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Phosphorous and Phosphate Solubilising Bacteria and their Role in Plant Nutrition

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Phosphorous (P), an essential nutrient element is the second most important element after nitrogen. It is unavailable to plants because in the soil it is mostly present in the fixed form. Soil bacteria having the phosphate solubilizing capacity are called as Phosphate Solubilising Bacteria (PSB). They convert the insoluble phosphate into soluble form through the production of organic acids and make it available for plant uptake and nutrition. They are also useful as biofertilizers as they belong to the plant growth promoting Rhizobacteria. This review is focused on the role of 'P' and 'PSB' in plant nutrition and sustainable agriculture.

Introduction

Plant-bacteria-soil interactions are the determinants of soil fertility and plant health. The success in the use of the beneficial microorganisms requires an excellent understanding of the complex interactions taking place between the different components of the complex plant-soil-microorganisms (Hani Antoun, 2012). The soil surrounding the germinating seed is known as spermosphere. This ecological niche is the first habitat used by any developed microorganisms by seed inoculation and supports microbial activity. This in turn influences plant growth. As the plant grows older the growing roots are surrounded by strongly adhering soil particles and this soil-root interaction zone is known as rhizosphere (Hani Antoun, 2012). Plant root, exudates the organic content into the rhizosphere and supports the microbial activities, termed by Hiltner as Rhizospheric effect (Flaishman *et al.*, 1996). Soil bacterial genera are involved in various biotic activities of the soil ecosystem to make it dynamic for nutrient turn over and sustainable for crop production (Munees *et al.*, 2014). Sufficient and balanced quantities of nutrients require for optimum plant growth (Almas Zaidi *et al.*, 2010).

P as a mineral nutrient in terms of quantitative plant requirement it is the second most important element after nitrogen. Although it is abundant in soils in both organic and inorganic forms, its availability is restricted to plants as it occurs mostly in insoluble forms (Pradhan and Sukla, 2005). Thus the release of these fixed and insoluble forms as soluble forms is a very important factor in increasing soil P availability. Soil microorganisms play a key role in soil P dynamics and subsequent availability of phosphate to plants (Khosro Mohammadi, 2012). Phosphate solubilising bacteria (PSB) in soils make the insoluble forms of P into soluble forms through various mechanisms and make them available for plant uptake there by promoting its growth (Chandler *et al.,* 2008). In this review different aspects of phosphorous nutrition, plant growth promoting rhizobacteria and phosphate solubilising bacteria will be discussed.

Phosphorous in soil and its role in palnt nutrition

Next to Nitrogen, Phosphorus (P) is the second most important macro-nutrient required by the plants. Unlike for nitrogen there is no large atmospheric source that can be made biologically available for P availability (Mc Vickar *et al.,* 1963). Phosphorus occurs in fully oxidized state as phosphate, but invariably forms a large number of insoluble chemical complexes with calcium, iron and aluminium, forming insoluble phosphate salts present in the soil, which indeed makes this nutrient a paradox. It is reported to be a critical factor of many crop production systems, due to the fact that the limited availability in soluble forms in the soils (Khan *et al.*, 2007). Phosphorus is the least mobile nutrient element in plant and soil compared to other essential macronutrients (Gyaneshwar, 2012). Soil P dynamics characterized by physico-chemical, sorption-desorption and biological, immobilization-mineralization (Mc Vickar, 1963). P either by adsorption or chemical precipitation becomes immobilise or less soluble in soil (Gyaneshwar, 2012). The concentration of P in soil solution is very low, varying from 0.001mg L^{-1} in very poor soils to 1mg L^{-1} in heavily fertilized soils. In India about 98% of soils including fertile ones are deficient in P, as the concentration of free P (available form for plants) is not more than 10µm even at pH 6.5 (Arnou, 1953). The form of phosphate taken up by the plant from soil solution is phosphate anions mainly $H_2PO_4^-$ and HPO_4^{2-} (Mc Vickar, 1963). Large amounts of P applied as P fertilizers get immobilized by the active and rapid chemical reactions with cations such as Ca^{2+} in calcareous or normal soils to form a complex Calcium Phosphate ($Ca_3(PO_4)_2$) and with Al^{3+} and Fe^{3+} in acidic soils to form Aluminium Phosphate ($AlPO_4$) and Ferrous Phosphate ($FePO_4$) which are sparingly soluble precipitates (Vassileva *et al.*, 2001) and ultimately resulting in the low concentration of P in soils making it unavailable to plants. Therefore, crop plants can utilise only a fraction of applied P and this make them poor in performance (Seema *et al.*, 2013). For example, P deficiency in legumes can severely affect plant growth and productivity where both plant and its symbiotic bacteria are affected posing deleterious effects on nodule formation and function. Release of this insoluble, fixed or adsorbed form of P by phosphate solubilising microorganisms is an important aspect of P availability in soils (Khosro, 2012).

Inorganic forms of P are solubilized by a group of heterotrophic microorganisms excreting organic acids that dissolve phosphatic minerals and / or chelate cationic partners of the P ions directly releasing P into solution (He *et al.,* 2002). Plant growth promoting (PGP) microorganisms, including PGP-Rhizobacteria (PGPR), phosphate solubilizing microorganisms (PSMs) and other symbiotic microorganisms like arbuscular mycorrhizas (AM) fungi, may play a major role in developing a sustainable use of P resources and making them solubilise in the soil (Hani Antoun, 2012). P, being an important constituent element of nucleic acids, enzymes, coenzymes, nucleotides and phospholipids, it is involved in the transformation of energy, transfer of hereditary characters and cell organization in plants (Arnou, 1953). The overall contribution associated with P nutrition to plants include, root development, stalk and stem strength and growth, formation of flower and seed, resistance to plant diseases, crop quality, maturity and production. N fixation is the major task associated with P nutrition in legumes (Deepshikha *et al.*, 2014). It is also involved in photosynthesis, macromolecular biosynthesis and respiration (Khan *et al.*, 2010). During the early phases of plant development an adequate supply of P is important for laying down the primordia of plant reproductive parts. Hence, P is important in every aspect, from molecular level to plant physical development.

Plant growth promoting rhizobacteria (PGPR)

Differential bacterial genera are vital components of soil. The term Plant Growth Promoting Rhizobacteria was first defined by Kloepper and Schroth in 1978 as soil bacteria that colonize the rhizosphere of plants, and are directly or indirectly involved in promoting plant growth and development via production and secretion of various regulatory chemicals in the vicinity of rhizosphere (Kloepper *et al.*, 2003). Rhizospheric microorganisms mediate soil processes such as soluble compounds exudation, storage and release of nutrients and water, nutrient mobilization and mineralization by roots and microorganisms, soil organic matter decomposition, phosphate and potassium solubilization and nitrogen fixation, nitrification, denitrification and sulphur reduction (Flaishman *et al.*, 1996; Deubel *et al.*, 2000). They have the ability to produce plant growth promoters such as indole acetic acid, gibberellic acid, ethylene and cytokinins (Yahya and Azawi, 1998), antagonism against phytopathogenic microorganisms by the production of sidophores (Parul and Dharmendra, 2014), antibiotics (Arshad and Frankenberger, 1993) and also cyanide (Scher and Baker, 1982), quorum sensing (QS) signal interference and inhibition of biofilm production, production of volatile organic compounds, induction of systemic resistance, promoting plant-microbe symbioses, interference with pathogen toxin production etc., (Mohammad *et al.*, 2012). Khan *et al.*, mentioned the following inherent capabilities of PGPR: (i) they must be capable to colonize the root surface (ii) they must survive, multiply and compete with other micro biota, at least for the time needed to express their plant growth promotion activities, and (iii) they must promote plant growth (Khan *et al.*, 2007). In general, PGPR function in three different ways in plant growth: synthesizing particular compounds for the plants, facilitating the uptake of certain nutrients from the soil, and lessening or preventing the plants from diseases (Rifat *et al.*, 2010). These beneficial effects can be achieved by the direct interaction between PGPR and their host plant and also indirectly due to their antagonistic activity against plant pathogens. Direct stimulation includes several mechanisms such as: production of 1-aminocyclopropane-1-carboxylate (ACC)-deaminase which reduces ethylene levels in the roots of developing plants; production of plant growth regulators like auxins, gibberellins, cytokines and certain volatiles; symbiotic nitrogen fixation; solubilization of mineral like phosphorus and other nutrients. Indirect stimulation is related to biocontrol, by mean of antagonistic activity against phytopathogenic microorganisms inducing plant systemic resistance responses, interfering in the bacterial Quorum Sensing (QS) systems, etc.

Phosphate solubilising bacteria

A variety number of microbial species have the capacity to solubilise P. These include bacteria, fungi, actinomycetes and algae and are collectively called as Phosphate Solubilising Microorganisms (Hani, 2012). Bacteria are more effective in P solubilization than fungi (Alam *et al.,* 2002). Phosphate solubilizing bacteria belong to the PGPR (Antoun and Kloepper, 2001). PSB are ubiquitous and varies in shape and population in different soils. Their population in soil depends on chemical and physical properties, organic matter and P content of the soil (Kim, 1998). PSB were found in majority of soils (Chhonker and Taraedar, 1984). Their population was generally low in arid and semi-arid regions, possibly due to the low level of organic matter and high temperature regime (Gupta *et al.*, 1986). The PSB population was higher in soils under mild and moist climates than in dry ones (Subba Rao, 1982). Agricultural and rangeland soils are found with larger populations of PSB (Yahya and Azawi, 1998). Among the whole microbial population in soil, phosphate solubilizing bacteria (PSB) constitute 1 to 50%, while phosphorus solubilizing fungi (PSF) are only 0.1 to 0.5% in P solubilization potential (Chen *et al.*, 2006).

Evidence for naturally occurring phosphate solubilizing microorganism dates back to 1903 (Khan *et al.*, 2007). PSB possess phosphate solubilizing ability and they can convert the insoluble phosphatic compounds into soluble forms in soil and make them available for plants to absorb (Khosro and Yousef, 2012). These bacteria in the presence of labile carbon serve as a sink for P by rapidly immobilizing it even in low P soils. Subsequently, PSB become a source of P to plants upon its release from their cells (Bunemann *et al.*, 2004). The solubilization of insoluble phosphates in the rhizosphere is one of the most common mode of action of plant growth promoting bacteria (PGPB) that enhance nutrient availability to plants (Richardson *et al.*, 2001). The PSB may release several organic acids including oxalic, citric, butyric, malonic, lactic, succinic, malic, gluconic, acetic, glyconic, fumaric, adipic, and 2-ketogluconic acid (Rose, 1957). Salstorm in 1903 first demonstrated the microbial solubilization of inorganic phosphates by incubating TCP (Tricalcium phosphate) with bacteria from milk and soil infusions as mentioned by Deepshika *et al.*, (2014) and Gerretson in 1948 demonstrated the microbial activity in the rhizosphere could dissolve the sparingly soluble inorganic P and increase plant growth, mentioned the same (Deepshika *et al.*, 2014).

Different bacterial genera and within genera different bacterial species have been reported to have P solubilising capacity. Strains from bacterial genera *Pseudomonas*, *Bacillus*, *Rhizobium* and *Enterobacter* (Whitelaw, 2000), *Bacillus megaterium*, *B. circulans*, *B. subtilis*, *B. polymyxa*, *B. sircalmous*, *Pseudomonas striata*, and *Enterobacter* are the most powerful P solubilizers (Subbarao, 1988). *Acetobacter* sp. (Joseph and Jisha, 2009), *Acetobacter diazotropicus* (Maheshkumar *et al.*, 1999), (Rodriguez and Fraga, 1999), *Agrobacterium* sp. and *Alcaligenes* sp., *Corynebacterium* sp. (Gupta *et al.*, 1998), *Azotobacter chroococcum* (Kumar and Narula, 1999), *Burkholderia* sp., *Gluconacetobacter* sp., *Enterobacter* sp. (Chung *et al.*, 2005; Kim *et al.*, 2003), *Flavobacterium* sp. *Micrococcus* sp. (Goldstein, 2001), *Pseudomonas*, *Bacillus*, *Rhizobium*, *Micrococcus*, *Flavobacterium*, *Achromobacter, Erwinia, Acinetobacter* sp. *and Agrobacterium* (Rodriguez and Fraga, 1999) are among the frequently reported PSB. Among all PSB, rhizobia has dual advantage; they can provide N, besides P solubilization and also improve legume growth with other PGPR or mycorrhizal fungi (Zaidi *et al* 2003). The only phosphate inoculum presently sold commercially on a large scale, is JumpStart, developed in Western Canada with a strain of *Penicillium bilaii*, and now sold by Novozyme (Jump Start, 2012).

Phosphate solubilization and mineralization by phosphate solubilising bacteria

Phosphate solubilizing microbes could play a pivotal role in making soluble phosphorus available to plants (Khan *et al.,* 2010). Although fungi are also known to solubilize P, the majority of the role is played by PSB in solubilising inorganic P. The principal mechanism in soil for solubilization of P is lowering of soil pH by microbial production of organic acids or the release of protons and mineralization by producing acid phosphatases (Tarafdar and Claasen, 1988) ultimately resulting in P availability in soil (White law, 2000; Khan *et al.,* 2007; Khosro, 2012). Soil phosphates mainly of phosphatic fertilizers under alkaline conditions are fixed in the form of insoluble phosphates. Many of the calcium phosphates, including rock phosphate ores (fluoroapatite, francolite), are insoluble in soil. Their solubility increases with a decrease of soil pH. Phosphate solubilization is the result of combined effect of pH decrease and organic acids production (Fankem *et al.,* 2006). PSB decrease the soil pH by producing organic acids. These organic acids compete with the P binding sites in the soil (Nahas, 1996). Through Organic acid production PSB mobilizes P from sparingly soluble phosphates and convert into soluble forms mainly by the chelation mediated mechanism (Whitelaw, 2000). Acidification of the surroundings of microbial cell releases proton through the production of organic acids (Villegas and Fortin, 2002). These metabolite organic acids as a result of anion exchange of P by an acid anion can either directly dissolve the mineral P or can chelate $Al^{3+,}$ Fe^{3+}, Ca^{2+}ions associated with inorganic P. The carboxyl and hydroxyl groups chelate the cation bound to inorganic P and convert it into soluble forms (Sagoe, 1998; Seema *et al.*, 2013) with the net result of an enhanced availability of it to the plant. As the soil pH increases the divalent and trivalent forms of inorganic P, HPO_4^{-2} and HPO_4^{-3} occur in the soil. The organic acids released by PSB into the soil consequently decreases the soil pH and acidifies the surrounding environment and lead to the release of P ions by H^+ substitution for the cation bound to phosphate (Goldstein, 1994).

The type of organic acid produced and their amounts differ with different organisms. Among them, gluconic acid and 2-ketogluconic acid seems to be the most frequent agent of mineral phosphate solubilization (Deubel *et al.*, 2000; Song *et al.*, 2008). Other organic acids, such as acetic, citric, lactic, propionic, glycolic, oxalic, malonic, succinic acid, fumaric, tartaric etc., have also been identified among phosphate solubilizers (Ahmed and Shahab, 2011).These organic acids are the products of the microbial metabolism, mostly by oxidative respiration or by fermentation of organic carbon sources like glucose (Trolove *et al.*, 2003).

PSB mineralize soil organic P by the production of acid phosphatases. Release of organic anions, and production of Siderophores and acid phosphatase by microbes, hydrolyze the soil organic P or split P from organic residues resulting in P availability (Dodor and Tabatabai, 2003).

Phosphate solubilising bacteria in sustainable agriculture

There are many factors responsible for increasing threat to sustainable agriculture. Some of them include energy crisis, environmental hazards and depleting soil fertility etc. Hence, the use of biofertilizers in agriculture has proven to be eco-friendly, productive and accessible (Sheraz *et al.*, 2010). PSB are the main contributors of plant nutrition in agriculture. Utilization of phosphate solubilizing microorganisms is considered to be a sound strategy in improving the productivity of lands that are currently under crop production. Phosphate solubilizing bacteria are being used as biofertilizers since 1950's (Krasilinikov, 1957). The technique is also claimed to show the ability to restore the productivity of degraded, marginally productive and unproductive agricultural soils (Gyaneshwar *et al.,* 2002). PGPR together with PSB can reduce P fertilizer application by 50% without any significant reduction in crop yield (Jilani *et al.,* 2007). Inoculation of seeds with PSB is a promising technique which alleviates the deficiency of P (Qureshi *et al.,* 2012). Inoculation with PSB such as *Pseudomonas, Bacillus, Rhizobium, Micrococcus, Flavobacterium, Achromobacter, Erwinia and Agrobacterium* has been reported in increasing solubilization of fixed P ensuring high crop yields (Rodriguez and Fraga, 1999).

Some of the recent reports showed their potency in solubilising Phosphorous. *Bacillus* and *Paenibacillus* reported to be the potential PGPR in sustainable agriculture and also are the major source of broad spectrum peptide antibiotics that are active against various microbial and nematode pathogens (Venkadasamy *et al.,* 2010). Ankit *et al.,* mentioned *Bacillus* as the PGPR in crop ecosystem (Ankit *et al.,* 2011). Diriba *et al.,* assessed for P solubilising ability of isolated strains of rhizobacteria associated with *Coffea arabica* L. in the presence of two P sources hydroxyapatite and tricalcium phosphate. From a total of 395 isolates tested, over 72% mostly *Pseudomonas erwinia* and *P. chlororaphis* were able to solubilize P sources strongly and HPCL analyses showed several organic acids, with 2-ketogluconic acid dominating (Diriba Muleta *et al.,* 2013). The isolates *Bacillus* sp., (67%) and *Burkholderia* sp., (58.5%) of maize rhizosphere were shown solubilisation of aluminium, phosphate ($AlPO_4$), and tricalcium phosphate ($Ca_3 (PO_4)_2$) (Oliveira *et al.,* 2009). Studies on *Pseudomonas* and *Trichoderma* to enhance growth yield and disease uptake showed positive IAA (indole-3-acetic acid) production, phosphate solubilisation and antagonistic activities against *Fusarium oxysporum* and *Rhizoctonia solani* (Jay *et al.,* 2014). Experiment on the effect of *Pseudomonas letiola* on mobilization of P and growth of Ligol (young apple trees) grown in a pot, significantly increased the total shoot length and solubilised insoluble P compounds (Ewa *et al.,* 2013). *Rhodococcus* sp. EC35, *Pseudomonas* sp. EAV and *Arthrobacter nicotinovorans* EAPAA when inoculated with *Zea mays* and grown in P deficient soils amended with tricalcium phosphate enhanced the plant growth (Sofia and Paula, 2014). *Pseudomonas* sp. enhanced the P availability and possessed tricalcium phosphate solubilization, ammonification and inhibited *Aspergillus niger* and *A. flavus* in a study conducted by R. Dey *et al.,* (Dey *et al.,* 2004).

Many PSB are proved to be effective biofertilizers or biocontroling agents. PSB can be regarded as broad spectrum biofertilizers (Gupta, 2004). PSB such as *Bacillus megaterium*, *Bacillus circulans*, *Bacillus subtilis* and *Pseudomonas straita* are effective biofertilizers. *Burkholderia cepacia* from maize rhizosphere showed tricalcium phosphate solubilization and promoted the growth of both healthy and *Helminthosporium maydis* infected maize plants, indicating that the isolate was a good candidate to be applied as a biofertilizer (Ke Zhao *et al.,* 2014). *Pseudomonas* sp*., Serratia marcescens* and *Bacillus cereus* were known to reduce the bacterial wilt caused by *Ralstonia solanacearum* in tomato and hence proved to be effective biocontrol agents (Henok and Kerstin, 2013). In a pot experiment *Pseudomonas striata* when co-inoculated with an endophytic fungi *Piriformospora indica* resulted in significantly higher dry plant biomass in chick pea and increase in the population of *P. striata* in the rhizosphere (Kamlesh *et al.,* 2010). *Pseudomonas chlororaphis*, *Bacillus cereus*, and *Pseudomonas fluorescens* inoculated with walnut seedlings improved plant height, shoot and root dry weight, and P and nitrogen (N) uptake of the seedlings (Xuan *et al.*, 2011). Evaluation of the effect of application of PSB, *Bacillus* M-13, with and without varying amounts of phosphorus on growth and yield of sunflower under field conditions resulted in highest yield of sun flower seeds (Zehra, 2010). *Bacillus* sp. enhanced the growth and yield of cotton in a field experiment conducted by Qureshi *et al*., (2012).

In addition to the above phosphate solubilising microorganisms also faciliatate plant growth and development in the presence of various stresses. *Pseudomonas* sp. enhanced plant growth in salt stress (Shimaila *et al.*, 2014) and *Pseudomonas putida* (Pandey *et al.,* 2006), *Pseudomonas corrugate* (Trivedi and Sa, 2008), *Mycobacterium* sp. (Egamberdiyeva and Hoflich (2003) are showed to be cold tolerant. *Pseudomonas* sp. (Sandhya *et al.*, 2010), *Arthrobacter* sp., *Bacillus* sp. (Banerjee *et al.*, 2010) showed tolerant towards drought stress and *Bacillus* and *Hallobacillus* towards salinity stress (Dhanushkodi *et al.,* 2013).

In conclusion although, chemical fertilizers offer benefits to some extent to the crop plants, their extensive use beyond which damage the agricultural soil health and further there will be no increase in the crop production. Furthermore, the use of chemical fertilizers is also an environmental concern. Phosphate solubilising microorganisms promise a better alternative to this problem. It is eco-friendly and cost effective agro technology to improve crop production. Hence, there is an urgent need to improve better research in this field for developing this technology and to minimise the use of chemical fertilizers and make use of biofertilizers in large scale in agronomic practices to obtain better results.

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