Microbes and Plant Mineral Nutrition

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R. Rajkumar and C. Kurinjimalar

Abstract

Plants and microbes are inseparable constituent of ecosystem for plant mineral nutrition availability. The prime important factors for the plant productivity are macro and micronutrients next to water. A few plants can assimilate macronutrients and micronutrients such as nitrogen, phosphorus, potassium and iron, zinc, copper, manganese, respectively, from soil, while other cannot take up readily. The soil nutrient cycling and its availability to plants are invariantly caused by soil microbes and thus soil health is determined by soil microbes. The different modes of nutrients acquisition by plants are direct uptake from the soil or symbiotic association with soil microbes and mycorrhizal interaction with plants. The indirect way of soil nutrients availability to plants are biological nitrogen fixation, phosphate and sulfate solubilization. The important role of soil microbes in plant growth promotion includes improved plant health, plant growth, plant yield, and also antagonistic to plant pathogens. This chapter highlights different classes of plant nutrients and efficient microbes (cyanobacteria, bacteria, and fungi) helpful in plant nutrition availability are discussed.

Keywords

Bioavailability · Soil nutrients · Plant growth-promoting Rhizobacteria · Biofertilizer · Macro and micronutrients · Bioavailability of nutrients

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5.1 Introduction

The biological soil fertility is maintained by the soil microbial habitants, namely bacteria, fungi, actinomycetes, algae, and protozoa (Muller et al. 2016). The importance of microbes in soil is recycling of nutrient and thus plant nutrition has been realized for many years. The plants are not an individual entity as they co-habit with the microbes. The different plant–microbial interactions are symbiotic, pathogenic, epiphytic or endophytic (Iniguez et al. 2005). The beneficial plant-associated microbiota increases plant nutrient availability by different microbes including cyanobacteria, bacteria including N-fixing bacteria, actinomycetes, fungi (Arbuscular Mycorrhizal), and other Plant Growth-Promoting Rhizobacteria (PGPR) (Miransari 2010, 2011a). Commonly, soil nutrients are present as insoluble precipitates or bound to inorganic and organic components in the soil. Thus direct plant nutrients are not present in available forms. The soil microbes colonizing the plant root either decompose or mineralize organic matter and thus released nutrients in sustainable plant productivity (Hirel et al. 2011). Together with physical and chemical factors, biological factor improves the agricultural drylands. Thus plant–microbe interaction improves the plants growth under nutrient deprived soils.

The fundamental of life on the planet is maintained by soil microbes by nutrient recycling process. Bacteria are the fundamental decomposers of organic waste from inaccessible forms to usable forms of different nutrients. The *Pseudomonas* sp., *Streptomyces* sp. bacterial species and *Trichoderma harzianum,* and *Polyporus ostriformis* lignocellulolytic fungi after consumption for their nutrition release inorganic plant nutrients (Woo et al. 2014). The increase in soil fertility and thus improves plant productivity. In other ways, increasing world population necessitates the increased food production by the use of fertilizers and herbicides of chemical origin. This leads to irreversible environmental damages of ground water pollution and soil degradation. It is therefore need an alternate biological approach of plant nutrients availability without affecting the environment (Miransari 2011b). Therefore, soil inoculation with indigenous microflora is a bioprospecting approach for the necessary plant–microbe interaction. Gopal and Gupta (2016), shows plant dependence on plant-associated microbes including biofertilization, protection from diseases and tolerance to abiotic stresses.

Plant growth directly depends on soil, soil-borne organisms and its interaction with plants. When nutrients are not present in readily available forms for the plant growth, it causes reduction in crop yields or quality. This leads to reduction in overall biodiversity of living creatures, as plants being the primary producers of food web chain. A diverse range of ecological interactions between soil-borne organisms and plants is developed (competition, neutral, commensalism, and mutualism). The symbiotic association of mycorrhizal and legume-*Rhizobium* findings are the base of present studies on microbial role for plant growth. Recent biotechnological advances of next-generation 16S rRNA gene sequencing show major contribution of bacteria present in the core of plant microbiomes. Hawkes et al. (2007) reported as many as 1200 bacterial taxa associated with rhizosphere of 14 different plant species.

Nutrient deficiency can have a significant impact on agriculture, resulting in reduced crop yield or reduced plant quality. Plants require 17 essential nutrients which are derived from the soil. Macronutrients, required in large quantities includes carbon (C), nitrogen (N), oxygen (O_2), hydrogen (H), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), and sulfur (S). Among these, carbon, hydrogen, and oxygen are the building block of organic macromolecules of the cell. Micronutrient includes iron (Fe), zinc (Zn), manganese (Mn), copper (Cu), chlorine (Cl), and boron (B) are the cofactors for enzyme activity required in very small amounts. These elements are required to plant growth for both structural and biochemical functions. The source of essential elements such as hydrogen, carbon, and oxygen are derived from carbon-di-oxide and water, while the others have to be absorbed from mineral nutrition in soil.

The soil microbes are an important component of ecosystem with essential function in plant nutrient nourishment and protecting plants. The use of soil-borne organism for promoting plant growth is biofortification (Miransari 2011b). These soil microbes metabolize soil-borne nutrients for their nutrition and thereby the elemental nutrients for plant use (Uroz et al. 2009). In other way N, P, S, and K are present in various organic molecules as complexes that are minimally bio-available to plants. This can be overcome by the conversion of organic to inorganic forms (N, P and S) through the process of depolymerization and mineralization (van der Heijden et al. 2008). Thus chemical fertilizer application can be minimized by the use of microbes and making easy availability of nutrients to plants. The microbe mediated nutrient availability is proved to be effective by keeping the environment clean and enhancing soil nutrient availability. Thus understanding the linkage between plant and microbes allows better nutrient management. The different mechanisms to increase the solubility of soil nutrients by symbiotic or non-symbiotic association of microbes with their host plant are: (1) Plant metabolism, (2) Increasing solubility and availability of soil nutrients, and (3) Interaction with other soil microbes (Miransari 2013). Therefore, sustainable agriculture can be developed by the application of plant growth-promoting bacteria as a new management strategy.

The different beneficial role of soil microbes by symbiotic or non-symbiotic association to boost growth of host plants are (1) Bioavailability of complex soil nutrients by solubility, (2) Microbial pathogenic strains control, (3) Manipulating the hormonal signaling of plants, (4) Nutrient cycling by mineralization of soil organic matter, (5) Production of different biochemicals such as plant hormones and enzymes, (6) Bioremediation of the toxic heavy metal species and degrading xenobiotic compounds in the polluted soils, (7) production of siderophores, (8) production of 1-aminocyclopropane-1-carboxylate (ACC) deaminase, (9) improving abiotic stress resistance, (10) drought stress tolerance (van der Heijden et al. 2008; Mendes et al. 2013; Verbon and Liberman 2016; Vurukonda et al. 2016) (Fig. 5.1).

Soil microbes perform essential functions of nourishing as well as protecting plants. The understanding of plant and soil microbe interactions allow better nutrient management for sustainable crop production. The niche of plant roots is habitat for microbial communities. The microbial conversion of organic complex material into

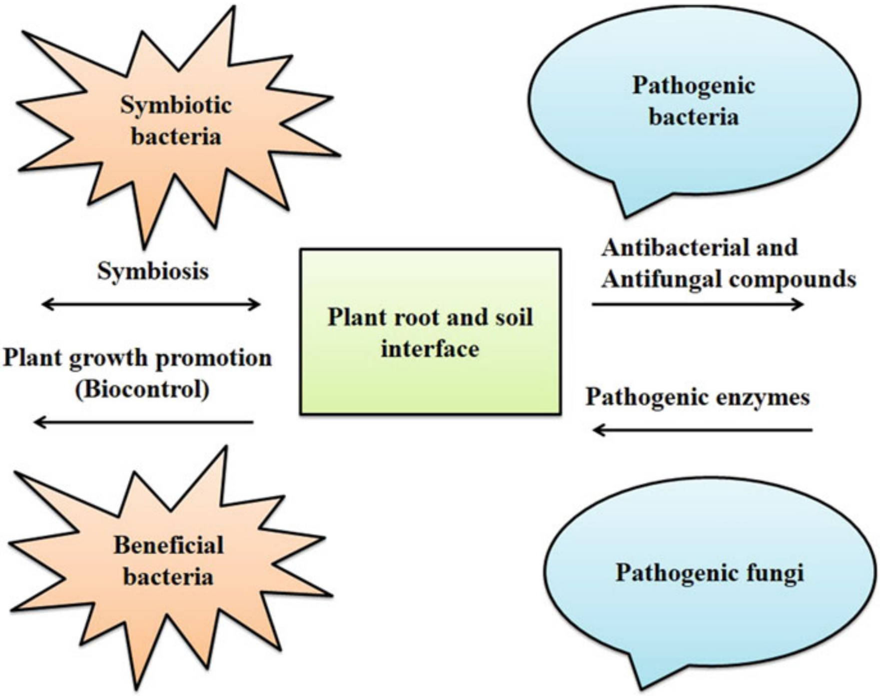

Fig. 5.1 Interaction of plant roots and microbes

Table 5.1 Different mechanisms of plant nutrient availability mediated by soil microbes

Nutrient	Mechanism of transformation by microbes
Nitrogen	Mineralization, Nitrification, Denitrification, N_2 fixation, extracellular enzyme activity (protease and chitinase)
Phosphorus	Mineralization, Solubilization, Extracellular phosphatase activity, organic acid mediated dissolution
Potassium	Mineralization, K solubilization
Iron	Chelation, production of siderophores, changing oxidation states
Zinc	Solubilization, Facilitated uptake by mycorrhizal fungi
Copper	Production of carboxylase and phenolic compounds, Facilitated uptake by mycorrhizal fungi
Manganese	Change in oxidation and reduction state

plant available forms as N, P, and S are carried over by soil microbes by various mechanisms (Table 5.1). This chapter will focus on the mechanism of increasing the soil-borne nutrients bioavailability to the plants.

5.2 An Overview of Soil Microorganisms for the Availability of Nutrients in Plants

The different roles of symbiotic and free living soil microbes in plant growth are nitrogen fixation, improving soil structure which promotes root growth and to control plant pathogens (Coyne and Mikkelsen 2015). Figure 5.2 shows the role of soil microbes involved in the major nutrients accessibility for plant growth. The nitrogen recovery process is carried out by mycorrhizal fungi either ecto-mycorrhizal or endo-mycorrhizal fungi. The process involves solubilization of organic matter to soluble forms by enzymatic process. Nitrogen fixation carried out by symbiotic bacteria, namely *Frankia* through infection in woody species. In root-associated asymbiotic bacteria, namely *Azospirillum* can provide nitrogen to the roots of grasses. Good soil structure enhances plant root growth and extraction of nutrients. The organic molecules like protein released by soil microbes bind soil particles and improve soil structure. The mechanism of pathogens control by plant rhizospheric organisms is competition between pathogens and beneficial microbes for essential nutrients. Many studies reported pathogen control by the application of antagonistic beneficial microbes in disease control.

Soil microbes in 1 g of root niche habitat estimates as 10^{11} microbe (Rolli et al. 2015). The root microbiome inhabiting soil microbes of food crops include maize (Peiffer et al. 2013), rice (Edwards et al. 2015), sugarcane (Yeoh et al. 2015), and sweet potato (Marques et al. 2014). Rhizosphere organisms are categorized into biofertilizers and biocontrol agents which enhance the nutrient availability to plants and prevention of plant diseases (Glick 2012). The rhizobacteria may be extracellular or intracellular, present in the rhizoplane and inside the root cells as nodules. The plant beneficial microbes are significant in agriculture due to sustainability, environmental safety, and multiple beneficiaries as improved nutrient acquisition, plant growth and tolerance to environmental stresses (Sharma et al. 2017). The direct soil nutrients availability to plants are the production of different compounds such as

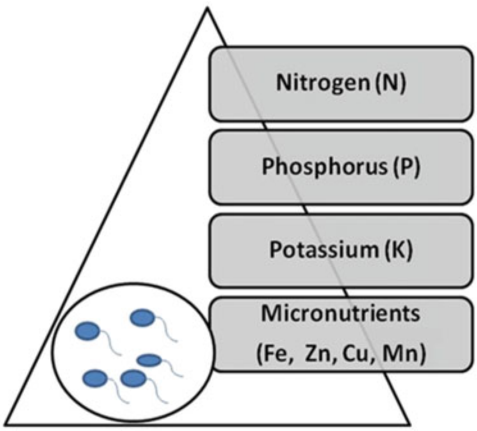

Fig. 5.2 Role of soil microbes in major nutrients accessibility for plant growth

organic (namely glucose, fructose, sucrose, ribose, maltose), organic acids (namely citric, lactic, pyruvic, malic, succinic, and oxalic acids), fatty acids, amino acids, vitamins, and putrescine by plant roots as signaling molecules which influences microbial population for the solubility and availability of nutrients (Ortíz-Castro et al. 2009; Johnson et al. 2010).

The different types of plant–microbe interrelations are neutral, negative, and positive interaction (Whipps 2001). The neutral interaction, namely commensalism have no significant effects on plant growth (Beattie 2007). In negative association, phytopathogenic microbes affect the plant growth by producing phytotoxic substances such as hydrogen cyanide (HCN) or ethylene, (Khalid et al. 2004). Therefore, in positive association the microbes can promote plant growth either directly or indirectly (Glick 2012). Therefore, different plant parts are colonized by different microbe's which are grouped into three groups such as rhizosphere microbes (resides on root surrounding area), rhizoplane microbes (resides on root surface), and endophytic microbes (resides within host tissues) (Andrews and Harris 2000).

A well-known endo-symbiotic association of plant and microbes are between plants and mycorrhizal fungi as well as nodulated bacteria in leguminous plants recognized date backs to the nineteenth century (Morton 1981). Mycorrhizal fungi have increased surface area with improved nutrient absorptive capacity of roots (Rillig 2004). A holistic approach to improve plant growth and yields are developed by crop seeds coating with bacterial cultures such as *Azotobacter* and *Bacillus megaterium* (Brown 1974). Rhizobacteria such as *Pseudomonas* and *Azospirillium* are commonly known as Plant Growth Promoting Rhizobacteria (PGPR) that enhances the plant growth (Burr et al. 1978). Thus plants access the recalcitrant soil-borne nutrients by the metabolic activities of soil microbes. Therefore, selection of soil microbes for biofertilization is based on the (1) inoculation potential, (2) persistence in soil and (3) able to survive under stress condition.

The major PGPRs genera include *Frankia*, *Azotobacter*, *Streptomyces*, *Arthrobacter*, *Rhizobium*, *Azospirillum*, *Pseudomonas*, *Bacillus*, *Pseudomonas*, *Flavobacterium*, *Thiobacillus*, *Enterobacter*, *Serratia*, *Chryseobacterium*, *Achromobacter*, *Aeromonas*, *Acetobacter, Bradyrhizobium*, and *Sinorhizobium* have been reported in plant growth promotion (Vessey 2003; Dimkpa et al. 2009; Etesami and Maheshwari 2018; Etesami and Beattie 2018) (Table 5.2). The nitrogen fixing PGPR, namely *Rhizobia* spp. develops symbiotic association with the host plant (van Loon 2007). The other beneficial benefits of PGPR are production of enzyme, 1-aminocyclopropane-1-carboxylate (ACC) deaminase, production of phytohormones, production of plant pathogens control products such as HCN, and rhizoxin, increased nutrient uptake in plants, induction of antioxidant enzymes, production of polysaccharides, production of carboxylates which chelate micronutrients, production of compounds like humic acid, riboflavin, phenazines, and quinines and induction of systemic tolerance (Hernandez et al. 2004; Uroz et al. 2009; Zhao et al. 2010).

Table 5.2 Important soil microbes in plant nutrient availability from soil

Rhizobacteria role	Mechanism of action	Microbes	References
Increase in plant macronutrients uptake	Solubilizing and mineralizing insoluble phosphate	*Rhizobium, Pseudomonas, Bacillus, Enterobacter,* and *Pantoea*	Sharpley et al. (1992); Sharma et al. (2013); Etesami and Maheshwari (2018)
Not mentioned	Solubilizing K-containing minerals by the synthesis of organic acids, inorganic acids, siderophores	*Bacillus mucilaginosus, Bacillus circulans, Bacillus edaphicus, Paenibacillus spp., Pseudomonas, Acidithiobacillus ferrooxidans*, and *Burkholderia*	Botella et al. (1997); Ahmad et al. (2016); Sindhu et al. (2016); Etesami et al. (2017)
Not mentioned	Symbiotic and non-symbotic N_2 fixation by enzyme nitrogenase; Mineralizing organic forms of N	Not mentioned	Feigin (1985); Glick (2012); Santi et al. (2013); Etesami and Beattie (2017)
Increase in plant micronutrients uptake-Fe, Zn, Mn, Cu, Mo, Ni, Co	Generation of iron chelators, namely siderophores	*Bacillus, Pseudomonas,* and *Geobacter*	Zhuang et al. (2007); Iqbal et al. (2010); Etesami (2018a)
Decrease salinity stress	IAA-containing PGPR stimulate ACC levels	*P. putida, P. fluorescens, Variovorax paradoxus, Enterobacter* sp., *Arthrobacter* sp., *Bacillus* sp., and *Pantoea dispersa*	Bal et al. (2013); Glick (2014); Wang et al. (2016)
Production of phytohormones	PGPR synthesize IAA and cytokinin which induces root growth for positive effect on water acquisition	*Pseudomonas aurantiaca*, *Pseudomonas extremorientalis*, and *Bacillus subtilis*	Ilangumaran and Smith (2017); Barnawal et al. (2017); Etesami and Beattie (2018)
Salinity stress alleviation	Taking up K^+ within their cells and amassing compatible solutes such as polyols and derivatives, amino acids and their derivatives, sugars and derivatives, betaines, and ectoines	*Pseudomonas fluorescens, Serratia* sp., *Pseudomonas*, *Bacillus*, *Flavobacterium*, *Azospirillum*, *Chryseobacterium*, *Achromobacter*, *Sinorhizobium*, *Bradyrhizobium*, *Aeromonas*, and *Acetobacter*	Lugtenberg et al. (2013); Paul and Lade (2014); Qin et al. (2016); Etesami and Beattie (2017, 2018); Etesami and Maheshwari (2018)

(continued)

Table 5.2 (continued)

Rhizobacteria role	Mechanism of action	Microbes	References
Accumulation of osmolytes in plants	Production of proline and glycine betaine	*B. subtilis, Bacillus amyloliquefaciens, Bacillus aquimaris, Azospirillum brasilense, P. dispersa, Rhizobium tropici*, and *Paenibacillus polymyxa*	Ilangumaran and Smith (2017); Etesami and Maheshwari (2018)
Induction of antioxidant enzymes	Scavenging ROS by the antioxidant enzymes such as CAT, POD, SOD, polyphenol oxidase, phenylalanine ammonia-lyase, phenolics, and lipoxygenase	*Bacillus pumilus, B. cepacia, Promicromonospora* spp., *A. calcoaceticus, Bacillus* spp., *Exiguobacterium oxidotolerans, Pseudomonas pseudoalcaligenes*, , *B. subtilis*, and *Arthrobacter*	Jha et al. (2011); Upadhyay et al. (2012); Damodaran et al. (2014); Etesami (2018b)
Production of exopolysaccharides	Augmenting water and fertilizer availability to raise from seeds and plants	*Pseudomonas mendocina, Halomonas variabilis, Planococcus rifietoensis, Enterobacter* sp., *Bacillus* sp., *Bacillus amylolequifaciens, Bacillus insolitus, Microbacterium* spp., and *Pseudomonas syringae*	Tewari and Arora (2014); Sandhya and Ali (2015); Etesami and Maheshwari (2018)
Induction of systemic tolerance	Generation of volatile organic compounds	*B. subtilis*	Egamberdieva and Lugtenberg (2014); Etesami and Maheshwari (2018)

In nutrients assimilation, plant growth-promoting bacterial strains should possess successful colonization in the niche of rhizosphere. In nitrogen fixing symbiotic leguminous host plant nitrogen fixing diverse bacterial taxa possesses nitrogenase genes (Gyaneshwar et al. 2011; Mus et al. 2016). Rhizobia fixes free atmospheric nitrogen to the host plant and in turn depend on host for photosynthates (Hunter 2016). The Arbuscular mycorrhizal (AM) fungi develop symbiotic association with host plants called mycorrhizosphere with organelles called vesicles and arbuscules as storage organ and as hyphal branched structure, respectively (Smith and Read 2008). Endo-symbiotic Arbuscular mycorrhizal (AM) fungi establish increased water and nutrients uptake for their host plant in the exchange for carbon (Rogers and Oldroyd 2014).

5.3 Soil Microbes Induced Nitrogen Uptake by Plants

One of the most important plant growths limiting nitrogen element is not present in readily available form used by the plant. Despite nitrogen is the most abundant gaseous element which constitutes of about 78% in the atmosphere it cannot be directly assimilated by plants due to the presence of triple bonds between two N atoms. Green plants can only readily acquire inorganic nitrate (NO^{3-}) and ammonium (NH^{4+}) from the soil through the plant roots. In the absence of nitrate in the soil, it can be replenished using soil microbes (PGPR) by fixing atmospheric nitrogen (N_2) in the atmosphere.

Therefore plant species has evolved mechanisms of beneficial symbiotic and non-symbiotic process of nitrogen fixation with soil-borne microorganisms called diazotrophs. It can be classified based on the trait of N_2 fixation into three subgroups: symbiotic, free living, and associative. In symbiotic association plant species of Fabaceae family by the process of biological nitrogen fixation develops symbiotic relationship with a group of nitrogen fixing bacteria such as *Rhizobium* and other related genera. The interactions are based on chemical signaling between plant and microbial compounds, flavonoids and lipochitooligosaccharides, respectively. This cause root hair curling to envelop the bacteria through which infection thread grows into the cells of the root cortex and differentiate into structures called bacteroids. The subsequent division produces the nodules, which converts atmospheric nitrogen to ammonia catalyzed by nitrogenase enzyme complex, a readily available form to plants (Ferguson et al. 2010). As a result of this biological nitrogen fixing association between the host plant and microbes, both are benefited with productivity and survival, respectively. The deleterious approach of using nitrogen-rich fertilizers to combat nitrogen deficiency leads to ground water pollution with eutrophication in aquatic ecosystem. The root or legume associated bacteria fixes atmospheric nitrogen into usable N (176×10^{12} g $year^{-1}$).

The other types of non-symbiotic associative relationships of host plant with atmospheric nitrogen fixation bacteria are Cyanobacteria, *Azospirillum* spp., *Acetobacter* spp., *Azotobacter* spp., *Bacillus* spp., *Pseudomonas* spp., *Rhodospirillum* spp., *Corynebacterium* spp., *Beijerinckia* spp., and others (Saharan and Nehra 2011). Furthermore some bacteria involve mineralization of organic N compounds into inorganic forms (NH^{4+} and NO^{3-}) that are readily available for growth of plants. Non-symbiotic organisms degrade organic matter and fix the atmospheric nitrogen for plant use. For example, the plant parts that remain after harvest are the source of N to the soil upon decomposition. During the decomposition organic nitrogen is converted to inorganic ammonium into the soil and the process is called bio-mineralization. The different steps in bio-mineralization are aminization, ammonification, and nitrification, where the initial step involves break down of complex proteins to amino acids, amides, and amines, further converted to ammonium and finally nitrate formation occurs. The two steps of nitrification are carried out by different bacterial groups, namely *Nitrosomonas* and *Nitrobacter*, respectively. The common nitrogen fixing rhizobacteria either endophytic or free-living genera includes *Azotobacter, Azospirillum, Bacillus, Bradyrhizobium, Burkholderia,* and *Pseudomonas* are having positive effects on food crops (Igiehon and Babalola 2018).

5.4 Soil Microbes Induced Phosphate Uptake by Plants

The second most essential element phosphorus (P) in inorganic phosphate form is also a plant growth limiting nutrient. In natural plant habitat phosphorus is present in the form of rock phosphate, mineral salts, hydroxyapatite or organic compounds. This helps in root development, seed production, improves BNF and resistance to diseases (Murrell and Munson 1999). Phosphorus is an integral component of biochemicals such as nucleic acids, and phosphoproteins. Thus a large proportion of about 95–99% of phosphorus are present in unavailable forms as present in insoluble or precipitates, which causes phosphorus limitation. The two kinds of phosphate available to the plants are mineral phosphate and organic phosphate. Generally for phosphate fertilization triple super phosphate is applied to soil only 20% of soil phosphate is in available form and the remaining will precipitate. Soil pH affects the plant nutrient availability in the soil, in which solubility of nitrogen, potassium, and sulfur are not much affected as phosphate. At acidic and basic pH, phosphate ions react rapidly with Al, Fe, Ca, and Mg and they become less soluble forms. Therefore, phosphate availability is a pH-dependent. A number of studies reported different strains of both fungal and bacterial solubilize inorganic P, and also mineralize organic P (Ahemad and Kibret 2014).

The mechanism of inorganic and organic phosphate acquisition involves solubilization and mineralization by the release of microbial phosphatases (Illmer et al. 1995; Gouda et al. 2018). This bio-solubilization of P is most important in agricultural soils for enhanced utilization of P by plant. A wide range of soil bacteria especially PGPR and fungi could convert precipitated and organic phosphate in the form $H_2PO_4^-$ and HPO_4^{-2} ions (Whitelaw 2000). The lowering in pH of the medium by organic acids production in phosphate solubilizing microbes (PSB) dissolves organic phosphorus into inorganic form. The different organic acids are acetic acid, citric acid, fumaric acid, oxalic acid, lactic acid, propionic acid, malonic acid, succinic acid, 2-ketogluconic acid, glycolic acid, and gluconic acid are produced in PSB (Krishnaraj and Dahale 2014). Among the several soil bacterial communities, *Pseudomonas* and *Bacillus* spp. have been excellent phosphate solubilizers (Goswami et al. 2014). The common mechanisms of microbial action involves production of enzymes (phosphatases) and products such as low molecular weight organic products (carboxylic acids) pH, anions, and cations can readily increase phosphate availability (Houser and Richardson 2010; Salimpour et al. 2010). The PSB solubilizes inorganic soil phosphates of Ca, Fe, and Al via production of siderophores, several acids (organic), and hydroxyl and carboxyl groups, and chelating them to the bound phosphates and the available calcium (Sharma et al. 2013).

Among bacteria, the most efficient phosphate solubilizer belongs to genera such as *Rhizobium*, *Bacillus,* and *Pseudomonas*. The other two chickpea nodulating species, *Mesorhizobium ciceri* and *Mesorhizobium mediterraneum*, are reported as phosphate solubilizers (Rivas et al. 2006). A large number of phosphate solubilizing microorganisms has been reported by in vitro studies. The most commonly reported phosphate solubilizing organisms of bacteria such as *Azospirillum brasilense, Arthrobacter, Rhizobium, Pseudomonas*, *Arthrobacter*, *Beijerinckia, Erwinia*, *Thiobacillus ferrooxidans Bacillus,* and *Nitrobacter sp.* (Sharma et al. 2013); fungal genera are *Penicillium Aspergillus, Fusarium,* and Chaetomium spp. of the plant microbiome hydrolyze inorganic phosphorus into soluble forms (Uribe et al. 2010; Sharma et al. 2013). The different mechanisms involved in phosphorus availability by microbes are release of H^+, OH^-, organic acid, anions such as citrate, malate, and oxalate and also mineralization of organic P by release of various phosphatase enzymes (Marschner et al. 2010). Thus soil organisms can be applied as potent soil inoculants for plant growth.

Phosphate solubilizing bacteria produce organic acids helps in dissolution of glucose to gluconic acid. Organic acids have good chelation properties by the substitution of divalent cation of Ca^{2+} coupled with the release of phosphates from insoluble complexes (Behera et al. 2017). Thus most phosphate solubilizing microbes cause a reduction in the pH of the medium either by production of inorganic acids as H^+ extrusion (sulfuric and nitric acids) or by secretion of various organic acids like malic, citric, succinic, tartaric, and oxalic acids; and by the production of enzymes acting on fatty substrates (Alori et al. 2017). The organic acids secretion by microbes is mainly dependent on environmental properties and gene induced in bio-solubilization of phosphate (Zhen et al. 2016). In this study, revealed a clear relationship between profile of organic acids and source of phosphate. The other common P-mineralization process is governed by hydrolyzing enzymes, namely phytases and phosphatases produced by fungi and bacteria (Alori et al. 2017).

Other rhizospheric bacteria produce siderophores, phytohormones, including auxins, gibberellins, cytokinins, ethylene, and abscisic acid involved in plant growth and yield improvement through N_2 fixation. The phosphate solubilizing for P availability to plants occurs either by chelation with cations or in exchange of organic acid by ligands (Parker et al. 2005). A number of reports show plant growth promotion activities by the microbes besides making soluble P accessible for plants uptake (Sharma et al. 2013). Indole-3-acetic acid (IAA), produced by various PGPR are involved in plant growth and development, such as cell elongation, cell division, and tissue differentiation (Misra et al. 2012; Oves et al. 2013; Kaushal et al. 2017). The processes in plants like promotion of seed germination, nutritional signaling, expansion of leaf, and delay of senescence are also greatly influenced by cytokinins produced by PGPR (Wong et al. 2015).

Egamberdiyeva (2005) isolated and reported rhizospheric bacteria from the field, namely *Bacillus laevolacticus*, *B. amyloliquefaciens*, *Pseudomonas denitrificans*, *P. rathonis*, *and Arthrobacter simplex* from wheat, alfalfa, cotton, and tomato. *Acinetobacter* sp. and *Bacillus* sp. isolates from *Phyllanthus amarus* showed phosphate solubilizing property with promoted higher vigor index, phosphorus content, percentage of germination, plant biomass, phenolic content, and also antioxidative activity compared to uninoculated control. Therefore, many researchers reported the role of phosphate solubilizing bacteria towards enhancing plant growth and reducing the usuage of fertilizer with high salt tolerance (Alori et al. 2017). A large number of field-based studies evidenced a high uptake of phosphate that enhance the crops yield (Sawers et al. 2017).

5.5 Soil Microbes Induced Potassium Uptake by Plants

Potassium is the third essential macronutrient present in soil is absorbed by plants for its growth and yield. The different forms of potassium (K) in the soil are non-exchangeable K, exchangeable K, mineral non-exchangeable K, and K in soil solution (water-soluble K). The important functions of potassium within plant cell include control of stomatal opening/closing, enzyme activation, and balancing the charges of cellular anions. The deficiency of potassium leads to chlorosis (yellowing), browning of leaves, and curling of leaf tips with ultimate reduced growth and yield. The application of chemical and organic fertilization can make potassium availability for plant use. However, owing to soil erosion, leaching, intensive cropping, imbalanced fertilizer application, and presence of insoluble K sources, the availability of potassium to plants is decreasing (Zorb et al. 2014). As a result, deficiency of K in soils is reducing crop production. Only tightly bound mineral form of K constitute about 90–98% of soil K and it is unavailable for plant (Sparks 1987). Therefore K solubilizing microbes have been applied for sustainable production by mineralizing insoluble potassium into usable forms. Microbes solubilize K from insoluble sources of feldspar, mica, and others by extracellular production of organic acids, extracellular enzymes, siderophores, extracellular polysaccharides, organic ligands and formation of biofilms are the different key processes involved in the release of K by the dissolution of complex minerals (Keshavarz Zarjani et al. 2013; Meena et al. 2015; Das and Pradhan 2016).

Ullman (1996) reported that the bacterium, *Bacillus mucilaginosus* are able to solubilize potassium rock by the secretion of organic acids. Thus K-solubilizing microbes (KSB) play an effective role in K cycle to fulfill the K requirement of crops (Meena et al. 2014; Sindhu et al. 2014). The process involves conversion of mineral K into available K to plants. A number of genera reported to release K from K-bearing minerals, namely *Pseudomonas* spp., *Burkholderia* spp., *Acidithiobacillus ferrooxidans*, *Enterobacter hormaechei, Paenibacillus glucanolyticus, Arthrobacter* spp.*, Paenibacillus mucilaginosus, P. glucanolyticus, Bacillus mucilaginosus*, *B. edaphicus*, and *B. circulans* (Lian et al. 2002; Keshavarz Zarjani et al. 2013; Zhang et al. 2013).

Overall the direct mechanisms used by KSB include: (i) acidolysis, a process of dissolving mineral K by organic acids (Shelobolina et al. 2012), (ii) chelation, a mechanism of forming complexes with reaction products with organic acids which can enhance dissolution (Ullman and Welch 2002), (iii) oxidation, involves breakdown of K-bearing minerals microbial Fe(II) oxidation in the rhizosphere, and (iv) production of CO_2 for the breakdown of K-bearing complex which result in carbonic acid formation (Barker et al. 1998).

5.6 Soil Microbes Mediated Micronutrient Acquisition in Plants

The plant nutrients that are required in significantly in lesser amounts in comparison to other macronutrients are micronutrients. The soil is a good reservoir for all plant nutrients including micronutrients. The inoculation of soil with rhizospheric microbes stimulates the micronutrient acquisition. The action mechanism of micronutrient availability to plants by soil microbes are organic and inorganic acids, chelating agents and also play a key role in disease control. Eight essential micronutrient elements required for plant growth are iron (Fe), zinc (Zn), manganese (Mn), chlorine (Cl), copper (Cu), boron (B), molybdenum (Mo), and nickel (Ni) (Kumar et al. 2016). As similar to macronutrients, micronutrient availability from soil to plants is highly dependent on interaction between plant roots and soil microbes. The process involves secretion of organic acids and chelating agents by the microbes for solubilization and mobilization of nutrients (Suri and Choudhary 2012, 2013). Thus, rhizospheric microbes play an important role towards micronutrient availability to plants such as iron, zinc, copper, and manganese.

5.6.1 Iron

Iron is relatively abundant element with an average concentration of 40 g kg^{-1} present in soil (Cornell and Schwertmann 2003). The iron deficiency in plant nutrient leads to chlorosis which ultimately leads to reduced agricultural productivity. The cellular processes of chlorophyll synthesis, mitochondrial respiration, oxygen transport, and as constituent of some enzymes and proteins in plants are dependent on iron (Jin et al. 2014). The mechanism of solubility of iron in soil by microbes and plants are carried out by the chelation of insoluble iron in producing siderophore (Sharma et al. 2003). The iron deficient conditions stimulate siderophore production in rhizobial strains to enhance bioavailability of the nutrient in the environment (Terpolilli et al. 2012). In leguminous plant roots, secretion of signalling phenolic compounds establish rhizobia nodulation in Fe-deficient soil. Further, microbes produce different types of siderophores such as ferrioxamines, enterobactin, pyoverdine and ferrichromes (Marschner et al. 2010) which plays key role in plant growth. The siderophore producing rhizobia are considered as the potential iron acquisition in leguminous plant. This process involves siderophore mediated chelation of ferric (Fe^{3+}) to ferrous (Fe^{2+}) ion in the cell surface (Mendes et al. 2013). Yaseen et al. (2018) show increased iron uptake in the wheat with co-inoculation with endophytic bacteria *Enterobacter* sp. and *Burkholderia phytofirmans*. The iron content was increased up to 10.14% with enhanced leaf area, height, and biomass of plant.

5.6.2 Zinc

Zinc is an essential micronutrient for plant growth. The concentration of zinc is generally very low (80 mg kg^{-1}) in soil. It is the most important nutrient required for the synthesis of auxin, proteins, carbohydrates, lipids, nucleic acid, and involved in chlorophyll and seed formation (Seilsepour 2006; Broadley et al. 2007). It also helps in catalytic roles in different enzyme classes such as isomerase, transferase, oxido-reductase, hydrolases, and ligases (Hafeez et al. 2013). In soil various mechanisms of zinc solubilization are achieved by soil pH reduction by the release of organic acids and chelation (Subramanian et al. 2009; Whiting et al. 2001). The acidification of medium by gluconic acid production also make Zn availability to plants by bacteria such as *Curtobacterium, Plantibacter, Pseudomonas, Stenotrophomonas, Streptomyces* reported by Costerousse et al. (2018). The other way includes beneficial symbiotic relationship by Arbuscular mycorrhizal fungi (AMF) with the crop plants for sustained crop productivity (Yadav et al. 2018). This can increase root surface area which helps in high Zn uptake from the soil. Jha (2019) shows zinc-solubilizing microbes, namely *Bacillus pumilus* and *Pseudomonas pseudoalcaligenes* protect plants from osmotic stress by enhancing antioxidant enzymes catalase (CAT), and peroxidase (PO).

Kamran et al. (2017) shows maximum shoot and root length with high zinc content in wheat plant tested with *E. cloacae*, similarly maximum zinc content in wheat plant observed with *Pseudomonas fragi* and *P. agglomerans*. The Zn-solubilizing bacteria such as *Pseudomonas aeruginosa*, *Ralstonia pickettii*, *Burkholderia cepacia*, and *Klebsiella pneumonia* aids in the Zn-biofortification in rice seedlings with potential for utilizing insoluble zinc compound with exopolysaccharide (EPS) production, 1-aminocycloproparane-1-carboxylic acid (ACC) utilization, and potassium and phosphate solubilization (Gontia-Mishra et al. 2017). Singh et al. (2017) show two endophytic bacteria *Bacillus subtilis* and *Arthrobacter* sp., enhanced two folds increased Zn content in the wheat plant. The Zn-solubilizing bacterium *Pseudomonas* sp. is also a plant growth-promoting rhizobacteria in wheat cultivation (Lasani-2008 and Faisalabad-2008). Foliar spray application of microbes significantly increase Zn-biofortification in wheat grains (Rehman et al. 2018). Together Zn-solubilizing rhizobacteria have the ability of phosphate solubilization and production of IAA, siderophore, HCN, ammonia, exopolysaccharides, with catalase, protease, chitinase and lipase activity which increase the plant growth of wheat (Mumtaz et al. 2017).

5.7 Copper

The other essential micronutrient for plant growth is copper. Comparatively lesser amount of copper is required as compared to other micronutrients. It plays important role in the process of respiration and enzyme activation in the plants. The copper improves plant growth as it is important cofactor for enzymes (Makoi and Ndakidemi 2007). The copper availability to plants is made by soil microbes by the release of carboxylase and phenolic compounds (Badri and Vivanco 2009). The role of copper is acting as a catalyst for respiration and activator of several enzymes.

5.7.1 Manganese

The other essential micronutrient for plant growth manganese concentration in the soil is in an average amount of 1000 mg kg^{-1}. Manganese is a part of multiple enzymes and is a catalyst of other enzymes and used in metabolism of nitrogen and inorganic acids, formation of vitamins, and other metabolic process. The microbial activities in the soil largely affecting enhanced plant growth activities (Dutta and Podile 2010).

5.8 Future Perspectives and Challenges in Plant Microbe Based Agro-Inputs

Growing world population and climate change causes a big challenge towards crop production. In this context, intensify agricultural production is required to combat abiotic stress agents, pathogens, and pests in a sustainable manner. Research efforts may be made at developing agricultural yields through the management of soil microbes. In fact, developments of microbial formulations are global interest which is very useful to increase the soil fertility, particularly in N- and P-deficient agro-systems. The combined usage of beneficial microbes and mineral nutrients can stimulate plant growth and protect the environmental health. This is considered as the novel approach and an emerging research area to study the various activities of beneficial soil microbes, especially in interaction with plants and mineral nutrients. Currently researches are directed towards finding individual organism and its gene in a community. However, in future it can be widened with molecular approach. The scientific knowledge on plant-associated bacteria is scarce and therefore interaction between plants and microbes has to be studied intensively.

5.9 Conclusion

The role of soil microbes on soil nutrient availability to plants is discussed in this chapter. In addition to that, the usage of mineral nutrients with beneficial microbes is greatly required to improve higher yield in a sustainable way. Indeed, appropriate combination of mineral and microbial resources with favorable climatic conditions are highly essential for enhancing crop productivity and soil fertility. Moreover, systemic approaches are required to maintain biodiversity and environmental health. This mainly shows way forward towards efficient soil microbes as biofertilizers in order to reduce chemical fertilizers and pesticides. Thereby protecting the niche of soil habitat by biological approach is the proven efficiency.

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