ca^{2+}) ions and further becomes unavailable for uptake by crop plants following this fixation. The solubility of different inorganic phosphorus compounds is influenced by pH of the soil, with soil pH values of 6 to 7 favouring more availability of free soluble phosphate ions for uptake by plant. At pH values exceeding 7.3, phosphate ions become lesser available due to fixation in form of calcium phosphates [$Ca_3(PO_4)_2$] (Zhang *et al*., 2010; Sharma *et al*., 2013) while at pH values less than 6, phosphates ions are fixed as aluminium phosphates ($AlPO_4$) and at pH values below 5, phosphate ions are fixed as iron phosphates ($FePO_4$). The second major portion of soil phosphorus exists in the organic form, principally as inositol phosphate accounting for approximately 50% of the entire organic P. The remaining organic-P form constitutes of humus alongwith other soil organic components. Through the process of mineralization by soil microbes the phosphorus available in soil organic fractions is freed and released. The concentration of free phosphorus in soil which is accessible for plant uptake ranges from 0.05 to 10 ppm (Bhattacharyya and Jain, 2000). Various processes like adsorption, precipitation and conversion to organic forms make nearly 80% of the P immobile and fixed in soil with soil minerals and organic complexes (Holford, 1997). These fixation and precipitation of P in soil are in general dependent chiefly on soil type and its pH value (Subba Rao, 1999; Adhya *et al*., 2015).

Although the total P content of soil usually exceeds the plant requirements, but the amount of available P for plants could be restricted by lower mobility of soil P. Plant demand for soluble P in soil solution near rhizosphere is build up by several times replacement in a day by transfer from bulk soil to the zone of rhizosphere (Shen *et al*., 2011). Phosphorus dynamics in the rhizosphere zone is chiefly influenced by growth and activity of roots, and the physicochemical properties of the soil also affect the same (Neumann and Romheld, 2001). Biochemical processes operative in the rhizosphere zone not only determine mobilization and acquisition of soil nutrients plus microbial dynamics, but also achieves nutrient-use efficiency of crops, and thus greatly influence productivity of crops (Richardson *et al*., 2009; Zhang *et al*., 2010; Shen *et al*., 2011; Adhya *et al*., 2015). To enhance the availability of P in soil or to make it available for uptake by plants, application of chemical fertilizers to soil came into practice in the last century. Introduction of chemical fertilizers into the agricultural fields resolved several of the problems being faced by farmers related to crop yield. But with time the usage of chemical fertilizers had shown their adverse effects in agro ecosystem and environment ultimately harming human and other animals. Regular applications of P fertilizers have resulted into large reserves of P in many of the agricultural soils owing to its accumulation (Richardson, 1994). However, a major quantity of soluble inorganic phosphate used for application in agricultural soils as chemical fertilizer is soon immobilized following its application and becomes unavailable for uptake by plants (Bhattacharyya and Jain, 2000; Dey *et al*., 2004). Extensive usage of P fertilizers often causes environmental pollution, including heavy metal contamination of soil and phosphate runoff contributing to eutrophication of the water bodies (Chien *et al*., 2009). Owing to this, use of biofertilizers for nutrient supply and crop improvement is a better option in terms of sustainable approach.

Biofertilizers are basically the microorganisms existing in the soil near the roots of the plants and offering plant growth promoting activities. These microorganisms have been and are being explored by many researchers for their activities related to growth promotion of plants and include bacteria, fungi, actinomycetes, protozoan and others. The microbial intense zone nearby the roots called rhizosphere is highly nutrient rich owing to accumulation of diverse organic compounds released by plant roots through processes like exudation, secretion and deposition. Hence rhizosphere is like a home to various bacteria associated with root and commonly known as rhizobacteria. The bacteria which exhibit plant growth promoting potentials are called plant growth promoting rhizobacteria (PGPR) and the root associated fungi contributing positively towards growth promotion of plants are referred as plant growth promoting fungi (PGPF). These beneficial microbes have capability to convert nutritionally important macro elements like nitrogen, phosphorus, potassium and micro elements such as zinc and iron from unavailable to available form through several types of biological processes. Apart from solubilisation of phosphate these phosphate solubilising microbes are also used as potent agents for biocontrol against several types of plant pathogens. They check pathogens by providing number of antifungal compounds like flavonoids, phenolics and HCl, lytic enzymes and antibiotics; all of which enhance inhibition of the growth of plant pathogens (Ahmed and El-Araby, 2012; Alori *et al*., 2017).

In this article, a review of the status and mechanisms concerned with microbes either PGPR or PGPF, for enhancing phosphate solubilisation and mobilisation for recovering and maintaining the fertility of P in soil is being presented.

2. Need for Microbial Phosphate Mobilizers

Microorganisms play a very vital role in soil P cycle and in relocating P between various soil P pools. Therefore, use and management of soil microbes had gained impetus in the recent past to recover the P nutrition of plants and to enhance the overall efficiency of P-use in agricultural practices. This interest originates from the fact that deficiency of P is pervasive in soils all over the globe; that P fertilizer represents a significant cost for agricultural production; and that the efficacy of P-use by plants available from soil and fertilizer sources is poor. Mining of rock phosphate for manufacturing fertilizers is a global concern. Application of P fertilizers over the agricultural fields is neither eco-friendly, unfeasible economically nor it is sustainable and moreover presents following constraints; (i) emission of the fluoride as extremely volatile and poisonous HF gas; (ii) disposal of gypsum; (iii) accumulation of Cd and other heavy metals in agricultural soils as a result of repetitive use of P fertilizers. Moreover, P resource is finite and the finest quality rock phosphate reserves will get exhausted within the current century if it gets consumed with the same rate of application to the agricultural lands (Isherwood, 2000). Beyond this time, the production of P-based fertilizers will require the processing of lower-grade rock phosphates at a significantly higher cost. Alternatively, the direct application of rock phosphates as fertilizers will demand a more effective process for its solubilisation. These issues are in particular pertinent to soils throughout developing world and on acidic soils in tropical and subtropical regions (Hedley *et al*., 1995). The idea of using soil microbial populations to mobilize poorly available P in soil is not new. As early as 1948 it was shown that cultures of soil bacteria in pure form could increase solubility of Ca-phosphates thereby increasing P nutrition of plants (Gerretsen, 1948). A large volume of literature is available on the soil microorganisms enhancing P efficiency in plants. But still the challenge for efficient P solubilisation and mobilization remains. Indeed, prospects for exploring soil microorganisms for P mobilization have improved as knowledge of the processes and understanding of the ecology of microbial populations in soil environments has increased. Such prospects are further enhanced with the advent of new techniques. These include the possible involvement of gene technology for direct manipulation of microorganism.

Enriched phosphatic rocks deposits in India are limited, hence annual imports of 2 million tons of rock phosphate is required to meet out the current P fertilizers demand. Only 1-9% of agricultural lands in India are rich in phosphorus status and about 90-98% are poor in available forms of soil phosphorus. Intensive agricultural cropping during the green and white revolution also produced a widespread scarcity of available P in the soil. Although several amendments exists for management of P in different soil types, all are high priced and practically difficult to apply. Thus, despite total soil P being sufficiently high and also with regular application of P fertilizers the pH dependent chemical fixation of P determines the quantity of available P. An eco-friendly and cost effective approach is microorganism mediated management of P for sustainable agricultural productivity. Phosphate solubilising microorganisms (PSM) through different mechanisms of phosphate solubilisation and mineralisation are capable to convert insoluble inorganic and organic soil P respectively into the plant available form facilitating its mobilization and uptake by roots of plants (Khan *et al*., 2010). It is imperative to determine the actual mechanism of P solubilisation by PSM for optimal exploitation of these microbes under variable field conditions. Hence it is important to better understand the plant-soil-microbial P cycle with an aim to reduce dependence on chemical P fertilizers. This has by and large led to increased interest in the harnessing of microbial mediators to support P cycling in agroecosystems.

3. Phosphorus Mobilization by Soil Microorganisms

Microorganisms have been and are being used past many years to increase the availability of P in soil for plant uptake (Gerretsen, 1948). A number of microbial species including bacteria, fungi and actinomycetes have been identified as phosphate solubilisers which help in mobilizing insoluble phosphates for plant uptake (Table 1).

Microorganisms directly influence plant competency to obtain P from soil through structural and process-mediated mechanisms. The mechanisms include, (i) an increase in the root surface area by either extension of existing root systems (e.g., mycorrhizal associations) or by increasing root branching and root hair development (by phytohormones mediated stimulation of growth); (ii) by shift of sorption equilibria resulting in elevated net transfer of phosphate ions into soil solution or an enhancement in the movement of organic forms of P; and (iii) through stimulation of metabolic processes that are operative in direct solubilisation and mineralization of P from scarcely available forms of inorganic and organic P. These processes principally include mechanisms deployed by soil microbes which are secretion of organic acid anions, protons, hydroxyl ions, production of the siderophores, production of the extracellular enzymes like phosphatases, phytases and phosphonatases that are able to hydrolyse soil organic P and release of P during substrate degradation (McGill and Cole, 1981; Richardson, 2007; Sharma *et al*., 2013). In particular, organic anions and associated protons are most effective in solubilising the various precipitated forms of soil P. A study performed by Wang *et al*. (2015) demonstrated enhanced plant yield and increased P uptake both in pot experiment and field conditions, when *Aspergillus niger* was used as a biofertilizer. According to Zhu *et al*. (2011) a strain of *Kushneria* sp. YCWA18 was capable of solubilising both inorganic and organic form of P.

4. Mechanisms Involved by PSMs to Solubilise Inorganic and Organic Forms of Soil P

The main mechanisms known for phosphate solubilisation by microbes are depicted in Figure 1.

4.1. Inorganic P solubilisation

The main mechanism involved in solubilising inorganic P is production of organic acids either by lowering of pH, through chelating P bound cations, formation of soluble complexes with the metal ions (Ca, Al, and Fe) associated with insoluble P and thus making release of P. Production of organic acids has been suggested during lowering of pH of the medium (Whitelaw *et al*., 1999; Sharma *et al*., 2013) through microbial metabolism including direct oxidation pathways or fermentation of organic carbon source i.e. glucose (Atlas and Bartha, 1997; Omar, 1997; Trolove *et al*., 2003; Zaidi *et al*., 2009). These acids mineralize P through anion exchange or through chelation of cations like Fe, Al, and Ca. In gram negative bacteria direct oxidation of glucose to gluconic acid (GA) has been proposed as the key mechanism for mineral phosphate solubilisation (MPS) (Goldstein, 1994). Low pH favours occurrence of soluble form of inorganic phosphate i.e. monovalent anion phosphate $H_2PO_4^-$. The divalent and trivalent forms of inorganic phosphate occur as the pH of soil gets elevated. Thus production of organic acids by PSMs lowers the pH of their surrounding environment through acidification which ultimately leads to increase in soluble P from mineral P source through substitution of H^+ with cations bound to P (Goldstein, 1994). Some of the acids released by PSM in the solubilisation of insoluble P are gluconic acid (Di Simine *et al*., 1998; Bar-Yosef *et al*., 1999), oxalic acid, citric acid (Kim *et al*., 1997b), lactic acid, tartaric acid, aspartic acid (Venkateswarlu *et al*., 1984). Observations from a study using HCl and gluconic acid to solubilise P also indicated that chelation of Al^{3+} by gluconic acid may be a factor in the solubilisation of colloidal Al-phosphate (Whitelaw *et al*., 1999).

Table 1: Microbial genera showing P-solubilisation for plant uptake and growth.

Genus showing P-solubilisation	Plant	Mechanism involved	References
Glomus and *Enterobacter*	Tomato	Production of organic acids and phosphatases alkaline and acidic	Kim *et al*. (1997a)
Aspergillus and Glomus	*Triticum aestivum* L.	Production of enzyme phosphatases	Tarafdar and Marschner (1995)
Sinorhizobium	*Medicago truncatula*	Production of organic acids and acid phosphatases	Bianco and Defez (2010)
Pantoea, Microbacterium and *Pseudomonas*	Potato	Production of organic acids and phosphatase enzyme	Malboobi *et al*. (2009)
Pseudomonas	Maize	Production of organic acid	Vyas and Gulati (2009)
Trichoderma	*Cucumis sativus* L.	Production of phosphatases, phytases and organic acid	Garcia Lopez *et al*. (2015)

Other mechanism operative in solubilsing inorganic P is H_2S production, which reacts with ferric phosphate to produce ferrous sulphate with immediate release of soluble phosphate (Swaby and Sperber, 1958). It has been suggested that MPS activity occurs as a consequence of microbial sulphur oxidation, nitrate production and CO_2 formation (Rudolph, 1922). These processes result in the formation of inorganic acids like sulphuric acid (Sperber, 1958). However, their efficiency has always remained a subject of acceptance, while concept of production and involvement of organic acids in solubilisation of inorganic P has been majorly accepted (Kim *et al*., 1997b).

4.2. Organic P solubilisation

Organic P may contribute 4–90% of the total soil P (Khan *et al*., 2009). Release of P from organic compounds in soil occurs through several types of enzymes:

4.2.1. Non-specific acid phosphatases

Non-specific acid phosphatases (NSAPs) which dephosphorylate phosphoester or phosphoanhydride bonds of organic matter. The maximum and best studied classes of phosphatase enzyme produced by PSM are, phosphomonoesterases (often called phosphatases) (Nannipieri *et al*., 2011). These enzymes are classified depending on their pH optima, into acid and alkaline phosphatases and both can be produced by PSM depending upon the external conditions (Kim *et al*., 1998). Typically, acidic soils are predominate by acid phosphatases, whereas alkaline phosphatases are predominant in neutral to alkaline soils (Eivazi and Tabatabai, 1977; Juma and Tabatabai, 1988; Renella *et al*., 2006).

4.2.2. Phytases

Phytases, are the enzymes which particularly release P from phytate degradation. Phytate is one of the major constituent of organic P in soil. It is a chief source of inositol and the major stored form of P in seeds and pollen of plants (Richardson, 1994).The ability to acquire P directly from phytate was very restricted, yet the growth and P-nutrition of *Arabidopsis* plants supplied with phytate was significantly enhanced when they were genetically transformed with a phytase gene (phyA) derived from *Aspergillus niger* (Richardson *et al*., 2001). This led to an increase in P-nutrition to such an extent that the growth and P-content of the plant was equivalent to control plants supplied within organic P. Hence microorganisms are in fact akey driver in regulating the mineralization of phytate in soil and their presence within the rhizosphere may compensate for a plants inability to otherwise acquire P directly from phytate (Richardson *et al*., 2011).

4.2.3. Phosphonatases and C–P lyases

Phosphonatases and C–P lyases, these enzymes cleave the C–P bond of organophosphonates (Rodríguez *et al*., 2006).

4.3. Using microorganisms to improve soil phosphorus availability

Microorganisms are important for P mobilization in soil has led to research effort directed at improving plant P nutrition. Essentially, there are two major strategies for manipulating soil microorganisms.

4.3.1. Management of existing microbial populations to optimize their capacity to mobilize P

This approach needs detailed knowledge of soil management practices like crop rotations, soil amendments etc. and their impacts on abundance of microbes, diversity and existence of different functional groups and their relation with each other in terms of magnitude and availability of different soil P fractions. An example of how populations can be managed to enhance the availability of soil P in plants is through manipulation of VAM in soil by means of crop rota-

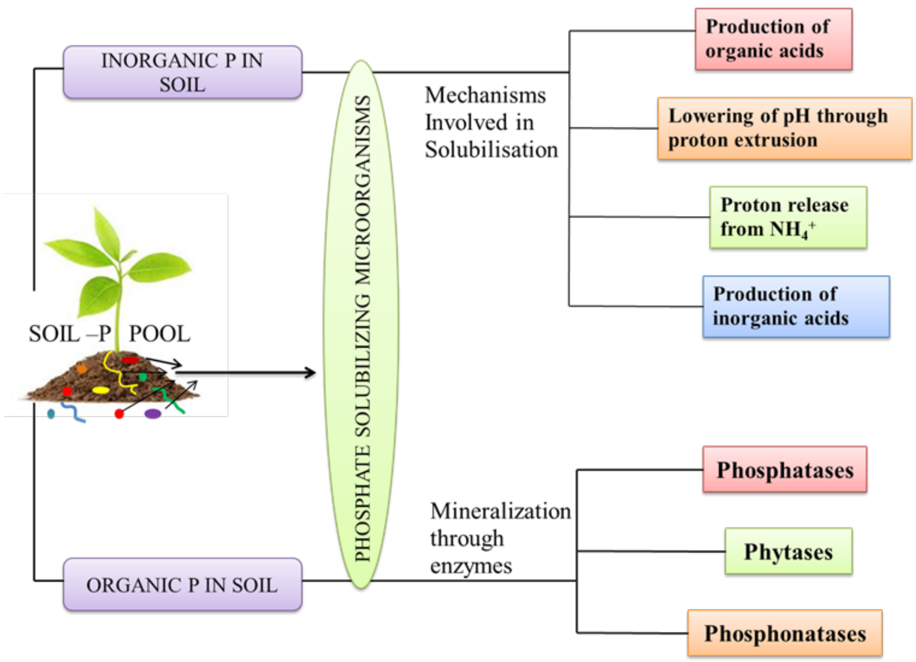

Fig. 1: Overview of mechanisms involved in P-solubilisation by phosphate solubilising microbes.

tion (Thompson, 1994). In response to soil cultivation and crop rotation enhanced mineralization of organic P has been observed in general. Integration of organic residues through legume rotation produced enhanced biological activity and increased microbial P uptake and release (Oberson *et al*., 2001). Although the contribution in terms of total P released through such processes needs to be evaluated in relation to P uptake by plants, such observations provide an indication that management opportunities do exist for improving and enhancing the cycling of P and its maintenance in plant-available pools.

4.3.2 The use of specific microbial inoculants to increase P mobilization

Species of *Pseudomonas* and *Bacillus* amongst bacteria and *Aspergillus* and *Penicillium* in fungi are found to be commonly associated with the plant rhizosphere and upon inoculation onto plants result in healthier growth and P nutrition under both glasshouse and field conditions (Kucey *et al*., 1989; Rodrı́guez and Fraga, 1999; Whitelaw, 1999).

Microbial phosphate solubilises have also been commercialized providing sustainable solution to meet the growing demands of the population. A bacterial consortia comprising of four microbial species *Enterobacter cloacae*, *Citrobacter freundii*, *Pseudomonas putida* and *Comamonas testosterone* named Mammoth P™ has been commercially developed (Growcentia, Fort Collins, CO, USA). Selected for its superior capacity to solubilise soil Pandit had been found effective in increasing plant productivity upto twofold when application of inorganic fertiliser was combined with Mammoth P™. Mammoth P™ also facilitates superior plant emergence and faster blooming. Mammoth P™ additions had successfully enhanced productivity among a wide variety of crop species (hard red winter wheat, fescue turfgrass, jalapeno, cherry tomato, and basil). The inoculation with the four-species consortia in Mammoth P™ enhanced productivity by upto 91% (Baas *et al.*, 2016).

A combination of two types of naturally occurring phosphate solubilizing bacteria *Pantoea agglomerans* strain P5 an organic acid producer and *Pseudomonas putida* strain P13 a phosphatase enzyme producer was observed to increase number and biomass of potato tubers under greenhouse and field conditions (Malboobi *et al*., 2009). Based on these observations another commercial P biofertilizer Phospho BARVAR-2 containing *P. agglomerans* P5 and *P. putida* P13 capable of releasing soluble phosphate ion from inorganic and organic compounds by producing organic acids and robust phosphatase enzymes around plant roots had been developed in Iran (GreenBiotech, Tehran, Iran). These evidences suggest that microbial inoculants have potential to control plant development and consortia based inocula can be used for enhancing phosphate solubilisation and mobilization to increase agricultural productivity. There are various parameters influencing the potentials of PSM's during generation of soluble phosphate forms from insoluble phosphate forms. These include nutritional status of the soil and colonization pattern of the PSM's. The PSM's isolated from soils of extreme environments like saline-alkaline soils, highly nutrient deficient soils or from soils of extreme temperature are capable of solubilising higher amount of P than those PSM's which are from moderate soil conditions (Zhu *et al*., 2011). A wide range of optimum temperature for maximum P solubilisation by microbes has reported by several workers. It ranges from lowest 10°C as reported by Johri *et al*. (1999) to extreme temperature of 45°C in desert soil as demonstrated by Nahas (1999); Nautiyal *et al*. (2000).

Some additional factors effecting phosphate solubilisation includes microbial community interaction, climatic and ecological conditions, soil types, plant variety and among soil's physicochemical properties organic matter and soil pH influence solubilisation of phospahte (Seshachala and Tallapragada, 2012). Warm humid climate and well aerated soils favours faster phosphate solubilisation than cool dry climates and saturated wet soil. Soil rich with organic matter favours microbial phosphorus solubilisation.

5. Factors Influencing the Efficacy of P Release by Microorganisms in Soils

Plant inoculations with PSM had shown inconsistent effects on plant growth and crop yields in field experiments. The colonization and survival of the rhizospheric microbial communities is influenced by various environmental factors and variations in soil and crop. Some factors responsible for survival of the inoculants in fields are:

5.1. Root colonization ability

Inoculants survivability is mainly influenced by root colonization ability. Secretion of high amount of root exudates is responsible for abundance of microbes in the rhizosphere. Majority of the microbial population found in the soil are associated with the plant roots where their population can reach up to 10^9 to 10^{12} per gram of soil (Metting, 1992), leading to biomass equivalent to 500 kg ha^{-1} (Bhattacharyya *et al*., 2013; Adhya *et al*., 2015).

5.2. Soil properties

Soil properties vary in term of texture, particle and pore size of soil. The efficacy of the microorganism is determined by distribution of the pore size and different soil texture determines behavioural pattern in bacteria.

5.3. Abiotic stresses

Variety of abiotic stresses challenge the PSMs under field conditions. Many PSMs have potential to retain their ability under stress condition also. Efficiency of PSMs differs significantly with high or low temperatures. PSMs in tropical countries need to tolerate 35–45°C temperatures, while temperate regions require cold tolerance. Many *Bacillus*, *Streptomyces* and *Aspergillus* strains exhibited very good P solubilisation ability at 50°C, which could facilitate composting, *Acinetobacter* CR 1.8 could grow up to 25% NaCl, between 25°C and 55°C and at pH 5–9, but maximum solubilisation of tricalcium phosphate and aluminium phosphate was obtained at neutral pH, and 37°C (Das *et al*., 2003).

5.4. Substrate availability

Substrate availability for carbon in laboratory studies is very high as compared to that present in plant rhizosphere. Substrate availability often limits the performance of the inoculants. Plant secretes various kinds of compounds used by microbes as substrate like sugars, organic acids and many more.

6. Conclusion

Phosphorus is an important limiting factor in agriculture production, and considering the negative effects of chemical P fertilizers, intervention of PSM seems to be an effective way to solve the phosphorus availability inn soil. However P-solubilisation in soil is much more difficult to study than solubilisation of P in broth culture. The crops respond differently to the inoculation of PSMs and are dependent on several factors such as the soil temperature, moisture, pH, salinity, and source of insoluble P, method of inoculation, the energy sources and the strain of microorganism used. Hence study of PSM activity in correlation with these factors has to be done extensively before PSM can be used as a biofertiliser with promising results. Looking at the possible avenues which can open up with exploring these environmental friendly microorganisms, it is necessary to study the composition and dynamics of these microbial populations to reach a better understanding of soil PSM diversity and P uptake by plants.

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