

Chapter 2

Microbes: A Sustainable Approach for Enhancing Nutrient Availability in Agricultural Soils



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Abstract The soil scientists along with microbiologists had a big responsibility to come forward with a sustainable solution to enhance soil nutrient supplying capacity, without applying the agrochemical and mineral fertilizers. The only way out to this problem is through the use of efficient microbes which plays a vital role as organic or biological agents in facilitating uptake of many primary and secondary nutrients. Moreover, the fertility of any soil is directly proportional to the microbial biomass and its potential of functional activity and diversity. Billions of microbes which are present in soil are major key players of nutrient cycling and their solubilization and mineralization. This fact has been known and scientifically reported for a number of decades, but still its significance has not yet channelized into the mainstream of intensive agriculture. Thus, in this chapter, exhaustive overview of the different groups of agriculturally important microbes has been given which are responsible for enhancing nutrient availability particularly nitrogen, phosphorus, potassium, sulphur, iron and zinc in agricultural soils.

Keywords Nutrient supplying capacity · Efficient microbes · Solubilization · Mineralization

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2.1 Introduction

Soil nurtures incredibly diverse community of microorganisms that mediate the soil nutrient cycling at local, regional and global scales. In natural systems, these microbial communities live in harmony and keep balance in respect of food and space (Bélanger and Avis 2002). Around 1 billion microbes per gram of agricultural soil represent the largest and most diverse biotic group in the soil. Soil health is defined as the capacity of soil to function as a vital living system, by recognizing that it contains biological elements that are key to ecosystem function within land-use boundaries. In the agricultural context, it may refer to its ability to sustain productivity. Microorganisms possess the potential to give an integrated measure of soil health, an aspect that cannot be obtained with physical/chemical means and analyses of the diversity of higher organisms (Meena et al. 2013a, 2016a; Bahadur et al. 2014; Maurya et al. 2014; Jat et al. 2015; Kumar et al. 2015, 2016b; Ahmad et al. 2016; Kumar et al. 2016b).

Microbes are key players in the cycling of nitrogen, sulphur and phosphorus and the decomposition of organic residues. They affect nutrient and carbon cycling on a global scale. Production of extracellular polysaccharides and other cellular debris by microorganisms help in maintaining soil structure as well as soil health. Thereby, they also affect water holding capacity, infiltration rate, crusting and susceptibility to compaction. Changes in microbial populations provide an early sign of soil degradation. But the sustainable agricultural system alters this balance in the microbial community. These soil microorganisms have been differentiated as “beneficial” or “harmful” depending on their role and effect on soil quality, crop growth and yield. The beneficial microorganisms can fix atmospheric N, enhance nutrient cycling by decomposing organic wastes and residues, suppress soil-borne pathogens, detoxify pesticides and produce many bioactive compounds, viz. vitamins, hormones and enzymes, for better plant growth.

Such beneficial rhizospheric microbes are generally termed as agriculturally important microorganisms (AIMs). Soil microbes play a vital role in the cycling of nutrients which are essential for life. This chapter is the comprehensive understanding of the role of microbes in nutrient cycling, solubilization, mineralization and release (Parewa et al. 2014; Prakash and Verma 2016; Meena et al. 2016b; Jha and Subramanian 2016; Kumar et al. 2016a).

2.2 Microbe-Mediated Nutrient Release and Cycling of Nitrogen

The nitrogen (N) cycle is a fundamental process of nutrient cycling intimately linked with the ecosystems functional stability essential for ecosystem services (Virginia and Wall 2000). The dynamics of N transformation in various ecosystems is highly focused by the ecologist because N is a major elemental component of life

consist of proteins and nucleic acids and its supply can limit primary productivity in many natural terrestrial and aquatic ecosystems.

The microorganisms play vital role for N cycling in the ecosystems, and organic matter is the main contributor of N pool in the plant soil environment. The significant fraction of N pools present in organic matter is unavailable to the plants because of its complicated process of decomposition, and some fractions are locked as the recalcitrant fraction or just opposite to labile organic matter fraction (Haynes 2005). Organic matter decomposition is primarily mediated by soil biota mostly through fungi, bacteria/rhizobacteria and actinomycetes which resulted in the release of nutrients in mineral form and loss of C from the soil as CO₂ via respiration. The microbial biomass that is the living part of the soil organic matter has a pivotal role in the soil N cycle (Aislabie and Deslippe 2013; Priyadharsini and Muthukumar 2016; Kumar et al. 2017; Meena et al. 2015b; Jaiswal et al. 2016).

The continuous transfer of mineral N into organic materials via the incorporation of N into soil microbial biomass and the subsequent release of that immobilized N back into the soluble mineral N pool is known as mineralization-immobilization turnover (MIT) that governs the mineral N availability in agricultural land (Luxhoi et al. 2008). Gross N mineralization in soil is the great contributor of the release of volatile ammonium by non-specific heterotrophic soil microorganisms under aerobic and anaerobic conditions. The bulk of N mineralization occurs in the biologically active surface soil (~5 cm) that contains most of the dead and decomposing plant and animal litter (McNeill and Unkovich 2007).

These microorganisms play an important role in the breakdown of organic material and nutrient cycling with few compounds becoming recalcitrant fraction. The diversity of bacterial functions contributes a significant role in nutrient recycling and plant litter decomposition, thereby shaping and executing a system (Lynch 1983; Collins et al. 1992). They represent a vibrant source and sink of nutrients in all ecosystems and occupy a significant place in the ecosystem and soil food web (Raghavendra et al. 2016; Zahedi 2016; Meena et al. 2015c, f; Rawat et al. 2016; Dominguez-Nunez et al. 2016; Dotaniya et al. 2016).

Bacterial cells break down several intricate compounds into simpler organic forms. Therefore, they improve the status of soil organic carbon (SOC), soil structure and aggregate stability and increase water retention capacity and nutrient availability. The symbiotic relationship between N-fixing bacteria and legumes is one of the most dynamic plant-bacteria relations between N-fixing bacteria and legumes in one of the most dynamic plant-bacterial interactions (Sprent 1979). However, environmental conditions and the host determine the distribution and diversity and interaction of specific N-fixing bacteria (Hirsch et al. 1993; Moawad et al. 1998).

The nitrogen is the key elemental component of the soil-plant-animal continuum in the terrestrial ecosystems (McNeill and Unkovich 2007). The nitrogen distribution in the ecosystems regulated the microbial component of the soil. The limitation of N in the soil environments also renders the process of nitrogen cycling because of the essential requirement for microbial growth. Soil microorganisms play a crucial role in relation to nutrient cycling, and plant growth is regulated by the plant usable form of nutrient mediated through microbes. A comprehensive understanding

of nutrient cycling in agroecosystem and the microorganism that perform is thus essential for managing the soil health and ecosystem sustainability (Yasin et al. 2016; Meena et al. 2016c,d; Saha et al. 2016a, b; Yadav and Sidhu 2016; Bahadur et al. 2016b; Das and Pradhan 2016).

Nitrogen is present in different forms in the biosphere, among which dinitrogen (N_2) is the most abundant (~ 80%) fraction, whose bioavailability is limited (Robertson and Groffman 2007). In biological nitrogen fixation, the atmospheric nitrogen is converted to organic nitrogen which is the principal process to enter into the soil biological pools. Other major N transformations in soil include N mineralization, which is the conversion of organic N to its inorganic forms; N immobilization, which is the assimilation of inorganic forms of N by soil heterotrophs or plants, and nitrification, which is the conversion of ammonium (NH_4) to nitrite (NO_2^-) and then nitrate (NO_3^-); and denitrification, which is the conversion of nitrate to nitrous oxide (N_2O) and then dinitrogen gas (N_2). Other N species are involved in these conversions primarily as intermediaries and during conversion can escape to the environment where they can participate in chemical reactions or be transported elsewhere for further reactions (Verma et al. 2014, 2015a, b; Meena et al. 2013b, 2014a, 2015e; Sharma et al. 2016; Teotia et al. 2016).

Nitrogen cycles are strongly mediated by the microorganism and comprise five main processes which are **nitrogen fixation**, nitrogen uptake (microbial assimilation), nitrogen **mineralization** (decomposition), **nitrification** and **denitrification**. Nitrogen fixation is the conversion of N_2 to ammonia with the help of nitrogenase enzyme *Rhizobium* and *Bradyrhizobium* associated with legumes and *Frankia*, *Nostoc* and *Azolla* associated with nonlegumes. The ammonia produced by N-fixing bacteria is usually quickly incorporated into **protein** and other organic nitrogen **compounds**, either by a host plant, the bacteria itself, or another soil **organism**. After nitrogen is incorporated into organic matter, it is often converted back into inorganic nitrogen by a process called nitrogen **mineralization** or decomposition (Shrivastava et al. 2016; Velazquez et al. 2016; Meena et al. 2015d, 2016e; Masood and Bano 2016).

When organisms die, soil heterotrophs consume the organic matter and the process of decay continues. During this process, a significant amount of the nitrogen contained within the dead organism is converted to an available form of N. Nitrogen, in the form of ammonia, is available for use by plants and subsequently converted to nitrite (NO_2^-) and nitrate (NO_3^-) by nitrification process mediated by *Nitrosococcus* and *Nitrobacter* bacteria, respectively. Conversion of nitrogen products such as nitrates and nitrites back to nitrogen gas occurs through a process known as denitrification by common denitrifying bacteria including several species of *Pseudomonas*, *Paracoccus*, *Alcaligenes*, *Bacillus*, etc.

This process occurs in anaerobic conditions where bacteria use nitrogen, due to the absence of oxygen, for anaerobic respiration. The nitrogen cycle has a very significant agricultural and environmental role as it affects soil fertility, due to the fact that nitrogen is often the limiting nutrient for crop growth and it can also be a source of the greenhouse gas N_2O (Fig. 2.1).

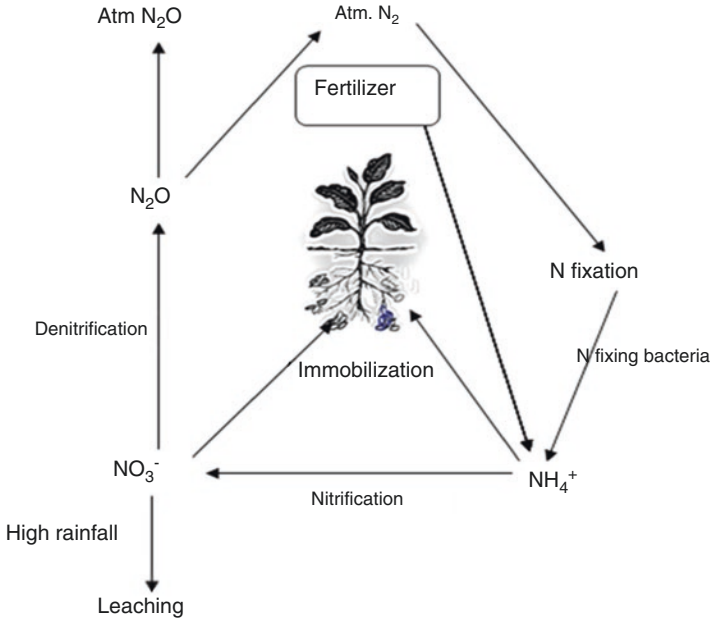
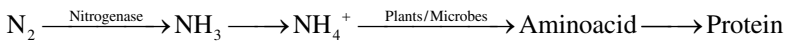
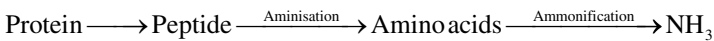


Fig. 2.1 Nitrogen cycle in the agroecosystem

Nitrogen fixation



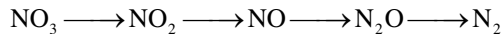
Ammonification



Nitrification



Denitrification (Pseudomonas, Bacillus, Paracoccus, Thiobacillus)



The primary source of N_2O emission is through the application of N-containing fertilizer and manure N inputs in the agricultural field (Davidson 2009). The presence of excess moisture has an adverse impact on nitrification. Nitrification progresses when the water content is one-third to one-half of water holding capacity and would be less in the case of dry and extremely dry conditions. The soil temperature of 25–40 °C is optimum for the nitrification process. At the freezing point and

50 °C, the nitrification ceases. The temperature coefficient (Q_{10}) between 5 and 40 °C is 2.0.

Soil microorganisms will preferentially use the plant rhizodeposition because they are more readily decomposable with optimum N availability. Increased microbial biomass may result in enhancing denitrification rates, immobilize more soil N and initiate a shortage of available N for the plants. Increased decomposition of carbon into more resilient pools of carbon increases immobilization of soil N. Arbuscular mycorrhizal fungi (AMF) are also known to play a crucial role in nitrogen cycling and nutrition in soil by increasing plant nitrate uptake and efficient utilization. Report of McFarland et al. (2010) established that a significant amount ~ 50% of plant N requirement is supplied by the plant-mycorrhizal association (Sindhu et al. 2016; Meena et al. 2013c, 2014b, 2015d; Singh et al. 2015, 2016; Bahadur et al. 2016a).

This mycorrhizal inoculation enhanced the activities of nitrate reductase, glutamine synthetase and glutamine synthase in the roots and shoots of mycorrhizal corn (*Zea mays* L.) as reported by Subramanian and Charest (1999). The main supply of nitrogen in leguminous plants occurs via symbiosis, a process that is highly associated with phosphorus cycle.

2.3 Microbe-Mediated Phosphorus Solubilization

Phosphorus (P) is one of the significant growth-limiting nutrient having no biologically available source (Saharan and Nehra 2011; Hrynkiemicz and Baum 2011). This nutrient is associated with the development of root, providing shoot strength, and flower as well as seed formation, for N-fixation in legumes and to develop resistance in plants against diseases. In soil phosphorus dynamics can be characterized by physicochemical (sorption-desorption) and biological (immobilization-mineralization) processes. A large amount of P fertilizer reacts with Fe^{3+} and Al^{3+} in acidic soils and Ca^{2+} in calcareous or neutral soils through precipitation reaction and remains immobile (Hao et al. 2002). Thus, P fertilizer has only 10–25% efficiency throughout the world (Isherword 1998). Further, the concentration of soil bioavailable P is only 1.0 mg kg^{-1} (Goldstein 2000).

Soil microorganisms play a vital role in triggering the availability of phosphate to plants vis-a-vis soil P dynamics (Misra et al. 2012; Pingale and Popat 2013). The occurrence of Phosphorus-solubilizing microbes (PSMs) has been evidenced long back and is listed in Table 2.1 (Sharma et al. 2013; Khan et al. 2007), and various acids produced by them are given in Table 2.2. Gaiind (2016) studied that *A. niger* and *T. harzianum* could be the potential candidate for developing microphos inoculants to facilitate P supply to different crops in alkaline and acidic soils with organic and inorganic P content. While developing microbial formulations, the cultivation conditions can be manipulated to favour the production of organic acids. It is also known that bacteria solubilize phosphorus more potentially than fungi.

Table 2.1 List of Phosphorus-solubilizing microbes (PSMs) in soil

Microbial group	Phosphorus-solubilizing microbes (PSMs)
Actinomycetes	<i>Actinomyces</i> sp., <i>Streptomyces</i> sp.
Bacteria	<i>Agrobacterium</i> sp., <i>Achromobacter</i> sp., <i>Azospirillum</i> sp., <i>Alcaligenes</i> sp., <i>Bacillus</i> sp., <i>B. cereus</i> , <i>B. fusiformis</i> , <i>B. pumilus</i> , <i>B. megaterium</i> , <i>B. polymyxa</i> , <i>B. coagulans</i> , <i>B. subtilis</i> , <i>Bradyrhizobium</i> sp., <i>Pseudomonas</i> sp., <i>P. putida</i> , <i>P. striata</i> , <i>P. fluorescens</i> , <i>Flavobacterium</i> sp., <i>Nitrosomonas</i> sp., <i>Micrococcus</i> sp., <i>Escherichia</i> sp., <i>Enterobacter</i> sp., <i>Serratia phosphoticum</i> , <i>Nitrobacter</i> sp., <i>Thiobacillus ferrooxidans</i> , <i>T. thiooxidans</i> , <i>Rhizobium meliloti</i> , <i>Xanthomonas</i> sp., <i>Anabaena</i> sp., <i>Nostoc</i> sp.
Fungi	<i>Aspergillus awamori</i> , <i>A. terreus</i> , <i>A. flavus</i> , <i>A. niger</i> , <i>A. nidulans</i> , <i>A. foetidus</i> , <i>Fusarium oxysporum</i> , <i>Alternaria tenuis</i> , <i>Penicillium digitatum</i> , <i>P. lilacinium</i> , <i>Cephalosporium</i> sp., <i>Cladosporium</i> sp., <i>Candida</i> sp., <i>Chaetomium globosum</i> , <i>Humicola</i> sp., <i>Helminthosporium</i> sp., <i>Paecilomyces fusisporous</i> , <i>Pythium</i> sp., <i>Phoma</i> sp., <i>Micromonospora</i> sp., <i>Rhizoctonia solani</i> , <i>Rhizopus</i> sp., <i>Mucor</i> sp., <i>Trichoderma viride</i> , <i>Sclerotium rolfsii</i> , <i>Glomus fasciculatum</i>

Source: Sharma et al. (2013)

Table 2.2 Organic acids produced by phosphorus-solubilizing microbes (PSMs)

PSMs	Organic acid produced	References
<i>Aspergillus niger</i> , <i>Penicillium</i> sp., <i>Bacillus megaterium</i> , <i>Pseudomonas</i> sp., <i>Bacillus subtilis</i> , <i>Arthrobacter</i> sp.	Lactic, malic, citric, gluconic	Bajpai and Sundara Rao (1971), Fankem et al. (2006), Vyas and Gulati (2009), and Gaind (2016)
<i>Aspergillus japonicus</i> , <i>A. foetidus</i> , <i>B. pumilus</i> , <i>Citrobacter</i> sp.	Oxalic, succinic, 2-ketogluconic, heptonic, caproic, isocaproic, formic, valeric, succinic, oxalic, oxaloacetic, malonic	Banik and Dey (1983), Singal et al. (1994), and Puente et al. (2004)
<i>Bacillus amyloliquefaciens</i> , <i>B. licheniformis</i> , <i>Vibrio proteolyticus</i> , <i>Xanthobacter agilis</i> , <i>Enterobacter aerogenes</i> , <i>Pseudomonas aerogenes</i>	Isobutyric, acetic itaconic, isovaleric	Vazquez et al. (2000)

Among the soil PSMs, P solubilization potential of phosphorus-solubilizing bacteria or rhizobacteria (PSB and PSR) is 1–50%, whereas that of phosphorus-solubilizing fungi (PSF) constitutes only 0.1–0.5% (Chen et al. 2006). Bacterial strains like *Pseudomonas*, *Bacilli* (ectorhizospheric) and endosymbiotic rhizobia with fungal strains like *Penicillium*, *Aspergillus* and *Arthrobotrys oligospora* (nematofungus) have been reported as effective phosphate solubilizers (Duponnois et al. 2006; Igual et al. 2001).

Heterotrophic microorganisms solubilize inorganic forms of P by excreting organic acids (gluconic and ketogluconic acids) which dissolve phosphatic minerals or by chelating the cations bound to phosphate (through their hydroxyl and carboxyl groups) or by lowering the pH of rhizosphere (through production of proton/bicarbonate release and O₂/CO₂ gaseous exchange) (Nenwani et al. 2010; Stevenson

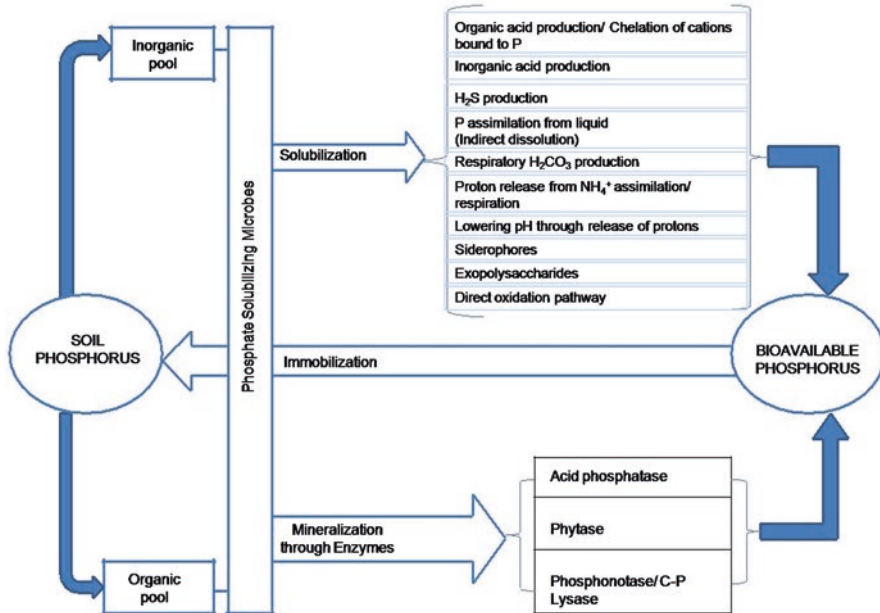


Fig. 2.2 Schematic representation of mechanism of soil P solubilization/mineralization and immobilization by PSMs

2005; He et al. 2002). Figure 2.2 shows the schematic representation of mechanism of soil P solubilization/mineralization and immobilization by PSMs. Wyciszewicz et al. (2016) confirmed that the decrease of pH observed during the solubilization process resulted from the synthesis of organic acids and the spectrum of synthesized organic acids on different phosphorus sources used in the microbial solubilization as a method for producing the phosphate fertilizers.

2.3.1 Mineralization of Organic P

Total soil P constitutes 4–90% of organic P. Soil organic P (Po) mineralization plays a major role in phosphorus cycling. Po mineralization takes place by almost half of the PSM in soil and plant roots in the presence of phosphatase/phytase/lyase enzyme (Tarafdar et al. 1988; Hilda and Fraga 2000). The releases of these enzymes either by plant roots or by microbes hydrolyse the Po or extract P from organic residues (Dodor and Tabatabai 2003; Yadav and Tarafdar 2001; Tarafdar and Claasen 1988). Consortia of PSMs (*Bacillus*, *Pseudomonas*, *Streptomyces*, etc.) are highly effective in mineralizing Po (Molla et al. 1984).

2.3.2 *Solubilization of Ca-Bound P*

Under alkaline conditions, most of the calcium phosphates, including ores of rock phosphate (like fluoroapatite, francolite), are not soluble in soil with respect to the release of inorganic P (Pi) (Goldstein 2000). Literature shows that PSM has potential to feed the P requirement of plants by decreasing rhizospheric soil pH through organic acid production and thereby increasing the solubility of Ca-phosphates (Gerretsen 1948; Fankem et al. 2006). Microorganisms break the bound forms of phosphate like $\text{Ca}_3(\text{PO}_4)_2$ through secretion of different types of organic acids, e.g. carboxylic acid. Acidification releases P from apatite by excretion of H^+ or proton substitution or through the release of Ca^{2+} (Villegas and Fortin 2002; Deubel and Merbach 2005).

2.3.3 *Solubilization of Al-Bound P and Fe-Bound P*

Phosphorus-solubilizing microbe releases proton which solubilizes Fe and Al and thereby reduces the negative charge of adsorbing surfaces and facilitates the sorption of negatively charged P ions. Acidification occurs through proton release that can also decrease P sorption by increasing H_2PO_4^- with respect to HPO_4^{2-} (Henri et al. 2008; Khan et al. 2007). Acids (carboxylic) mainly solubilize Al-P and Fe-P which results in anion exchange of PO_4^{3-} by acid anion or by chelation (via siderophores) of both Fe and Al ions associated with phosphate (Altomare 1999) or by ligand exchange (Whitelaw 2000). Chelating ability of organic acids is mainly influenced by its molecular structure (viz. number of carboxyl and hydroxyl groups). Moreover effectiveness of solubilization process is determined by ligand type and position in addition to its acid strength (Kpombrekou and Tabatabai 1994).

2.4 **Microbe-Mediated Potassium Release and Its Solubilization**

Injudicious application of chemical fertilizers in India has a considerable negative impact on the economy and environmental sustainability. There is a growing need to turn back to nature or sustainable agents that promote evergreen agriculture. Potassium (K) is the third primary essential plant nutrient and plays a critical role in enzyme activation, protein synthesis and photosynthesis and quality of produce. It is a major constituent of several soil minerals and quite abundant in many soils, particularly in India. However, the K levels have dropped in many soils due to continuous mining through crop removal without replenishing it.

In India, the cost of K fertilizers is very high because of non-availability of K-bearing minerals for manufacturing of conventional K fertilizers, and the total

Table 2.3 Import and consumption of potassic fertilizers in 2013–2014 and 2014–2015

Name of fertilizer	Import (Mt)		Consumption (Mt)	
	2013–2014	2014–2015	2013–2014	2014–2015
Muriate of potash (60% K ₂ O)	3.180	4.197	2.280	2.853
Sulphate of potash (50% K ₂ O)	0.058	0.078	0.031	0.019

Source: <http://www.faidelhi.org/statistical-database.htm>

consumption is imported, costing an enormous amount of foreign exchange (Table 2.3).

In this context, it is obvious that attempts should be made to harness the microbial potential in releasing potassium into plant available form from potassium-bearing mineral reserve in soils. Furthermore, the potentiality as potassium-solubilizing microbes also needs to be tested for sustainable crop production and maintenance of K status in soils.

2.4.1 Potassium-Solubilizing Microbes and Their Occurrence

The very first study which surfaced evidence of the involvement of microbes in rock potassium solubilization dates back to 1890 (Muentz 1890). Apart from this, the role of silicate bacteria in the dissolution of potassium, silicates and aluminium from insoluble minerals have also been reported (Aleksandrov et al. 1967). A diverse group of soil microbes (Table 2.4) has been reported to be capable of solubilizing insoluble and fixed forms of K into available forms of K (Li et al. 2006; Zarjani et al. 2013; Gundala et al. 2013).

2.4.2 Potassium-Solubilizing Mechanisms

The primary agent responsible for the potassium-solubilizing capacity of K-solubilizing microbes is the low-molecular-weight organic acids, viz. citric, oxalic, tartaric, succinic acids, etc. (Sheng and He 2006; Prajapati and Modi 2012). Apart from this production of ferulic, coumaric, syringic and malic acid by K-solubilizing bacteria has also been reported to be responsible for K solubilization (Setiawati and Mutmainnah 2016). Organic acids produced by microbes facilitate K solubilization and mobilization through the following mechanisms (Fig. 2.3).

The following are the mechanisms involved in K solubilization:

- (a) Weathering of micas, illite and orthoclase by direct dissolution of K from the minerals.
- (b) Mobilizing K from unavailable to available form by creating metal-organic complexes/chelates with Si₄⁺ ion to bring the K into solution (Song and Huang 1988; Friedrich et al. 1991; Bennett et al. 1998).

Table 2.4 Different phosphorus-solubilizing bacterial species reported by various researchers

Bacteria	References
<i>Bacillus mucilaginosus</i>	Zhao et al. (2008), Basak and Biswas (2009), Sugumaran and Janarthanam (2007), and Zarjani et al. (2013)
<i>Bacillus circulans</i>	Lian et al. (2002)
<i>Bacillus edaphicus</i>	Zhao et al. (2008), Basak and Biswas (2009), Sugumaran and Janarthanam (2007), and Zarjani et al. (2013)
<i>Burkholderia</i> sp.	Sheng and Huang (2002) and Sheng and He (2006)
<i>Acidithiobacillus ferrooxidans</i>	Sheng and Huang (2002) and Sheng and He (2006)
<i>Arthrobacter</i> sp.	Zarjani et al. (2013)
<i>Enterobacter hormaechei</i> (KSB-8)	Prajapati et al. (2013)
<i>Paenibacillus mucilaginosus</i>	Liu et al. (2012) and Hu et al. (2006)
<i>Paenibacillus frequentans</i>	Argelis et al. (1993)
<i>Cladosporium</i> sp.	Argelis et al. (1993)
<i>Aminobacter</i> sp.	Uroz et al. (2007)
<i>Sphingomonas</i> sp.	Uroz et al. (2007)
<i>Paenibacillus glucanolyticus</i>	Sangeeth et al. (2012)
<i>Agrobacterium tumefaciens</i>	Meena et al. (2015a)
Fungi	
<i>Aspergillus niger</i>	Prajapati and Modi (2012)
<i>Aspergillus terreus</i>	Prajapati and Modi (2012)
<i>Penicillium</i> sp.	Sangeeth et al. (2012)
<i>Glomus intraradices</i> , <i>Glomus mosseae</i>	Wu et al. (2005)
Ectomycorrhizal fungi	Alves et al. (2010)

- (c) The mineral structural cation released by the attack of H⁺ ion from organic acids form the cation-organic complex with COOH⁻ and OH⁻ ions. The chemisorption of the cation-organic complexes on the mineral surfaces causes a shift of electron density toward the framework of the mineral. This charge transfer increases the electron density of the cation-oxygen bonds and makes them more susceptible to hydrolysis (Chen et al. 2000).
- (d) Dissolution of feldspar by decreasing the pH of the surrounding soil environment (Bennett et al. 2001).
- (e) Dissolution of K from orthoclase by carboxylic acids and capsular polysaccharide produced by *Bacillus mucilaginosus* and *Bacillus edaphicus* (Lin et al. 2002; Sheng and Huang 2002).
- (f) Mineral weathering by a mixture of polymers and low-molecular-weight ligands produced from *Bacillus mucilaginosus* (Malinovskaya et al. 1990).
- (g) Biofilm formation on the rhizospheric mineral surfaces can also solubilize K from unavailable sources (Balogh-Brunstad et al. 2008). Biofilms embedded with ectomycorrhizal hyphae and root hairs of non-ectomycorrhizal trees are reported to solubilize K from biotite and anorthite through weathering process.

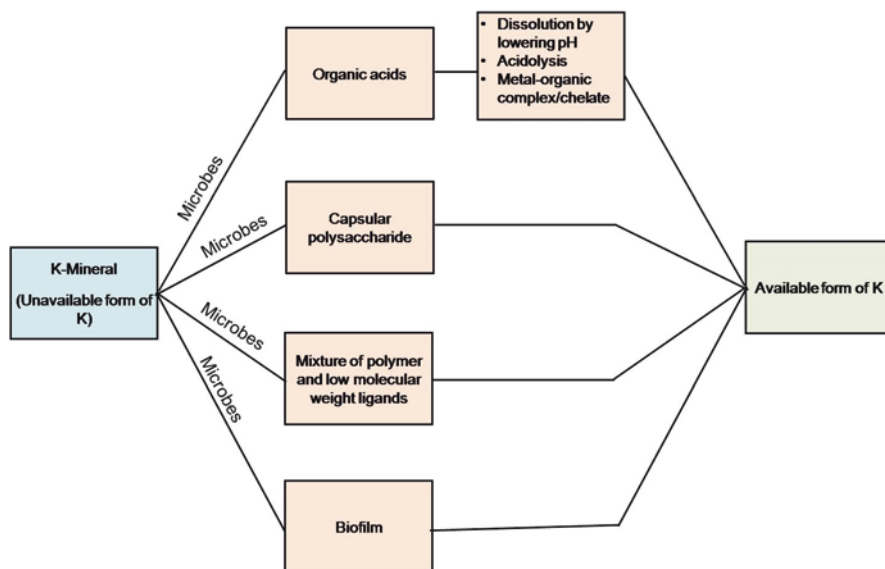


Fig. 2.3 Mechanisms involved in potassium solubilization by soil microbes

2.4.3 Potential Role of Potassic Biofertilizer

Chemical fertilizers are the major sources for replenishing soil potassium reserve; however, it bears a considerable negative impact on the environment. Moreover it incurs a great expenditure as the total consumption of potassium fertilizer has to be imported. In this respect, potassium-solubilizing bacteria could serve as an eco-friendly tool which could be utilized for converting insoluble form mineral potassium in the soil into a plant absorbable form. This strategy will ensure improved plant absorption of potassium simultaneously reducing the dependency on chemical fertilizer (Zhang and Kong 2014).

Potassic biofertilizers have already been reported to play a vital role in improving soil fertility, yield attributing characters and eventually yield (Basak and Biswas 2010; Awasthi et al. 2011; Zhang et al. 2013). Furthermore, potassic biofertilizers also promote soil biota as well as plant growth. It is well known that Indian soil is the reserve of sufficient potassium containing secondary mineral; nevertheless, the greatest challenge is its lower availability to plant. Henceforth, it surfaced the urgent need of inoculation of potassium-solubilizing microbes alone or in consortia with other beneficial soil microbes to augment the potassium availability from natural sources to harvest good sustainable yield of crops as well as to reduce the reliance on chemical fertilizer.

2.5 Role of Microorganisms in Mineralization and Immobilization of Sulphur

Sulphur is very essential macro element known as the secondary element required for the all living organisms to form their important biomolecules like protein, hormones, enzymes and vitamins. Sulphur is a structural part of the 2 of the 21 amino acids such as cysteine and methionine in which sulphur is used to form disulphide bridges (c-s-s-c) which provide structural stability to the protein molecule.

Sulphur is available in the organic and inorganic form. The availability of sulphur in soil depends on the soil microbial population, and they are solely responsible for generating sulphur pool by oxidative transformation of organic sulphur (Vidyalakshmi et al. 2009). The chemolithotrophic and photoautotrophic bacteria complete their energy requirement by oxidizing sulphur and generating sulphate which is used by plants.

Sulphur cycle (Fig. 2.4) splits into four steps which form soluble sulphur used by plants for their growth and development:

1. Mineralization of organic sulphur by prokaryotic organisms.
2. Formation of sulphate (SO_4^{2-}) by oxidation of elemental sulphur, hydrogen sulphide (H_2S) and sulphide (S^{2-}).
3. Reduction of sulphate generates sulphide.
4. Assimilatory reduction of sulphate into organic compounds.

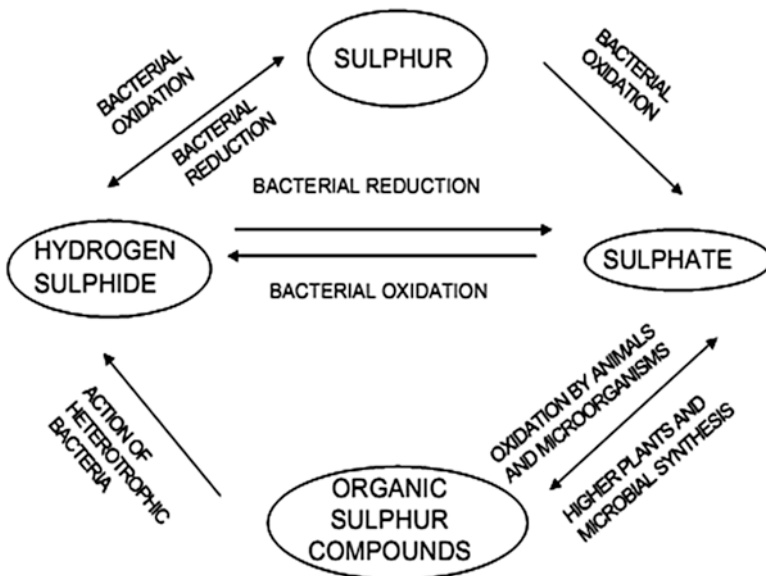


Fig. 2.4 The oxidation of sulphur in soils (Burns 1967)

Table 2.5 List of sulphur-oxidizing microbes (SOMs)

Microbes	Species	References
Bacteria	<i>Acidithiobacillus</i> sp., <i>Aquaspirillum</i> sp., <i>Aquifer</i> sp., <i>Bacillus</i> sp., <i>Beggiatoa</i> sp., <i>Paracoccus</i> sp., <i>Pseudomonas</i> sp., <i>Starkeya</i> sp., <i>Xanthobacter</i> sp., <i>Thiobacillus thiooxidans</i> , <i>Thiobacillus ferrooxidans</i> , <i>Thiobacillus</i> , <i>Allochromatium</i> sp., <i>Chromatium</i> sp., <i>Rhodobacter</i> sp., <i>Rhodovulum sulphidophilum</i> , <i>Rhodopseudomonas acidophila</i> , <i>Thiocaspa</i> sp., <i>Chlorobi</i> sp.	Teske and Nelson (2004), Beller et al. (2006), Frigaard and Bryant (2008), Imhoff et al. (1998), and Kelly et al. (2000)
Archaea	<i>Sulfolobus</i> sp., <i>Acidianus</i> sp.	Setter et al. (1990) and Kelly and Wood (2000)
Fungi	<i>Aureobasidium pullulans</i> , <i>Alternaria tenuis</i> , <i>Epicocum nigrum</i> , <i>Penicillium</i> sp., <i>Scolecobasidium constrictum</i> , <i>Myrothecium cinctum</i> , <i>Aspergillus</i> sp.	Wainwright (1978) and Shinde et al. (1996)

2.5.1 Sulphur-Oxidizing Microorganisms (SOMs)

Sulphur oxidation is the major step in the sulphur cycle to produce sulphate with the help of some sulphur-oxidizing microorganisms such as chemolithotrophs (*T. ferrooxidans* and *T. thiooxidans*), photoautotrophs (including purple and green S bacteria) and heterotrophs (including a wide range of bacteria and fungi). Oxidation of sulphur occurs in both oxic and anoxic condition with the help of aerobic chemolithotrophs and anaerobic phototrophic bacteria. The SOMs are mostly Gram-negative chemolithotrophic bacteria which take part in the mineralization, transformation and oxidation of various organic and inorganic sulphur compounds (Table 2.5).

The biological sulphur oxidation comprises in principle the following oxidation steps: $S \rightarrow S_2O_2^{-3} \rightarrow S_4O_2^{-6} \rightarrow SO_2^{-4}$. These SOMs are known as chemolithotrophs which meet their energy requirements from reduced organic and inorganic sulphur compounds such as hydrogen sulphide, sulphide and elemental sulphur. In acidophilic chemolithotrophic *Thiobacillus* sp., oxidation of sulphur is a complex process involving the formation of various intermediate products such as thiosulphate, tetrathionate and sulphite. The thiosulphate oxidizer, *Thiobacillus thioparus*, grown on thiosulphate as an energy source has a pH optimum of 4.5–5.0 (Masau et al. 2001). The oxidation of sulphur requires a close bacteria-substrate interaction. *Thiobacillus* sp. consumes substrate by acting at the surface of crystalline sulphur, which decreases the fractal dimension at a small scale. In the early oxidation stage, microorganisms near the surface area of small sulphur particles can lead to a faster oxidation rate. However, in the later stages of oxidation, large particles remaining in soils provide less contact area to microorganisms, resulting in a low oxidation rate in the later stage.

The accumulated amount of SO_2^{4-} may also affect sulphur oxidation because of a high osmotic pressure (Harahuc et al. 2000). Oxidation of sulphur improves soil fertility and also improves alkali soil by the formation of sulphate (SO_4^{2-}). Decline in soil pH due to the sulphur oxidation increases solubilization of other nutrients in the rhizosphere. In addition to the release of H^+ and SO_2^{4-} after sulphur oxidation,

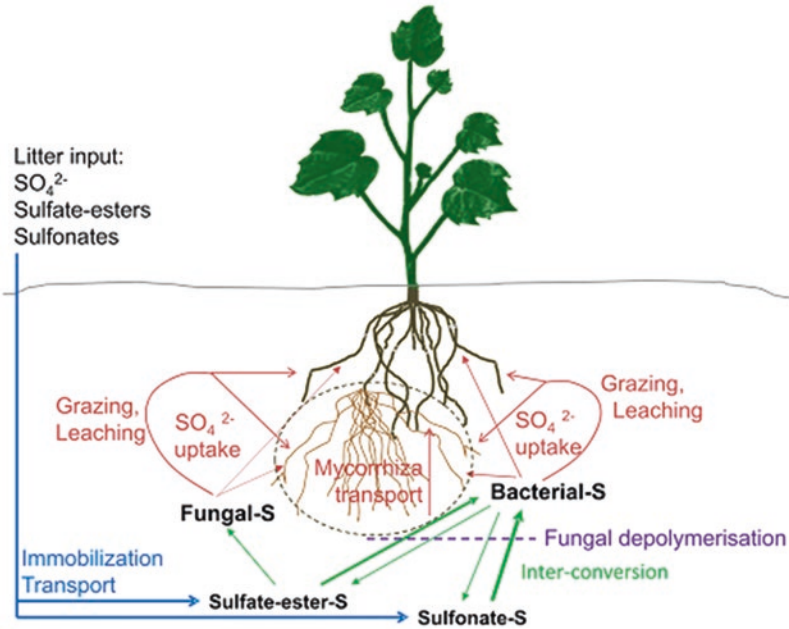


Fig. 2.5 The sulphur cycle in soil and plant sulphate uptake (Autri and Fitzgerald 1990; Kertesz and Mirleau 2004)

other nutrients such as phosphorus and Zn are dissolved and increase electric conductivity values (Zhou et al. 2002; Jaggi et al. 2005).

2.5.2 Rhizosphere Sulphur Cycle and Its Utilization

In plants, requirements of sulphur depend on species and stage of development (Leustek et al. 2000). Sulphate (SO_4^{2-}) is the primary source of sulphur which is used by plants for their growth and development (Fig. 2.5). The sulphur pools in the soil are not static but immensely dynamic. Importantly, although some of the organosulphur present in soils are plant and animal derived (Kertesz 1999), much is also synthesized in situ. Inorganic sulphur forms are immobilized to organic sulphur, different organosulphur forms are interconverted, and immobilized sulphur is simultaneously mineralized to yield plant available inorganic sulphur. These processes occur concurrently, and many of them are linked to the microbial community present in the soils which composition varies significantly between two plants (Gomes et al. 2003; Kent and Triplett 2002; Marschner et al. 2001; Smalla et al. 2001; Van den Koornhuysse et al. 2003).

Sulphate esters and sulphonates act as the significant contributor of sulphur in the soil. Deposition of biological material and subsequent humification increases

the organic sulphur pool. Fungi and bacteria release sulphur from sulphonates which are catalysed by a bacterial multicomponent monooxygenase system and from sulphate esters using sulphatases (Gahan and Schmalenberger 2014).

Thiosulphate oxidation via formation of the tetrathionate intermediate (S_4I) pathway is observed in several *Beta*- and *Gammaproteobacteria* such as *Acidithiobacillus*, *Thermithiobacillus* and *Halothiobacillus* (Trudinger 1965; Guay and Silver 1975; Pronk et al. 1990; Kelly et al. 1997). Acidophilic species preferred S_4I pathway of thiosulphate oxidation because it appears that oxidation of thiosulphate to sulphate via intermediate such as tetrathionate is stable in acidic condition (Johnston and McAmish 1973). In S_4I pathway, thiosulphate is said to be oxidized to tetrathionate in the periplasmic space by the enzymatic action of thiosulphate dehydrogenases that use c-type cytochromes as cosubstrates.

Acidianus ambivalens, a thermoacidophilic archeon, have a membrane-bound, tetrathionate-forming thiosulphate:quinone oxidoreductase (TQO), involved in sulphur chemolithotrophy (Muller et al. 2004). Hydrolysis of tetrathionate produces sulphite followed by its oxidation to sulphate in the cytoplasm or in close vicinity to the inside of the cell membrane (Kelly and Harrison 1989; Hallberg et al. 1996; Kelly et al. 1997; Dam et al. 2007). Complete oxidation of tetrathionate needs the participation of active membranes. Sulphite oxidation takes place in the cytoplasm by a sulphite dehydrogenase involving a ubiquinone-cytochrome b complex transferring electrons from SO_3^{2-} to oxygen (Dam et al. 2007).

2.6 Iron Transformation in Soil by Soil Microbes

Iron is the fourth most abundantly available element in the earth's crust (Radzki et al. 2013). However, its availability to the plants mainly depends upon the state in which iron is present in the soil. Iron is a crucial element for plant growth since it constitutes cofactor of many vital enzymes of plant system (Radzki et al. 2013). Deficiency of iron may lead to disruption of many metabolic processes and thus an overall reduction in growth and yield of the plant. pH and redox potential of the soil system determine the state of the metal and thus affects its availability. Microbes are key driver for transformation of metal from one form to other. Under aerobic condition, oxidation of iron by soil microbes dominates in the acidic environment, whereas chelation is promoted under neutral environment. Iron reduction and precipitation of iron sulphides are prevalent in the anaerobic environment (Coyne 1999).

Many physiological groups of microbes can use iron as a substrate for energy generation and change the oxidation state of iron which facilitates its availability. Under aerobic and acidic condition, iron oxidation can be mediated by *Thiobacillus ferrooxidans* and *Sulfobacillus acidophilus* for energy generation. The oxidation of iron is not always associated with energy generation. In neutral soil, the microbial

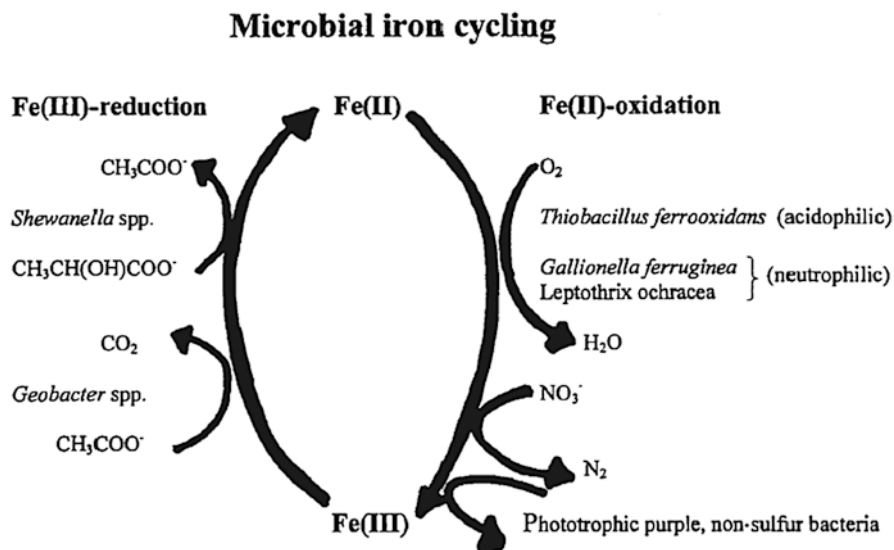


Fig. 2.6 The microbial iron cycle (Erbs and Spain 2002)

conversion of Fe(II) to Fe(III) can be carried out by microbes including *Crenothrix*, *Gallionella*, *Leptothrix*, *Metallogenium*, *Sphaerotilus*, etc. without any energy generation (Coyné 1999).

In anoxic condition and neutral soil pH, nitrate-dependent Fe(II) oxidation can be mediated by *Acidovorans* sp. and *Azospira oryzae* (Fig. 2.6), whereas phototrophic iron oxidation with CO_2 as an electron acceptor was reported in *Rhodobacter ferrooxidans* SW2 and *Rhodovulum iodosum* (Kappler and Straub 2005).

2.6.1 Iron Reduction

Till date a wide diversity of Fe(III)-reducing microorganisms have been identified where hydrogen, short and long fatty acids, amino acids, sugars and aromatic compounds are reported to serve as electron donors for Fe(III) reduction. The enzyme responsible for dissimilatory Fe(III) reduction is a membrane-associated ferric reductase. The Fe(III) reducers may utilize alternative electron acceptors such as O_2 , nitrate, S^0 , sulphate, humic substances, contaminant metals and metalloids and chlorinated solvents. The first organism shown to couple respiratory growth to dissimilatory iron reduction was *Shewanella oneidensis* (previously known as *Pseudomonas ferrireductans*).

Various dissimilatory Fe(III) reducers, including the well-known *Geobacter* sp. and *Shewanella* sp., have frequently been isolated from marine and freshwater sediments. The obligate anaerobic *Geobacter* sp. belongs to the δ -proteobacteria,

Table 2.6 Microbes involved in different soil conditions

Soil condition	Microbial processes	Organism involved
Acidic, aerobic	Oxidation with energy generation	<i>Thiobacillus ferrooxidans</i> and <i>Sulfobacillus acidophilus</i>
Neutral, aerobic	No energy generation	<i>Gallionella</i> and <i>Leptothrix</i>
Anaerobic Fe(II)-oxidizing phototrophic bacteria		Purple sulphur bacteria (<i>Halothiobacillus</i> sp.), purple non-S bacteria (<i>Rhodomicrobium</i> sp., <i>Rhodobacter</i> sp., <i>Rhodopseudomonas</i> sp.) Green bacteria (<i>Chlorobium ferrooxidans</i>)
Acidophilic Fe(III)-reducing microorganisms		<i>Acidiphilium</i> sp.
Reduction of Fe(III) at neutral pH		<i>Shewanella putrefaciens</i> and <i>Geothrix fermentans</i>

whereas the facultatively anaerobic *Shewanella* sp. belongs to the γ -proteobacteria (Erbs and Spain 2002). Table 2.6 shows the microbes involved at different soil conditions.

2.6.2 Bacterial Siderophores

Among the benefits for plant fitness attributed to plant growth-promoting rhizobacteria (PGPR) is the ability to release siderophores, compounds capable of chelating iron with high affinity and in a reversible manner (Budzikiewicz 2010; Neilands 1995). Under iron-limiting conditions, PGPR produces low-molecular-weight ligands called siderophores to competitively chelate ferric ion (Saharan and Nehra 2011). Siderophores include catecholates, hydroxamates and carboxylates (Louden et al. 2011). Berraho et al. (1997) demonstrated production of salicylic acid and 2,3-dihydroxybenzoic acid as phenolate-type siderophores in strains of *Rhizobium ciceri*, specific to chickpea. Many siderophores producing soil microbes are used as potential plant growth-promoting rhizobacteria. For example, soil bacterial isolates including *Azotobacter vinelandii* MAC 259 and *Bacillus cereus* UW 85 produced siderophores and can be used as potential PGPR to increase the yield of the crop (Husen 2003).

Bacillus megaterium from tea rhizosphere was able to produce siderophore, and thus it could help in the plant growth promotion and reduction of disease intensity (Chakraborty et al. 2006). *E. coli* isolated and characterized from endorhizosphere of sugarcane (*Saccharum* sp.) and rye grass (*Lolium perenne*) was found to produce siderophores and thus was found to help in the growth of the plants (Gangwar and Kaur 2009).

2.7 Zinc Transformation

Zinc plays very important role in plant metabolism by influencing the activities of enzymes like hydrogenase and carbonic anhydrase. It also helps in stabilization of ribosomal fractions and synthesis of cytochrome (Tisdale et al. 1984). Deficiency of zinc results in the developmental abnormalities in plant and also adversely affects the quality of harvested products (Hafeez et al. 2013). In soils, Zn is mostly present in unavailable fraction rendering its lower availability to plant. The factors responsible for its lower availability include low total Zn content, neutral or alkaline pH, high salt concentration and high calcium carbonate content in calcareous soil (Kumari Sunitha et al. 2014). Thus, some researchers had explored few microbial genera such as *Bacillus* sp., *Pseudomonas* sp. and *Aspergillus* sp. for their zinc-solubilizing potential (Saravanan et al. 2003).

Secretion of organic acids by microbes has been identified as the prime mechanism of zinc solubilization. These released organic acids, viz. acetic, citric, lactic, propionic, glycolic, oxalic, gluconic acid, etc., can sequester cations and acidify the microenvironment by lowering the rhizospheric pH (Bapiri et al. 2012; Saravanan et al. 2007). Organic acid secreted by microflora increases soil Zn availability in two ways; they are probably exuded both with protons and as counter ions and, consequently, reduce rhizospheric pH. Also the anions can chelate Zn and increase Zn solubility (Jones and Darrah, 1994) which result in the conversion of the available form (Zn^{2+}) to plants. Vaid et al. (2014) showed improved growth and productivity of rice upon inoculation with zinc-solubilizing bacteria of genus *Burkholderia* and *Acinetobacter*. Goteti et al. (2013) reported seed bacterization with zinc-solubilizing bacteria at 10 g kg⁻¹ enhanced total dry mass (12.96 g) and uptake of N (2.268%), K (2.0%), Mn (60 ppm) and Zn (278.8 ppm) in maize.

2.8 Concluding Remarks

Nitrogen, phosphorus, potassium, sulphur, iron and zinc are the vital elements from crop nutrition point of view. In addition to fertility status of a particular soil, the mineral fertilizers fulfil the major requirement of nutrients by the crops. However, the injudicious application of mineral fertilizer along with nutrient mining under the intensive agriculture have resulted in the emergence of multi-nutrient deficiency along with deteriorated soil health finally stagnating crop productivity. Moreover, the skyrocketing prices of mineral fertilizers have made the situation worse. These conditions have compelled us to find an alternative and sustainable approach for improving nutrient availability as well nutrient efficiency in agricultural soils to meet the burgeoning global demand for food. In this respect, soil microbes is the only resort that are responsible for a range of soil processes that affect nutrient transformation and thus influencing the subsequent availability of these nutrients to plant roots. It is already well perceived that microorganisms have the potential to

solubilize and mineralize nutrients from inorganic and organic pools and their use could open up a new horizon for better crop production and productivity with improved soil health. Nonetheless, their wide acceptability as biofertilizer has faced a major drawback of lower viability due to low-quality inoculants and lower shelf life.

These issues impaired the end users (farmers) to rely on the efficacy of microbes. Hence, there is a need for constant and continuous research efforts to explore, characterize and identify more microbes with greater efficiency for nutrient transformation and preparation of improved inoculums with higher shelf life and viability for their final application under field conditions.

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